BIOLOGY

Its Human Implications

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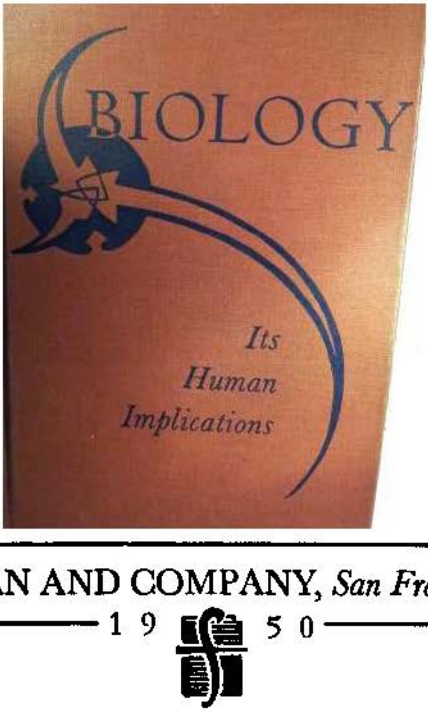

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Preface

WHAT should a student learn in a college course in biology if he will never again be exposed to formal instruction in the subject? This question has been constantly before me during the writing of this book. The question is a difficult one, yet, in my mind at least, it can be answered fairly satisfactorily. The kinds of knowledge I would hope to impart to the student may be divided into three categories.

Generalizations. The great generalizations of any important science should be part of the intellectual equipment of every well-educated man and woman. In biology, one thinks naturally of such generalizations as the cell doctrine, the gene theory, and the theory of evolution. These great generalizations integrate the field and make sense of it. Properly presented to the intelligent student, they create an intellectual excitement not to be found in mere details, however "practically" important the details may be.

Details. Details should, I believe, be of two sorts: (1) the minimum technical details needed for a firm foundation of the great generalizations, and (2) those details that have a fairly immediate bearing on human welfare and human problems, e.g., the facts of human physiology, of soil conservation, and of the biological background of population problems. Discussion at some length of such problems as these surely needs no apology.

Method. We are not sure what we mean when we use the phrase "the scientific method"; but whatever this method is, it is clear that the use of it has revolutionized the life of mankind. Few would doubt the desirability of imparting an appreciation of the meaning and significance of this method to the student. How can this be done? We know something about imparting knowledge of a science to others. But the scientific *method* is not a science; it is an art. It is difficult to discuss an art concisely and definitively. Like all arts, the scientific method is best imparted by indirection, repetition, and example. Difficult though it may be to teach this art, we can hardly excuse ourselves from the attempt. Many of us have a feeling that the method of science has the potentiality of reaching into fields that are not yet considered proper areas for its operation. Is this feeling a sound intuition or an unjustified hope? We do not know. But it is surely worth while to try to exhibit the method of science to the "general" student, that is, to the student who may be instrumental in developing other fields of human knowledge.

One useful device for developing the meaning of the scientific method is almost omitted from this book, namely the approach through history. When soundly presented, a story of the historical development of a science is second only to laboratory work in conveying the meaning of science. Such a presentation may be found in James B. Conant's *On Understanding Science.* However, to secure the benefits of the historical approach, one must recount a story in considerable extension, as Conant has done. It is not practically possible to give such extended treatment to more than a very few subjects either in a text or in a course. The problem of selection of topics becomes acute. Scarcely any two individuals would agree in their selections, and the selection frozen into a text would suit very few teachers. All in all, I think it best for the lecturer to determine for himself the topics to be treated historically; thus, will his enthusiasm be highest. A detailed description of the history of a few discoveries, plus frequent historical sidelights interpolated throughout the course by a flesh-and-blood instructor, will give history a sense of life and immediacy that the cold, printed page can scarcely aspire to convey.

Although this book has been planned primarily for the student who is not to become a biology major, I believe that it is not without merit when examined from the point of view of the beginning biologist. True, there will not be found here the abundance of terms with which the professional biologist must soon become acquainted. However, I think it is better first to see the forest whole even at the risk of missing some of the trees, rather than skirt too near the contrary danger. In a word, I think that the treatment of biology which is best for the general student is also the best introduction for the professional biologist.

So much for generalities; what of the specific organization of the book? The writer of a textbook is confronted with two nearly mutually exclusive alternatives: to write a book that is a closely integrated whole and which, consequently, cannot be adapted to more than one order of presentation; or to turn out a book that has no integration at all but is infinitely adaptable. I have purposely steered closer to the former course. However, the *Parts* of the book can be successfully interchanged to some extent. Within a part, the chapters are best taken up in the order given. An exception to this rule is Part III, The Variety of Living Things, which is consciously designed as a service section. The peculiar demands of laboratory work at each institution make necessary a systematic treatment of plants and animals so developed that it can be taken piecemeal and in any of several orders. The other parts of the book are not as flexible as this, but I hope that the system of division into sections (indicated by § §) will permit the individual teacher a reasonable amount of freedom in the organization of his course. Numerous cross-references embodied in the text should help the reader who skips to pick up the knowledge prerequisite to each section.

To conclude, I wish to thank a few of the many friends who have helped bring this work to birth. Encouragement at critical periods was given by Miss Janet MacRorie, Mr. W. H. Freeman, and Dr. G. W. Beadle. For excellently detailed criticisms, I am greatly indebted to Dr. Ralph Emerson, Dr. D. M. Whitaker, and Mr. John Behnke. A special word of thanks is due the artist, Mr. Evan L. Gillespie, for the splendid way in which he has clarified the text by simple and imaginative sketches; and to Mr. Ralph Sweet for his sound counsel in artistic matters. I would also like to express a word of gratitude to my family for putting up with an author in the house.

Lastly, for the molding of the viewpoints which have determined the character of this work, I must needs express my indebtedness to a half-dozen great teachers and personalities, to one of whom it is my pleasure to dedicate this book.

GARRETT HARDIN

Santa Barbara
January, 1949

PART I

Introduction to the Science of Biology

Chapter I

On Scientific Method

1. What Is Biology?

It is not unreasonable for a person who is setting out on a journey to ask: what is the goal of this adventure? What am I going to see? If, for instance, a man in New York were persuaded to visit the Royal Gorge of the Arkansas River, his interest would probably be heightened if he were told in advance something of the topography of the intervening country and details of the Gorge itself—that it is, for example, a 2600-foot gash cut almost perpendicularly through colorful granite walls; that, in the same region, are found tourmalines, beryls, and aquamarines; that . . . and so on. Of course, no words, however numerous and well chosen, could give the traveler the veritable experience of seeing the Gorge itself.

Words can never be a complete substitute for experience. But good verbal descriptions often make the subsequent experience keener by focusing, in advance, one's critical and observational abilities upon the most significant features of the thing to be observed. Observation is usually more perceptive and accurate if one has some preconceptions (not too tenaciously held, however) of what one is going to see.

Setting out to survey a new field of knowledge is not unlike starting on a journey. What the aim and content of the subject really are cannot be known until one is fairly in it; but a preliminary discussion should give one a reasonably good idea of the sort of things to expect of the projected intellectual adventure. To get down to the case before us, what do we expect to find in the field labeled "biology"?

The word "biology" is made up of two parts: "bio" from *bios*, a Greek word for life, or mode of life; and "logy" from the Greek *logos*, meaning word, thought, speech, or discourse—by extension, a body of knowledge or a science. By way of simple definition, then, we may say that **biology is the science of life.**

2. How Good Is a Definition?

Notice that the definition given above does not dispose of the problem of what biology is in any complete or ultimate way; it merely tells what the word means *in terms of other words*, viz., "science" and "life"—which were not defined. This sort of side-stepping is characteristic of definitions; they define words only in terms of other, *undefined*, words. One may, of course, follow the primary definition with others which define the terms of the first and continue this process indefinitely, but sooner or later a halt must be called. At this point, one is necessarily left with at least one definition which has undefined terms in it; and a little thought should convince us that there is no way to avoid this situation. If we are to avoid later misunderstandings, it is essential that our undefined terms be ones which nearly everyone understands in the same way.

A definition is only as good as its undefined terms. Are we quite clear as to what we mean by the terms "science" and "life"? Observation and reflection will show that not all people understand these terms in the same way. That being so, it would be advisable to try to define them as explicitly as possible before going on.

3. What Is Science?

Interestingly enough, not even the practitioners of science are in agreement as to the essential nature of science if one is to judge by their statements. To appreciate the sort of variation of opinion that exists, consider the following quotations:

"Science is ordered knowledge of natural phenomena and of the relations between them." [William Cecil Dampier (1867-), a historian of science.]

"Science is the search for the reasons of things." [Havelock Ellis (1859-1939), a psychologist and physician, best known for his studies in the psychology of sex.]

"Science is, I believe, nothing but *trained and organized common sense,* differing from the latter only as a veteran may differ from a raw recruit: and its methods differ from those of common sense only so far as the guardsman's cut and thrust differ from the manner in which a savage wields his club." [T. H. Huxley (1825-1895), an English biologist and friend of Darwin.]

"Science is knowledge, not of things, but of their relations." [Henri Poincaré (1854-1912), a great French mathematician.]

"Natural science is the attempt to understand nature by means of exact concepts." [Georg Friedrich Bernhard Riemann (1826-1866), a German mathematician whose novel ideas helped to pave the way for Einstein.]

"Science is the process which makes knowledge." [Charles Singer (1876-), a historian of medicine.]

"Science is an attempt to systematize our knowledge of the circumstances in which recognitions occur." [Alfred North Whitehead (1861-1947), a leading twentieth-century philosopher.]

No two of these definitions are alike, but comparison reveals that they can be separated into two groups, namely, those (see Dampier and Poincaré) which, in effect, define science *as organized knowledge;* and those (see Ellis, Riemann, Singer, and Whitehead) which define science *as the process* which leads to organized knowledge.* The first would make science a static thing; the second a dynamic one. Surely they can't both be correct? Which is right?

Both; or either. It depends on which science one is thinking of; how mature the science is when it is being considered; and the context in which the science is being considered. Sometimes, one wishes to consider all the branches of scientific study as being but parts of a whole which one speaks of as "Science"—usually with a capital *S,* for dignity. At other times, one speaks of plural "sciences"—the science of geology, the science of chemistry, the science of astronomy, and so on. In trying to frame a satisfactory definition of "Science," most men unconsciously think of the one or the few sciences that are best known or dearest to

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* How would you classify Huxley's definition?

them and generalize from these limited cases. It is undeniable that there are considerable differences between the sciences; between, for instance, anatomy and physiology, between historical geology and atomic physics.

To take an example from biology, let us consider the character of **anatomy** (derived from the Greek *temno*, cut, and *ana*, up). Gross human anatomy, the science which deals with such human structures as are visible to the naked eye, could be described satisfactorily by a definition of the first sort, the static sort. The principal parts of the human body are very completely and accurately known; it is exceedingly unlikely that a new bone or muscle will be discovered. Anatomists, that is, scientists who specialize in anatomy, are concerned primarily with passing on the organized knowledge about anatomy to another generation of medical men and anatomists. Unconsciously thinking of his own "science," an anatomist would probably be satisfied with a static definition of "Science."*

On the other hand, a satisfactory definition of **biochemistry** would most likely be couched in dynamic terms. Biochemistry (note that root *bio* again) deals with the chemistry and chemical reactions of living things. It is a field in which much more remains to be discovered than is already known. Consequently, biochemists are less active as teachers than they are as investigators. The typical biochemist would probably define "Science" in a dynamic way, as a process or method of finding answers.

The differences between the sciences of anatomy and biochemistry may not be fundamental and eternal, but merely temporary, valid as of the middle of the Twentieth Century. Anatomy had its real beginning in the work of Vesalius, in Italy, in the Sixteenth Century. After four centuries of rapid development, it is a mature, well-rounded body of knowledge with little more to be discovered or described. Biochemistry, however, began in earnest only a century ago and is still in its vigorously

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* It is possible that the "anatomists" spoken of here no longer exist. Most of the men in good, modern anatomy departments do their research in the field of physiology and hence are really physiologists, whatever they may be called. Departments of anatomy are actually filled with physiologists (to whom the above remarks do not apply). This situation is an illustration of the general rule that human institutions (such as academic departments) tend to retain their superficial form and symbolism as they change to meet new conditions.

growing childhood. Perhaps some day its field will be as completely known as is the field of human anatomy and biochemists will be concerned primarily with passing on a body of existing, organized knowledge to a new generation of scientists.

All Science, including biology, is both organized knowledge, and method. The first aspect is easier to comprehend for it is nearer to the things of our daily lives. Consider the telephone directory, a magnificent piece of organized knowledge. It is organized so well that anyone who can read, providing he knows the alphabet, can use it. Its accuracy probably transcends that of any scientific book ever published. Yet, we do not think of the telephone directory as a work of science. Why not? Is it because we think it too prosaic, too commonplace? Partly, perhaps. But probably more important is the fact that, unlike an anatomy book, the facts within it were not assembled by methods that would be called scientific methods, excellent and adequate to the task though they were. Assembling a telephone book is merely a glorified job of record keeping. Developing a science is much more than that and involves *certain modes of thinking and methods of observation and experimentation* which collectively are spoken of as "the scientific method."

What is this method that seems so foreign to our everyday activities? What is its strength? What its weaknesses? How widely applicable is it?

4. The Scientific Method: Discussion of a Problem

At the outset, it is necessary to appreciate the self-imposed limitations of Science. **It deals only with material things,** with things that can be reported on in an objective fashion, things that can be seen, heard, felt, tasted or smelt, and with no others.

Does a human have a soul? By definition, a soul is an immaterial thing which cannot be seen, heard, felt, tasted, or smelt. Therefore, it cannot be investigated scientifically. *Is Stravinsky's "Rites of Spring" a thing of beauty, or just so much cacophonous caterwauling?* "Beauty," whatever it is, is not to be apprehended by the senses; one cannot see beauty or hear beauty. True, one hears musical tones or sees color, but what one calls beauty is something that is connected with one's internal appreciation of the form of the thing that is seen or heard, and this internal appreciation is clearly not material. *Is it good or bad to honor one's parents?* Again, we have posed a question which deals with something ("good" or "virtue") which is not material. Again, the problem cannot be answered *scientifically.*

Half-informed folk sometimes imply that only Science is important, that questions not answerable by scientific means are either unimportant or else are not real questions. But consider the three nonscientific questions we have just discussed. Who will say that all of them are of no human importance? Who will say that the answers, however arrived at, will entail no consequences of importance to humans?

Whenever we voluntarily limit our attention to scientific matters, we must, at the outset, exclude all questions like those of the preceding paragraph, questions which deal with nonmaterial things. Possibly someday, the definition of Science may be extended to include the investigation of nonmaterial things; but at present, by common consent of practicing scientists, the definition of Science and the delimitations of its methods are made too severe to include these other questions, however humanly important they may be.

The scientific method is limited, but within its prescribed field it is exceedingly powerful, a truism today too trite to merit serious discussion. But what is this method? How does it work? Let us take an example of its application to a biological problem and examine it in detail. The example is an imagined one, somewhat simplified for ease of understanding.

Any investigation may be regarded as beginning with a question, which one may frame as a **hypothesis**—a supposition, a sort of tentative guess, a hunch, a possibility to be tested. For our example, let us suppose that there is some inconclusive evidence (little better than a hunch, perhaps) which indicates that a certain chemical, say brucine, will cure a certain disease, say bubonic plague. Expressed in a formal way, our investigation starts with this hypothesis:

Hypothesis: brucine cures bubonic plague.

How can we test the hypothesis? Obviously, by administering brucine to plague victims. So we go to a hospital which has a good supply of victims and administer brucine to them. If they get well, the hypothesis is true. If they don't, it is false. No?

No! That would be a miserably planned experiment. For many reasons, it would yield a most ambiguous answer. First, the experiment can be criticized because of the well-known fact that patients often "spontaneously" get well without any treatment. Suppose we had treated one hundred patients and all of them had recovered. Could we have concluded that it was the brucine which had cured them? No; for a critic could have pointed out that perhaps these *particular* hundred patients would have gotten well if left entirely alone. We would be unable to answer a criticism of that kind.

Plainly, the thing to do is give the brucine only to some of the patients, say half of them. These patients we will call the **experimentals.** The other fifty patients we will save as **controls;** their recovery will tell us the "normal" rate of recovery with our particular lot of patients. We must make every endeavor to see that the controls and the experimentals differ *in only one respect,* namely the administration of the drug. We would not, for instance, put all the people over forty years of age in one group and all under forty in the other, for it is well known that age influences resistance to, and recovery from, disease. Nor would we have all the patients on the south side of the building be controls, and those on the north side be the experimentals, for a scientific critic might then suggest that the difference in lighting and temperature of the two groups made a significant difference in their recovery rates. Also, we should keep in mind the very real possibility that the patient's mental attitude may influence his recovery. It is important that the design of the experiment does not introduce any factor which will produce a difference in the mental attitudes of our two groups of patients. We must not, for instance, openly administer to one group of patients while we neglect the other, for the mere feeling of neglect might affect the recovery of the control group. To avoid this possibility, it would be good practice to administer to the controls a similar-appearing and similar-tasting substance which is known (from previous experiments) to be without effect on the disease.

There may be other factors which should be taken into consideration in designing the experiment, but the rationale of the design of experiments should be sufficiently clear without a discussion of every possible factor. To repeat, the aim in setting up a **controlled experiment** is to insure that the controls and the experimentals differ in only one respect. This is an ideal which may never be completely realized but it must always be borne in mind. The reliability of the results will be limited by the degree to which the actual experiment conforms to the ideal.

5. The Degree of Certainty of Scientific Truth

So much for designing a "controlled experiment." How shall we interpret the results when we get them?

To illustrate some of the problems of interpretation, let us consider three different sorts of results which conceivably might turn up in such an investigation.

TABLE 1-1

Results	Treatment	
	Controls	Experimentals
Recovered	8	9
Died	42	41

Suppose the results were those appearing in Table 1-1; would we conclude that the drug had aided the recovery of the patients? Probably not. True, one more patient recovered in the experimental group than did in the control group, but that might have been only "chance" or "luck." To illustrate what we mean by the idea of chance, consider Table 1-2. In this table, the figures are the same as they were in the first table, but they refer to different things; instead of to the behavior of diseased patients, they refer to the behavior of dice. Different brands of honest dice should behave the same way. Suppose that we had a hunch (hypothesis) that the dice sold as "X Brand" were weighted differently from those of the "Y Brand." To test this hypothesis, we might throw 50 of the X Brand of dice and compare the results with those obtained by throwing 50 of the Y Brand. As a simple means of recording the data, we might note the number of dice which turned up

TABLE 1-2

Results	Brand of Dice	
	X Brand	Y Brand
No. of 3's thrown	8	9
All other numbers	42	41

a *3* against the number which turned up any other number. Suppose our hypothetical experiment gave the results shown in Table 1-2. Would we regard these results as proving that X Brand is different from Y Brand? Certainly not. For similar reasons we would not regard the results recorded in Table 1-1 as justifying any statement that the drug-treated patients were significantly better off than the untreated controls.

Now let us consider quite a different set of results which one might turn up in such an investigation. In Table 1-3, we have recorded a case in which 45 out of 50 of the experimentals recovered, as opposed to only 8 out of the 50 controls. Such results would unquestionably lead any reasonable person to the conclusion that the experimental group of patients received treatment which was effectively different from that of the controls; and if the administration of the drug was the only difference, that the drug had definitely aided recovery. Results like these are the sort one hopes for, of course—nice, clean-cut results that admit of no uncertainty in their interpretation. Unfortunately, the results of our experiments are not always as clean cut as this.

TABLE 1-3

RESULTS	TREATMENT	
	Controls	Experimentals
Recovered	8	45
Died	42	5

TABLE 1-4

RESULTS	TREATMENT	
	Controls	Experimentals
Recovered	8	14
Died	42	36

All too frequently, a well-designed experiment leads to results that can be interpreted only with difficulty. In Table 1-4, are recorded some imaginary (but highly possible) results of the more unsatisfactory sort. In this case, 14 of the experimentals recovered as compared with 8 of the controls. Is 14 out of 50 significantly greater than 8 out of 50 or not? It is difficult to say. If Table 1-4 represented the results of a dice-throwing experiment (as did Table 1-2), would we say that the two sets of dice were different? Different persons would probably arrive at opposite conclusions regarding the significance of such data, which emphasizes the difficulty of the problem and the ambiguous significance of the results. To analyze such data rationally, recourse must be made to the science of **statistics** which deals with the problem of the significance of differences. Such analysis is beyond the scope of this book, but it is important that the student realize that much of modern experimental biology leans heavily on the reasoning and the methods of statistics.

One more point should be made before leaving these hypothetical experimental results. Look again at Table 1-3. When we first discussed it, we said that these results would "unquestionably lead any *reasonable* person to the conclusion that the experimental group received treatment which was effectively different from that of the controls." There is something not quite straightforward about an appeal to *reasonable* people. After all, some person might maintain that 45 out of 50 was not significantly different from 8 out of 50. Then, what would we say? How could we answer such a critic? By calling him unreasonable? *Assume* that there *was* no real difference between the two groups of patients: could not one occasionally find 8 recoveries in one group and 45 in the other, just as a matter of chance? It is certainly *possible.* It might be highly *improbable* (and here the statistician would step in to tell us precisely how improbable), but it is not impossible. The differences exhibited in Table 1-3 could have been caused by chance alone.

Further thought along this line will convince most men that there are *no* results that could prove, *with absolute certainty,* that the tested drug cures the disease. Always there would be at least a slight possibility that chance alone could account for the differences in the recovery rates of the two groups of patients.

6. The Scientific Method: The Stages of an Investigation

In retrospect, what seem to be the principles of scientific method as illustrated by the above example? One can, without undue oversimplification, regard an investigation as taking place in four stages:

1. The invention of a hypothesis.
2. The development of a program of observation or experimentation to test the hypothesis.
3. The carrying out of the program.
4. The interpretation of the observations or experimental data.

Concerning the first stage, the invention of a hypothesis, it is not possible to say much that is useful to a person who is interested in becoming a scientific investigator. Most conceivable hypotheses never lead to any discoveries of note; only a few are fruitful of results. The art, of course, is in discovering these useful hypotheses without wasting too much time developing and testing useless ones—and it is an *art*, not a science. Clearly some scientists (e.g., Pasteur and Einstein) are more proficient in this art than others, but no one, not even a Pasteur or an Einstein, has succeeded in laying down rules for discovering useful hypotheses. Only one thing seems to be true: the discovery of useful hypotheses cannot be a spare-time occupation. Hypotheses grow out of long-continued concern with a problem, arising as the by-products of intensive investigation and many observations.

The second stage, the development of a program of attack, we have already discussed at considerable length in § 4. However, the reader should not suppose that the controlled experiment is the only method of arriving at the truth. Frequently, practical considerations force one to use other means. In medicine, for instance, humanitarian considerations often conflict with a desire for scientific rigor* and necessitate the design of other sorts of experiments. In addition, there are many fields of science, for instance, much of astronomy, where experimentation is impossible. In such fields, accurate and critical observation is the means of arriving at the truth. This does not imply any fundamental difference between the so-called experimental sciences and the so-called observational sciences; both of them depend on accurate observation. **An experiment is merely a method of arranging opportunities to observe.** If this method is possible in a given science, progress will be faster; but progress can be made, though with less speed and greater difficulty, even in a field where experimentation is impossible.

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* Those who have read Sinclair Lewis' *Arrowsmith* will recall the important role of this conflict in the novel.

The third stage of an investigation, the actual carrying out of the program of observations, varies so much from science to science that there would be little profit in making generalizations about it. However, in all scientific investigations, there is one common factor: the attitude of mind which makes accurate observations possible. It is important that the observer repress in himself the desire "to prove something." He should not be trying to prove anything but, rather, he should be trying to find out the truth, whatever it is—whether it proves or disproves his pet ideas, whether it is pleasant or unpleasant. Experience has shown that men who too passionately believe in the truth of a certain hypothesis make poor (inaccurate) observers. In scientific investigation, the true scientist is not an advocate; he is the judge. The facts must be their own advocate. For this reason, the training of scientists always includes a great deal of work in the laboratory or in the field, making experiments and observations. Laboratory work for beginners is not for the purpose of making new discoveries—that is unlikely in a field already well developed. Rather, it is designed to instil in the student the habit of "going to Nature" for the answers to questions instead of falling back on textbooks or preconceived ideas. This habit is, in a real sense, a natural one, yet in most cases it must be developed in the would-be scientist.

Finally comes the time for interpreting the results of the observations. Interpretation must be based soundly on logic and, in many sciences, on mathematics which is but a special kind of logic. The ideal is to state nothing that is not absolutely certain. However—recall the discussion of the previous section—since nothing is absolutely certain, one states what is probably true, making assertions in such a way as to reveal the evidence on which the assertions are based. In this way, others can appreciate the degree of certainty established by the evidence.

In Science, our aim is always to discover facts whose truth is *beyond reasonable doubt;* there is no absolute certainty in Science. To some minds, this lack of absolute certainty may be disturbing but most scientists find it part of the beguiling quality of their work. Because nothing is known with absolute certainty, there is always the possibility of making new discoveries by reexamining old generalizations in a more finely critical way. As Émile Duclaux, one of Pasteur's most perceptive students, has said: "It is precisely because science is never sure of anything that it always advances."

QUESTIONS AND PROBLEMS

1-1. In § 4, it was stated categorically that the investigation of certain sorts of questions does not fall within the realm of science. Is the question involved one of fact or of definition?

1-2. What definition of the science of statistics is implied in the text (§ 5)? Does this definition differ from that most laymen would give? (See, for instance, an unabridged dictionary.) If so, how?

1-3. Define: biology, anatomy, biochemistry, and "control," as used in experimental sciences.

1-4. Suppose you read in a book that is universally regarded as the greatest authority on insects that all houseflies have four pairs of legs; and suppose you could never find more than three pairs of legs on houseflies: would you deny the authority of the book or of your senses?

1-5. Of the four stages of a scientific investigation, as given in this text, which one is the most difficult to describe in such a way as to help others carry out a program of scientific investigation?

1-6. Consider the question: How many "perfect crimes" are committed annually in the United States? Can this question be attacked scientifically? If so, how; if not, why not?

1-7. Suppose, in the experiment designed to see if brucine cured bubonic plague (§ 4), we had available only two nurses for the care of the patients, one pleasant and friendly and the other a veritable termagant. How should we make use of these nurses in order not to have their personality differences affect the interpretation of the experimental results?

1-8. Suppose the experiment of § 4-§ 5 had given the results recorded in Table 1-5, below. In this case, could one say that the drug had cured the patients beyond the shadow of a doubt, that is, that it would have been *impossible* for all the experimentals to have recovered if chance only had been operating?

TABLE 1-5

Results	Treatment	
	Controls	Experimentals
Recovered	8	50
Died	42	0

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Chapter II

Characteristics of Living Things

7. What Is Life?

Biology, we said, is the science of life. We have tried to gain some idea of the meaning of the word "science" by describing and analyzing the activities involved in its operation. But what is "life"?

There are reasons why it is unwise to do more than begin to attack this question at this point. For one thing, the entire book may be said to be an attempt to answer the question. For another, experience shows that asking the question, "What is Life"? (with a capital *L*), all too frequently leads to answers of uncertain sense. Perhaps not all answers to this question need be nonsense; but, in fact, so many of them are that it is sound strategy to avoid the question at first by asking others which, though difficult, are more easily answered, namely: "What are living things? What do we mean when we say 'living'? How can we tell living things from dead, so that we will know what we are to study in biology?" These questions are perhaps less profound than the original question, but they are more easily answerable; so we will ask them first. A most important part of the strategy of science is asking answerable questions.

8. Recognizing Living Things

In dealing with the things that make up the ordinary man's life, we seldom have trouble telling a living thing from a nonliving one. Birds, sunflowers, and men are living. Stones, houses, and sidewalks are not. The ability to distinguish living from nonliving is not an instinctive one as any parent knows. Children have to be taught what is living and what is not. Listening to the prodigal flow of commentary with which small children accompany their play, one realizes that pictures and spring-wound toys seem nearly or quite as animate to the child as do cats and dogs; and certainly the idea that trees and flowers are alive does not come easily.

If we can recognize living things only because we have learned how to do so, it must be that we have learned, however unconscious the process of learning may have been, what the characteristics of living things are. What do birds and flowers have in common that stones, houses, and sidewalks lack? The familiar things of everyday life we have mentally sorted into two classes, "living" and "nonliving"; but suppose we come up against an object we never saw before—how, then, do we decide whether to call it alive or not? What are the characteristics we look for? Are these characteristics unique in living things, or are they sometimes observed in the nonliving? Consideration of these questions at some length may help us to gain insight into our own intellectual processes as well as show us, in outline, some of the fundamental problems of biology.

9. Characteristics of Living Things: Movement

Probably the characteristic that we unconsciously rely on most to help us recognize living things is movement. Certainly, it permits the most rapid judgment. Whenever we see a hummingbird hover over a flower, a trout break the water in pursuit of a fly, or a slug slowly laying a trail of slime across the garden walk, we unhesitatingly say, "It's alive!" Not all living things move, of course. A mushroom, as far as the eye can tell, never moves. Not all living things move; but do we call all things that move *living?*

A rock may roll down the hill; why do we not say that *it* is alive? (Some primitive people do.) Clearly, it is because we have arrived at a certain stage of sophistication, a stage in which we distinguish between "spontaneous" movement and "forced" movement. The movements of nonliving things are always of the latter sort; a rock moves because it is forced to by gravity, dynamite, a small boy's arm, or some similar force. On the other hand, the movements of a dog are not easily attributed to a simple force. We speak of the dog's movements as being *spontaneous*, and *unpredictable*, the rock's movements as being *forced*, and *predictable.*

Casual observation alone permits us to recognize many living things by the spontaneous movement they exhibit. Most plants, however, do not exhibit any *gross* movements, that is, movements readily apparent to the naked eye. However, microscopic examination of such immobile plants will usually show movement of some of the parts.

To summarize, we may say that if a thing moves spontaneously, it may be called living; if it does not exhibit spontaneous movement, we must look for other characteristics before we can classify it as living or nonliving.

10. Characteristics of Living Things: Responsiveness

Stroke a cat and the cat's back arches. Speak to a dog and the dog's ears stand erect as he turns his head toward the source of the sound. Shine a flashlight in a man's eyes and his pupils contract. In each of these situations, the first action is called a **stimulus** (the Latin word means *goad*. Plural: stimul*i*) and the resultant reaction of the organism is called a **response.** Generally, the stimulus comes from the outside, though sometimes it is internal; for instance, certain sensations in the region of a man's stomach may stimulate him to get into his car and drive to the doctor's office. As a generalization, **the stimulus furnishes only a small fraction of the energy involved in effecting the response.** For example, the scarcely audible ticking sound emanating from a package may stimulate an apprehensive postal clerk to turn and run hundreds of feet at truly Olympic speed. It cannot be said that the ticking sound furnished enough energy for the sprint. The energy was furnished by the man's body; the tiny sounds acted merely as a stimulus to release the energy.

Most animals show prompt and gratifying responses to stimuli of all sorts, whereas most plants do not. However, plants do respond to many stimuli, though their responses are usually much slower and more subtle. A seedling, developing in a dark cellar illuminated by only one window, will show a response to the lighted window by growing towards it. Plant responses to gravity, water, and other stimuli can also be demonstrated by suitable means. It is probably true that responses to stimuli are shown by every living thing. However, all plants and animals do not respond to the same kind of stimuli, and for some very simple organisms* it is often difficult to find an effective stimulus.

Although responses to stimuli are typical of living organisms, no inhabitant of the modern world need be told that stimulus-response systems are not confined to the living world. Flicking a tiny switch may turn on a light or start up a giant dynamo; the interruption of a beam of light that normally shines on a photoelectric cell may open heavy doors or set off a burglar alarm. Much thought and work are expended these days on devising mechanical stimulus-response systems which, in many cases, involve stimuli too delicate to affect any known organism and which, in turn, may lead to responses of a rapidity or a magnitude unknown in the biological world.

To summarize, it may be said that responsiveness to stimuli is definitely characteristic of living things but it is not confined to them.

11. Characteristics of Living Things: Growth

All living things grow. Some increase in size so rapidly that we can "almost see them grow"; for instance, a mushroom (the fruit of an underground mold) may suddenly protrude through the surface of the soil and grow two or three inches upward in the course of a single day (whence one meaning of the verb "to mushroom"). At the other extreme, a scrawny, wind-twisted pine near timberline in the Rockies may take fifty years to grow to the height of a man. But, fast or slow, all living things grow.

It is not easy to find phenomena in the nonliving world that approximate the process of growth in the living. Perhaps the closest approach is that of the growth of crystals in a supersaturated solution of a salt. Consideration of an example of crystal growth will serve to point up both the resemblances and the contrasts between growth in the nonliving world and growth in the living.

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* An **organism** is any plant or animal, anything that is or has ever been living; i.e., one may speak of dead organisms as well as of living ones.

Salts are usually more soluble in hot water than they are in cold. Sodium thiosulfate (the photographer's "hypo"), for instance, can be dissolved in hot water to the extent of more than a gram of salt per cubic centimeter of water. In near-freezing water, however, the salt is less than half as soluble. What will happen if we make, in hot water, a saturated solution (i.e., one that has as much salt as the water can possibly hold) and then cool the water? Evidently, some of the dissolved salt will have to come out of solution. Under certain conditions, as it comes out of solution, it will form large and obvious crystals which grow in size until all the surplus salt has been removed from the solution.

To the eye, the resemblance of crystal growth to growth in living things is immediately apparent. The crystal increases in size while still maintaining a fairly constant form characteristic of the kind of crystal. Crystals of "hypo", for instance, are of one shape; crystals of table salt of another. Each substance crystallizes out of solution ("grows") true to form.

Similarly, a small dog grows in size until it is a larger version of the same shape of animal. Each of the different kinds of puppies grows into a different kind of dog; a dachshund puppy grows into a large dachshund, a St. Bernard puppy into a large St. Bernard, just as different types of crystals grow true to their types.

What are the differences between these two kinds of growth? First, there is the matter of the kind of raw material used. In the case of the crystal, the raw material is essentially the same as the final product itself. A chemist would tell us that the "hypo" in solution is the same substance as the "hypo" that we see in the crystal. But when a living thing grows, it grows at the expense of things unlike itself. Dogs, normally not cannibalistic, grow at the expense of things, e.g., dog biscuits, that are chemically quite different from themselves. It does not take a very good chemist to tell a dog biscuit from a dog.

In living things, growth takes place by complex processes of **ingestion** (taking in) of food, **digestion** of it (breaking it up into smaller particles), and **assimilation** of the particles—that is, turning them into larger particles once more which are now different from the original food particles, and which, in fact, are like the particles of the living thing which is carrying out the process of assimilation. Of these processes, we shall learn more later, but at this point it should be emphasized that the nature of assimilation is such that there is little relation between the kind of raw material used and the resulting product. The nature of the final product is determined primarily by the organism which is taking in the raw material. A dachshund and a St. Bernard puppy may always be fed from the same box of dog biscuits, but they do not, therefore, come to resemble each other. Each grows true to its (not the food's) type. Such growth is in striking contrast to the growth of crystals, the chemical composition and mode of growth of which are determined by the nature of the raw material.

12. Characteristics of Living Things: Reproduction

One of the most characteristic features of living things is their ability to reproduce themselves. Men beget men and mice beget mice, and an individual of one species of plant or animal does not give birth to an individual of another. Offspring are slightly different from their parents, but the exactness of the reproduction is remarkable and indicates underlying forces which operate with great precision. The attempt to identify these forces is one of the principal activities of the modern science of **genetics** (from the Greek *genesis*, meaning origin), a science concerned with what it is that young organisms inherit from their parents that makes them grow to resemble them, as well as with the causes that make children slightly different from their parents.

In the nonliving world, there is no phenomenon that closely approximates biological reproduction. But, although it is true that only living things reproduce, an object need not necessarily possess the ability to reproduce for it to be called living. Most ants, for instance, are completely *sterile*, that is, incapable of reproducing themselves; yet, no reasonable man would doubt that they are alive. The special forms of ants which are capable of reproducing are usually out of sight, in a nest underground. Such ants reproduce not only their own kind, that is, other reproductive ants, but also produce the many sterile ants which make up the bulk of an ant colony.

A given species or kind of plant or animal must always include some reproductive individuals if the species is to continue to exist, but an *individual* member of the species may be unquestionably alive even though it never reproduces.

13. Characteristics of Living Things: Metabolism

Organisms require energy to carry on all their activities. That movement and response to stimuli require energy should be no surprise to us, for these same activities require energy when they are carried out by nonliving things, e.g., automobiles, and electric-eye door-openers. Much evidence indicates that growth and reproduction, which are unknown in the nonliving world, also require energy for their performance. If, then, all the known activities of living things require energy, what is the source of this energy?

The immediate source of energy for all these activities is energy-rich food. Food contains locked in it (in a chemical sense) energy which can be released in various ways. One common way of releasing the energy is by oxidizing the food, that is, combining it with oxygen, an invisible substance present in the air around us. As a result of the **oxidation** of the food, i.e., the combination of the food with oxygen, simpler compounds are produced. These compounds are relatively poor in energy. The energy that is no longer locked in chemical compounds now appears as free energy, available for other uses. The process of oxidation may be simply written as follows:

$$\underset{\text{(energy rich)}}{\text{Food}} + \text{oxygen} \longrightarrow \text{water} + \underset{\text{(energy poor)}}{\text{carbon dioxide}} + \text{energy} \qquad (1)$$

Equation (1) is a simple example of a *chemical equation*, and may be read: "Food plus oxygen yields water plus carbon dioxide plus energy."

The released energy appears in part as heat. The remainder of the energy is used to produce movement, reactions to stimuli, and to make possible the manufacture of new chemical compounds used in growth and reproduction.

It would be difficult to write an equation which would represent a greater oversimplification of the facts than does equation (1). Actually, the process by which food is broken down to form water and carbon dioxide takes place in scores of separate chemical steps, and the way in which the released energy is trapped again and used to make possible all the activities of the organism involves hundreds of imperfectly known chemical reactions. All of these reactions, both those that release energy and those that trap and use the energy, are known collectively as **metabolism.**

That is, **metabolism is the name given to the entire complex of chemical reactions by which an organism obtains and uses the energy available in its food.**

Metabolic reactions are at the base of all biological actions, and the study of metabolism is of fundamental importance to all of biology.

The above definition is perhaps too general to be of much help in understanding the nature of the chemical activities of organisms but there are two good reasons why this definition must suffice for the present. First, the detailed picture of metabolism, in so far as it is already known, is fairly complicated and will need to be approached gradually if confusion is to be avoided. Second, we know quite well that the greater part of the story of metabolism remains to be discovered. Only a small fraction of the known activities of organisms can, at present, be thoroughly explained in terms of the metabolic reactions underlying them.

Lavoisier, one of the fathers of modern experimental science, said: "Life is a chemical function." At the time he said this his statement was more prophecy than known fact. By now, more than 150 years later, much meaning has been given to Lavoisier's statement through the discovery of the exact sequence of many of the chemical reactions in living things. But we have unravelled only a little of that tangled web of chemical reactions that we call metabolism. Most of the chemical processes of living things are yet to be elucidated and, what is more important, we have yet to discover how the chemistry and physics of living organisms can account for all their manifold activities. To the beginner, the quantity of books already written about plants and animals indicates a very impressive amount of knowledge about the living world. But the professional biologist knows that the work of making this world understandable has scarcely begun.

QUESTIONS AND PROBLEMS

2-1. Define *stimulus.* Define *response.* Can one be defined without the other?

2-2. What characteristics of living things can be used to distinguish living things from dead things?

2-3. One biologist has defined life as the "sum total of all phenomena common to all living things." And, of course, we may say that "living things are those things which possess life." Thus, have we definitions in which there are *no undefined terms,* thus disproving the contention of § 2? (Compare the above definition of life, with a definition of a once noted English wit: "An Archdeacon is a person who performs archidiaconal functions.")

2-4. Is it necessary to have a perfectly clear-cut and unobjectionable definition of a characteristic or thing before investigating it? Is it desirable?

2-5. It takes energy for a man to walk upstairs. Where does the energy come from? Give the answer in the form of an equation.

2-6. What is meant by the word *organism*?

SELECTED REFERENCES

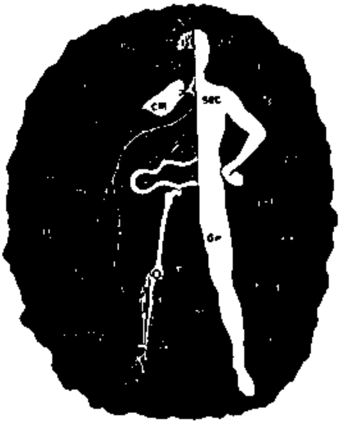
(Students frequently experience difficulty with the vocabulary of a new study such as biology. This difficulty is best met head-on by *studying* the terms rather than *avoiding* them. For such study, a good unabridged dictionary is most useful. In addition, the following books are highly recommended. The book by Andrews can be read like a novel, for pleasure. Jaeger's book is a useful reference.)

Andrews, Edmund, *A History of Scientific English*. New York: Richard R. Smith, 1947.

Jaeger, Edmund C., *A Source-Book of Biological Names and Terms*. Springfield, Ill.: Charles C. Thomas, 1944.

PART II

The Measure of Man



Chapter III

The Skeleton: The Cell Doctrine

14. Why Study Man?

We shall begin our account of biology with Man. If we could be perfectly objective about the matter—which we cannot—we might seriously ask: why study this particular organism in detail? There are at least a million different kinds of plants and animals in the world. Why single out this one from the million for detailed study? If we were studious mice or wasps or earthworms, would we consider Man such a thing of interest? Is he so remarkable?

It must be confessed, as regards most of the characteristics and activities of living organisms, Man is not remarkable. He is neither the largest nor the smallest, the strongest nor the weakest, the fastest nor the slowest of living things. He is perhaps not as beautiful as the bird of paradise, nor as precisely fashioned as certain microscopic plants called diatoms. He is not a rare beast, nor is he very numerous; there are more ants in one county than men in the whole world. The only remarkable thing about him seems to be his highly developed intellect, his ability to reason. With this one exception—and it is an important one—Man seems to be a rather mediocre being, hardly the sort that would strike any nonhuman creature as worth writing a book about. Yet, if we are to study living organisms in general, Man's very mediocrity can be considered a justification for studying him. It is precisely because he is, in most respects, so little distinguished from his fellow creatures that an account of his abilities and problems will tell us something about the abilities and problems of a large proportion of organisms. Then, too, we cannot forget—nor should we—that we are ourselves men, and not mice or wasps or earthworms; which means that, consciously or unconsciously, we subscribe to the belief of the poet, Pope, that "the proper study of mankind is Man."

However, even if our interests in biology were very narrowly confined to Man, we would soon find that we could not learn a great deal about Man by studying him alone. Most of our fundamental knowledge of Man's biology has been gained from the study of other living things. A dog whose pancreas was removed for experimental purposes gave the first clue to the cause of diabetes in humans. The study of frog's eggs has explained Siamese twins. Because so much human effort has been expended in the breeding of fruit flies, we understand better why a son looks like his father. The study of the metabolism of beer yeast has revealed secrets of the metabolism of human muscles. Even the study of reasoning ability, man's only specialty, has been notably advanced by experimentation with dogs and other nonhuman, reasoning creatures. It would, in fact, be difficult, if not impossible, to name a field of human biology which has not been enriched by the study of other organisms. In this section of the text, the emphasis will be on Man and his biology, but not exclusively so. Since much of the knowledge about Man has been gained from the study of other, similar creatures, any account of the experimental background of the facts must necessarily bring in other organisms.

15. Analysis: The Systems of the Body

The human body is such a complex machine that it would be scarcely feasible to try to understand it all at once. Study will be facilitated by **analysis** (from the Greek *lysis*, a loosening, and *ana*, up; that is, a loosening up of a complex). We will, in imagination, separate the parts of the body into various **systems,** each system subserving some function or group of related functions. The anatomical elements of each of these systems are revealed in Figure 3-1.

It must not be forgotten that the analysis of the body into the various systems is made only as a matter of convenience. In carrying out even the simplest function, more than one system is involved. The muscular

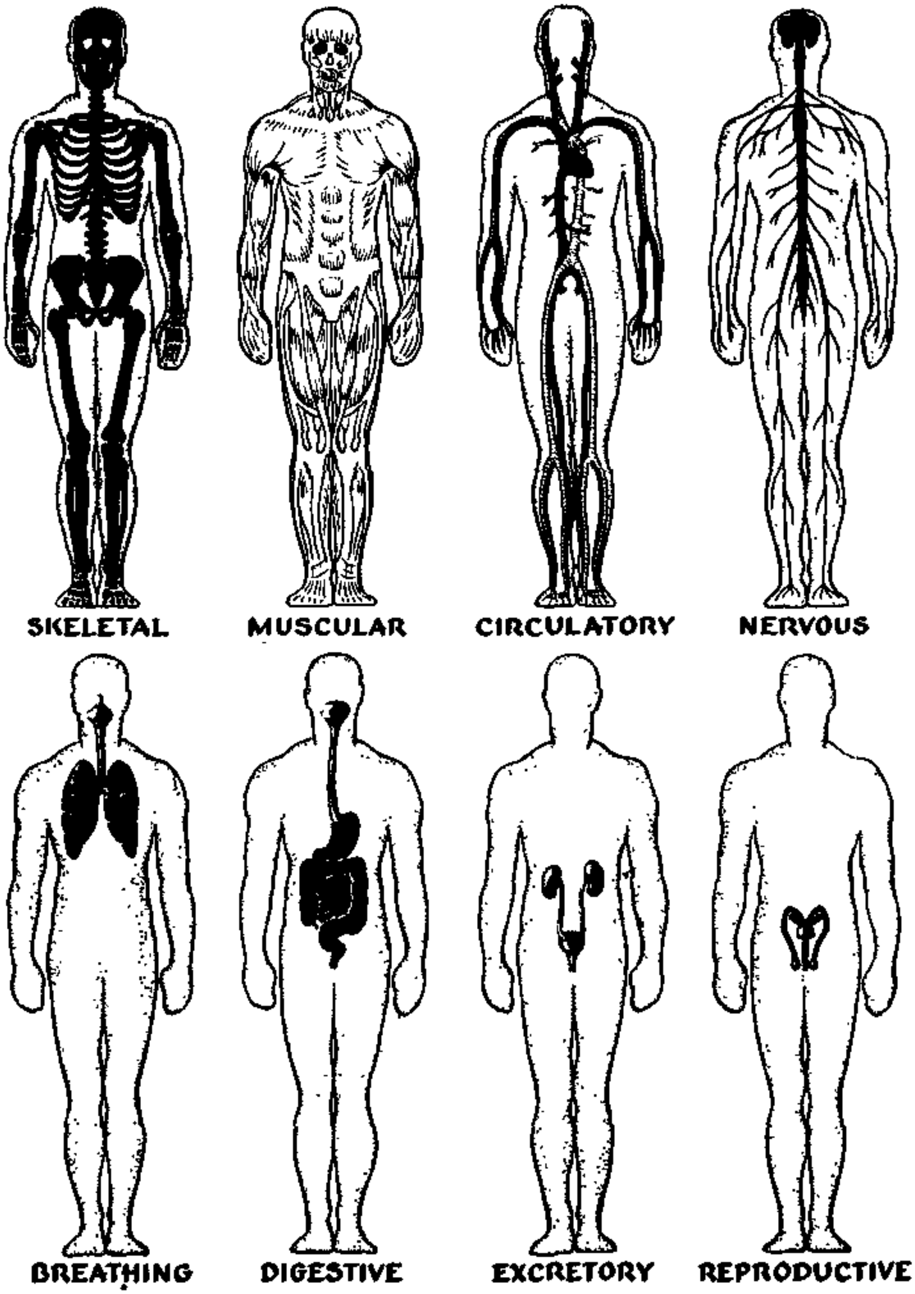


Fig. 3-1. Although the body is really a well-integrated whole, one may think of it in terms of the separate systems illustrated above. Such analysis is an aid to investigation and study.

system, for instance, moves the body, but it can do so only because the muscles are firmly attached to the skeleton; the muscles are stimulated to move by nerves; and repeated movements are possible only as long as the breathing, circulatory and digestive systems are functioning, to mention only the more obvious interrelationships. Analysis alone would lead to a false impression of independence of the various systems; therefore, following the analytical treatment of the body, there will be a **synthesis** of the various parts and functions in Chapter XIV. (The word **synthesis** comes from the Greek *syn*, together, and *tithemi*, place; that is, it implies a bringing together of different things in one place.) The employment of both analysis and synthesis is a methodological necessity in all the sciences. Analytical treatment is necessary if the student is to avoid being confused by the complexity of the total picture. Eventually, there must be a synthesis of the parts into a whole again if one is to avoid the danger of "not seeing the forest for the trees."

16. The Skeletal System

The skeleton may be said to consist of two divisions: the **axial skeleton,** the more central part which constitutes a central axis on which is hung, so to speak, the **appendicular skeleton.** (See Fig. 3-2.) The axial skeleton consists of the **vertebrae** (backbone), the **skull,** and the **ribs** and **sternum.** The appendicular skeleton consists of the **appendages** (legs and arms) together with the **pelvic girdle** to which the legs are attached, and the **pectoral girdle** to which the arms are fastened. Altogether, the body contains more than 200 bones; the number varies somewhat from individual to individual because of variation in the number of the small, replicated bones, such as the vertebrae, which show a normal variation in number from 32 to 37 per individual.

The skeleton fulfills three major functions: **protection, support,** and in conjunction with the muscles, **movement.** Discussion of the last function will be deferred to Chapter IV. The other two functions will be considered here.

17. Protection

Among the most delicate and vital portions of the human body, are the brain and the spinal cord. These structures, as will appear later, control in large measure the activities of the entire body. The material of which they are composed has no intrinsic strength or resistance to mistreatment. It is not surprising, therefore, to find that no other part of the body is so thoroughly protected.

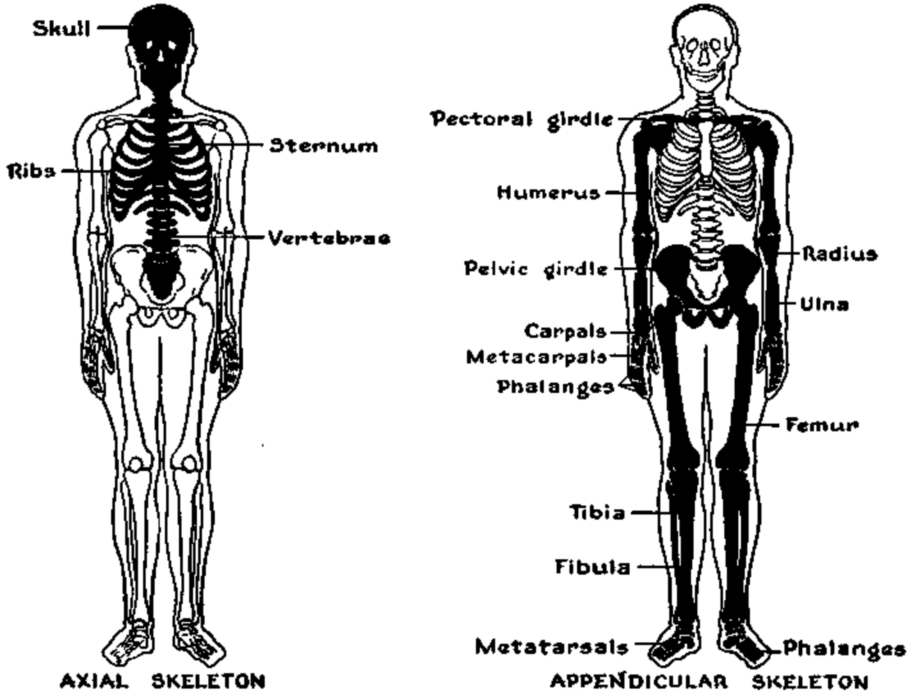


Fig. 3-2. The human skeleton analyzed into axial and appendicular components.

The brain, located in what would otherwise be a dangerously exposed position at the very top of the axial skeleton, is almost completely enclosed in a bony box, the skull. The skull is not a single bone but rather a number of variously shaped, platelike bones which grow together and fuse at their edges as the individual grows older. During development, which starts before birth, the skull bones begin as widely separated, growing plates. By the time a child is born, these plates have grown until they are touching each other in most regions, but not in all. At the points where more than two bones meet, there are usually small areas not completely covered over with bone, called **fontanelles,** the most prominent of which is the one near the top of the head of a newborn child. Moreover, even where the skull bones have already met by the time of birth, the **suture** (Latin *sutura*, a seam) between the two is not very firm, permitting considerable distortion of the shape of the skull. The pliability of the infant skull is of importance at this time, for it permits a more easy passage of the rather oversize head down the birth canal.

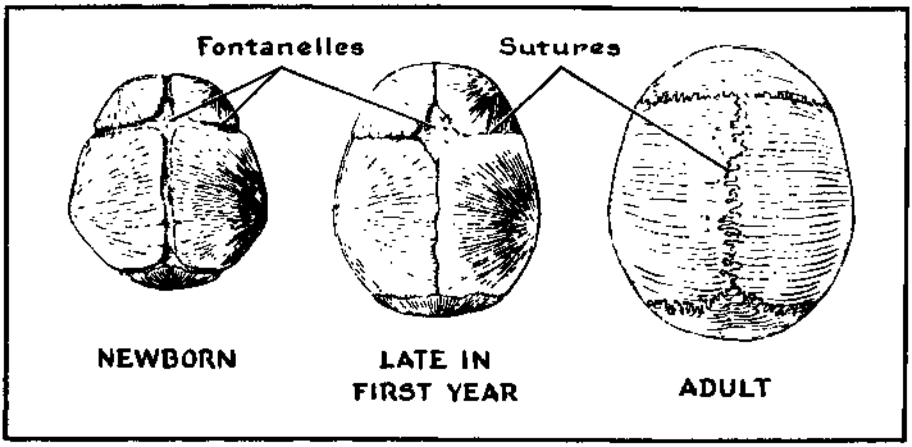


Fig. 3-3. Development of the brain case from separate bones which fuse as they grow together.

Such a pliable skull would not, however, be good protection after birth for the brain of a human exposed to the myriad dangers of this world; and on the other hand, once the crisis of birth is passed, there is no advantage to having a delicate brain case. It is not surprising, therefore, to find that within a year or so after birth the fontanelles close as the skull bones grow together, and the sutures of the skull bones become more firmly knit. As this growth occurs, the outline of the suture increases in complexity, year by year (Fig. 3-3). The skull bones do not, however, become completely welded together until about the twentieth year. During all the intervening time, the brain is growing in size. Once the skull bones have completely grown together, no further increase in brain size is possible. Since the course of development of these sutures is fairly constant throughout the race, their appearance constitutes one of the means by which the archaeologist is able to determine the age at death of individuals whose skulls he finds.

The skull protects the brain. The other great part of the central nervous system, the spinal cord, is equally well protected by **vertebrae** (Latin singular, *vertebra*, a joint, derived from *verto*, turn). Note, in Figure 3-4A, how small a portion of a vertebra is occupied by the spinal cord itself and how much by protective bone. The construction and organization of the vertebrae represent an admirable compromise between the ideals of complete protection and complete mobility. The delicate nerve cord runs from the mid-region of the body clear up to the brain to which it is joined. It is most important that the nerve cord not be injured in the slightest way. From this point of view, the ideal protection would be a solid bony tunnel running the length of the back. Such a solid structure would be very inflexible and, hence, would not allow much in the way of movement of the body. The way in which the protective

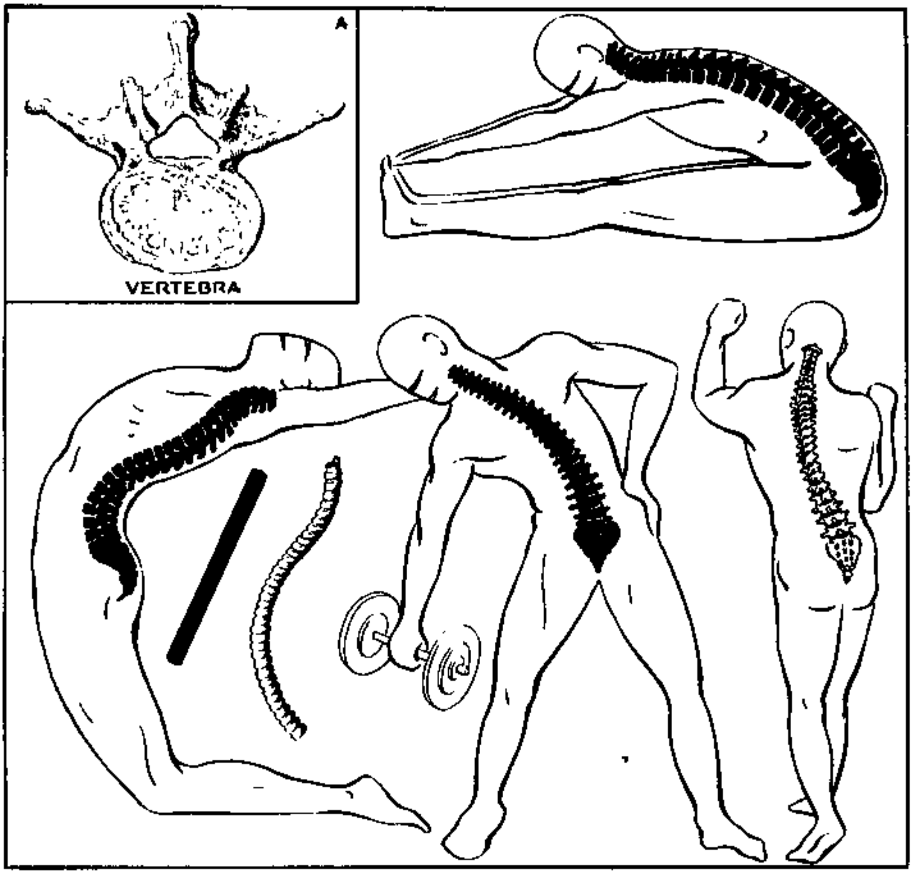


Fig. 3-4. The pliability contributed to the backbone by its construction which is analogous to flexible armored cable rather than rigid conduit pipe. The individual vertebrae (see A) furnish massive protection to the delicate spinal cord, while their articulation with one another permits movement.

bony covering of the nerve cord is actually constructed affords nearly as much protection as a solid bony tube, while conferring an amazing amount of flexibility to the body. (Fig. 3-4.)

In humans, the skull and the vertebrae constitute the major portion of the skeleton which may be said to be protective in function. Most of the body is not protected from external blows by anything more solid than skin. In many other animals, however, the protective role of the skeleton is of much greater importance; consider, for instance, the turtle.

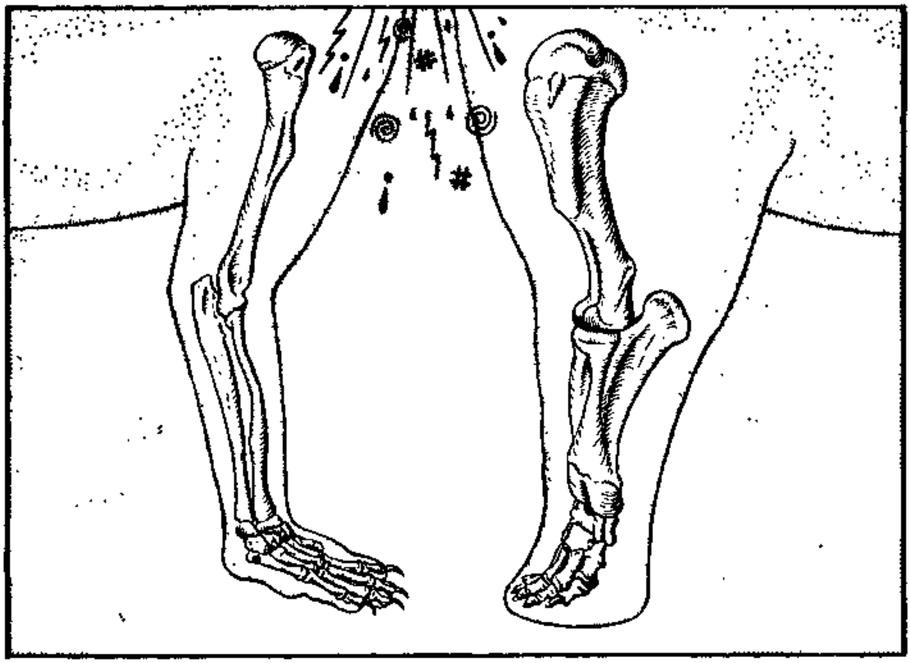


Fig. 3-5. A mouse (left) and an elephant (right) drawn to the same size, illustrating the fact that the supporting bones of large animals are *proportionately* larger than those of small animals. This principle sets a limit to the size of land animals.

18. The Skeleton as Support

Most of the bones of the human body are concerned with support. The heaviest load falls on the leg bones which, it will be noted (Fig. 3-2) are considerably more stoutly built than the otherwise similar arm bones. *The heavier the load it must bear, the greater must be the diameter of* *the bone.* This is a commonplace: the legs of an elephant are thicker than those of a mouse. What is not so easily remarked is that they are disproportionately thicker. In Figure 3-5, the front legs of mouse and elephant are drawn *to the same size;* notice how much more slightly built is the mouse's leg; i.e., the diameter of the bones is less. We have taken two particular animals for comparison, but the same relationship would hold for any two animals of similar mode of life which differ greatly in size. Larger animals are more coarsely built. **Of two bones which fulfill the same function, the one which bears the heavier load will be disproportionately larger in diameter.**

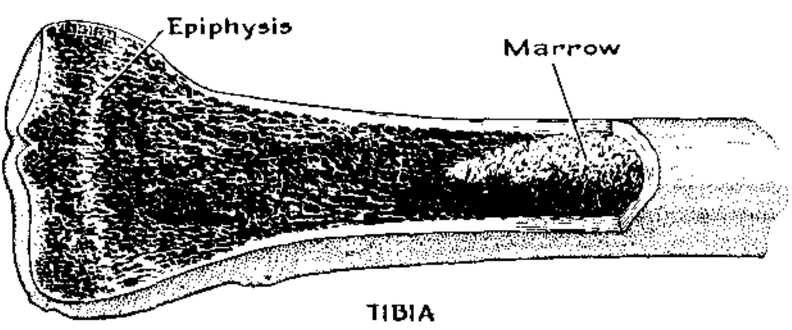


Fig. 3-6. The structure of one of the long bones of the body.

A large animal has disproportionately large bones. As one consequence, large size is correlated with lack of agility. A mouse is much quicker in its movements than an elephant. Also, since the larger animal has bones which are disproportionately large, the nonbony part of its body must be disproportionately small. The larger the animal, the smaller proportion of it will be made up of the necessary muscles and internal organs. If an animal were to grow indefinitely, there would come a time when it would have to consist of nothing but supporting structure, which would be so heavy that it would be unable to support anything else. Actually, of course, growth would have to stop considerably short of this. It is not possible to state precisely the upper limit in size for land-living animals, but it should be apparent that the problem of adequate support is one of the factors which determine the limit.

19. What a Bone Is Made of

Although many of the bones of the human body are hollow, it should not be inferred that they are empty. In the center (see Fig. 3-6) of the long bones, there is a soft material, called **marrow**, which is of great importance in the formation of blood. Since the marrow is of no structural importance, discussion of it will be deferred to Chapter IX.

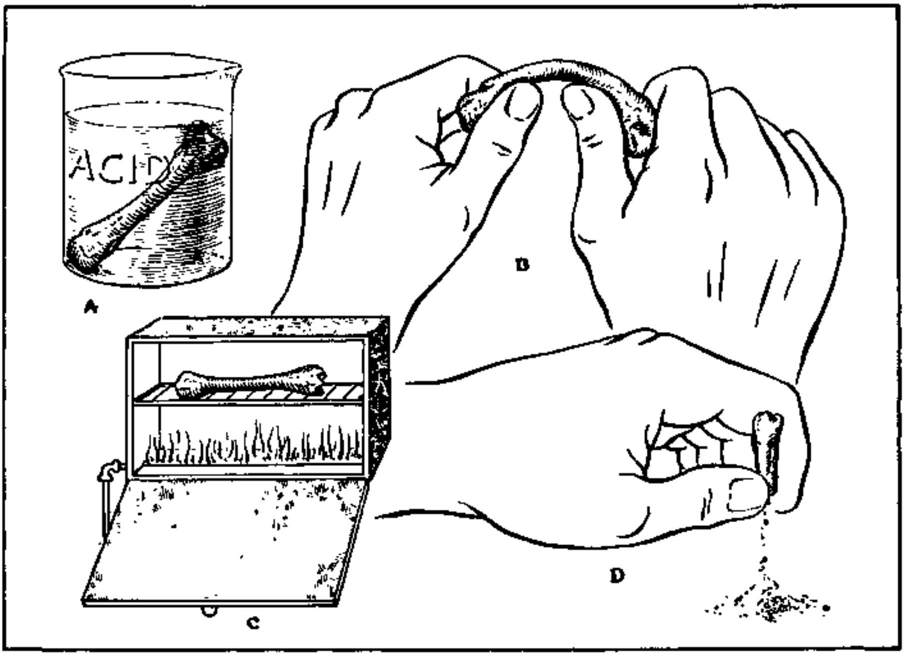


Fig. 3-7. Bone consists of two sorts of materials closely intermixed: organic materials, insoluble in dilute acid, which contribute flexibility to bone (A,B); and inorganic materials (calcium salts), which can withstand burning, and which contribute rigidity (C,D).

The hard or bony part of bone is made of the chemical substances calcium phosphate and calcium carbonate. The latter substance occurs also in such things as oyster and clam shells and in limestone which is often composed largely of such shells. Both calcium phosphate and calcium carbonate are soluble in acids. One might suppose, then, that a bone immersed in acid would completely disappear. Such, however, is not the case. Although all the calcium is removed from the bone by this treatment, the bone has the same shape after acid treatment as it does before, but it is now very flexible. (See Fig. 3-7.)

The material that is left after treatment with acid resembles *cartilage*, the material one calls gristle in meat, and the material, softer than bone, that is found at the ends of "short ribs." Evidently, bone consists of two sorts of material: calcium-containing substances that are acid-soluble, and non-acid-soluble material which is cartilage-like.

A further experiment is enlightening. Instead of putting the bone in acid, let us subject it to great heat for a considerable time. In this case, the cartilage-like material burns and disappears, but the calcium-containing substances, being nonburnable, remain. Again, the experimental treatment leaves the bone unchanged in shape, but this time its structural characteristics are changed in a different way. Loss of the cartilage-like material makes the bone very fragile. (See Fig. 3-7D.)

Since the shape of the bone is not changed by removing either of the two materials, these materials must be very intimately intermixed. In its structural properties, whole bone resembles reinforced concrete. Rigidity is contributed by the calcium-containing substances, while the less fragile cartilage-like material acts as a reinforcing agent, just as steel rods reinforce rigid, but fragile, concrete.

20. How Does a Bone Grow?

The way in which bones grow can be determined by fastening small metal markers to the bones of a young animal, letting the animal grow for a while and then determining the new positions of the markers. The results of such experiments are shown diagrammatically in Figures 3-8A and B. Notice that, as growth proceeds, the spacing between markers 2, 3, and 4 remains the same, whereas the space between 1 and 2 increases, indicating that the region where growth takes place must be located somewhere between markers 1 and 2. The growth region is, in fact, quite near the end of the bone and is called the **epiphysis** (Greek *epi*, on or upon, and *physis*, growth) because it brings about growth by additions on the end of the previous bone. (Note position of epiphysis in Fig. 3-6.)

Bones, however, grow not only in length but also in thickness. How is this accomplished? Again, an experiment with a metal marker will answer our question. This time a metal ring should be fastened around a long bone of a very young animal. The subsequent positions are diagrammed in Figures 3-8C to E. Notice that the ring is first covered over with bone, indicating that bone is added from the outside. Later, the ring appears free in the marrow cavity as the bone in which it was embedded is destroyed to make room for the enlarging marrow cavity.

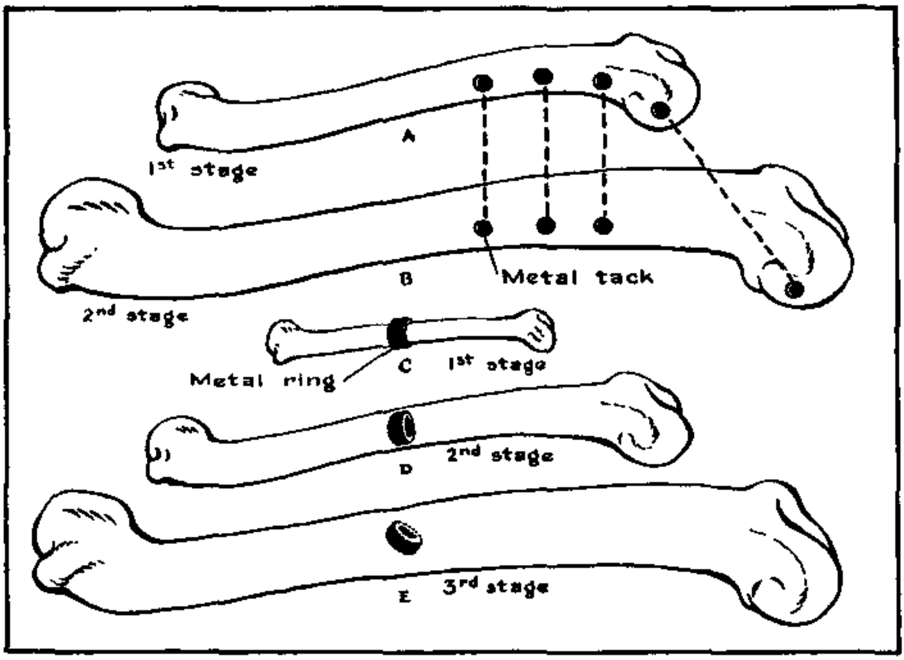


Fig. 3-8. The experimental data which reveal the location of the growing regions of a long bone as explained in the accompanying text.

Growth in thickness of the bone is brought about by a slightly different method from that which causes growth in length. Every long bone of the body is surrounded by a soft sheath called the **periosteum** (Greek *peri*, around, and *osteon*, bone), which lays down new bone from the outside. It can readily be seen that the activity of the periosteum accounts for the burial of the ring in the bone. The subsequent freeing of the ring occurs by another process which will be discussed in § 21.

By analytical experiments, we have shown that growth of the long bones of the body occurs by two different processes: growth in length being brought about by the epiphy*ses* (plural of epiphy*sis*), in thickness by the perioste*a* (plural of perioste*um*). In what we call normal growth, the epiphyses and periostea continue to be active until about twenty years of age. There is, however, a type of abnormal growth in which the epiphyses cease activity prematurely. In such a case, a short-limbed dwarf is produced (Fig. 3-9). Such short-limbed dwarfs were the court jesters of the Middle Ages. In some parts of the world, e.g., in the Congo River valley and in some of the mountains of Mexico, races of this sort have developed locally. The same growth abnormality is known in many other kinds of animals and has been deliberately bred for in certain fancy breeds, notably the dachshund and the Basset hound.

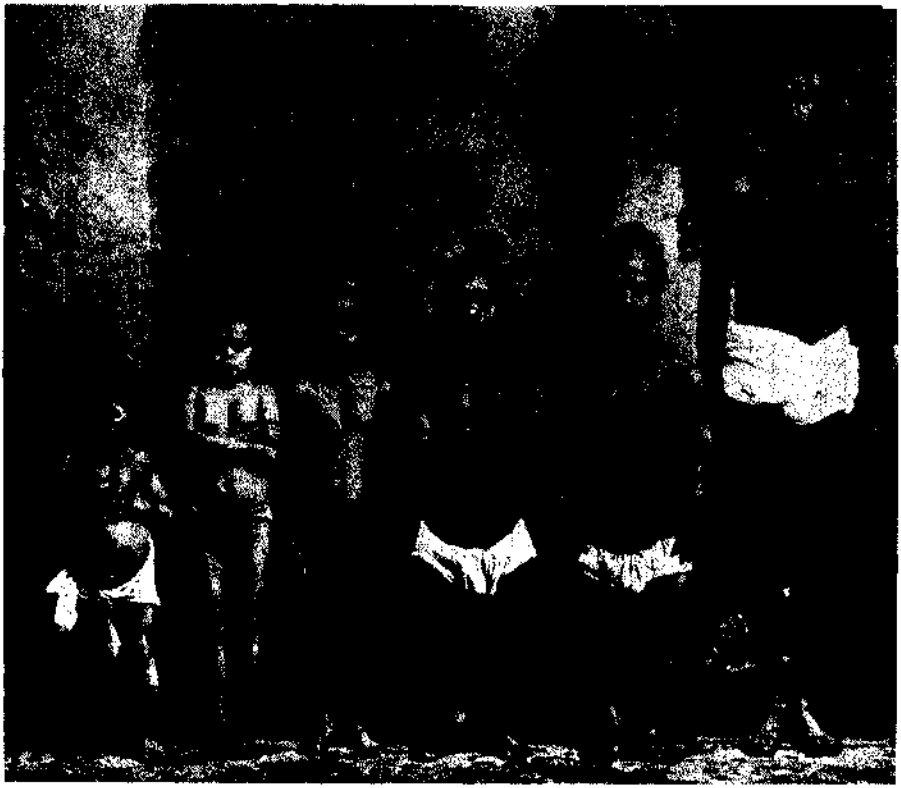


Fig. 3-9. All individuals in this photo are more than twenty years of age. From left to right: a cretin imbecile, the result of insufficient secretion of thyroid hormone; two midgets of the symmetrical (Lorain) type; two short-limbed dwarfs (see § 20); normal man. (From *Physical Diagnosis* by Ralph H. Major, W. B. Saunders Co., Philadelphia.)

21. By What Means Does a Bone Grow? The Cell Doctrine

A long bone grows through the activity of its epiphyses and periosteum; but what is this activity? By what means do these growing

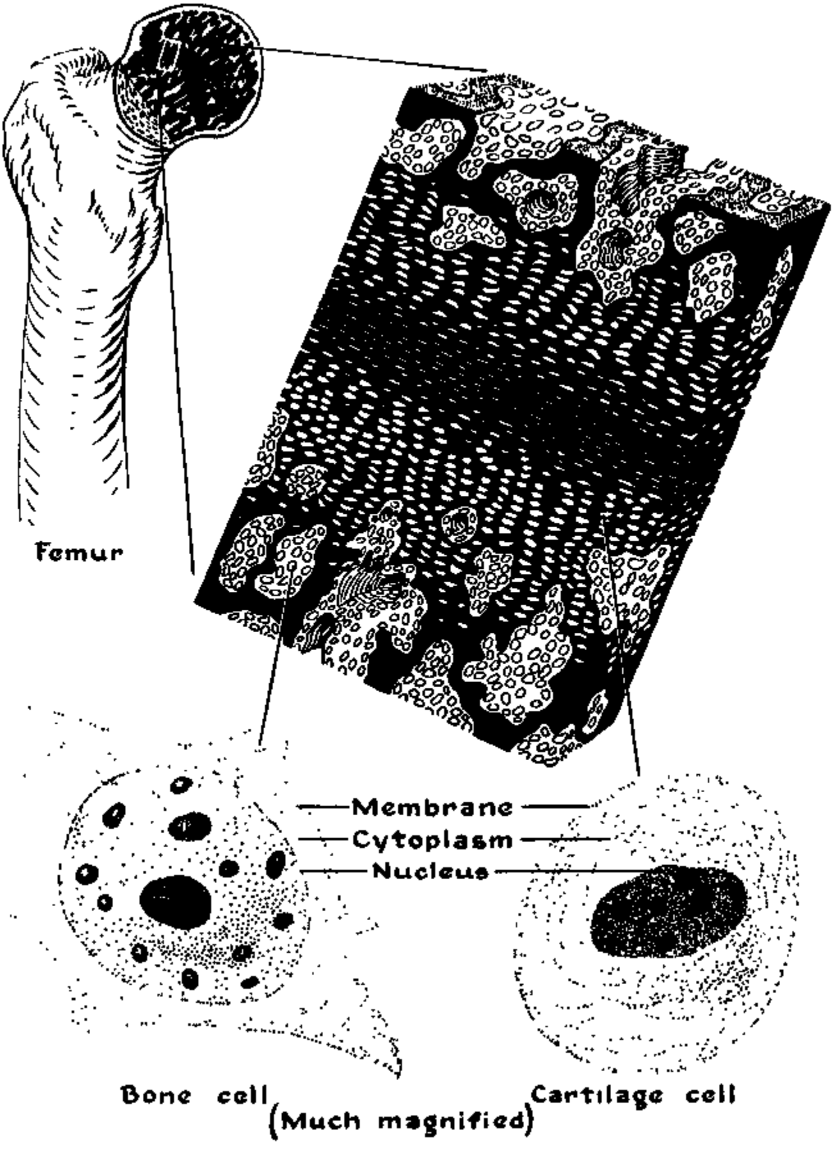


Fig. 3-10. The living cells to be found in the growing section (epiphysis) of a long bone.

regions add to the previously existing bone? What is the *mechanism* of this growth? In answering this question, we will, for simplicity, consider only the mechanism of growth brought about by the epiphysis. The story of the periosteum is slightly different; but, since it is not *essentially* different, there would be little to be gained by telling it, too.

First, we must see what an epiphysis really looks like. To the naked eye, it appears as an irregular plane. But if we look at this region with a microscope, we see that it is composed of a great many smaller elements of definite form, surrounded by formless material. (See Fig. 3-10.)

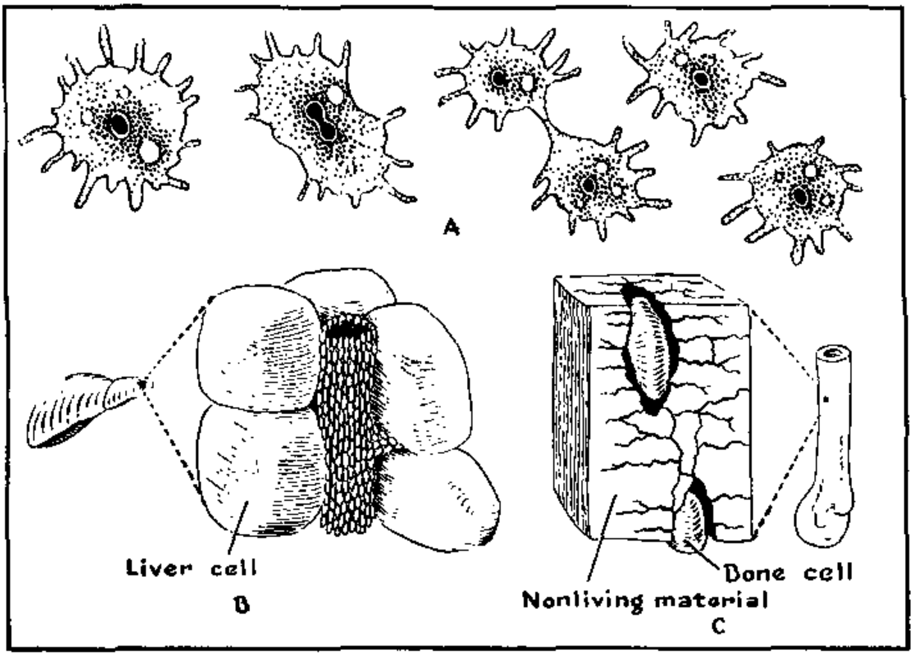


Fig. 3-11. Cells multiply in number by dividing in two (A). Some tissues, e.g., the liver (B), are composed almost entirely of cells. Other tissues, e.g., bone (C), are made up mostly of the nonliving secretions of cells.

Each one of the elements of definite form is called a **cell.** The cell is made of soft, jelly-like material enclosed within a **cell membrane** which is somewhat firmer. Within the cell, there is usually a special structure called a **cell nucleus** (Latin *nucleus*, a little nut, the kernel, the inner part). The rest of the cell, which shows relatively little structure, is called the **cytoplasm** (Greek *kytos*, a hollow vessel—now used to mean a cell—and *plasm*, something formed).

Each cell is in certain respects an independent living thing. It is possible, for instance, for a cell to live all by itself in a laboratory vessel, provided it is supplied with the proper environment. It exhibits all the properties of living things (see Chap. II) including that of reproduction. After being kept well-nourished for some time, a cell divides, forming two cells, each of which is exactly like the original (Fig. 3-11A). The original is usually referred to as a parent cell or **mother cell,** and the two offspring cells are called **daughter cells.** Of course, if the environment is favorable, the process goes on indefinitely, so each daughter cell ultimately becomes a mother cell.

In a suitable environment, each daughter cell is, or soon becomes, like the parent cell in every respect, including size. As one cell increases to two, two cells to four, four cells to eight, and so on, the amount of living material increases in the same proportion. Reproduction of the individual cells of the body results in growth of the body as a whole. In some parts of the body, e.g., the liver, this is the only process concerned in growth. In the bones, as we shall see, it is a relatively minor factor in their growth. Correlated with this difference, we find that the liver is made up almost entirely of cells closely packed together (Fig. 3-11B); whereas, in bone, the living cells are surrounded by a great deal of nonliving material (Fig. 3-11C). Experiments and observations show that **the nonliving material is, in every case, derived from cells.**

How is bone formed? Evidence indicates that it is formed in several stages which we will now describe. Imagine that you are situated on the region of the epiphysis, and that you are small enough (or the cells large enough) so that you can see what is going on from a cell's-eye view*, so to speak. Picture, if you will, first a horde of **cartilage cells.** Each of these cells produces some sort of material inside itself, which passes through its membrane to the outside where it turns into the tough, resilient substance we call cartilage (Fig. 3-12). This process is called **secretion** (Latin *secerno*, to place apart, to separate). Any substance so secreted is called *a secretion.* Each cartilage cell continues to secrete cartilage until it is finally entirely surrounded by its own secretion. Before this happens, however, it has divided several times (as in Fig. 3-11A). Some of the daughter cells are trapped in their own secretion, while others manage to remain in front of the advancing wall of cartilage that is being built up.

There are, of course, regions of the body in which cartilage is the end product; in the long bones of the legs and arms, it is only an inter-

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* This is a figure of speech. None of the cells of the body have eyes.

mediate product, not destined long to survive. If, from our cell's eye, we look at the rear of the wall of cartilage, we discover that it is in a process of disintegration. Looking more closely, we see that the rear of the cartilage wall is heavily infested by an army of a new kind of cell, cells ordinarily called **bone-forming cells** (Fig. 3-12), but which might better be called *cartilage-destroying-and-bone-forming cells.* These cells move slowly forward, literally dissolving tunnels in the cartilage, probably by means of some sort of digestive secretion. Their burrowing through cartilage reminds us of the burrowing of termites or shipworms through wood. There is an important difference, however, in that the bone-forming cells are constructive as well as destructive. As they dissolve away the cartilage, they lay down a layer of bone on the walls of their tunnels. Bone, too, then is a secretion.

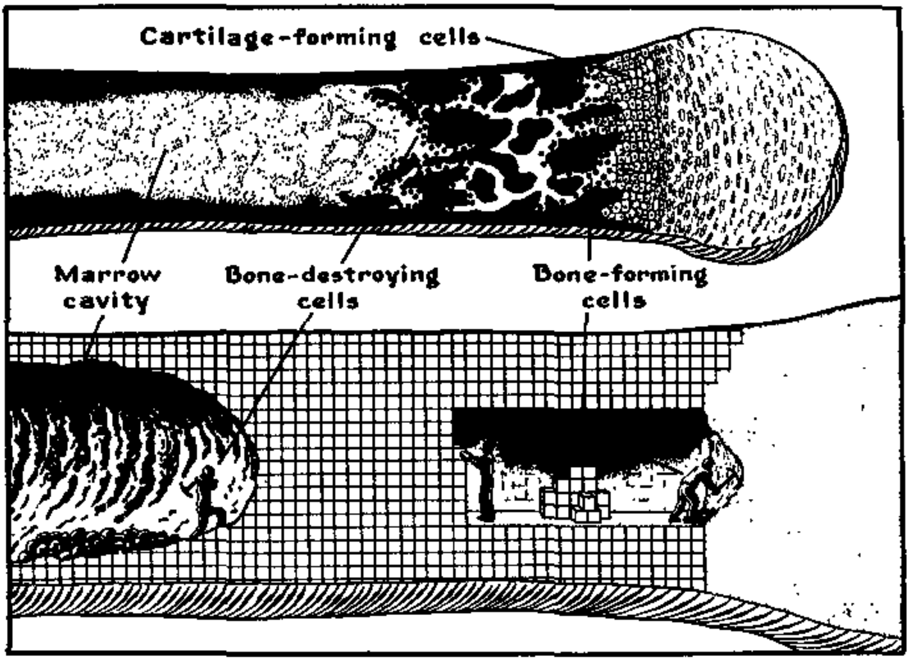

Fig. 3-12. Diagram and picture-analogy of the method of formation of cartilage, followed by cartilage destruction and bone formation, and ultimately bone destruction to make way for the marrow cavity, as described in text.

Thus is bone, the substance, made. But the making of *a bone*, the object, involves more than this. Notice, in Figure 3-6, that a large part of a bone is not occupied by bony material, but by a much softer stuff, marrow. This central cavity in the bone can come into existence, and can grow as the bone grows, only if much of the bone that is formed is subsequently destroyed. Bone-destruction, like cartilage-destruction, is carried out by cells which in this case are called **bone-destroying cells.** In Figure 3-12, these cells can be seen as the last army of cells moving forward toward the end of the bone, destroying bone material as they go.

Such is the activity involved in the linear growth of the long bones. Other types of bone growth differ in details but the principles are the same. Growth is always the result of cellular activity and consists either of increase in the number of cells or in the amount of secreted substance, or both. Furthermore, a fact we might not have predicted beforehand, growth frequently involves destructive aspects as well, as the juvenile scaffolding is removed to make way for the adult structure. Even in adults, as a matter of fact, both construction and destruction continue, but at very slow rates, and at rates that are almost exactly equal. Even in adults, bone material is being slowly destroyed and as slowly replaced without, however, substantial change in the form of the whole. It is as though we had a house made of bricks and that continuously, year after year, we slowly removed a brick here and a brick there, always replacing it by another. The house remains, but the bricks change. So in the adult bone, the object we call *a bone* remains, but individual bits of the substance, *bone*, disappear to be replaced by new material of the same sort.

We have considered at some length the process by which the long bones are made. This is a special case of the process of growth, but it is in no sense exceptional. The story of growth varies from part to part throughout the body; but wherever it occurs, it is the result of cell activities. Indeed, it is well to emphasize two facts:

The body is made up entirely of cells and the products of cells.

All the normal activities of the body, both constructive and destructive, are the result of the activities of cells.

QUESTIONS AND PROBLEMS

3-1. Define the following terms: *suture*, *epiphysis*, *periosteum*, *secretion*.

3-2. Give the plural forms of the above terms.

3-3. Distinguish between: (a) *analysis* and *synthesis;* (b) *axial skeleton* and *appendicular skeleton*.

3-4. What are the functions of the skeleton?

3-5. Although the text is not explicit, would you hazard a guess as to whether or not the periostea of human and animal dwarfs exhibit normal activity, or cease activity prematurely? (Regard Fig. 3-9.)

3-6. Describe the process by which a long bone grows in length.

3-7. It is common knowledge that the diet must include some calcium in it. For what purpose is the calcium used?

3-8. Would you expect the daily need of calcium to be greater in a child of, say, ten years, or in an adult? Why?

3-9. A whale has proportionately less of its body weight in skeleton than a land animal of corresponding size would have. Account for the possibility of such a difference.

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Gerard, R. W., *Unresting Cells.* New York: Harper & Brothers, 1940.

Chapter IV

The Muscular System

22. How the Muscles Move the Bones

At the outset, it is important to realize this fact: **a muscle is capable of only one positive action,** namely, **contraction.** Its only other action is a passive one, **relaxation.**

Muscles move the parts of the body in various directions. To take a simple example, the forearm can be either **flexed** (Fig. 4-1A) or **extended** (Fig. 4-1C). Both flexion and extension are the result of muscular action. Since all muscles have the same primary action (contraction), different movements must be possible only because muscle contractions are utilized in different ways. The relationships of the muscles to the associated bones show how this is possible (Fig. 4-1B and D).

In the example illustrated, the two bones act as two parts of a lever; the upper arm bone, the **humerus,** acts as the fulcrum, while the forearm bone, the **radius,** acts as the lever arm. (There are two bones in the forearm, the radius and the **ulna,** but for simplicity we will speak of only one.) There are several muscles involved in moving the forearm, but no harm will be done if we focus our attention on only two of them, the **biceps** muscle on the "front" part of the upper arm and the **triceps** on the back part.

Both muscles are attached to the shoulder bones above the humerus. From knowledge of the point of attachment to the radius (see Fig. 4-1C), one can readily predict that contraction of the biceps will lead to a flexing of the arm. Similarly, since the triceps is attached to the other side of the forearm, one can predict that contraction of this muscle will

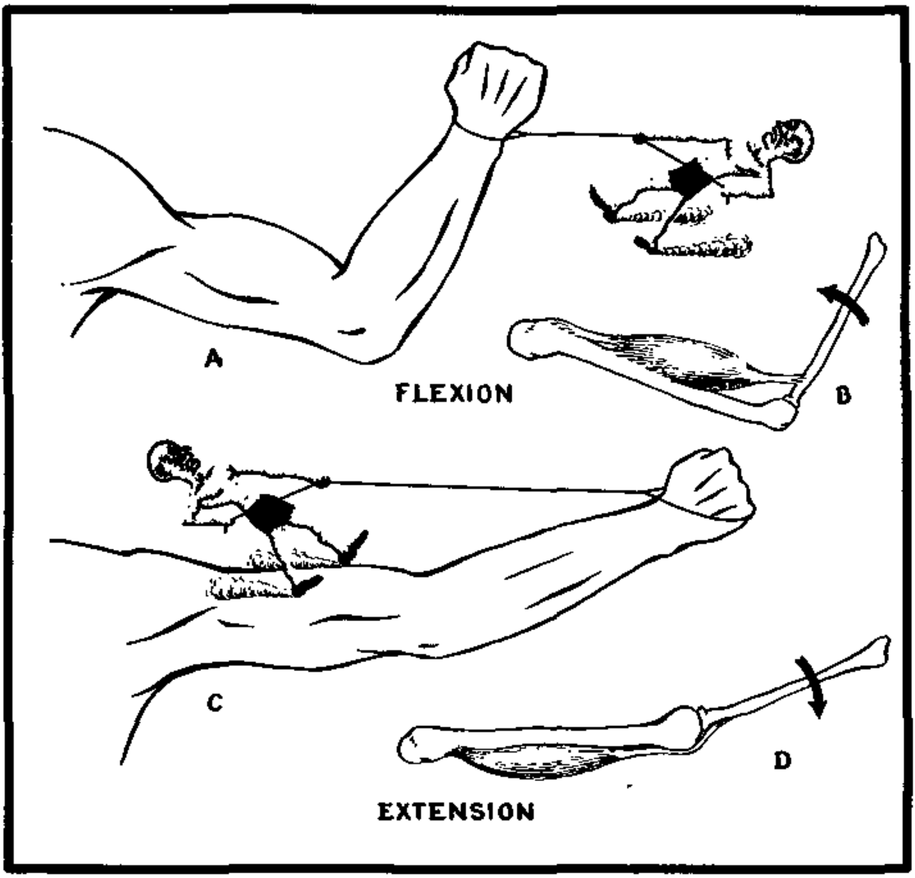

Fig. 4-1. Showing how the points of attachment of a muscle determine whether the muscle's one action (contraction) results in flexion (A,B) or extension (C,D).

result in extension of the arm. By the proper cooperative use of these two muscles, the arm can be flexed or extended to any degree. Muscles which act contrary to one another in this way are called **antagonists** or are said to be *antagonistic* to each other.

These terms are partly apt, partly inept, for with muscles, we have the paradoxical situation that **antagonistic muscles always cooperate** in carrying out the movements of the body. Theoretically, an arm could be flexed by the use of the biceps alone. Actually, the triceps, too, is always called into play during flexure. To verify this, the reader should slowly flex, say his right arm, while with his left hand he feels the underneath side of his right arm. During flexure, a noticeable tenseness develops in the triceps muscle, showing that it is contracted to a certain extent. The triceps does not contract as forcibly as the biceps, for if it did, the two equal and counteracting forces would prevent any movement at all, but it does contract somewhat whenever the arm is flexed. Similarly, in extension, the biceps contracts, though less strongly than the triceps. The cooperative action of antagonistic muscles is important in bestowing smoothness to the movements of the body.

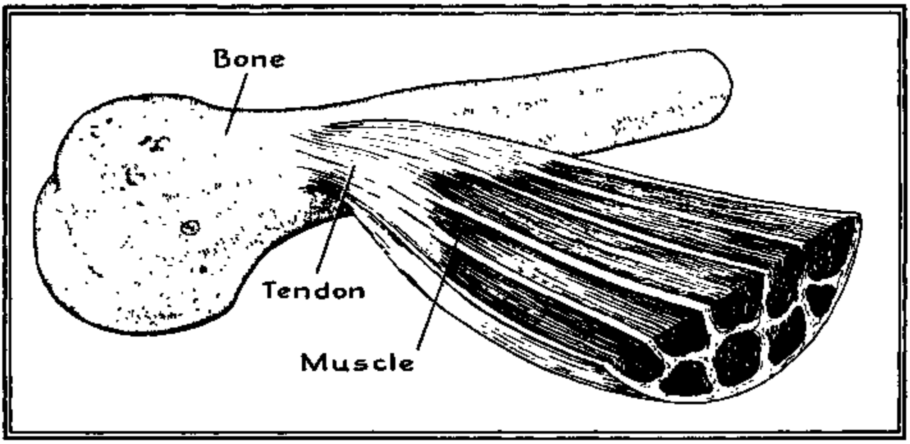

Fig. 4-2. The attachment of a muscle to a bone by means of a tendon, the usual method.

Sometimes a muscle appears to be attached directly to a bone; more frequently the muscle terminates in a **tendon** which in turn is attached to the bone (Fig. 4-2). This tendon belongs to a class of tissues called **connective tissue**—of which cartilage is another example—tissues which serve principally to connect and tie together the other tissues of the body. A tendon is made up largely of cell secretions, rather than cells, and it is very tough and flexible, but not elastic. The tendon acts as a cable to transmit the pull from the contracting muscle to the bone to which it is attached at the other end.*

There is an important benefit conferred by the tendons; a tendon permits a muscle to act at a considerable distance from the bone that it is moving. Notice, in Figure 4-3, that the muscles which move the

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* Suppose the tendon were elastic. What effect would this have on its manner of functioning?

fingers in the left hand are actually at a considerable distance from them, being well up in the forearm. The reader can verify this by moving his fingers vigorously and noticing how the muscles can be seen rippling under the skin of the upper part of the corresponding forearm. The position of these muscles explains the feeling of fatigue experienced in the forearm following long-continued and intensive use of the fingers, as in typing or playing a musical instrument. (See right hand in Fig. 4-3.)

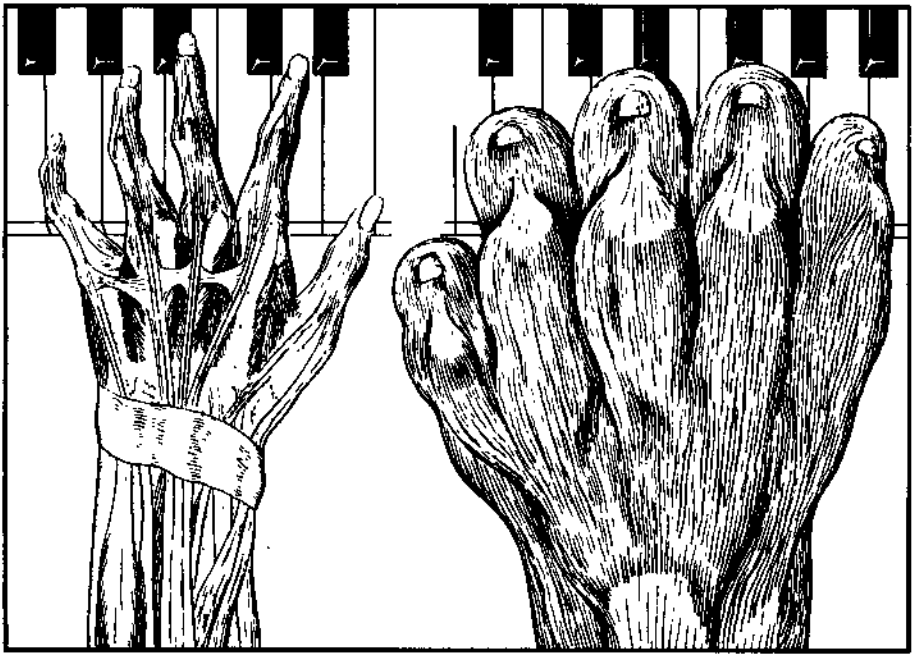

Fig. 4-3. How the tendons permit action of muscles at a distance is shown by the left (normal) hand. At the right, is the artist's conception of what the human hand would be like if muscles had to be attached directly to the bones they move.

When one thinks of activities of this sort, it is easy to appreciate the advantage of the tendon system of transmitting power; if muscles had to be always fastened directly to the bones that they move, our fingers, if they were as powerful as they are now, would be great, clumsy muscle-padded digits, quite incapable of the delicate movements they now perform. Many of man's arts and skills would no longer be possible, except at a very crude level. Without the action at a distance permitted by slender tendons, we would be truly "muscle-bound." (See Fig. 4-3.)
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There are over 600 recognized skeletal muscles in the human body. As was true of the bones, the number varies somewhat from person to person; smaller and relatively unimportant muscles are frequently missing. The more important muscles are almost always present but they show a considerable amount of variation in their points of origin and insertion. In one study of over 500 human corpses, it was found that, in more than twenty per cent of them, one or both of the biceps muscles had *three* heads, i.e., three points of attachment, thus belying the name which implies two heads. Many other variations in muscle attachment are known. Probably some of the individuality shown in gait is attributable to such variations.

23. Structure of a Muscle

We need no microscope to tell that a muscle is not a homogeneous structure. A beefsteak is a cross section of a cow's muscle or of several muscles. Either inspection or eating makes it apparent that there are three sorts of tissue present in such meat: muscle tissue (which makes up the bulk of the steak); fatty connective tissue which, in a good steak, is flecked throughout the muscle; and tough connective tissue* or gristle which, from a gastronomic point of view, is better absent.

To the animal, the presence of fat in a muscle is perhaps of no particular benefit; this is just one of the many places where fat can be stored. The presence of tough connective tissue, however, is of first importance. The strands and sheaths of connective tissue which surround the muscle fibers (Fig. 4-4) join with each other and with the tendon. They constitute part of the machinery by which the muscle is connected with the bone in such a way that the contraction of the muscle moves the bone. The proportion of connective tissue to muscle tissue increases with age. As evidence, compare the dated sections shown in Figure 4-4, or compare the masticability of genuine lamb with admitted mutton.

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* Histologists, that is, scientists who study tissues (Greek *histos*, web or tissue), recognize about a dozen different kinds of connective tissue, among which are loose connective tissue, fatty tissue, tendons, cartilage, and bone. Corroborative evidence that bone is but one variety of connective tissue is furnished by a rare disease (bearing the impressive name of *myositis ossificans progressiva*) in which the connective tissue of muscles gradually turns into bone. The eventual result is complete immobility of the muscles affected and the sufferer could be said to "turn to stone."

24. The Fine Structure of Skeletal Muscle

In Figure 4-5, it is apparent that a muscle is made up of strands of muscle fibers which run parallel to the length of the muscle. When these muscle fibers contract, the muscle contracts. Not all fibers contract at the same time. The greater the number of fibers contracting at any instant, the stronger the contraction of the whole muscle.

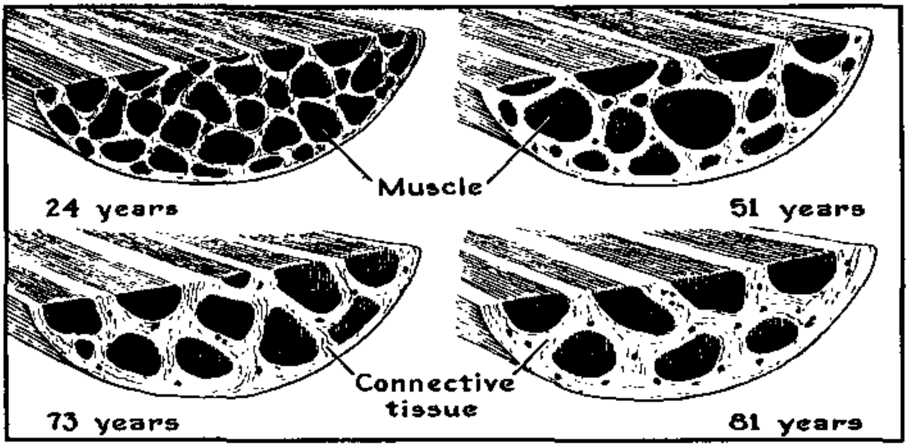

Fig. 4-4. Cross sections of muscles taken from men of several ages. Note the proportionate increase of connective tissue and decrease of muscle tissue with advancing age. This is one reason why the muscles of an old man are not as strong as those of a young one.

Previously (§ 21), we were introduced to the cell doctrine which, as concerns the human body, states that the entire body is made up of cells and the products of cells. Also, there were exhibited cells of a relatively simple sort, each of which consisted of a nucleus and cytoplasm enclosed in a membrane. Most of the tissues of the body are made up of cells of this nucleus-cytoplasm-membrane construction. The skeletal muscles are, however, an exception. Examination of one of the muscle fibers shows that it contains many nuclei but no membranes separating the nuclei. The only membrane is the one surrounding the whole fiber. Cells that are **multinucleate,** i.e., contain many nuclei, are not uncommon, but usually the number of nuclei is small, less than a half-dozen. Since the muscle fiber contains such an exceptionally large number of nuclei, there is a certain reluctance among some biologists to refer to it as a muscle *cell*, although it is unquestionably the unit of structure and function of the muscle. Because of this reluctance, this unit is usually referred to as a muscle fiber, a usage to which we will adhere.

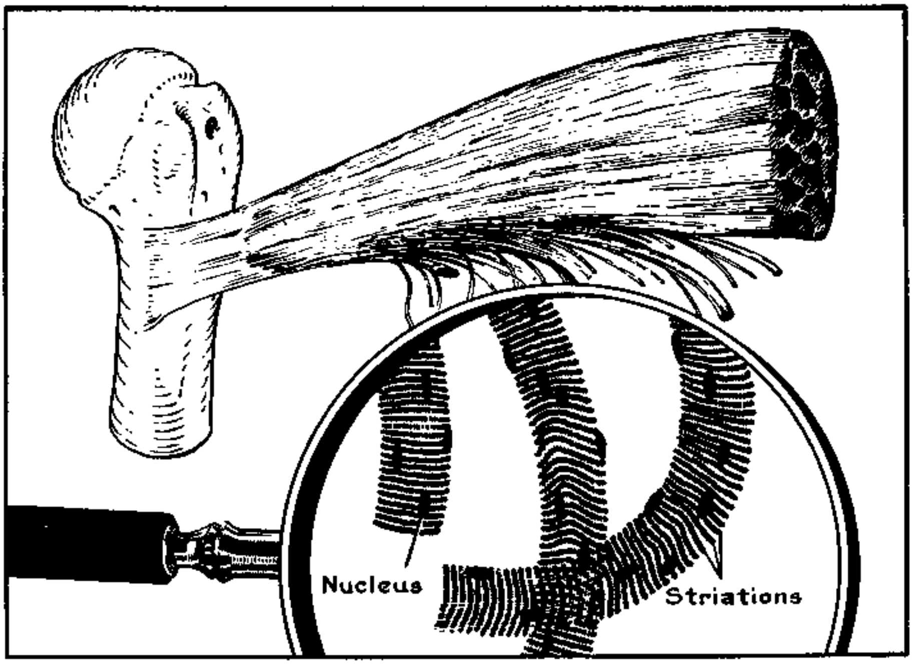

Fig. 4-5. The striations to be seen in skeletal (voluntary) muscle when it is examined with the highest magnification of the microscope.

One of the most remarkable features of skeletal muscle fibers is the cross-banding which is visible under the microscope. (Fig. 4-5.) Every skeletal muscle has alternating light and dark bands oriented at right angles to its long axis. What these bands really are is at present a mystery. It has been observed that when a muscle fiber contracts, the light bands become dark and the dark bands light, but no one knows why.

Not all muscles show this banding or *striation*. The muscles that move the skeleton do; hence, the skeletal muscle is frequently referred to as **striated muscle.** But there are other muscles that are not striated. The wall of the stomach, for instance, contains unstriated, or **smooth muscle.** In general, the organs in the central body cavity possess smooth muscle, striated muscle being comparatively rare. Smooth muscle differs from striated muscle in a number of ways (see § 60), the most conspicuous of which is in the speed of action. Smooth muscle contracts and relaxes very slowly, striated muscle much more rapidly. Completion of contraction may take several seconds in the case of the former, and less than one second in the case of the latter.

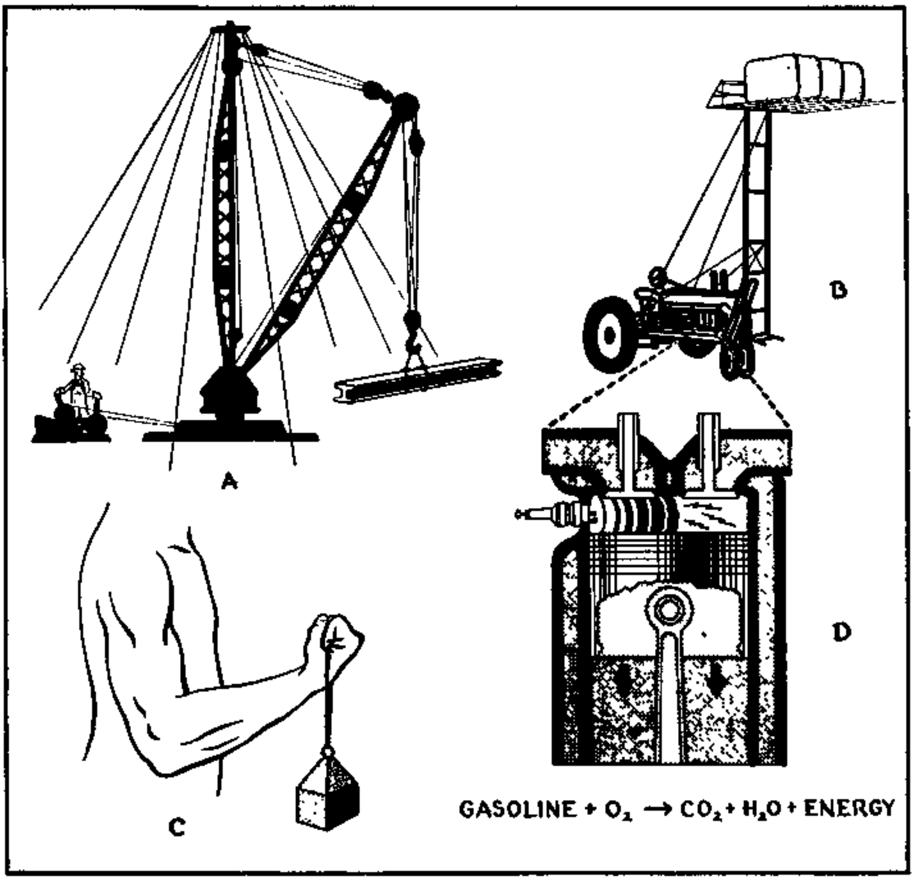

Fig. 4-6. Lifting a weight through space is work, whether the agent is a crane (A), a tractor (B), or a human arm (C). In the case of the gasoline motor, a chemical reaction (D) furnishes the energy needed. An analogous chemical reaction takes place in muscle as explained in the text.

Rapidity of muscle action is associated with presence of striations of the muscle, though we do not know why. The association is true not only in the sense of presence-or-absence mentioned above, but also there is, in a rough way, a *quantitative* relationship between activity and striation among striated muscles. The most active muscles of a bird are the wing muscles, which are attached to the breastbone; these muscles have very pronounced striations. Less active muscles, such as the leg muscles and muscles between the ribs, have less pronounced striations.*

25. Where Does the Energy Come From?

The 600-odd skeletal muscles of the body enable us to do many things: swim, climb mountains, play the piano, paint, write, perform sleight-of-hand tricks, or (in some fortunate individuals) wiggle the ears. All these diverse activities can be considered as variations of one basic action—lifting a weight through space (Fig. 4-6), that is, doing work. In the nonliving world, such work can be done only by the expenditure of energy. The weight in Figure 4-6A is raised when electrical energy is expended in running the electric motor. Work done by a living machine must also be paid for in the same coin—energy. Where does the energy come from in this case?

The source of the energy for movement of a living muscle can be made clearer by first considering work done by a gasoline engine (Fig. 4-6B). The source of the energy in this case is the gasoline which the engine burns. That gasoline can be a source of energy can be attested by anyone who has used a lighted match to see if a gas tank was empty, provided he has survived to bear witness. The reaction which releases the energy can be written thus:

$$\text{Gasoline} + \text{oxygen (from the air)} \longrightarrow \text{carbon dioxide} + \text{water} + \text{energy} \qquad (1)$$

Inside the gasoline engine, the same explosive reaction takes place, only the explosion is more carefully controlled. A little bit of gasoline is mixed with air in the carburetor, and the mixture is sprayed into a cylinder (Fig. 4-6D). Here the mixture is ignited by a spark plug. The energy released in the resulting explosion causes the piston to move, and it is this movement which is utilized to work a crane or run a car.

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* It happens, also, that the less active muscles are darker in color but this is due not to absence of striations, but to the greater presence of a coloring matter called muscle hemoglobin. "Light meat" has less muscle hemoglobin and more marks or striations, and more work to do. Veal, the meat of a younger, more active animal, is likewise lighter in color than beef.

The waste products of the reaction, the carbon dioxide and water (together with small amounts of carbon monoxide and some foul-smelling gases), pass out through the exhaust pipe, the water in the form of a hot vapor contributing to the rapid rusting of the automobile muffler.

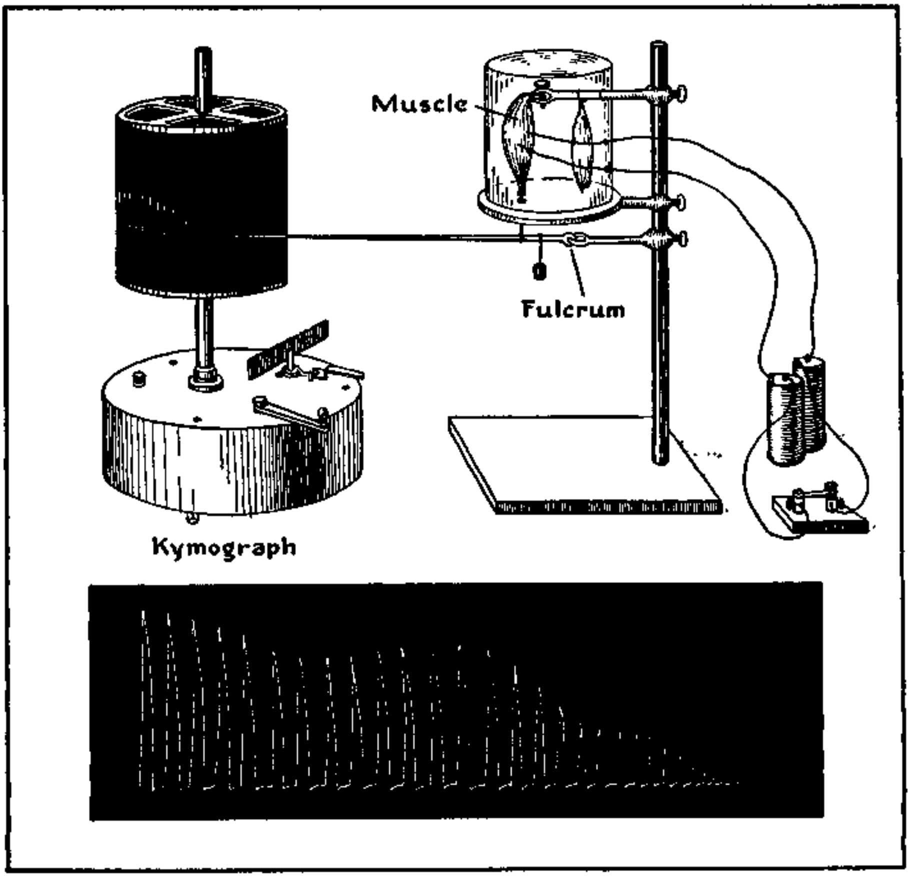

Fig. 4-7. A method of causing contraction of muscle by an electric stimulus. A record is made on the moving drum of smoked paper. Below is seen a typical record of successive muscle contractions ending in fatigue.

A muscle gets its energy also from a reaction, or rather a series of reactions, in which energy-rich compounds are "burned" with oxygen. The discovery of these reactions has taken many years and the story is not yet complete, but enough of it is known so that a reasonably firm outline can be sketched. A convenient way of doing this will be by describing some idealized demonstration experiments. In these experiments, we will use muscles from a frog. There is much evidence that a frog's muscle is not significantly different from a man's or a dog's, and its use is justified by its convenience. Not only is it cheaper, but it is much hardier. A muscle taken from a freshly killed frog will remain alive, i.e., capable of contraction, for many hours, provided it is kept properly moist. Since a frog is a "cold-blooded" animal, the temperature need not be closely controlled as it would have to be for a muscle from a warm-blooded animal like man. This is an important practical advantage in carrying out experiments.

Before beginning an account of the experiments on which are based our present concepts of muscle action, it might be well to prepare the reader for what is ahead. (Here we erect a sort of SLOW—STEEP HILL sign.) We could summarize the present state of our knowledge of the chemistry of muscle contraction forthwith by a column of brief equations. Such a display, however, would have relatively little meaning to the neophyte. Moreover, it would give him little insight into the method by which physiologists arrived at these equations. At the risk of spending overmuch time on this small part of physiology, we will give, in simplified form, the essential experiments that led to our present knowledge of muscle physiology in the hope that this extended treatment will be more meaningful than a briefer and more elegant presentation.

Suppose, now, that we take two frog muscles and place them in a moist chamber. One of these will be attached to a weight (Fig. 4-7). Periodically, it will be caused to contract by a suitable stimulus which had best be a small electric shock. The shock will be very small, not nearly enough to furnish the energy expended by the muscle in raising the weight. That is, the electric shock is only a *stimulus* (§ 10). Each time the muscle is stimulated, it contracts and lifts the weight, thus doing work and undoubtedly expending energy. For reasons which will appear subsequently, successive stimuli will be administered at rather long intervals of time, perhaps a minute or two. If we follow this procedure, the strength of the contractions will grow less and less and finally cease altogether.

It would seem reasonable to suppose that the final inactivity of the muscle results from an exhaustion of the "fuel," i.e., the source of energy, just as an automobile will come to a stop when its supply of gasoline is exhausted. But what is the fuel that the muscle uses? Is there anything present in the control muscle, which has not been working, that is not present in the experimental muscle which has worked to exhaustion?

Chemical analysis shows that there is a difference in the two muscles. Only the control, unexercised, muscle contains a chemical substance called **glycogen** (Greek *glykys*, sweet, Latin *gen*, giving rise to; so named because glycogen can be changed into sugar). This substance contains energy, as the chemist can show by burning it with oxygen. From this experiment, one might suppose that the reaction which furnished the energy for muscular contraction could be written:

$$\text{glycogen} + \text{oxygen} \longrightarrow \text{carbon dioxide} + \text{water} + \text{energy} \quad (2)$$

This reaction, which differs from (1) only in the fuel used, looks reasonable. It is chemically possible. Is it truly what takes place in the muscle?

A simple experiment will show that equation (2) is not the whole chemical story. The experiment consists in having the muscle act in a chamber in which no oxygen is present. *A muscle can contract even when it has no access to oxygen.* Therefore, the primary reaction cannot be one that involves oxygen.

This does not mean that oxygen is not involved in muscular function. It has been noticed that a muscle contracting in the absence of oxygen soon fatigues. As long as the fatigued muscle is deprived of oxygen, it remains incapable of contraction. But if oxygen be readmitted to the chamber in which the muscle is placed, in a short while the muscle recovers its ability to contract. It is evident, then, that *oxygen is required for the* **recovery phase** of muscle activity.

Further studies have shown that the chemical equation involved in the **contraction phase** involves neither oxygen nor glycogen but rather an entirely different substance which can be called **phosphate-creatine.** This substance can be broken down into two parts, phosphate and creatine, and this breakdown releases the energy which is used in muscle contraction. As an equation:

$$\overset{\text{CONTRACTION}}{\text{Phosphate-creatine} \longrightarrow \text{phosphate} + \text{creatine} + \text{energy}} \quad (3)$$

In the recovery of muscle, glycogen is "burned" with oxygen, yielding energy. Part of this energy appears as heat, just as it would if we burned the glycogen in a test tube. But, more important, another part of the energy is used to remake phosphate-creatine—that is, to restore the muscle's ability to contract. In equations:

RECOVERY

$$\begin{tikzcd}
\text{Glycogen + oxygen} \arrow[r] & \text{carbon dioxide + water +} & \text{energy} \arrow[d] \arrow[dll, bend right] & (4) \\
 & & \text{heat (waste)} & \\
\text{Energy + creatine + phosphate} \arrow[r] & \text{phosphate-creatine} & & (5)
\end{tikzcd}$$

notice that the energy of (4) is followed by two arrows indicating that part of the energy appears as heat, and the remainder is the energy that makes the reaction of equation (5) go. Notice also that equation (5) is simply (3) written in reverse.

At this point, it might be well to stop and ask, *What of it?* What if muscle function does involve two separate phases, (equations (3), (4), (5)) as just described, instead of only one phase (equation 2) as first supposed? Is this of any importance to the organism? A little thought will suggest (and experiments confirm) that it is exceedingly fortunate that the two phases exist and that the contraction phase does not involve oxygen. As we shall learn later, oxygen is brought to the muscle (as well as to other parts of the body) by the blood stream; there is no appreciable reservoir of oxygen in the muscle. There is, however, a considerable reservoir of phosphate-creatine. For contraction, therefore, the muscle does not have to wait for the blood stream to supply it with anything; it is ready, on an instant's notice, to contract. It cannot contract for very long, however, before it runs through its supply of ready-made phosphate-creatine; then it becomes dependent on a supply of oxygen to remake these energy-rich compounds. If an analogy will help, the phosphate-creatine complex amounts to a sort of wound-up spring which can release its energy upon suitable stimulus. The oxidation of glycogen (equation (4)) is the means whereby the spring is rewound, thus making possible new contractions.

In the light of these facts, consider the practical example of a man running a hundred-yard dash. While he is running for this brief time, he is using up—breaking up—the phosphate-creatine complex faster than the muscle's oxygen supply (dependent on the blood stream) will permit remaking it. As a result, the man ends the race in a thorough state of exhaustion, his muscles being virtually incapable of further contraction. For a considerable time after the race, his breathing is very deep and rapid; thus, more air (hence oxygen) is brought to his lungs, hence to his blood stream, hence to his muscles. His body must function in this way to bring more than the normal supply of oxygen to his muscles, because during the preceding period of excessive activity the muscles built up an **oxygen debt,** represented by the unreconstructed phosphate and creatine. This debt is paid off after the race by increased intake of oxygen, and not until the phosphate-creatine is remade is the man able to run again.*

26. Equations As Approximations to the Truth

It will be worth while to reexamine the path of discovery described in the preceding section in the light of the remarks made earlier (see § 5) about the lack of absolute certainty in science. We are now in a position to recall this basic idea in a new context and give it more meaning.

Let us suppose that our experimentation had stopped earlier, after the experiment which led to equation (2), namely:

$$\text{glycogen} + \text{oxygen} \longrightarrow \text{carbon dioxide} + \text{water} + \text{energy} \qquad (2)$$

This equation was postulated because of its analogy to equation (1) which we accepted without evidence. Our experiment showed only that glycogen disappeared as energy appeared in the form of heat and muscular work. However, other experiments could have been carried out which would have shown that oxygen disappeared as carbon dioxide appeared. There are also means (which we will discuss in later chapters) by which it could be shown that at least some of the carbon in the carbon dioxide came from the glycogen. The source, or even the appear-

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* In describing the experiment diagrammed in Figure 4-7, it was stated that the successive stimuli should be administered at rather long intervals. In dealing with a muscle isolated from the rest of the frog, if the stimuli are sufficiently widely spaced in time, no oxygen debt is incurred. The recovery rate being the same as the rate of contraction, equation (2) is a satisfactory description of the whole process since it represents the *net* result of completely "paid-for" muscle activity.

ance of water, we could probably not determine. Nevertheless, it would have been possible to establish, with a fair degree of certainty, the validity of equation (2) in describing the results of an experiment of the sort mentioned, namely, an experiment in which the muscle was *slowly* fatigued in the presence of plenty of oxygen.

If asked for a brief summary of the results of our work at this point, we might have replied: "We have found that the energy needed for muscle contraction is furnished by the oxidation of glycogen." Let us call this "Statement One."

Is Statement One true? Had we gone no further in our experiments, we might have concluded that it was. We might even have called it a *Law* (say the Law of Muscle Energy). In time, we might, from forgetfulness or unscientific arrogance, have concluded that it represented Absolute Truth. Yet only a single, simple experiment would be needed to overthrow this "Absolute Truth", namely, the experiment of stimulating an unfatigued muscle in the absence of oxygen. If we had been overly impressed with the absoluteness of scientific truth, we would likely also have been unduly disturbed by the apparent fickleness of the absolute. In any case, it might have seemed that what was true one day became false the next, and this is not a pleasant situation.

But need we, after performing the experiments that led to equations (3), (4), and (5), conclude that Statement One is false? Not necessarily; it is still true—in a sense. In the long run, the oxidation of glycogen *is* the source of energy for muscle contraction, but it is not the immediate source. Equations (3), (4), and (5) do not flatly contradict Statement One; they elaborate on it. If we are to capitalize on the information furnished by the new equations, we need to make a new summary statement:

Statement Two: "The immediate source of the energy needed for muscle contraction is the breakdown of phosphate-creatine to phosphate and creatine; the remaking of the phosphate-creatine complex is made possible by energy furnished by the combination of oxygen and glycogen to form carbon dioxide and water."

Statement Two takes account of all the experimental facts described above. Is this statement true? Is it Absolutely True? In the light of previous experience, it would be foolhardy to say it is. Statement Two is undoubtedly closer to the truth than is Statement One. But, by analogy, one would suspect that further experiments would lead to a Statement Three which would be still closer.* At no time, can we say of a statement: *This is the truth*. The best we can say is: *This is an approximation to the truth.*

It would be well at this point to emphasize a characteristic of textbooks of science. The student should realize that almost all sciences have progressed to such a stage now that it is impossible to give all the facts and evidence in even a small corner of a science in an elementary textbook. As a consequence, all elementary textbooks (including this one) are necessarily false. However, the errors of a textbook should be only ones of *om*ission, never of *com*mission. The author should tell "the truth, . . . and nothing but the truth"—but not the whole truth. To refer to the present problem, it should be permissible for an author to say: "The energy for muscle contraction comes from the burning of glycogen." However, he should *not* say: "The burning of glycogen causes a muscle to contract," or "A muscle cannot contract unless it burns glycogen."

The student mastering a new science cannot learn the truth, the whole truth, and nothing but the truth at one fell swoop. He must work with the facts and evidence that are given him and inch his way forward, so to speak, arriving at ever-closer approximations to the truth. In this necessity, however, the rawest recruit learning how to handle the weapons of a science does not differ from the research scientist struggling at the outermost frontier. As one great chemist† has stated:

> "The scientist is a practical man and his are practical aims. He does not seek the *ultimate* but the *proximate*. He does not speak of the last analysis but rather of the next approximation. His are not those beautiful structures so delicately designed that a single flaw may cause the collapse of the whole. The scientist builds slowly and with a gross but solid kind of masonry. If dissatisfied with any of his work, even if it be near the very foundations, he can replace that part without damage

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* As a matter of fact, much more is already known of the chemistry of muscle activity. For instance, the reaction which is the immediate source of energy for equation (5) is a breakdown of glycogen to form lactic acid, a reaction in which oxygen is not involved. Subsequently, some of the lactic acid is completely oxidized.

† Lewis, Gilbert N., *The Anatomy of Science.* New Haven, Conn.: Yale University Press, 1926.

to the remainder. On the whole, he is satisfied with his work, for while science may never be wholly right it certainly is never wholly wrong; and it seems to be improving from decade to decade."

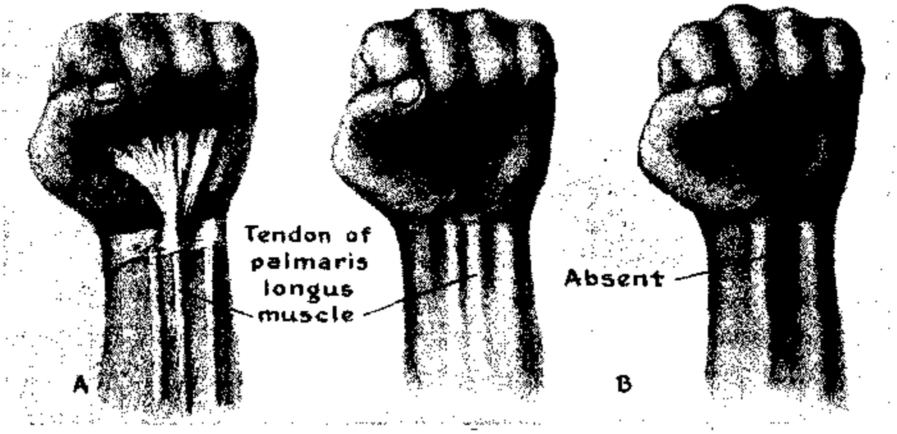

Fig. 4-8. Demonstration of the tendon of the *palmaris longus* muscle. This muscle and tendon are absent in many normal humans.

QUESTIONS AND PROBLEMS

4-1. A muscle has only one positive action: contraction. How do you account for the fact that opposite movements of an appendage are possible?

4-2. What is connective tissue? Why is it so called? Name as many kinds of connective tissue as you can, telling the importance of each, in so far as you know.

4-3. What is striated muscle? Where is it found? Where is muscle of other sorts found?

4-4. What is the function of the striations in striated muscle?

4-5. Give a simple equation for the reaction that takes place in the cylinders of a car when running. Does this equation represent "the truth, the whole truth, and nothing but the truth"? If you say "No," give your reasons.

4-6. What are the comparative advantages of using man, dog, or frog for experimentation in the field of muscle physiology?

4-7. Criticize: "All actions of all living organisms require oxygen."

4-8. What are the chemical reactions involved in contraction and recovery of a muscle?

4-9. What is meant by the phrase, "oxygen debt"? What phenomena well known to athletes does this concept help explain?

4-10. A muscle from a young frog is compared with a muscle from an old frog. Both muscles are of exactly the same size and weight and both are treated the same, yet the old muscle cannot lift as heavy a weight as the young one. Suggest at least one factor that may account for the difference.

4-11. The *palmaris longus* muscle is one of the muscles involved in flexing the fingers.

Its presence or absence can be easily determined on a cadaver (Fig. 4-8A), and with some accuracy on a living person by placing the forearm palm up on a table, flexing the middle finger and looking for a dimpling of the surface of the lower forearm, as shown in Figure 4-8B. Do you have this muscle? In both arms? Is it present in your parents and siblings?

4-12. Consider Table 4-1. Could one use the presence or absence of this muscle in an individual human as a means of determining his "race"?

TABLE 4-1
Frequency of Presence of *Palmaris Longus* Muscle in Different "Races" or Species

"Race"	PER CENT OF INDIVIDUALS POSSESSING THE MUSCLE
Chinese	98
Japanese	97
Negroes, U.S.A.	95
Russians	87
Whites, U.S.A.	86
Poles	81
French	75
Nonhuman Species	
Gibbons	100
Chimpanzees	95
Gorillas	15

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Chapter V

Interlude: Molecules

27. The Dimensions of Molecules

The science of biology leans heavily on the sciences of physics and chemistry. For that reason, many phases of biology cannot be understood without some grasp of the elementary concepts of the related sciences. To understand the problem of breathing, one must know something about molecules—not a great deal, perhaps, to begin with, but as much as one would learn in a high-school course in chemistry.

The student who has a fair grasp of elementary chemistry can begin immediately with Chapter VI. For the benefit of the student who has not previously been exposed to this material, the current chapter is presented. Certain basic theories of the physical sciences will be presented here *without proof*, but with some corroborative evidence, in the hope that the theories will seem reasonable enough for the student to be willing to accept them tentatively.

All matter, all materials, consist of (1) discrete bodies called **molecules,** and (2) empty **space** between the molecules. These molecules are extremely small, so small that no one has ever seen them with even the highest magnification of an optical microscope,* yet the evidence

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* The ordinary microscope uses ordinary light rays and is called an *optical microscope.* The *electron microscope* uses beams of electrons and produces an image that cannot be seen by the human eye. It can, however, be photographed, and the photograph can then be examined. Thus, only in an indirect sense do we "see" objects with an electron microscope. With this instrument the larger molecules, such as the protein molecules, can be "seen."

of their existence is very convincing. Or, to put it another way, we know of a great many facts that can all be very easily accounted for by assuming that invisible molecules exist, but we have not been able to devise any other assumption which will tie the facts together in an integrated, easily understandable picture.

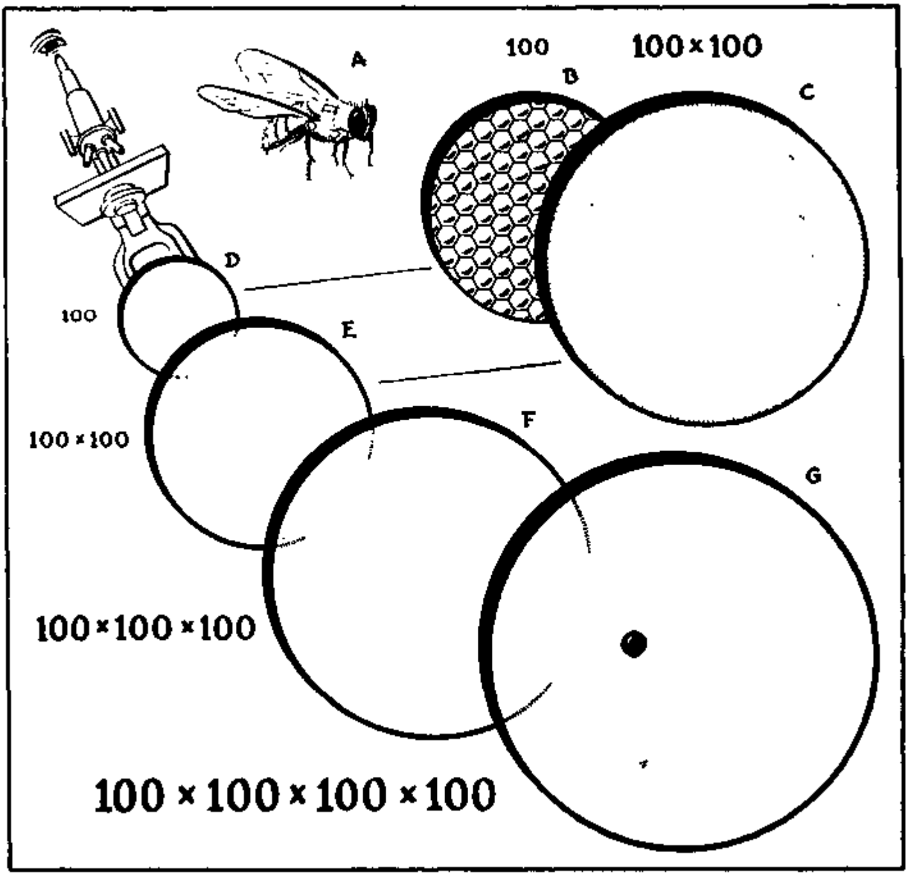

Fig. 5-1. The amount of magnification that would be needed to make a molecule visible. A magnification of around one hundred million times would be required to make the molecule look as big as the sphere in G. By comparison, a magnification of only one hundred times (B) reveals the facets of a fly's eye; 10,000 times (C) is too much to see the boundaries of a single facet, but not enough to reveal molecules.

How small are molecules? We might most easily get an appreciation of them by *assuming*, for the moment, that we had a microscope powerful enough to reveal them. And let us suppose that our microscope magnifies in successive stages of 100, that is, each new stage presents the previous picture magnified so that a line that was 1 mm long in the previous picture becomes 100 mm long.

First, to see what a magnification of 100× ("one hundred times") amounts to, let us examine the eye of a housefly before and after magnification (Fig. 5-1A-C). It takes only one such hundredfold magnification to reveal the beautiful structure of the surface of the eye. No additional detail is revealed by another one-hundredfold magnification.

Now, let us try to see the molecules present in air by, in imagination, magnifying it in successive steps of 100× (Fig. 5-1D-G). Without magnification, we see nothing; similarly, for magnifications of 100 times; 10,000 times (100 × 100); and 1,000,000 times (100 × 100 × 100); but at a magnification of about one hundred million times, we at last see a little something about half as big as the eraser on the end of a lead pencil. We have indicated this "something" in Figure 5-1G.

It will be noticed that the circle in Figure 5-1G includes only one molecule; that is because the next nearest molecule happens to lie a little bit outside the frame of our picture. At any instant, the molecules present in air are various distances apart, but on the average the distance between molecules of air is about ten times the apparent diameter of the molecules.

An important characteristic of molecules is their continuous motion. The molecule indicated in Figure 5-1G would be visible only for an instant; the next moment it would be off someplace else, and perhaps we would be seeing some other molecule, also in rapid motion. At any given instant, the molecules of air in a room are moving with a great variety of velocities but the average velocity is extremely great; a molecule moves a distance equal to about two million million times its own diameter per second, or *about one-third of a mile per second.* In other words, the magnified molecule of Figure 5-1G would have an apparent (magnified) velocity of about thirty million miles per second.

A molecule of gas moves with very great velocity, until it strikes another molecule. The two molecules then rebound from each other with the directions and the speeds that one would predict if they were perfectly elastic billiard balls. On the average, each molecule of air moves a distance of about 1000 times its own diameter before it strikes another molecule.

From the facts of the two preceding paragraphs, it follows that the number of collisions suffered by a given molecule in each second is extremely great. Expressed in terms of its own diameter, a molecule:

(A) has a speed of 2,000,000,000,000 diameters per second

(B) goes about 1,000 diameters between collisions.

Hence:

(C) the number of collisions per second $=A/B=2{,}000{,}000{,}000$ collisions per second.

It should be stressed that the above figures represent *average* values. Actually, the speed of molecules varies over a wide range. The speed of any given molecule varies widely, too; every time it bumps into another molecule, its speed is either increased or decreased. Also, the distance between collisions and the number of collisions per second varies a great deal. But the above figures give the approximate average values. Notice the great number of collisions per second for each molecule—*two billion.*

Another point should be emphasized once more: the molecules act as if they were perfectly elastic bodies. Friction does not exist in the submicroscopic world. The movement of the molecules is a form of energy called **kinetic* energy.** If we think of having a box of molecules completely insulated from all the rest of the world, i.e., not in contact or communication with any molecules outside the box, then we should realize that the kinetic energy of the molecules inside the box will forever remain the same. The kinetic energy of each *individual* molecule will change every time it bumps into another molecule, but the kinetic energy that is lost by one molecule is gained by another. So the average kinetic energy of the "system"† remains the same.

We have spoken only of molecules of a gas. But all substance, whether

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* Derived from the Greek *kineo,* move. The same root is seen in *cinema* (short for cinematograph).

† The word "system," as here used, refers to a number of elements (e.g., molecules, space) that are imagined to exist all by themselves, completely uninfluenced by the rest of the world which, for the moment, is imagined not to exist. Physicists may speak of a frictionless pulley, or an infinitely small point, or a completely isolated system. Such things do not exist, save in the imagination, but beginning with these concepts we can, by methods of successive approximations, come closer and closer to the conditions that actually exist in the real world and eventually solve our problems.

solid, liquid, or gas, is made up of molecules and empty space. The chief difference between a gas and a liquid is this: there is much more space between the molecules of a gas than there is between the molecules of a liquid. At 100° Centigrade, water can be either a gas or a liquid. In the gaseous condition (steam), the molecules are about ten times as far apart, and a given number of molecules occupies about one thousand times as much space as the same number of molecules in the liquid phase.

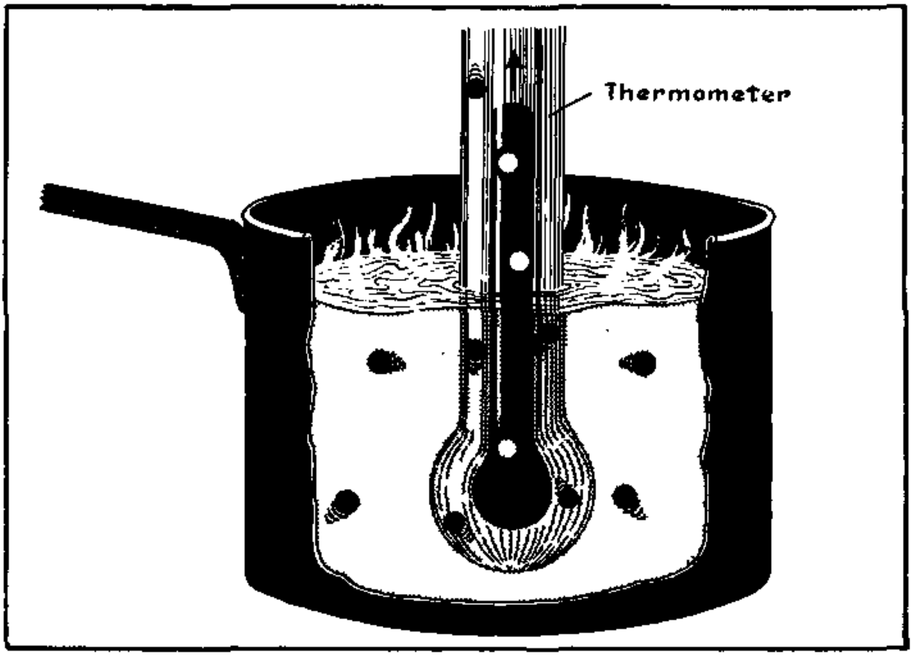

Fig. 5-2. Temperature, a measure of molecular motion. Rapidly moving water molecules make the molecules in the glass move faster, and these, in turn, increase the activity of the mercury molecules. The mercury expands because its molecules push harder against one another.

Solids, too, consist of molecules and space. The distance between molecules of a solid is usually about the same as the distance between molecules of the corresponding liquid. However, the motion of molecules in the solid is different. The molecules of a solid move, but not freely. Mutual attraction between the molecules keeps each molecule more or less in one position, vibrating back and forth around a "home plate," as it were. For this reason, a solid retains a fixed form.

28. Kinetic Energy and Temperature

In an isolated system, the average kinetic energy of the molecules would remain forever the same. But any real "system" is in contact with the rest of the world and the kinetic energy of its molecules is influenced by the kinetic energy of the molecules around it. An example will make this clear:

Suppose we have a thermometer whose molecules initially have a low average kinetic energy and that we thrust it into a vessel of water (Fig. 5-2) whose molecules have a high kinetic energy. What will happen? The molecules of the water, striking against those of the thermometer glass, will exert more force against the glass molecules than that exerted by the glass molecules against the water molecules. As a result, the average kinetic energy and the speed of motion of the glass molecules will increase. As their speed increases, the glass molecules will exert more force against the molecules of the mercury in the thermometer than the latter do against the former. As a result, the mercury molecules will begin to move faster. *When molecules move faster, they push harder against each other, thus tending to increase the average distance between themselves.* Or, looking at the situation macroscopically, we say that when a substance is heated, it expands. We can see now why the mercury in the thermometer rises as the surrounding temperature increases. It is because the average speed and the average kinetic energy of the mercury molecules are increased.

Temperature is a measure of kinetic energy.

29. The Density of Molecules in a Gas: Avogadro's Law

We have been speaking of the molecules of air as though there were only one kind. This is not true. There are several different kinds of molecules in air; the principal kinds are nitrogen molecules and oxygen molecules, with a small proportion of carbon dioxide molecules and others. These molecules do not all weigh the same. If, as is commonly done, we take the weight of an oxygen molecule to be 32—not 32 pounds, or grams, or ounces, or any ordinary measure of weight, but just 32 "arbitrary" unnamed units—then nitrogen molecules weigh 28, and carbon dioxide molecules weigh 44. Each of the other kinds of molecules has its own characteristic weight.

Different kinds of molecules have different weights. But it is remarkable that the size, that is, the volume, of the different molecules is almost constant. More important, in gases the volume "occupied" by the molecules is almost the same regardless of the weight of the molecules. In other words, of the space in the air in a cool room, about 0.1% is occupied by molecules, and this is true regardless of the kind of molecules that make up the air. Or, to put it in the more usual way:

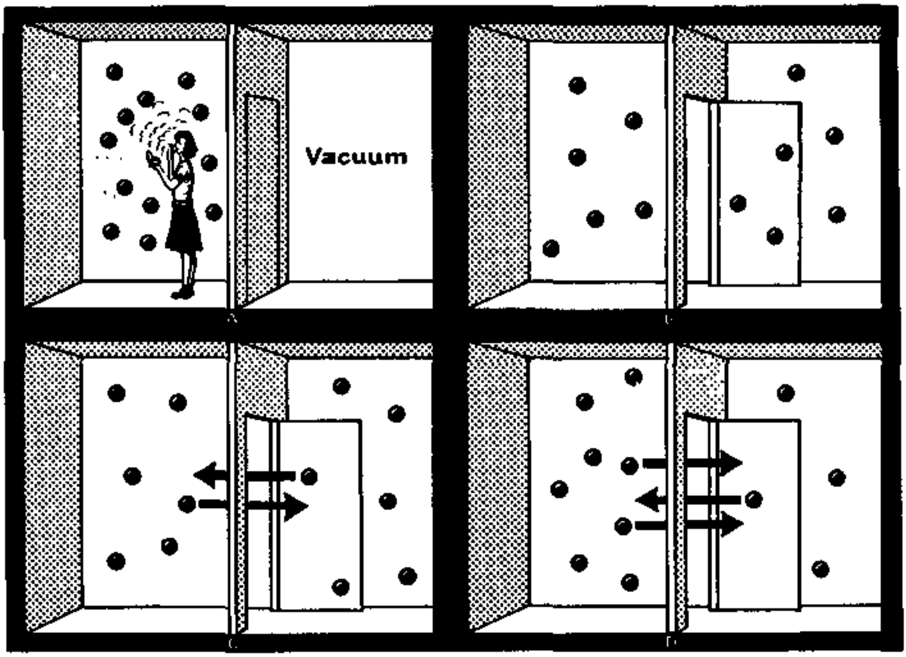

Fig. 5-3. When a door is opened between two compartments, the number of molecules in one becomes approximately equal to the number in the other (B). When this state has been reached, it will tend to continue because the probability of a molecule moving from left to right is the same as the probability of one moving from right to left, as indicated by the equal arrows in (C). Should the number of molecules in the left side be twice as great as the number in the right side (D), the probability of a movement from left to right is twice that of a movement from right to left, as indicated by the arrows. Hence, the inequality of the two sides will eventually be eliminated. The argument is stated in terms of a few molecules, whereas even a small volume (say that of a thimble) contains many millions.

The number of molecules in a given volume of gas at a given temperature and pressure is independent of the kind of molecules.

This is one way of stating a "law" proposed in 1811 by a chemist named Avogadro. It is often referred to as **Avogadro's Law.** A roomful of nitrogen contains the same number of molecules as the same sized room filled with molecules of hydrogen, oxygen, carbon dioxide, or any other gas, as long as the gases are subjected to the same temperature and pressure. *This rule applies only to gases.* There is no such rule for liquids or solids.

30. Consequence of Molecular Motion: Diffusion

Suppose we have a box divided in half by a removable partition. The partition, when in place, is gas tight, i.e., no gas molecules can get through it or around it to the other side.

Now suppose that, to begin with, with the partition in place, we put (Fig. 5-3A) twelve molecules in one half-compartment and none in the other. As long as the partition is not moved, this condition will remain unchanged, with the gas molecules continuously bouncing against one another and the walls of the left-hand compartment while the right compartment remains free of molecules.

What will happen if we suddenly remove the barrier? The first molecule to reach the region where the barrier once was will pass on into the right-hand compartment; it will continue moving until it strikes a wall and rebounds. Subsequently, other molecules will move from the left compartment to the right, the motion of each molecule continuing in a straight line until it bumps into other gas molecules or into the wall. In a very short time, a census of molecules would show that there would be the same number of molecules in the right-hand compartment as in the left-hand one (see Fig. 5-3B). Once this situation is reached, it will be maintained indefinitely unless outside forces interfere.

How does it happen that the numbers of molecules in the two compartments soon become equal and remain equal? It surely doesn't imply any intelligence on their part? We can most easily see what it is that makes the two numbers equal if we first *assume* that they are equal and ask what it is that keeps the numbers equal.

Assume that the situation diagrammed in Figure 5-3B has been reached, with six molecules in each compartment. All of these molecules are in continuous motion. *Their motion is of a random sort*, that is, if a molecule could be suddenly made visible to us, it would as likely prove to be moving in one direction as in another. All directions of motion are equally probable. Referring now to Figure 5-3C, it is apparent that the probability of some molecule moving from the left side to the right side is exactly equal to the probability of some other molecule moving from the right side to the left side. Therefore, it is most probable that the number of molecules will remain the same in the two equal compartments.

The argument can be put in another way. Suppose, by some chance, the molecules moved differentially until there were eight molecules on the left side and only four on the right side (Fig. 5-3D). The motion of the molecules is of a random sort. Any particular molecule is as likely to be moving in a specified direction as is any other molecule. That is, the probability that a particular molecule on the left side will be moving toward the right is exactly the probability that another particular molecule on the right will be moving toward the left. *But there are twice as many molecules on the left side as there are on the right.* Therefore, the probability that some molecule will move from left to right is twice as great as the probability that some molecule will move from right to left. The movement left to right will remain more probable than the opposite movement until the number of molecules in the two compartments is equal. From this time on a movement ⟶ will be as probable as one ⟵; therefore, the number of molecules in the two compartments will remain the same.

The critical reader will notice that underlying the preceding discussion is the unexpressed assumption that, of a number of possible events which have different probabilities of happening, the most probable one will happen. Is this true? Are we justified in making this assumption?

Everyone knows that sometimes the less probable event happens. To take a common example: *sometimes* a player wins money from a slot-machine—but not often. The odds of a slot-machine are arranged in favor of the machine and its owner. If a man plays the machine only a few times, he may come out winner. If he plays it a great many times, he is almost certain to lose, i.e., the probability of his winning becomes very small. Looking at the problem from the other side, the owner, since he is in effect playing a great many games, with the odds in his favor, is almost certain to win. Where large numbers are involved, the possibility of the less probable event's happening can be disregarded as a practical matter. Paradoxically, a gambling house, which plays tens of thousands of games (with the odds in favor of "the house") is not engaged in gambling; only the customer gambles.

To return to our example of the distribution of molecules in the two compartments of the box: it is apparent that, by chance, the molecules might be unequally distributed in the two sides, but that the probability of a *significantly* unequal distribution will *decrease* as the number of molecules *increases*. By the laws of probability, the probability that *all* the molecules will be on one side (either side) with the opposite side empty can be calculated. The calculations for a few simple cases are shown in Table 5-1. With only two molecules there is a 50-50 chance that both will be together, but with as few as 12 molecules, the probability for this event is less than 1 in 2,000. In other words, if one made periodic observations, say every half hour, of the set-up pictured in Figure 5-3, only about once every 42 days would one expect to find all the molecules on one side. Other and less extreme inequalities in the distribution of the molecules would, of course, be more probable.

One is ordinarily dealing with how many molecules? Suppose the two compartments each had a volume of one pint and contained air at ordinary temperature and pressure. In this case, the number of molecules would be more than 20,000,000,000,000,000,000,000.

TABLE 5-1

THE PROBABILITY OF AN UNEQUAL DISTRIBUTION OF MOLECULES IN A TWO-COMPARTMENT BOX

NO. OF MOLECULES IN TWO-COMPARTMENT BOX	PROBABILITY THAT ALL THE MOLECULES ARE IN THE SAME COMPARTMENT (EITHER ONE) AT A GIVEN INSTANT
2	1/2
4	1/8
6	1/32
8	1/128
10	1/512
12	1/2048

From the trend of the figures in Table 5-1, it should be apparent that the chance that all of these molecules would be on one side of the box would be so ridiculously small that we can ignore it. Indeed, the chance that one compartment would contain as little as 1% more molecules than the other is very, very small; or, for that matter, as little as 0.00001% more. In a set-up of this sort, no one has ever observed any discrepancy in the number of molecules present on the two sides. Any difference that would be at all likely to happen would be far smaller than our most sensitive methods of measurement could detect.

31. Reality of Molecular Movement Verified with Radioactive Isotopes

Since no differences in the number of molecules in two connecting compartments of a box can ever be detected, how do we know that exchange between the two compartments goes on continuously?

One way to establish the fact that molecules are continuously moving from one side to the other would be by the use of radioactive isotopes. An accurate description of isotopes would take us too far into the field of chemistry. For our present purpose, we may content ourselves with saying that every element (such as carbon) exists in several forms called isotopes. The isotopes of a single element are chemically identical, that is, they all combine with the other elements in the same way. However, some of the isotopes can be detected by physical apparatus (e.g., Geiger counters), so that the position and movement of the isotopes can be followed. Isotopes that can be detected in this way are called *radioactive isotopes.*

By the use of radioactive isotopes, the continuous exchange of molecules in a two-compartment box such as that of Figure 5-3 could be easily established. If an equal number of molecules of carbon dioxide were put in both compartments, but the molecules in the left side were of radioactive carbon dioxide while those of the other were of ordinary carbon dioxide, then, by the use of a Geiger counter, one could detect the decrease in the number of radioactive molecules* in the left compartment and their increase in the right. Since other measurements would show no change in the total number of molecules in the right-hand compartment, it follows that some of the nonradioactive molecules must have moved to the left side.

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* A question for the student who has some knowledge of physics: which is the more accurate expression: "radioactive molecules," or "radioactive atoms"?

32. The Slowness of Diffusion

The process we have just described is often referred to as diffusion. In the example, radioactive carbon dioxide diffused into normal carbon dioxide, and normal carbon dioxide diffused into the radioactive material. Even if both compartments had initially had the same kinds of molecules, material from one side would have diffused into the other. But, in this case, no change would have resulted, and the term diffusion would not ordinarily be applied to such a case, though it is not fundamentally different. The term **diffusion** is ordinarily applied to cases in which **molecules of one substance mix with molecules of another substance, resulting in a change in the relative concentration of the two.**

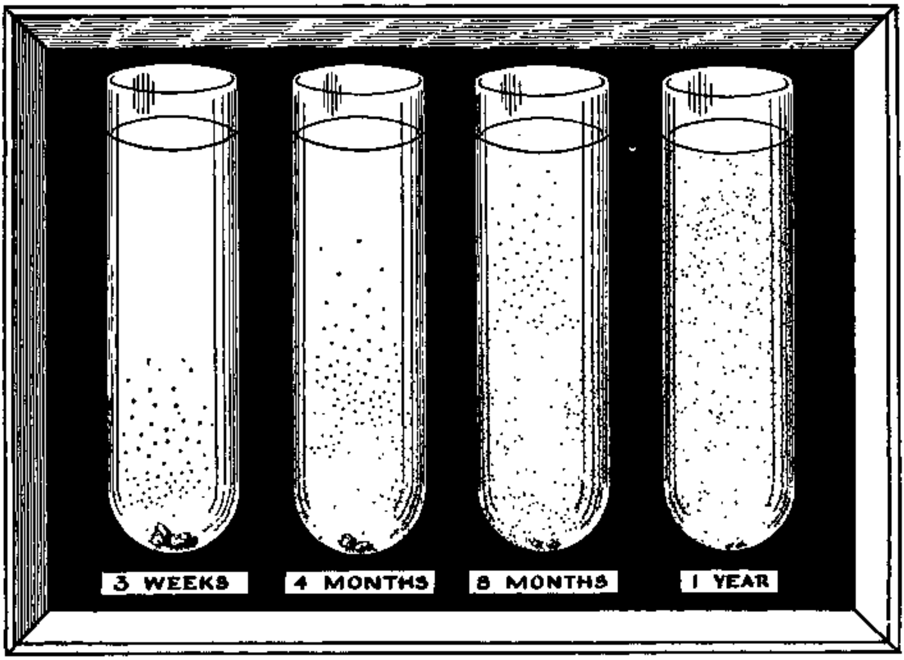

Fig. 5-4. The macroscopically visible diffusion of dye through water due to the continuous, random motion of the invisible molecules of dyestuff and water.

Examples of diffusion of one substance into or through another are common. The easiest to appreciate are those which involve the diffusion of an odorous gas molecule through the air. To mention only one example, a dog which has had a recent encounter with a skunk can be detected many feet away, by the nose alone. This is because certain molecules which were donated to the dog by the skunk diffuse through the air in all directions; our nose, as it happens, is a very sensitive detector of molecules of this kind. Only a few (perhaps a few million, really a trifling number of molecules) need reach the nose for it to be aware of them.

Diffusion can take place not only through gases but also, though more slowly, through liquids and even solids. A familiar experiment involves the placing of a brilliant dye at the bottom of a tall cylinder filled with water (Fig. 5-4). After a time, the color of the dye is visible at some distance from the bottom, showing that the dye is slowly diffusing through the liquid. As the days go by, the edge of visible color slowly creeps upward. Ultimately, though it may take years, the dye will be almost uniformly distributed throughout the cylinder of water.

At this point, a question naturally arises: if (as was pointed out in § 27) the speed of molecules is so very great, how does it happen that the rate of diffusion is so slow? The speed of oxygen molecules, given previously in terms of molecular diameters, is about $\frac{1}{3}$ mile per second at room temperature and pressure. Heavier molecules do not move so fast but, even so, have very great speeds as we ordinarily judge speed. Molecules of a dye such as methylene blue move at approximately the rate of 100 yards per second or over 200 miles an hour. With such a velocity, why does the dyestuff not diffuse faster?

Plainly, the answer lies in the impediment to movement offered by the other molecules. A molecule of dye may move at the rate of 200 miles per hour but it will not go even a millionth of a millionth of a mile before it bumps into another molecule which changes its direction of motion. A given molecule will collide with other molecules and change its direction many million times a second; hence, it is not surprising that measurable diffusion over a distance of inches takes days, months, or even years.

33. Molecular Motion and the Pressure of Gases

The pressure exerted by a gas is directly attributable to the motion of its molecules. Each individual molecule has very little weight (it takes more than 1,000,000,000,000,000,000,000,000 molecules of oxygen to weigh an ounce) but the molecules are moving with great speed and

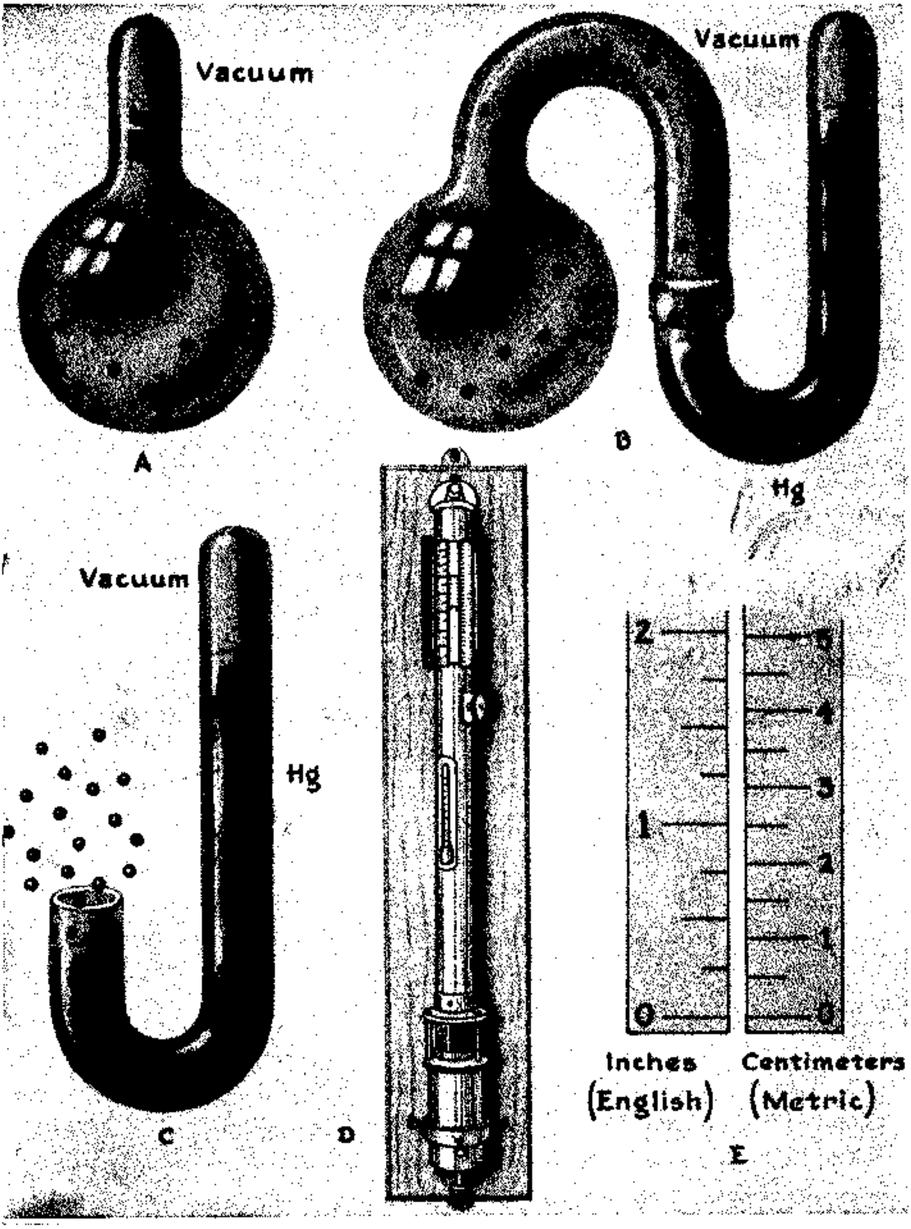

Fig. 5-5. The pressure exerted by moving molecules can support a weight (A). This pressure is most conveniently measured by means of a column of mercury (B). The normal atmosphere can thus support a column of mercury (C). The barometer (C and D) is a device for measuring the height of the column of mercury supported by the atmosphere.

there are a great many of them. As a consequence of their continual striking and rebounding from the walls of a container, the molecules exert a measurable *push* against the walls. We can show this by having one part of the upper (ceiling) wall made movable, by making it essentially a piston moving in a cylinder (Fig. 5-5). Such a piston, if of just the right weight, will remain motionless in the cylinder; the tendency of gravity to make it fall will be exactly balanced by the force of the molecules tending to push it up. If the scale of Figure 5-5 were correct, the piston would continuously bob up and down, moving upward each time a molecule hit its lower surface and downward, under the influence of gravity, between "hits." However, the size of the molecules in the figure is much exaggerated and their number minimized. Since millions of molecules hit the piston each moment, it shows no perceptible movement from moment to moment.

The push exerted by uncounted millions of molecules against the surfaces enclosing them we refer to as **pressure**. We could use a set-up of the sort illustrated to measure this pressure, but it would be inconvenient; it would take many trials to determine *exactly* the right weight to make the piston to keep it from moving either up or down. Moreover, for every slight change in pressure, the weight of the piston would again have to be adjusted. A more flexible device is needed for measuring pressure.

Such a device is the **manometer** (from the Greek *manos*, rare [probably because a gas is considered a rarified substance], and *metron*, measure). The essential construction is illustrated in Figure 5-5B. The resemblance, in principle, to the apparatus shown in Figure 5-5A is apparent. Again, the pressure of the gas raises a weight, but this time the weight is the weight of a column of liquid, usually mercury, moving in a tube. By having the column of mercury in contact with a reservoir of mercury, continuous variation in the weight of the supported column is permitted. Thus, it is easy to follow changes in the pressure of a gas. The pressure so measured is commonly expressed in terms of the height of the column of mercury it supports, e.g., "a pressure of 312 mm. Hg." *Hg* is an abbreviation for the Latin name, *Hydrargyrum*, and is written without a period. The abbreviation *mm.* (written either with or without a period) is an abbreviation for millimeters, a unit of measure in the metric system. The relation between the metric and the English systems is shown in Figure 5-5C.

An instrument constructed like the manometer of Figure 5-5B, even if not connected with an obvious source of gas molecules, will yet, in the usual environment, have its two "arms" of mercury standing at different levels (Fig. 5-5C). The reason for this is that the air surrounding us is made up of gas molecules that are continuously exerting a pressure on all surfaces. The difference between the two arms of mercury when only one of them is open to the air is normally in the neighborhood of 760 mm.

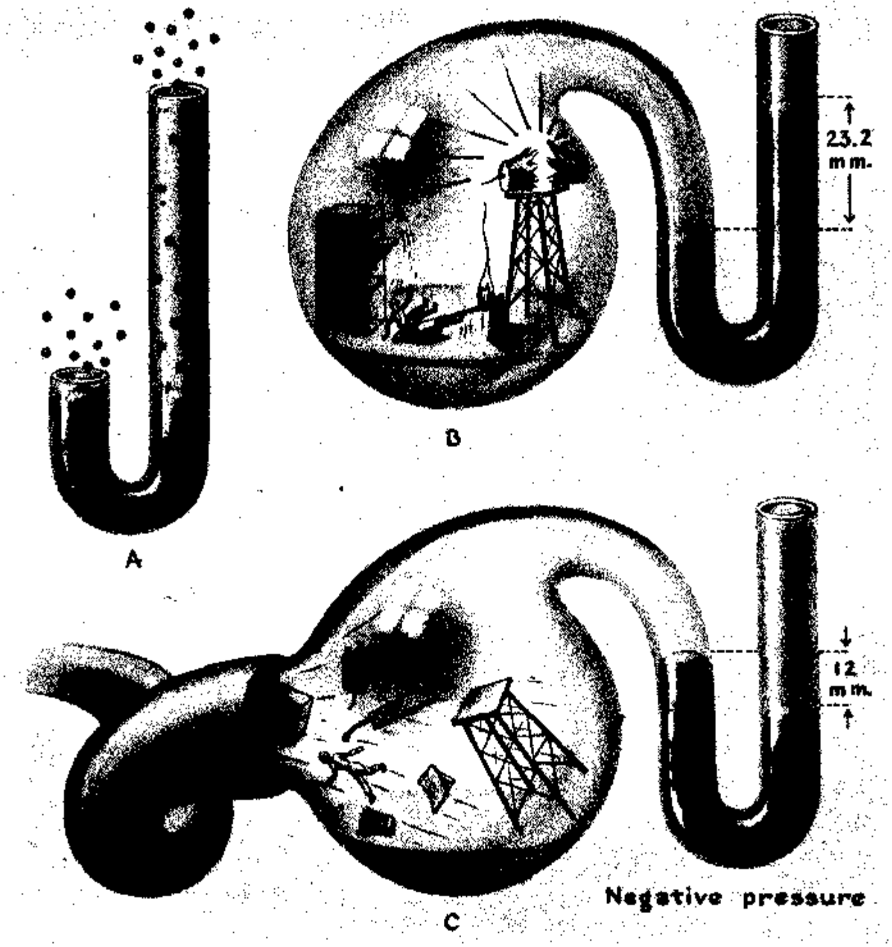

Fig. 5-6. A manometer (A) may be used to measure the pressure exerted in the experimental set-up shown in B. If the pressure exerted is less than that of the atmosphere, we refer to it as a negative pressure (C).

An instrument which is used to measure the pressure of the air around us is called a **barometer.** Figure 5-5C represents the essentials of its construction. A more usual form is shown in Figure 5-5D, which does not differ essentially from that of Figure 5-5C but is so constructed as to minimize the danger of dust falling into, or mercury falling out of, the reservoir.

Quite commonly, a manometer differs from a barometer in that neither arm encloses a vacuum (Fig. 5-6A). In such an instrument, both columns of mercury stand at the same height when they are both open to the air because the bombardment of molecules is equally powerful on both. If this sort of manometer is then connected to some chamber whose pressure we want to determine (Fig. 5-6B), the reading—say 23.2 mm—really means "23.2 mm plus atmospheric pressure" since the gas in the chamber is supporting both the weight of the atmosphere and the weight of 23.2 mm of mercury. However, if all the readings are being made with this sort of manometer, it may be possible to ignore the weight of the atmosphere and say merely that the pressure is "23.2 mm Hg." As long as the instrumental set-up is clearly understood by all, no harm is done by this sort of incomplete expression.

In making manometric measurements, still another incomplete expression is often used which sometimes causes misunderstanding. If the mercury in the arm connected with the experimental apparatus rises above the level of the mercury in the open arm, the result is often stated as a *negative pressure*, e.g., (see Fig. 5-6C) "a pressure of −12 mm Hg." On the face of it, a negative pressure is an impossibility. The amount of pressure is proportional to the number of molecules per unit volume; a negative pressure would imply a negative number of molecules, which is clearly ridiculous.

It will be easily understood that the true statement of pressure for the example given would be "atmospheric pressure minus 12 mm Hg," though such a full (and true) statement is almost never given in practice. It is assumed that the reader understands the experimental set-up and the method of measurement. Sometimes a negative pressure of x mm means a pressure which is x mm less than atmospheric. At other times, it means a pressure of x mm less than some other pressure supposedly known to the reader. The meaning of "x mm Hg" is usually clear from the context.

Nonscientists sometimes ascribe to science an exactness of expression which is inhumanly perfect. The example just presented is but one of many common scientific expressions which are, strictly speaking, quite inexact. Such elliptical expressions sometimes cause misunderstandings among the uninitiated; to scientists, they seldom cause trouble. In the realm of scientific expression, they correspond to the *idiom* of colloquial speech. When we speak of "carrying out a plan," we certainly do not mean that we carried the plan outside or that we discarded it, which a foreigner unlearned in English idiom might suppose. To those who really know the language, the idiom offers no difficulty. Similarly, the idioms or ellipses of scientific discourse (like "negative pressure") give no trouble once the idea behind the words is grasped.

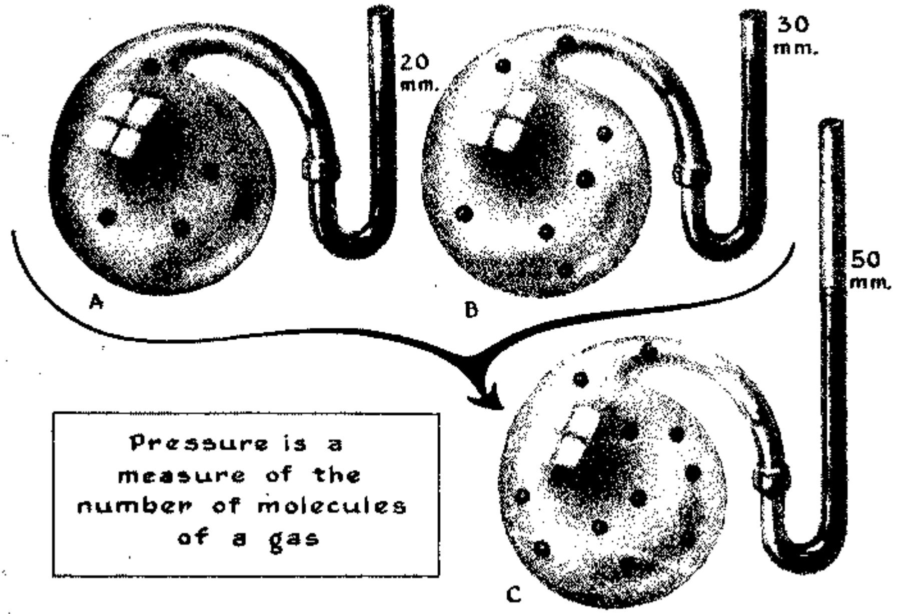

Fig. 5-7. Showing how the pressure, expressed in mm of mercury, is a measure of number of molecules.

34. Partial Pressures: Pressure as a Measure of Quantity of Material

The magnitude of the pressure is proportional to the number of molecules if the volume and temperature remain constant. From our picture of the cause of pressure, this would seem to be reasonable and it can be illustrated by essentially simple experiments.

In Figure 5-7, are shown three equal sized containers. The first, A, contains such a quantity of gas as to exert a pressure of 20 mm. The second contains a quantity which exerts a pressure of 30 mm. If, now, we transfer all the gas from both containers into a new container, of the same size as before, we will have A plus B molecules, and the total pressure will be increased correspondingly to 50 mm (20 plus 30).

Suppose the gases in A and B were composed of different kinds of molecules, what would happen? Assuming that there is no chemical reaction between the two, this situation is exactly as described above. The pressure in C (Fig. 5-7) will be 50 mm Hg (20 plus 30).

Clearly, the pressure in C is contributed by molecules of two different kinds, the A kind and the B kind. A contributes $\frac{2}{5}$ of the pressure of 50 mm. Therefore, it is customary to say that the **partial pressure** of A in vessel C is 20 mm. Similarly, the partial pressure of B in vessel C is 30 mm. Together, the partial pressures of all the constituent gases give the pressure of the whole mixture (50 mm Hg in this case).

When we deal with gases, we are usually interested primarily in the total number of molecules or with the number of each kind of molecule. But, experimentally, the number of molecules is difficult to determine. Volume, however, and pressure are easy to determine. Modern molecular theory (suggested, for the most part, without proof in this chapter) indicates that from the volume and the pressure (and the temperature), one can quite easily calculate the number of molecules. However, the experimental readings are usually in terms of volumes and pressures. To avoid the labor of converting these to numbers of molecules, discourse is kept at the level of volumes and pressures since this amounts to the same thing. But the student should not lose sight of the fact that when we speak of volumes and pressures, we are really concerned with numbers and concentrations of molecules.

35. Chemical Shorthand

So far, in speaking of molecules involved in physiological processes, we have designated them in the usual literary longhand, e.g., carbon dioxide, oxygen, nitrogen. Future progress will be expedited by introducing here conventional chemical shorthand. But, to do that, we must first introduce some new concepts, the concepts of *atoms* and *compounds.*

When discussing the movements of gases, the molecule is the most useful unit. Molecules, however, can be further broken down into smaller units called **atoms.** A molecule of carbon dioxide, for instance, consists of one atom of carbon and two atoms (hence, the *di*oxide) of oxygen. The standard symbol for carbon is C; for oxygen, O; and carbon dioxide is written CO_2. The subscript numbers indicate the ratios of the various atoms in the molecule. Strictly, we should symbolize carbon dioxide by C_1O_2 but the subscript 1 is understood; all others must be written.

The properties of a molecule are determined not only by the kind of atoms it contains but also by the number and arrangement of atoms in the molecule. There are two oxides of carbon, namely:

CO_2—carbon dioxide
CO —carbon monoxide

These both have the same atoms but in different proportions. With respect to their effect on the organism they are utterly different. If a man breathes in carbon *di*oxide, he soon starts breathing faster. If he breathes carbon *mon*oxide, he stops breathing entirely. Not all molecules are composed of different kinds of atoms. Oxygen molecules, for instance, are made up of oxygen atoms, two to a molecule. The formula for oxygen is O_2; similarly, for atmospheric nitrogen, N_2.

We must distinguish now between compounds and mixtures.

A compound is a substance all of whose molecules are made up of the same proportion of atoms combined in a definite way. CO_2 is a compound; CO is a compound. O_2 is not considered a compound because it is made of only one kind of atom.

A mixture is made up of different kinds of molecules. Air is a mixture of N_2, O_2, with a little CO_2, H_2O (water), and smaller amounts of other kinds of molecules.

It is important to realize that a mixture of two different compounds does not amount to the same thing as another compound with the same atomic proportions as the mixture. For example:

Two molecules of CO plus one molecule of O_2 has the same atomic proportions of C:O (namely 2:4 or 1:2) as the compound CO_2, but it will not have the same effect. The effect of CO plus O_2 on the organism is virtually the sum of the effects of the separate substances; it does not equal the effect of CO_2. Carbon dioxide (CO_2) stimulates breathing. Carbon monoxide (CO) stops breathing, thus causing death, and this effect is not prevented by the presence of oxygen (O_2).

QUESTIONS AND PROBLEMS

5-1. Ice floats in water. Which are farther apart (on the average), the molecules in ice or the molecules in water?

5-2. Referring to the experiment diagrammed in Figure 5-2, when the cool thermometer was put into the warm water, what must have happened to the average kinetic energy of the water molecules?

5-3. One quart vessel is filled with air at a temperature of 30° C; another one with air at 80° C. The pressure in both vessels is the same. Which one contains the greater number of molecules?

5-4. One vessel contains nitrogen gas at a temperature of 30° C and at atmospheric pressure; another vessel of the same size contains oxygen gas at the same temperature and pressure. What is the *ratio* of the number of nitrogen molecules in the one to the number of oxygen molecules in the other?

5-5. The left-hand compartment of a rigid box like that of Figure 5-3A is filled with oxygen at 50° C at atmospheric pressure; the other side is filled with oxygen at 30° C at the same pressure. After the temperatures of the two sides have become equal, the center gate is opened. *What happens?* Explain in two ways: (a) in terms of pressure; (b) in terms of a probability argument.

5-6. Mercury weighs about 13.5 times as much as water. If a barometer were made with water in it instead of mercury, about how high would the barometer have to be?

5-7. A "suction pump" operates by creating a vacuum above the fluid to be raised. About how high could the most efficient suction pump raise water from a well?

5-8. At high altitudes, atmospheric pressure is less than at low altitudes. Would the same suction pump be able to raise water higher from a well on Mt. McKinley or from a well at sea level?

5-9. Those to whom the beginnings of scientific ideas are interesting will enjoy reading Lucretius' "On The Nature Of Things," written in the century before the birth of Christ. Book I is well worth a careful reading with these two questions in mind: (1) What are the differences and resemblances between Lucretius' picture of the world and our present idea of the molecular structure of matter; and (2) what evidence and arguments does Lucretius marshal to support his theory?

Chapter VI

The Breathing System

36. The Need for Breathing

It often happens that phenomena that are best known are longest being explained. If a process is always before our eyes, we accept it unquestioningly and assume that, of course, we understand it. Breathing is such a process. For 50,000 years, men breathed regularly, day in, day out, without asking themselves why they were breathing. It perhaps was just as well they did not ask because the necessary related sciences of physics and chemistry were not well enough advanced to permit a biological answer to this question. Certainly, it is fortunate that men did not stop breathing until they learned the answer! But, gradually, the question forced itself to the surface of men's consciousness: *Why breathe? What useful purpose does breathing serve?*

The answers to these questions were various, and some of them were surprisingly close to the correct ones. But many of them were far from the mark. As late as 300 years ago, it was considered likely that the primary purpose of breathing was to keep the blood moving in the body, to mention but one of the prominent theories. The experiments by which the true significance of breathing was finally elucidated form an interesting chapter in the history of science, but one which we will not take time to recount here.

We may bring ourselves quickly to the modern position by restating

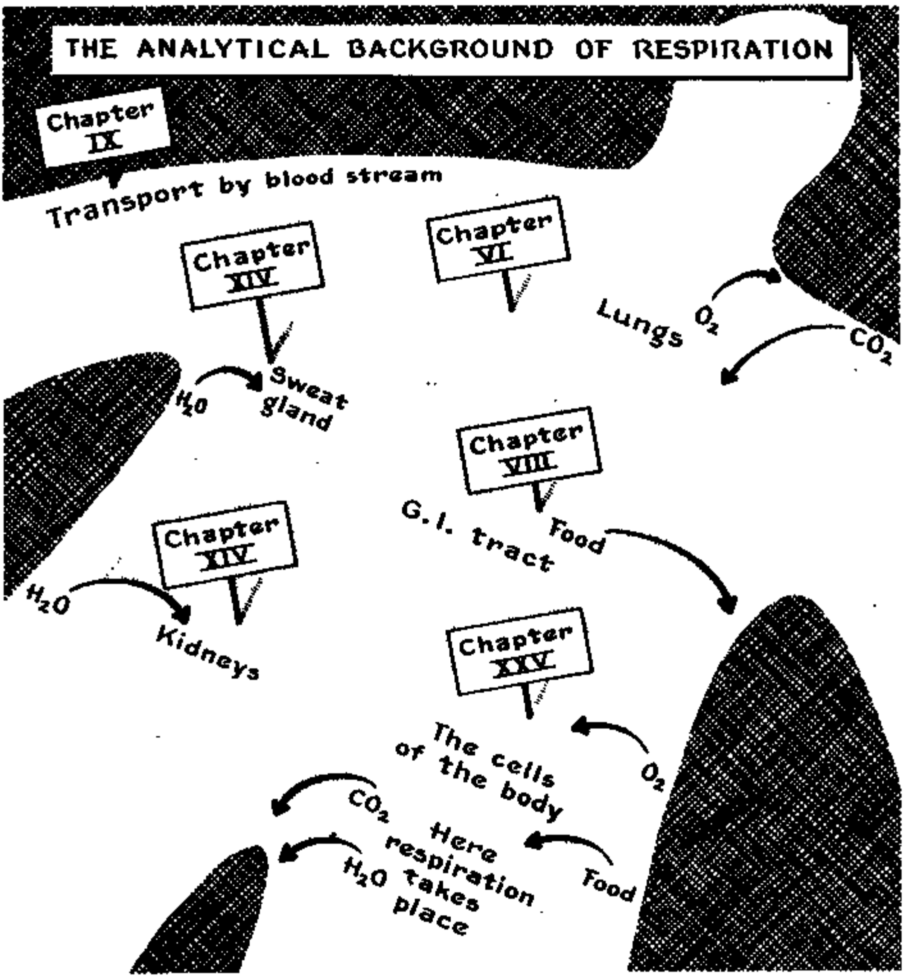

Fig. 6-1. It is difficult to understand the organism as a whole, and so the complex of processes involved in respiration is analyzed into separate subjects which are treated in various chapters, as indicated above. Respiration occurs in all the cells of the body.

once more the equation representing the gist of the most important chemical processes taking place in the body:

$$\text{Food} + \text{oxygen} \longrightarrow \text{carbon dioxide} + \text{water} + \text{energy}. \qquad (1)$$

This can be expressed more briefly with conventional chemical symbols:

$$\text{Food} + O_2 \longrightarrow CO_2 + H_2O + \epsilon \qquad (2)$$

"Food" we have not reduced to shorthand because it is not a compound but a mixture of compounds. In abbreviating energy, we have used a script "$\mathcal{E}$" rather than an ordinary capital "E", lest it be thought that the symbol represents a kind of atom.

The process indicated by this equation (2) is called **respiration.** It is a chemical process, taking place only **inside the individual cells of the body.** That being so, it is apparent that the body is confronted with the problems of getting food and oxygen to the cells and of carrying away the waste products of respiration, namely, carbon dioxide and water.

These problems, in turn, can be further subdivided. First, food and oxygen must be got into the body somewhere, through some portal of entry. The portal in the case of food is the gastrointestinal tract (the stomach, intestines, etc.) which will be discussed in Chapter VIII. The portal for oxygen is the lungs, and is discussed in the present chapter. Once oxygen or food has entered the body through the wall of the lungs or the intestine, it must be transported to the cells; transport is effected by the blood stream (discussed in Chap. IX). Discussion of the process of respiration taking place in the cells will be deferred to Part IV. Following respiration, the waste products are carried away from the cells by the blood stream, the carbon dioxide to be disposed of largely through the lungs, and the water through the kidneys and sweat glands.

The treatment which we propose to follow can be diagrammed as shown in Figure 6-1. The various problems connected with respiration, although interconnected to serve the same function, namely, respiration in the cells, will be analytically separated for treatment in different chapters, as stated above. Like all analysis, this separation of interconnected functions results in a certain falsification. Analysis is a practical necessity; the student should try to counteract the dangers of it by integrating each new bit of knowledge into a picture of the whole process.

One further warning before we go on: The word *respire* is derived from the Latin roots *re*, back (or again) and *spiro*, breathe; hence *respiration*, etymologically, is synonymous with *breathing*. Historically, this was the first meaning of the term. It is still listed as the primary meaning in dictionaries and is the commonest sense in which it is used in medical literature. However, more than a century ago, the term respiration was applied to the biochemical process indicated by equation (2). Respiration, in this sense, is a process that takes place in nearly all organisms, the majority of which do not breathe in the human sense at all. The use of the word respiration in this sense has increased to such an extent that it is today virtually the only sense in which it is used in research reports in biology, exclusive of medical literature. Confusion will be avoided if we use the term respiration in only one sense; we think that usage justifies choosing the more recent biochemical one. Therefore, in this book, the following definitions will be adhered to:

Respiration:

Definition: Food $+ O_2 \longrightarrow CO_2 + H_2O + \epsilon$ (in a living body)

Breathing:

Definition: The process by which O_2 is taken into the vertebrate body and CO_2 is expelled therefrom, the organs of breathing being the lungs and associated structures.

It is unfortunate, in a way, that a definition once made is not adhered to forever; at least, thus might awkward transition periods be avoided. But language is not fixed. As time passes, words acquire new meanings and lose old ones. It is a process against which reactionary lexicographers rail in vain. Most modern lexicographers and philologists recognize the inevitability of evolution in language and appreciate the essential soundness of Lewis Carroll's view of the nature of definition as expressed in *Through The Looking Glass:*

> "I don't know what you mean by 'glory'," Alice said.
>
> Humpty Dumpty smiled contemptuously. "Of course you don't—'til I tell you. I meant 'there's a nice knock-down argument for you'."
>
> "But 'glory' doesn't mean 'a nice knock-down argument'," Alice objected.
>
> "When *I* use a word," Humpty Dumpty said in rather a scornful tone, "it means just what I choose it to mean—neither more nor less."
>
> "The question is," said Alice, "whether you *can* make words mean so many different things."
>
> "The question is," said Humpty Dumpty, "which is to be master—that's all."

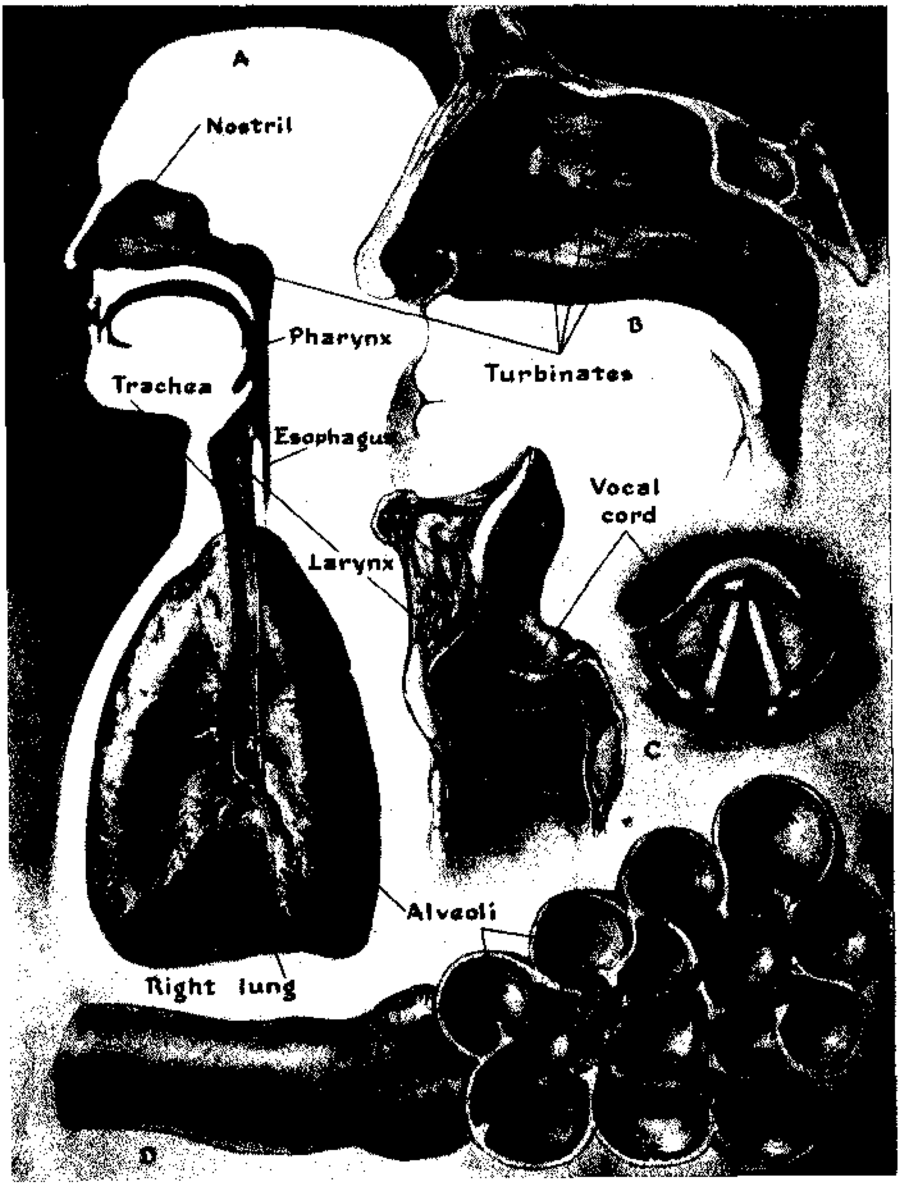

Fig. 6-2. The path of air in the breathing system. The long and somewhat tortuous path permits air conditioning—humidifying, warming, and cleaning of the air—before it gets to the alveoli where it can enter the body.

37. How the Air Gets to the Lungs

Using Figure 6-2A as a map, it will be worth while to trace the path of air from the outside to the lungs.

Normally we take in air through the nostrils. The structure of the nasal passages between the nostrils and the region of the pharynx constitutes a nicely designed air-conditioning system. Most of the time, the air outside is colder and dryer than it should be when it comes in contact with the lungs. The nasal passages are so constructed as to permit rapid modification of the temperature and humidity of the air. The over-all distance between nose and pharynx is only a few inches, but the air passage in that region is greatly complicated by the presence of bony structures (Fig. 6-2B) called **turbinates** (Latin *turbinis*, anything that whirls around, such as a whirlwind or top). These turbinates create eddies in the incoming air and thus increase the contact of the air with the extensive surface of the nasal passages. The bones of the turbinates are covered with a warm, moist tissue called **mucous epithelium** (Greek *epi*, upon, plus *thelys*, tender, delicate; that is, a delicate, outside tissue) which secretes **mucus.** Contact with the warm, watery mucus both warms and humidifies the incoming air.

The air is air conditioned in another way by the nose. Large particles of dirt are filtered out by the hairs lining those portions of the nasal cavities which are situated closer to the exterior. Smaller particles stick to the mucus and are eventually discharged with it. The filtering function of the mucus is brought home to us when we note the color of the nasal secretion following a sailboat trip (through an atmosphere that is already dirt free) as compared with that which follows a trip over a dusty road.

In filtering out small air-borne particles, the mucus performs a hygienic function. Many of these particles are bacteria, and a few of the bacteria are disease-producing kinds. The mucus keeps most of the bacteria from ever getting to the lungs. Moreover, mucus possesses marked bactericidal* properties.

Normally, the amount of mucus secreted is not enough for us to be aware of it. Evaporation of the water in the mucus and unconscious

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* The student should be able to deduce the meaning of this word from others already known to him; e.g., suicide, homicide, fratricide.

swallowing remove it as fast as it accumulates. In many diseases, however, e.g., "colds," the rate of secretion of mucus is greatly increased. This increase in rate of secretion of such a bactericidal material undoubtedly serves a useful function. However, the secretion of mucus and the attendant swelling of the mucous epithelium often proceed to such an extent that breathing through the nose becomes impossible, and air must be brought in through the mouth, thus by-passing the excellent air-conditioning apparatus of the nose. We see here an example of a type of reaction that is fairly common in the human body, an adaptive response which overshoots the mark, so to speak. The human body is wonderful; but it is not perfect.

Once air is in the **pharynx** (Greek *pharynx*, throat), two courses are open to it: the esophagus and the **trachea** (Greek *trachys*, rough: because of the bumpiness of this tube). The esophagus, which leads to the stomach, is normally collapsed and little air passes down it.* Instead, air passes into the trachea ("windpipe") which is permanently kept open by rigid rings of cartilage in its walls. Near the upper end of the trachea is the larynx or "voice box." This specialized part of the trachea supports several "vocal cords" (Fig. 6-2C) which are responsible for the primary production of the voice. These cords are stretched across the air passage. When the tension on them is increased and air is forced past them, a tone is produced, just as it is when we blow against a stretched rubber band. The vocal cords yield a higher pitched tone when they are stretched tighter. The length of the cords determines the pitch of the voice. Longer cords are pitched lower than short ones. Since the length of the cord is determined by the diameter of the larynx, men, whose larynxes are usually larger than those of women (and, hence, more often externally noticeable as the "Adam's apple") have, as a rule, deeper voices than women.

The vocal cords are the primary producers of the voice, but they are only part of the mechanism. The cavities of the pharynx, the mouth,

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* By closing the epiglottis over the glottis and "swallowing," air can be forced down the esophagus. It can later be permitted to return. The return can be silent or can be made strikingly audible by the vibration of movable structures (probably the uvula) which stand in the path of the returning air. The ability to control the time and tone of such a pneumoesophageal regurgitation is of considerable social importance in some societies (e.g., in Japan) where the execution of a resonant pneumatic rumble is considered a compliment to the cuisine.

and the nose also act as resonating chambers and vary the relative strength of the different overtones of the sounds produced by the vocal cords. These overtones can be greatly altered by modifying the resonating passages through movement of the tongue, the uvula, and other movable parts. The effect of the resonating chambers on the character of the voice is obvious when the nasal chambers are blocked off, for instance, by congestion with mucus, or by squeezing the nostrils shut. The tone produced is known as a "nasal" tone. We speak of singing or speaking "through the nose"—which is rather curious because that is precisely what we do not do in such a case. One wonders whether to regard the phrase "speaking through the nose" as an idiom or merely the result of inaccurate observation.

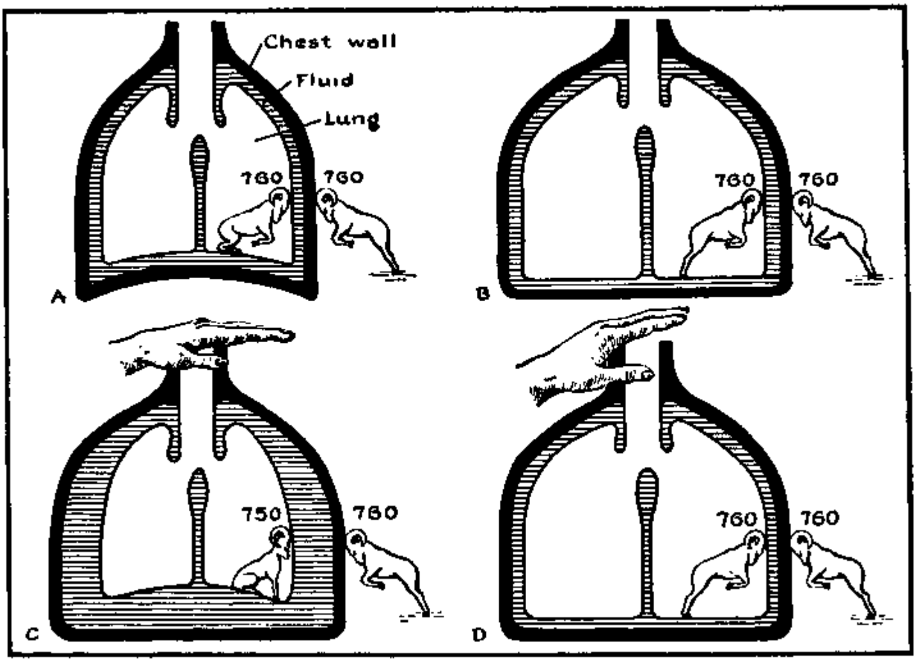

Fig. 6-3. Simplified diagram illustrating the pressure relationships of breathing. The pressure inside the lungs is the same as that outside at all times, whether the lungs are relatively collapsed (A) or inflated (B). *If* we could carry out the movements of breathing in while keeping the breathing passages closed (C), the internal pressure would be less than that outside until the passage was reopened (D). (Note: the layer of fluid between lungs and chest wall is only a very thin layer.)

Some distance below the larynx, well within the chest region, the trachea divides into two tubes called *bronchi* (singular, **bronchus**, Greek for windpipe); these bronchi in turn subdivide repeatedly, the ultimate subdivisions being blind-end sacs called *alveoli* (singular, **alveolus,** Latin, a small hollow). It is in the alveoli (Fig. 6-2D) that the real function of the lung is fulfilled, namely, getting oxygen into the body and carbon dioxide out of it. But more of this later.

38. The Process of Breathing

In the above section, the movement of air into and out of the air passages was often referred to but not accounted for. A little thought will convince one that there is a real problem here: how does air get from the outside of the nose all the way to the alveoli, a distance of perhaps fifty centimeters? An oxygen molecule might, of course, traverse the entire distance by virtue of its own molecular movement But, as we learned previously (Chap. V), the diffusion of any appreciable number of molecules is a slow process because of the jostling of other molecules which renders long-continued movement in one direction improbable.

As everyone knows, the movements of the chest have something to do with breathing. Simple observations show that when the chest increases in diameter, air moves into the body; when the chest decreases in diameter, air is expelled from the body. One might guess that the expansion of the lungs causes the chest to expand. The cause and effect relationship, however, is precisely the opposite, a fact which has some practical consequences.

It is first important to realize that a lung is incapable of actively expanding; in other words, there are no muscles in the lung which can cause it to expand. Functionally, the lung is but an elastic bag, living and complicated, but not too different from a rubber balloon. Once expanded, it can contract again by virtue of its elasticity, but it cannot expand itself anymore than a rubber balloon can expand itself.

The way the lung expands can be understood from the diagram of Figure 6-3. In a person who is momentarily not breathing, the gas pressure inside his lungs is the same as the gas pressure outside, say 760 mm Hg.

Now suppose the individual increases the volume of the thoracic cavity, the space which surrounds the lungs. The lungs are separated from the wall of the thorax by a thin layer of liquid. Since it is difficult to pull a hole in a liquid body, and since the lungs are elastic, the end result of an increase in the volume of the thoracic cavity will be an increase in volume of the lungs (Fig. 6-3B). The lungs will at all times be closely approximated to the wall of the thorax.

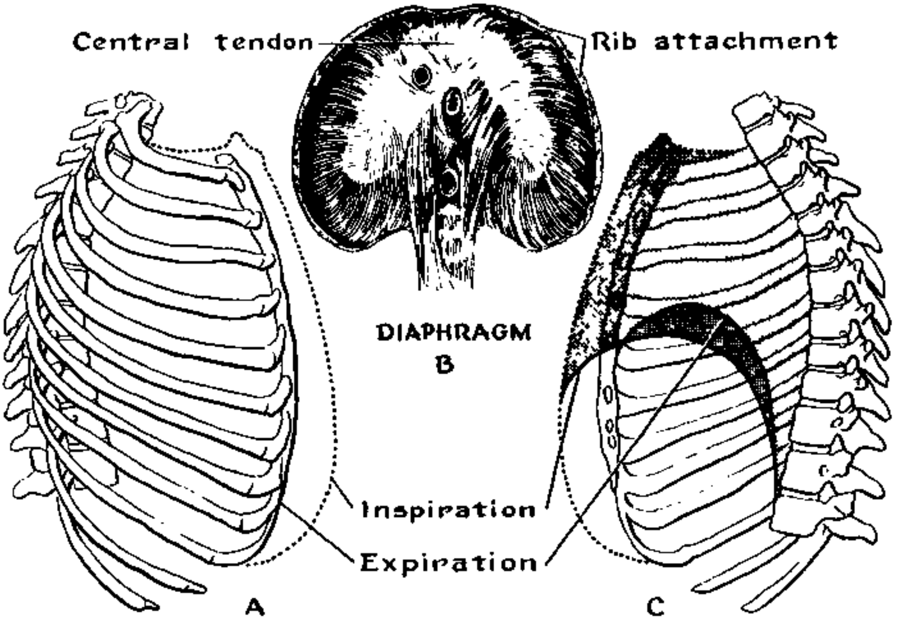

Fig. 6-4. Showing how the movements of the ribs (A) and of the diaphragm (C) increase the volume of the chest cavity, thus causing intake of air. The diaphragm, as seen from above, is shown in B; note that the muscle fibers are attached to the ribs and to one another by means of the central tendon.

When the thoracic cavity increases in size, the lungs expand too, remaining in close contact with the wall of the thorax. What will be the consequence of their expansion? We can perhaps best appreciate the consequence if we *imagine* the air passages to be kept closed during chest expansion (Fig. 6-3C). With the nose closed, no more air could get into the lungs. Since a given amount of air would have to fill a greater space, the air pressure inside the lungs would fall. If, after this had occurred, the air passage to the outside were opened (Fig. 6-3D), there would be an inrush of air because it is not possible to maintain different pressures in connecting vessels of gas. (An automobile tire, for instance, will not remain inflated after its valve is removed.)

The process of taking in air, called *inspiration*, does *not* occur in the discrete steps described because we normally do not try to expand the thoracic cavity while keeping our nose closed. Rather, at every instant, the "negative pressure"[*] which potentially might develop is prevented by the prompt inrush of air, so inspiration consists of a continuous adjustment of the inside pressure to the outside as the lung cavity is increased in size. In rapid inspiration, slight differences, a mm or so, in gas pressure may develop, but they last only momentarily.

The process of *expiration* is but the reverse of the inspiration and involves the same principles.[†]

39. The Anatomy of the Breathing Machinery

How is the change in the volume of the thoracic cavity effected? There are two ways in which this is accomplished: by movement of the ribs, and by movement of the diaphragm.

Figure 6-4A shows the anatomy of the rib arrangement in a simplified and somewhat exaggerated form. In inspiration, the ribs move up and outward, thus increasing the circumference of the thoracic cavity, hence, the volume of the cavity itself, which results in an increase in the volume of the lungs. The movement of the ribs is brought about through the contraction of numerous muscles that fasten the ribs to each other and to the rest of the axial skeleton.

Increase in chest volume can also be brought about by the action of the diaphragm. The diaphragm is a rather remarkable muscle in its method of attachment. The muscles we have previously considered (recall § 22) were attached to bones at both ends. By contracting, a muscle can move the bones closer together. The diaphragm, however, consists of a muscle whose fibers are arranged in a radial fashion (Fig. 6-4B) being attached at their extremes to the ribs and backbone, and at the center only to themselves (or rather to a central tendon). When we recall that the only positive action of a muscle is contraction, we realize that the sole effect of the contraction of the diaphragm muscles is to increase the tension of the diaphragm itself. When the diaphragm is not in the

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[*] Recall the discussion of § 34.

[†] It would be worth while for the student to make diagrams analagous to those of Figure 6-3 showing the process of expiration.

shape of a flat disk, the effect of its contraction tends to make it so.

In Figure 6-4C, it is seen that the diaphragm is not a flat disk. It is apparent that contraction of the diaphragm will increase the size of the chest cavity by pushing the contents of the abdominal cavity downward. As a result, there will be a slight protrusion of the abdomen, or belly.*

Breathing may be carried out principally by the muscles of the thorax, in which case it is called "thoracic breathing"; or principally by the diaphragm, in which case it is called "abdominal breathing"; or both types of breathing may be involved. There are considerable individual differences in the type of breathing employed. At one time, it was thought that there was a difference in the two sexes in this regard—and as a matter of fact there was; most women were thoracic breathers, whereas many men were abdominal breathers, studies made around 1900 A.D. showed. The difference observed was regarded by some as an inherent "secondary sexual characteristic" like the presence of a beard or a deep voice. It was, perhaps, a reasonable enough assumption, but when similar studies made around 1925 failed to reveal any difference between the method of breathing among men and among women, it was realized that the earlier observed thoracic breathing of women was necessitated by the formidable corsets that were once fashionable. . . . An error of interpretation of this sort makes the experimental scientist cautious about ascribing biological significance to any sex difference when the observation is made in only one society at one period. Folkways and customs can also corset or harness the minds of men and women and insure the appearance of striking differences between the adult sexes. . . . These remarks are not made to deny the existence of biological differences but only to enjoin caution in interpreting observations.

40. Some Consequences of Our Method of Breathing

That our lungs are expanded passively and indirectly by the expansion of the enclosing chest cavity might seem to be a technical particularity of small practical importance since the result is the same as if the lungs

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* It may be just as well, at this point, to get straight the synonymy of the mid-region. Thorax = chest. Abdomen = belly. Stomach = stomach, an organ in which food is digested. Professionally, biologists do not recognize "stomach" as a synonym for "belly." If, in certain circles, it seems desirable to avoid the use of "belly," *abdomen* must serve.

actively expanded themselves. In a sense, this is true, but situations sometimes arise in which the particular way our breathing mechanism works is of great importance.

As a result of war or accident, a hole may be opened in the chest wall. When this happens, air enters the thoracic cavity and surrounds the lung. This air is, of course, under the same pressure as the outside air; i.e., the pressure inside the lung is the same as the air surrounding it. Since the lung is elastic, it then collapses, just as a rubber balloon would collapse under the same conditions. Collapsed, the lung is of no use for breathing. Fortunately, in man, there is a wall, not too flexible, which separates the two lungs, so that a hole in the left side of the thorax will collapse only the left lung, leaving one lung still functional.

Collapsing a lung is sometimes done deliberately. In tuberculosis of the lungs, it is sometimes desirable to give one of the lungs a rest. This is very simply done by inserting a fine hollow needle between the ribs and letting clean, germ-free air enter the thoracic cavity. After enough air has been admitted, the needle is removed and the hole closed. The lung promptly collapses and remains collapsed and resting for a good many days. It eventually becomes active again because air that is introduced into the thoracic cavity is gradually dissolved in the fluid of the moist wall of the thorax and is removed by the circulatory system. If if it desired to keep a lung collapsed for a long period of time, air must be introduced into the thoracic cavity at frequent intervals.

41. The Capacity of the Lungs

A man at rest inspires and expires only a small amount of air each time he respires, approximately 0.5 liters* or about one pint. This "air" that goes in and out quietly and regularly, like the tides, is called **tidal air.**

If, at the end of a normal, resting inspiration, a man makes an extra effort and breathes in as much air as possible, he can take in an additional 3 liters of air. This extra air which can be taken in is called **complemental air.**

On the other hand, if, at the end of a normal expiration of tidal air,

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* A liter is almost exactly 1000 cubic centimeters; it equals 1.05 liquid quart (U.S.).

a man makes an extra effort and expels all the air he possibly can, the extra air expelled amounts to about 1 liter. This is called **reserve air.**

Reserve air + tidal air + complemental air = **vital capacity,** the total amount of air a man can breathe in and out by the most strenuous efforts. Notice that it is about 9 times the volume of the tidal air alone. The magnitude of the vital capacity varies some from one individual to another; it is generally greater in men than in women (heredity? training?), greater in athletes than in sedentaries, greater in healthy persons than in invalids.

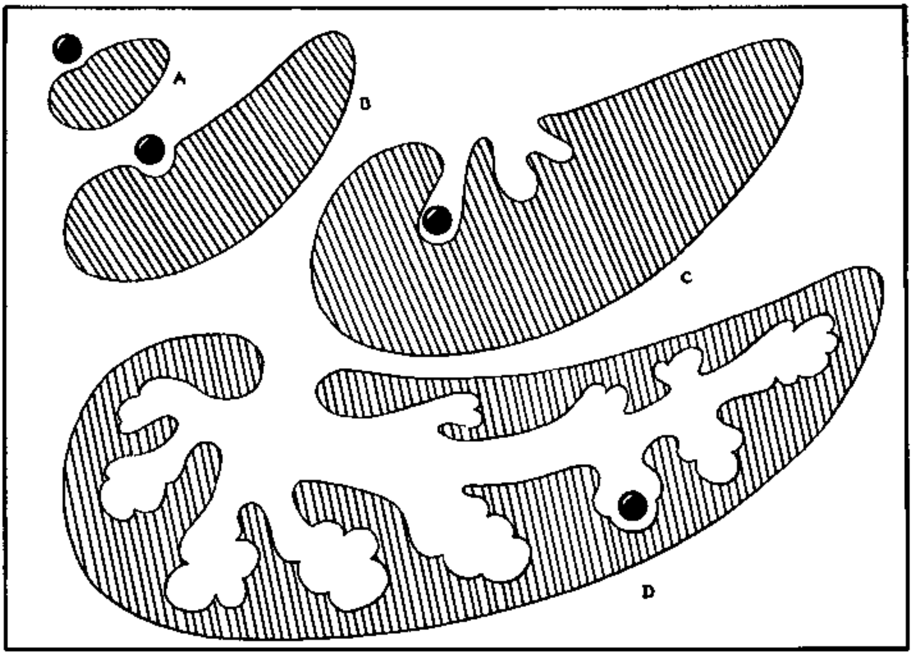

Fig. 6-5. The dark ball above is not inside the shaded body, no matter how convoluted may be the clear passageway, so long as the ball does not have to cross a limiting membrane. So it is with an oxygen molecule "inside" an alveolus. The molecule is not truly inside the body until it has passed through the epithelium of the alveolus.

From the previous discussion of the mechanism of lung inflation, it would be suspected that there must be air in the lungs after even the most forcible expiration, for the lungs are always touching the walls of the thorax which cannot be decreased in size very much. Such is indeed the case. There is an additional volume of air (called **residual air**), amounting to about 1.5 liters, still present in the lungs after the most forcible expiration. Part of this air can be released by letting air into the thoracic cavity from the outside as previously described (§ 40). But even removal of the lungs from the body does not result in their complete collapse. The remaining volume of air, called **minimal air,** is never released once it is taken in.* A newborn child has no air in his lungs until he takes his first breath. Thereafter, his lungs always have at least the minimal air in them. By placing a portion of its lung in water, we can tell if a dead infant was stillborn, or if it died after taking a breath, a difference that is often of legal importance. The lungs of the stillborn child sink, whereas those of the child born alive will float by virtue of the minimal air they contain.

42. Getting Oxygen into the Body and Carbon Dioxide Out

So much discussion of the mechanism of breathing, and still we have made no mention of getting air or any of its components into the body. Air that is in the lungs is still, in an important sense, outside the body.

Figure 6-5 will illustrate the point. In all four instances (A-D), the molecule indicated as a black ball is *outside* the body. In D, the molecule is almost entirely surrounded by the body, but logically we have to say that if the molecule in A is outside the body, so is the molecule in D. So, at least, would a mathematician tell us and, as we shall see later, the body acts as if it understood mathematics. To get truly inside the body, a molecule must cross some sort of limiting membrane such as that indicated by the continuous limiting line of each "body" in Figure 6-5.

Air in the dead-end alveoli of the lungs is still outside the body. How does it get into the body? To understand this problem, let us examine a diagram (Fig. 6-6) in which an alveolus is much magnified so as to show the relations of the air, the cells, and the blood in the blood vessel which winds around the alveolus. The molecules in this figure are much too large, of course.

The air in an alveolus consists mostly of nitrogen molecules, oxygen

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* That is, this *volume* cannot be expelled; the molecules of air are constantly exchanged for others. All of the "airs" referred to in this section are *volumes*.

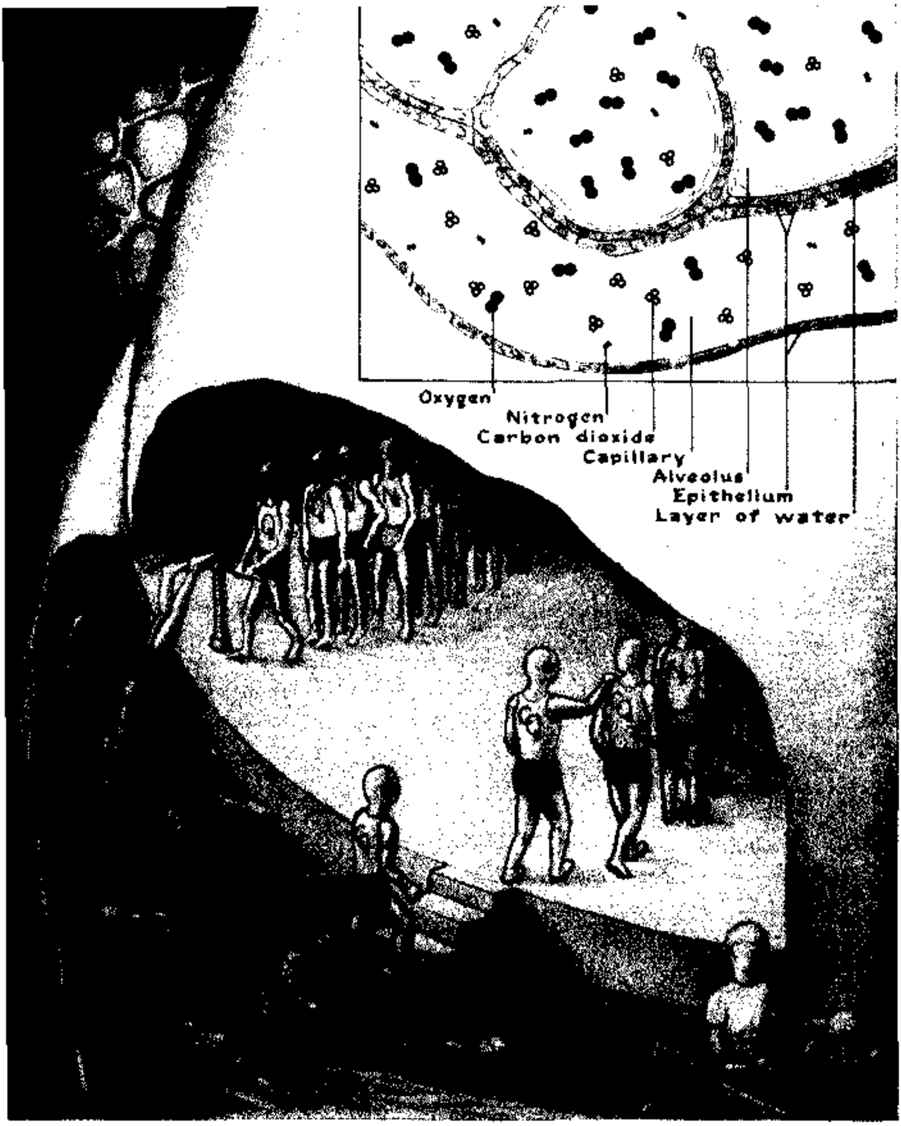

Fig. 6-6. A pictorial analogy of the process of absorption of oxygen from the alveolar space into the blood of a pulmonary capillary, and the release of carbon dioxide from blood to alveoli. Movement of both kinds of molecules occurs in both directions, but the *net* movement only is represented. The significance of the boat (RBC) in the analogy will appear later (§ 69).

molecules, and carbon dioxide molecules. Since it is oxygen molecules that we are interested in, we shall first deal with these.

Oxygen molecules in the alveolar air dissolve in the liquid that surrounds the cells of the alveolus. This liquid is, of course, made up of molecules, too; but, for simplicity, we have failed to indicate its molecular character in the figure. The O_2 molecules in the liquid move in all conceivable directions (as described in § 28)—back and forth in the liquid, across the membranes into the cells, through the cells, and into the liquid of the blood stream that is flowing past the alveolus. The blood stream also has some oxygen molecules in it and some of these diffuse in the opposite direction. However, the concentration of O_2 molecules is less in the liquid portion of the blood stream* than it is in the liquid of the inner wall of the alveolus. Consequently, although oxygen molecules move in both directions, the *net* movement is from the alveolus to the blood stream. The end effect is that, as the blood flows past the alveoli, it gains in oxygen content. Correspondingly, the air that comes into the alveolus loses oxygen.

The story of carbon dioxide is similar, but reversed. As a result of the process of respiration, the blood carries with it a considerable amount of CO_2. External air, however, has relatively little CO_2; consequently, the *net* movement of CO_2 molecules is from the blood stream to the alveolar air, and the CO_2 content of air is increased as a result of breathing.

The effect of breathing on the composition of air may be seen in Table 6-1. In comparing inspired air and expired air, notice the decrease in O_2, and the marked increase in CO_2. The partial pressure of H_2O also increases; this is due to evaporation of water from the warm, moist surfaces of the alveoli and other respiratory passages. The partial pressure of N_2 remains substantially the same.

43. The Importance of N_2: A Problem in Diving and High Flying

In Table 6-1, it will be noticed that the partial pressure of N_2 changes only a little when air is inspired and expired. It can be shown, in fact, that the *amount* of N_2 does not change at all. All organisms need nitrogen;

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* Consideration of the effect and importance of red blood cells is deferred to § 69.

but very few can use molecular nitrogen, N_2, to satisfy their nitrogen needs. Man cannot.

Molecular nitrogen (N_2) is chemically inert as far as man is concerned.

Physically, however, the existence of so much N_2 in the air is quite important. Its presence constitutes a problem for the deep-sea diver and the aviator. To understand this problem, it is necessary to realize that:

The solubility of a gas in a liquid is increased by pressure.

TABLE 6-1

Pressure stated in terms of mm Hg, taken from actual experimental readings. The decrease in the partial pressure of N_2 does not represent a decrease in actual amount of N_2; the relatively slight decrease in pressure is due to the warming of the air and to the increase in water-vapor content after inspiration.

	Inspired Air	Expired Air
Partial pressure of N_2	596	568
Partial pressure of O_2	158	116
Partial pressure of CO_2	0.3	29
Partial pressure of H_2O	5.7	47
Total pressure of all gases	760	760

Everyone has seen evidence of the truth of this. An unopened bottle of carbonated* beverage ("coke," ginger ale, "pop," etc.) is clear. No gas bubbles are present, showing that all the gas is in solution. When we remove the cap of the bottle, there is an outrush of gas, indicating that the contents were bottled under greater than atmospheric pressure. When we remove the lid, we reduce the pressure on the contents and, immediately, bubbles of gas start to form in the liquid and escape to the surface because, under the lower pressure conditions, the liquid is supersaturated with the gas.

Much the same sort of thing can happen to man (Fig. 6-7). When a man is put in surroundings where all the gas around him is under pressure, more gas is dissolved in the fluids of his body. This, by itself, is not harmful but if the pressure of the gas around him is suddenly

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* So called because the gas that is present in quantity is carbon dioxide.

decreased, the man's fluids have more gas in them than they can hold in solution; consequently, bubbles of gas are formed, just as they are in an opened bottle of ginger ale. In man, such bubbles may plug up blood vessels, thus stopping the circulation in the parts affected, often with serious consequences. The symptoms are extremely variable, depending on where the bubbles happen to lodge, which seems to be largely a matter of chance. They may stop part of the circulation in the spinal cord, thus causing partial paralysis; frequently, they affect the organs of the mid-region of the body, causing the affected individual to bend over in extreme pain—hence the common name "the bends."

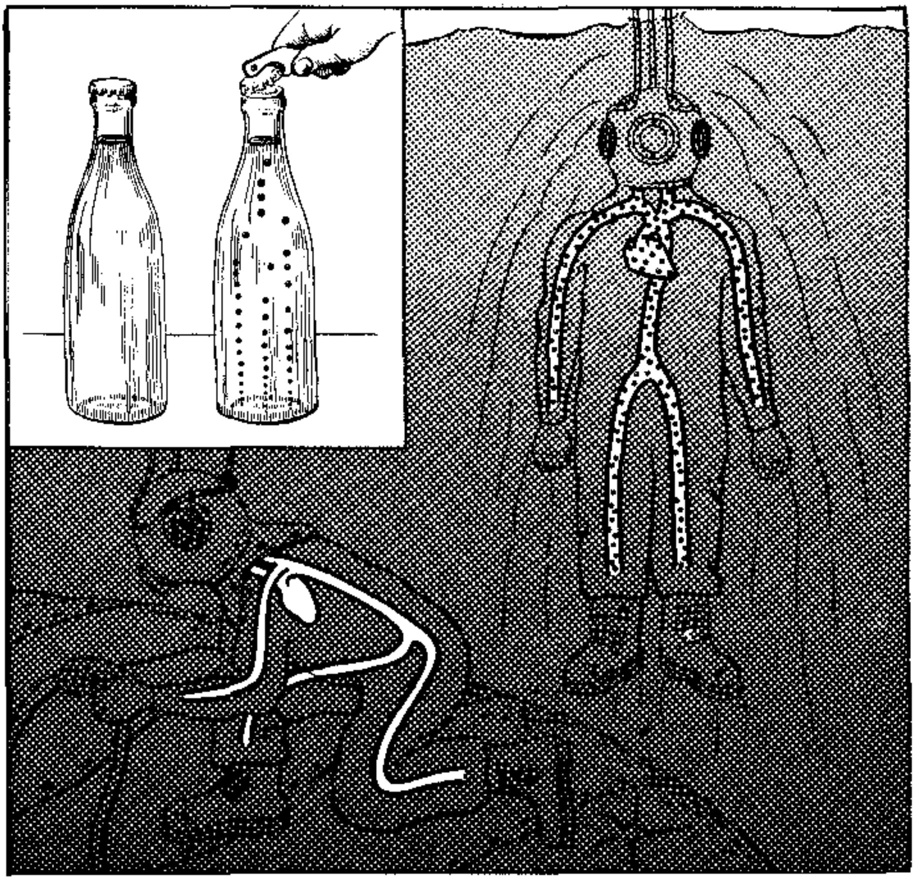

Fig. 6-7. The solubility of a gas in a liquid is directly proportional to the pressure. When a diver ascends to a region of lower pressure, gas may come out of solution in his blood and form gas bubbles which may occlude blood vessels.

A more general name is "decompression sickness"; this name indicates the invariable cause rather than a variable symptom.

The principal gas responsible for the effect is nitrogen because it is present in the largest concentration and because, being chemically inert, it is not used up by the body as is oxygen.

The probability of and the abundance of bubble formation depend on a number of factors (not all well understood), including the amount of gas dissolved in the body and the rate of release of the gas under decompression. How much extra nitrogen will dissolve in the body of a diver depends on how deep he goes (that is, how much pressure he is subjected to) and how long he stays down. Whether the gas will produce bubbles when he is decompressed depends on how rapidly the process takes place. If the diver is brought up slowly, he can get rid of the excess gas by breathing; when he is brought up rapidly, he may suffer decompression sickness. If this happens, the simplest remedy is to put him in a pressure chamber when he gets to the surface, raise the pressure inside the chamber until his bubbles redissolve, and then, by releasing the pressure slowly, simulate a slow ascent.

When an airplane ascends, it moves into regions of lower pressure. In air, of course, there is much less change in pressure per unit height than there is in water, air being much lighter. Decompression sickness is very unlikely to occur until the aviator has ascended to 20,000 or 25,000 feet, where the air pressure is about 40 per cent of normal. In water, a similar pressure change takes place in rising only about eighty-five feet. The speed of rise is important; in the days of the first sluggish airplanes, it was not possible to rise fast enough to experience decompression sickness. The development of more powerful motive forces brought this problem of the deep-sea diver to the attention of the aviation physiologist.*

There are individual differences in susceptibility to decompression sickness. These differences for the most part are not understood, but one thing is clear; fat men are more susceptible than thin men. The difference is apparently due to the fact that N_2 is about *five times as soluble in fat* as it is in water. A fat man, therefore, can accumulate a greater reserve of dissolved nitrogen that will have to be expelled when

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* There are other problems connected with flying in rarified air. These will be discussed in § 107-§ 108.

he is decompressed. It has long been known that fat men do not make good deep-sea divers.

The realization that the speed of elimination of dissolved gases was an important factor in decompression led to the search for gases which could be eliminated more rapidly. Of gases which can be safely introduced into the body, *helium* turned out to be most useful. It is chemically inert and quite harmless to animals. A surplus of it is eliminated about twice as rapidly as nitrogen. By breathing a mixture of helium and oxygen, instead of nitrogen and oxygen before ascending, an aviator or diver becomes less susceptible to decompression sickness.

QUESTIONS AND PROBLEMS

6-1. What distinction is made in this text between *breathing* and *respiration?*

6-2. Consider the following quotation from Richard Grant White: "There is a misuse of words that can be justified by no authority, however great, and by no usage, however general." Do you think that most scientists would be in accord with the sentiment here expressed?

It may be of interest to know that White was one of a band of aggressive grammarians who set out to refine American language after the Civil War, labelling, for instance, the ubiquitous "*It is me*" as an inexcusable barbarism and starting the custom, in America, of pronouncing *either* as though spelled *eye-ther*.

6-3. Do the lungs expand actively or passively? Explain.

6-4. What is a pneumothorax? It has been described in the text but not identified by this name. Try first to guess the meaning of this term by analyzing it into roots; then, look it up in a dictionary.

6-5. Dogs have no partition dividing the thoracic cavity into two chambers. Could the operation of pneumothorax be used successfully in treating canine disease? Explain.

6-6. Suppose an explosive shell blew up and injured a man near you by opening two small holes in his chest wall, one on the left side, one on the right side. Can you suggest an immediate first-aid measure that might save the man's life? Explain the rationale of the action.

6-7. An unwed mother is accused of having murdered her newborn child. The medical officer attached to the coroner's office performs a very simple test that exonerates her. What is the test and the reasoning behind its interpretation?

6-8. Trace the course of a molecule of oxygen from the time it enters the nose until it is in the blood stream. At what point would you consider it inside the body?

6-9. Repeat question 6-8, assuming that the man breathes through his mouth.

6-10. Etymologically, the term *epithelium* means a delicate outside tissue. How, then, can one justify the application of this term to the lining of the alveoli (see Fig. 6-6) which seem to be well inside the body?

6-11. Are there any advantages to breathing through the nose instead of the mouth?

6-12. Suppose the laryngeal cords were destroyed by disease, what would be the effect on the individual?

6-13. Suppose an animal had the ability to close completely all of its sweat glands and to stop all urination, could it, in a dry atmosphere, avoid losing water? Explain.

6-14. If we lived, and could live, in an atmosphere made up of 98 per cent O_2 and 2 per cent CO_2, would the problems of the deep-sea diver and the aviator be more or less serious than they are now? Explain.

6-15. "Decompression sickness" is a synonym for "the bends." Is there any reason to prefer the former term, aside from the fact that it is a longer term and hence more likely to impress our friends?

6-16. In 1849, a physiologist noted that men were usually abdominal breathers, women usually thoracic breathers, and considered this difference a secondary sexual characteristic. Later, it was noted that Indian and Chinese women were abdominal breathers. Is it probable that this difference between Oriental and Occidental women is an inherent racial difference?

Chapter VII

Interlude: A Bit of Chemistry

44. Authority, and the Scientific Attitude

Life being, as Lavoisier put it, a chemical function, it is not surprising that, to understand much about living things, one needs to know at least the elements of chemistry. In a way, this is unfortunate. The professional biologist is at a disadvantage compared with the professional chemist. The professional chemist can be almost completely ignorant of biology and still be a good chemist. The biologist, however, must attain a certain degree of competence in chemistry in order to understand his own field. There are many lines of biology which do not require a great deal of chemistry, but it is doubtful if there is a single specialty in the field of modern biology that does not require some grasp of elementary chemistry.

Ideally, the student should study chemistry for a year or so before tackling biology. Practically, this course of action is seldom possible. Therefore, it is necessary to make the best sense possible of biology, using only simple chemistry as a tool. Fortunately, at the elementary level, a fairly satisfactory picture of biology can be presented, utilizing only the rudiments of chemistry. But the rudiments at least are needed.

The treatment of biology given in this text presupposes a knowledge of elementary chemistry. For those students who lack this knowledge, the present chapter is inserted. Here certain facts of chemistry will be presented in a dogmatic fashion, without proof. If the student is willing to accept them thus, he can use these facts to gain a better understanding of biology. It may seem strange that we are urging the student to adopt an unquestioning attitude; surely this is not the much-praised scientific attitude. To accept without question, on the basis of authority —surely not!

Yet, in practice, this very attitude must be adopted *in part* by every practicing scientist. The interrelations of the sciences are so widespread, and there is so much to know, that no scientist can have a critical understanding of all the facts that he must use while working in his own small field. A biologist, in a day's work, may have to call upon knowledge in the fields of inorganic chemistry, organic chemistry, biochemistry, physical chemistry, electricity, electronics, atomic physics, or mathematics. No mere man can have a discriminating understanding in all these fields. Of necessity, the practicing biologist has a critical appreciation of the evidence in only one small segment of science. For lack of time and training, he must accept the conclusions in other regions on authority. The farther removed a field is from his own, the more uncritical must the investigator be in accepting the published facts.

No one can be completely critical in all his evaluations. To the question, "How many legs does a horse have?", we adopt a very critical attitude because it raises a question each of us can answer from his own observations. The weight of authority will count for little. But "How high is Mt. Everest?" must be attacked in a different way. Most of us will never be anywhere near Mt. Everest and so we seek statements of others. Indeed, most of us do not, of our own knowledge, even know that there *is* a mountain at 87° E longitude and 28° N latitude. Even its existence we accept on the basis of authority. If we seriously question the source of our information, we have no recourse but to go to Tibet and see for ourselves. But life is too short to attempt to prove every report so we, perforce, accept much of what we know on authority.

We are prevented from checking many facts by the practical limitations of time and material means. Many others we cannot verify because of lack of training. Here again, given time, we could remedy the deficiency. But, as a practical matter, we will accept many statements of scientific fact on the strength of authority, without asking the evidence. Even the scientific facts that are now matters of common knowledge may be so accepted. For instance, you undoubtedly believe that the world is spherical. What is the evidence? Do you know evidence that would rule out the possibilities of its being a disk; or a doughnut? This is not an easy question to answer!

The scientist, like other humans, accepts facts outside the field of his competence on authority. This is part of the scientific attitude. However, along with this willingness to accept, there is an insistence on remembering, at all times, when a fact is backed by direct evidence and when it is backed by authority; when the nature of the evidence is understood and when it is tentatively accepted without complete understanding. No scientist can live up to the popular stereotype of believing nothing except on direct evidence. But he can keep in mind at all times the nature of the evidence and the limits of his understanding. To the extent that he never forgets these limitations does he become a true scientist.

45. Molecules and Atoms

Chemistry is the science of substances and of the reactions that change them into other substances. All living things are in a constant state of change, i.e., the chemical substances of which they are composed are continually changing into other chemical substances. Any process in which chemical substances are changed is called a **reaction.** Every living organism takes in food substances and changes them into other materials by processes which we shall begin to study in the next chapter. But first it is necessary to elucidate the meaning of some common chemical terms, among them, the word **substance,** as used by the chemist.

A man eats a piece of cabbage. What would the chemist say the man is eating? He would say that the man is eating a complex **mixture** of many substances, including water, sugar, and salt. In the cabbage, thousands of different kinds of substances are mixed together. It is possible for the chemist to separate many of these substances from one another. When this is done, it is found that the most abundant substance in the cabbage is water. As a matter of fact, water is the most common substance in all living things, comprising from 70 to 95 per cent, by weight, of every living organism.

A sample of a pure substance is composed of only one kind of molecule. Each molecule is made of smaller particles called **atoms.** Every molecule of water is made up of one atom of oxygen and two atoms of hydrogen. This fact is indicated by the **molecular formula** of water, which is H_2O. Every molecule that is made of more than one kind of atom is called a **compound;** water is a compound. The oxygen molecules in the air are not compounds; their molecular formula is O_2. Our diet includes water and many other chemical compounds. One of the simple ones is table salt or sodium chloride, the symbol for which is NaCl. (*Natrium* is a synonym for sodium.) Other substances in our food are made up of more complex molecules, e.g., sugar, $C_{12}H_{22}O_{11}$.

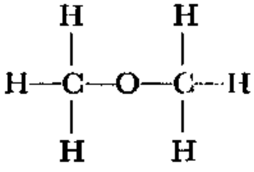
All substances are made up of the chemical building blocks we call atoms. Each different kind of atom is called an **element.** There are only ninety-odd elements in the universe, yet out of these few kinds of atoms are constructed literally millions of different kinds of molecules, or substances. **The molecules of each kind of substance are composed of (1) particular kinds of atoms which (2) are present in a fixed and definite proportion and which (3) are bound to each other in a specified way.** We can illustrate the three points made in this statement by some examples.

1. *With respect to kinds of atoms:* A molecule of H_2S has almost the same weight as one of H_2O. But these are quite distinct substances. The former is called *hydrogen sulfide*, and is a noticeable component of the bouquet of rotten eggs. The latter is water and is odorless. There are many other differences between them.

2. *With respect to proportions of atoms:* The substances, H_2O and H_2O_2, both contain hydrogen and oxygen atoms but in different proportions. The former is, of course, water; the latter is called *hydrogen peroxide* and is a strong antiseptic and bleaching agent.

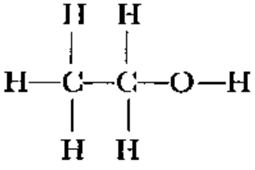
3. *With respect to molecular structure:* A molecule of *ether*, an anesthetic agent, has in it two atoms of carbon, six of hydrogen, and one of oxygen. A molecule of *ethyl alcohol*, the intoxicant, has the same atoms in the same proportion. But ether and alcohol are distinctly different substances. The properties of a substance are the properties of its molecules. Since ether and alcohol have markedly different properties, an ether molecule and an alcohol molecule must be different. Molecules are very small particles indeed (§ 27) but, fortunately, there are indirect but certain means of determining the struc-

ture of molecules, i.e., the arrangement of atoms within molecules. By these means, it has been shown that the structure of ether and alcohol are as indicated below:



$$\begin{array}{ccccccccc} & & H & & & & H & & \\ & & | & & & & | & & \\ H & - & C & - & O & - & C & - & H \\ & & | & & & & | & & \\ & & H & & & & H & & \end{array}$$

ether



$$\begin{array}{ccccccccc} & & H & & H & & & & \\ & & | & & | & & & & \\ H & - & C & - & C & - & O & - & H \\ & & | & & | & & & & \\ & & H & & H & & & & \end{array}$$

alcohol

In the above **structural formulas,** each atom of carbon is indicated by the letter C, each atom of hydrogen by H, and oxygen by O. The lines between the letters indicate the presence of forces which tend to hold the atoms near one another. These attractive forces are called **bonds** or *chemical bonds.*

One of the major cleavages in the field of chemistry is between **organic chemistry** and **inorganic chemistry.** Originally, the distinction between these two divisions was one based on the origin of the substances studied: organic chemistry was concerned with substances which were obtained, and could only be obtained, from organisms; inorganic chemistry was concerned with all others. However, in 1828, this distinction was shown to be untenable when a chemist named Wöhler made the organic substance urea, NH_2CONH_2, out of inorganic substances. After that date, with increasing rapidity, organic substance after organic substance was synthesized in the laboratory. In the light of these accomplishments, the old definition of organic chemistry became indefensible but the distinction did not. We now define the two fields as follows:

Organic chemistry is the chemistry of the carbon-containing compounds.

Inorganic chemistry is the chemistry of all other compounds.

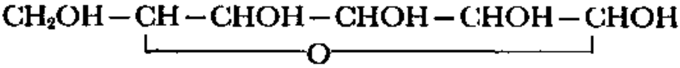
With few exceptions, these definitions fit the two fields of chemistry as presently conceived.

Students of organic chemistry are greatly concerned with the structure of molecules. We have discussed ether and alcohol to show how structure may determine properties. This example was not an exceptional one. Most organic molecules are made up of the same atoms, namely, carbon, hydrogen, and oxygen, with a few atoms of nitrogen, sulfur, or phosphorus often present. The proportions, and even the absolute numbers, of atoms present are often the same in a number of organic molecules that differ markedly in their properties. The problems of organic chemistry are principally ones of determining the way in which the atoms are bonded together. The atoms present in a cabbage and in a man are the same, and even the proportions of the atoms are almost identical. Many of the compounds are the same, too, but many others differ only (or principally) in the way the atoms are arranged. Among the major chemical problems that confront a man subsisting on cabbage are problems of modifying the architecture of the organic molecules of the cabbage so that they become human-type molecules, so to speak. The processes involved are many and complex. Before we can study them, we will need to learn something of the types of molecules that serve as food for man and other animals.

46. Some Compounds of Biological Importance

Anticipating the discussion of the next chapter, we may point out that a typical diet for a complex animal like man consists largely of carbohydrates, proteins, and fats. What are these substances, chemically speaking?

Carbohydrates. An example of a simple carbohydrate is *glucose* or grape sugar. The structure of this substance is indicated by its formula:



$$\mathrm{CH_2OH-\underbrace{CH-CHOH-CHOH-CHOH-CHOH}_{O}}$$

This is obviously a rather complicated molecule. For simplicity, we will hereafter refer to glucose by its molecular formula, $C_6H_{12}O_6$. Notice that the proportions of carbon: hydrogen: oxygen are as 1:2:1.

Another common carbohydrate is sucrose, $C_{12}H_{22}O_{11}$. Notice that the proportion of C:H:O is *approximately* as 1:2:1. The ratio shows a slight deficiency of H and O; as a matter of fact, it is shy two hydrogen atoms and one oxygen. The significance of this deficiency we will point out later (§ 49).

Examples of some other carbohydrates are: lactose, $C_{12}H_{22}O_{11}$; raffinose, $C_{18}H_{32}O_{16}$; and maltose, $C_{12}H_{22}O_{11}$. Notice that, in each of these, the atomic proportion of C:H:O is approximately as 1:2:1.

Fats. As an example of a fat, we may take *stearin*, the molecular formula of which is $C_{57}H_{110}O_6$. It is important to notice that *there is a much smaller proportion of oxygen in a fat molecule* than there is in a carbohydrate molecule.

Amino acids and proteins. Amino acids include one element not found in either fats or carbohydrates, namely, nitrogen. The simplest amino acid is *glycine*, NH_2CH_2COOH. The NH_2 group is called an *amino group.* The COOH group is called a *carboxyl* group and contributes some acidity to the molecule. Every amino acid has both of these groups in it.

Millions of amino acids are theoretically possible. Less than fifty different ones have been found in plants and animals. Only about two dozen amino acids are at all common. From these two dozen, however, are made a great variety of proteins.

A protein is a complex molecule made up of many amino-acid units. A typical protein may be made of as many as a thousand amino acid units. The ways in which these amino acids may be combined are so various that there seems to be no theoretical limit to the number of different kinds of proteins.

We cannot write the structural formula for a single protein, for **no protein has ever been synthesized by the chemist.** Proteins can easily be analyzed in the laboratory, that is, broken down, into their constituent amino acids. A living organism can take amino acids and make them into proteins again, but no chemist has yet succeeded in carrying out this synthesis in a test tube.

47. Ions and Ionization

Among the differences between inorganic and organic substances, is the greater tendency of inorganic molecules to separate partially into particles called **ions.** What are the relations between molecules and atoms and ions?

We usually think of a molecule of a substance as being the smallest bit of the substance that acts as a unit in moving around. However, with inorganic substances, the molecule itself is often separable into electrically charged particles that are capable of moving around more or less independently. Organic substances are not so prone to break up in this way.

Ordinary table salt is sodium chloride, NaCl. Much evidence indicates that when it is dissolved in water, each molecule splits into two particles that are somewhat independent of each other. These particles are *not* the atoms sodium and chlorine. These particles are *charged* with electricity, one of them positively (Na^+), the other negatively (Cl^-). The explanation of the charges is as follows: Every atom consists of a central core or **atomic nucleus** surrounded by one or more **electrons,** minute particles about the size of the nucleus. Each electron constitutes a negative charge of 1. The atomic nucleus is positively charged. The nucleus of an atom has a positive charge exactly equal to the total negative charge of the swarm of electrons around it, and so, the net charge of the entire atom is zero. If one of the electrons is *removed* from the outer swarm, this leaves the whole atom with a positive charge. Such a positively charged atom is called a **positive ion.** On the other hand, if a neutral atom *acquires* an additional electron, the atom thereby becomes negatively charged and is referred to as a **negative ion.** When NaCl is dissolved in water, the molecule separates into two parts but, in so doing, the Na part loses an electron to the Cl part. The result is the production of a positive ion of sodium, which we indicate by Na^+; and a negative ion of chlorine, indicated by Cl^-.

At any given instant in a solution of sodium chloride, some of the material is in the form of complete NaCl molecules and some of it is in the form of Na and Cl ions. Molecules of NaCl are continually breaking up, or **dissociating,** into ions, and ions are continually recombining to form molecules, facts which we indicate by writing:

$$NaCl \rightleftharpoons Na^+ + Cl^- \tag{1}$$

We read this as follows: "Sodium chloride dissociates to form positive sodium ions and negative chloride ions." Or, more briefly: "Sodium chloride ionizes."

Ionization is very characteristic of inorganic compounds and very *un*characteristic of organic. Many organic compounds do not ionize at all. Others ionize, but only weakly, i.e., only a small proportion of the molecules are dissociated at any given instant.

48. Acids and Bases

All **acids** taste sour. Among these substances, are: HCl (hydrochloric acid), HNO_3 (nitric acid), H_2SO_4 (sulfuric acid), and H_3PO_4 (phosphoric acid). It will be noted that the only element common to all of these is hydrogen. These substances dissociate as follows:

$$\begin{aligned} HCl &\rightleftharpoons H^+ + Cl^- \\ HNO_3 &\rightleftharpoons H^+ + NO_3^- \\ H_2SO_4 &\rightleftharpoons H^+ + HSO_4^- \\ H_3PO_4 &\rightleftharpoons H^+ + H_2PO_4^- \end{aligned}$$

It is the hydrogen ion that gives these substances their acidic properties, one of which is their sour taste. The acidic properties of these substances are dependent upon their ability to dissociate to form H^+ ions. The more readily a molecule produces H^+ ions, the more strongly acid we say it is.

A **base** is a substance that can produce the hydroxide ion, OH^-. NaOH (sodium hydroxide), and KOH (potassium hydroxide) are bases:

$$\begin{aligned} NaOH &\rightleftharpoons Na^+ + OH^- \\ KOH &\rightleftharpoons K^+ + OH^- \end{aligned}$$

A substance that can produce OH^- ions is said to be basic or alkaline.

When solutions of an acid and a base are mixed, the H^+ and the OH^- ions combine to form the weakly dissociated HOH, water (H_2O). If the proper proportions of acid and base are used, the resulting solution is neither acidic nor basic, but is **neutral.** H_2O is neutral.

As an example of such a reaction, we may consider:

$$NaOH + HCl \longrightarrow HOH + NaCl \tag{2}$$

which could better be written:

$$Na^+ + OH^- + H^+ + Cl^- \longrightarrow HOH + Na^+ + Cl^- \tag{3}$$

Any inorganic substance that can ionize to produce + and − ions, neither of which is a hydrogen or a hydroxide ion, is called a salt. NaCl, for instance, is a salt. Examples of other salts are KCl, $NaNO_3$, and Na_3PO_4.

Equation (3) may be generalized thus:

$$\text{a base} + \text{an acid} \longrightarrow \text{water} + \text{a salt} \tag{4}$$

Some organic substances are acidic. We have already pointed out two facts:

a. In general, organic substances dissociate into ions only slightly.

b. The strength of an acid is determined by the proportions of H^+ ions present in solution.

From these two facts, we would predict that:

c. Most organic acids are weak acids.

Such is, indeed, the case. The acidic group of an organic acid is the carboxyl group which can dissociate thus:

$$\begin{array}{ccccc} CH_3COOH & \rightleftarrows & CH_3COO^- & + & H^+ \\ \text{(acetic acid)} & \rightleftarrows & \text{(acetate ion)} & + & \text{(hydrogen ion)} \end{array} \tag{5}$$

Notice that the OH group does not act as a group at all in such organic compounds. The COOH group is not in any sense a basic group. It is acidic; it yields H^+ ions. The dissociation is usually not very extensive so the compound is only weakly acidic. In fact, most amino acids are only mildly acidic because the NH_2 group acts as a base, thus neutralizing part of the acidity.

49. Catalysis; Enzyme Action; Hydrolysis

$C_{12}H_{22}O_{11}$, sucrose, is a fairly stable substance. However, under certain conditions, it can be decomposed into two molecules of simpler sugars, glucose and fructose, both of which have the molecular formula, $C_6H_{12}O_6$. If we write:

$$C_{12}H_{22}O_{11} \longrightarrow C_6H_{12}O_6 + C_6H_{12}O_6 \tag{6}$$

we notice that the equation is not *balanced*, that is, that there are not the same number of atoms of carbon, hydrogen, and oxygen on the left side as on the right. The right side has two more atoms of hydrogen and one more of oxygen than the left. As written, equation (6) implies the spontaneous production of these atoms out of nothing—a phenomenon that has never been observed. If the two atoms of hydrogen and the one of oxygen must come from somewhere, whence do they come? The ratio of 2H:1O suggests the substance H_2O. Reaction (6) occurs only in water solutions; water is, in fact, the substance that completes the reaction:

$$C_{12}H_{22}O_{11} + H_2O \longrightarrow 2C_6H_{12}O_6 \tag{7}$$

Under most "ordinary" conditions, the above reaction does not appear to take place. However, if an acid, say HCl, is added to the solution, reaction (7) may then take place. At the conclusion of the reaction, the HCl is still present in the same amount. What is the role of the HCl? Since it promotes a reaction that would not otherwise occur at a perceptible rate, the HCl must, in some sense, enter into the reaction, but in such a way that, in the end, it comes out again, so to speak, in its original form. We can indicate its role by rewriting our equation:

$$C_{12}H_{22}O_{11} + H_2O \xrightarrow{(HCl)} 2C_6H_{12}O_6 \tag{8}$$

A substance that acts in this fashion is called a **catalyst. A catalyst is a substance that promotes a chemical reaction without itself being used up.** Many studies have shown that a catalyst does not induce a reaction that would not occur in its absence, but that it merely makes a spontaneous reaction occur very much more rapidly. *It does not change the course of the reaction; it merely changes the speed.* The reaction shown in (7) would occur without any catalyst, but it would take hundreds of years to go to completion. A catalyst can cut the time down to a few minutes or even a few seconds.

Catalysts are not substances set apart from noncatalysts. Any substance *may* be a catalyst for some reaction or reactions. In the above reaction, HCl is a catalyst; in some other reaction, it may be one of the reactants and some other substance may be a catalyst. Many reactions apparently require no catalyst to proceed at good speed. Many others are accelerated by catalysts. Many a substance can act as a catalyst in a great many different reactions. Finely divided metals, for instance, are used as catalysts in hundreds of industrial operations, e.g. in the catalytic breakdown of petroleum oils to form gasoline.

Living organisms, it has been found, make extensive use of catalysts. The catalysts of living organisms are proteins and are called *enzymes.* **All enzymes are proteins.** Since man has never succeeded in synthesizing a single protein in the laboratory, it follows that he has never synthesized an enzyme. The study of enzyme action must be carried out either with living organisms or with extracts of living organisms.

The ability to split sucrose into two C_6 sugars is very widespread among organisms. From an organism that can carry out this reaction, a protein can be obtained that catalyzes this reaction; this protein is, therefore, an enzyme. As contrasted with inorganic catalysts, **enzymes are highly specific.** Each enzyme is capable of performing only one chemical trick. The enzyme that splits sucrose apparently cannot catalyze any other reaction. To indicate this specificity of action, it is desirable to give the enzyme a unique and suggestive name. Although

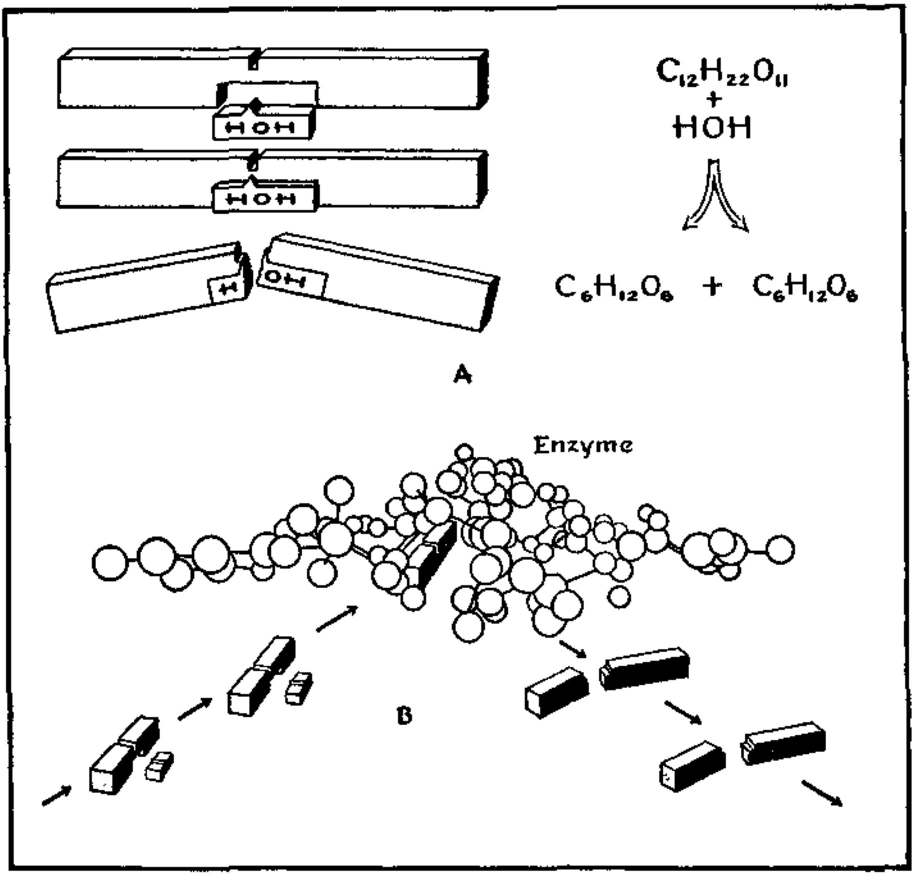


Fig. 7-1. In a hydrolytic reaction, a molecule of water splits into two parts as it brings about the splitting of a larger molecule (A). This process is hastened by a complicated protein molecule called an enzyme (B), which somehow makes more probable the proper juxtaposition of the two reacting molecules.

the nomenclature of the enzymes is not completely consistent, the modern practice is to make enzyme names by adding the suffix *-ase* to a root which indicates the substance upon which the enzyme acts. An enzyme which catalyzes the destruction of a protein is called a proteinase; or of urea, urease. The enzyme that catalyzes the splitting of sucrose is called *sucrase*. The reaction may be written:

$$C_{12}H_{22}O_{11} + H_2O \xrightarrow{\text{(sucrase)}} 2C_6H_{12}O_6 \qquad (9)$$

Reactions in which a molecule of water aids in the splitting of a large molecule into two smaller molecules are very common in biology. Such a reaction, in which water acts as a splitting agent, is called a **hydrolysis.** In Figure 7-1A, the probable nature of such a reaction is diagrammatically indicated.

How enzymes act is still one of the major mysteries of biological chemistry. An enzyme is always a huge molecule, with many of its atoms buried, so to speak, inside the molecule (see Fig. 7-1B). Other molecules come in contact only with the outer atoms of the enzyme molecule. The pattern of outermost atoms may be thought of as constituting the surface of the protein molecule. Much indirect evidence indicates that it is the structure of this "surface" that determines the compounds for which an enzyme can act as a catalyst. For purposes of visualization, we might imagine the enzyme to have a slight nook in it into which the reacting molecule can fit (Fig. 7-1B). Once in this position, the reactants can interact far more readily than they can ordinarily as free molecules. As soon as the reaction has taken place, the products break free and escape, leaving the nook for other molecules to occupy. An enzyme can bring about its characteristic catalytic reaction many thousands of times a second.

This picture of enzyme action, it must be admitted, is partly speculative. It does, however, fit the facts of enzymatic action as we know them today. It may not be an entirely true picture, but it will serve for the moment. Enzyme chemists often think in terms of this picture. Most students will find the facts of enzyme action easier to retain when visualized in terms of this picture.

There are many kinds of enzymatic action. Hydrolysis is not the only kind of reaction that is enzymatically catalyzed. However, it has been convenient to study it here because **all digestive processes brought**

about by the enzymes of the human digestive tract are enzymatic hydrolyses. The utility of these hydrolyses we shall see in the next chapter.

QUESTIONS AND PROBLEMS

7-1. Distinguish between a substance, in the chemist's sense, and a mixture.

7-2. Distinguish between organic and inorganic chemistry. How has the definition of organic chemistry changed in the last 200 years?

7-3. Two substances are made up of the same atoms in the same proportions. Is it possible for these substances to differ in their chemical properties? If so, can you account for the possibility of difference?

7-4. State a conspicuous chemical difference between fats and carbohydrates.

7-5. Will more or less O_2 be required to oxidize (burn) a pound of fat completely to CO_2 and H_2O than is required to oxidize completely a pound of sugar? Why?

7-6. Distinguish between an ion and an atom.

7-7. Write the reaction between nitric acid and potassium hydroxide. (The symbol for potassium is K.) Indicate ions correctly. What are the names of the products? To what class of substances does the more completely ionized product belong?

7-8. The *exact* name of an enzyme, according to the system described in § 49, is not always predictable, but the student should be able to make reasonably close guesses as to the names of the enzymes that attack the following substances: lactose, maltose, cellulose, lipids (fats), penicillin.

7-9. Analyze the word *hydrolysis* in terms of its roots.

7-10. From a student examination paper comes the following statement: "A catalyst is a substance that can bring about a reaction without entering into it."

What criticism can you make of this definition?

7-11. In terms of the picture of enzyme action developed in § 49, how would you account for the fact that enzymes are specific, that is, that each enzyme can catalyze the destruction of one, or at most a few, substances?

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Pauling, Linus, *General Chemistry.* San Francisco: W. H. Freeman & Co., 1947. (See especially Chaps. 1-4.)

Chapter VIII

The Digestive System

50. The Path of Food

Recall once more our equation of respiration:

$$\text{Food} + O_2 \longrightarrow CO_2 + H_2O + \epsilon \qquad (1)$$

In Chapter VI, we saw how oxygen was brought into the body, though we did not carry it as far as the cells where respiration takes place. In the present chapter, we propose to show how food gets into the body.

The path food follows is illustrated in Figure 8-1A. From the mouth, food passes through the pharynx into the **esophagus,** thence to the **stomach.** After considerable churning around, it moves on into the **small intestine** where much of the food passes from the intestinal cavity across the wall of the intestine and into the body itself. What remains in the intestine at the conclusion of this process goes into the **large intestine*** and, at intervals, leaves the body by way of the **anus.**

This, in brief, is the path of food through the body. But the story can be told still more briefly. Figure 8-1B is a simple yet, in a sense, accurate, picture of a man. Man may be said to be but an elongated doughnut. The hole of the "doughnut" is the gastrointestinal tract (G-I tract) or gut which, it happens, is differentiated into various parts: esophagus, stomach, etc. The upper orifice of the G-I tract is called the mouth; the lower is the anus.

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* Also known by its Greek name, *colon.*

This simplified view serves to emphasize the point that things within the G-I tract are not really inside the body. Is the saltcellar in Figure 8-1C *inside* the doughnut? Only in a trivial sense, a sense which we shall not consider further. Similarly, a piece of chicken in a man's stomach is not really inside the man.

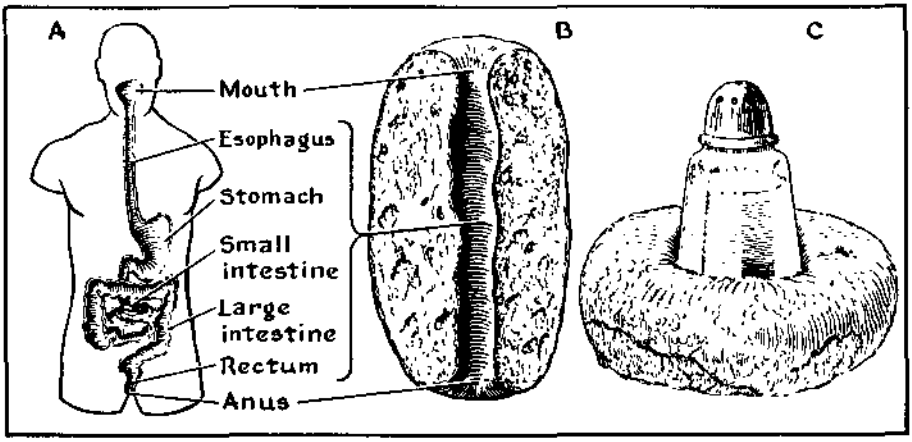

Fig. 8-1. Man (A) is an elongated doughnut (B). Things which are inside the hole of the doughnut (C) are not inside the doughnut.

This is a point of more than theoretical importance. The food that we take "into" the body *via* the mouth is not, at first, fit to enter the body. If, for instance, we should take this food, grind it up fine and inject it into the body proper (e.g., into the veins), the consequence would be a very sick man; death might even result. Even the finest menu is composed largely of substances that would be violently poisonous if taken directly into the body. Before they can safely be taken in, they must be considerably modified. The task of suitably modifying them falls to the G-I tract. The process takes place in stages, different parts of the tract specializing in different phases. We can best appreciate the division of labor by once more following food through the alimentary canal, this time at a more leisurely pace.

51. The Beginning of Digestion: The Hydrolysis of Starch

In the first stage of the preparation of food for digestion, it is cut into small pieces by the teeth. The utility of this action can be readily appreciated when it is realized that the digestive enzymes which will attack the food are initially on the outside of every food particle. To get at all the food molecules, the enzymes must diffuse through the gross particles of food. As pointed out in § 30, diffusion over a *ma*croscopic distance is very slow. When the size of the food particles is decreased in chewing, the distance the molecules of enzymes have to move to get to all the molecules of food is decreased. As a result, the speed with which contact is established between enzyme molecules and food molecules is increased; consequently, the rate of digestion of food by enzymes is increased.

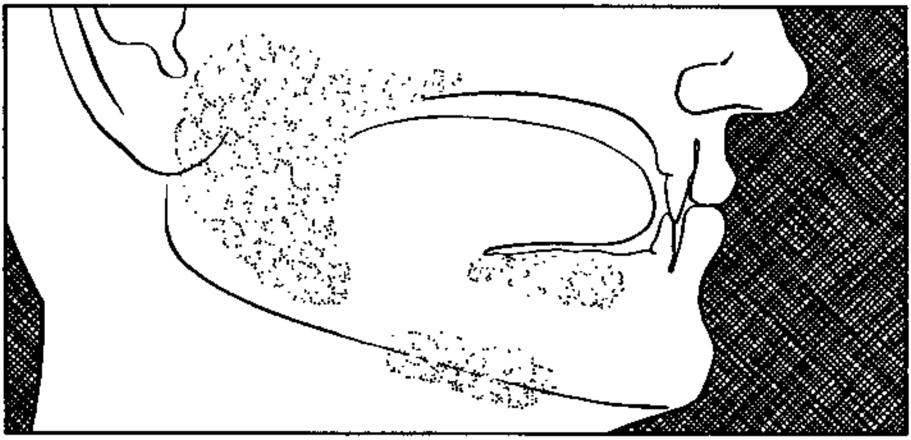

Fig. 8-2. The salivary glands occur in pairs. The location of the right member of each pair is shown above. The largest gland, the parotid gland, is the one whose infection by a virus causes the swelling known as "mumps."

But what is digestion? We may give a brief and simple answer: **digestion is the process of breaking large organic molecules into smaller ones, through the aid of hydrolyzing enzymes.**

The first step in digestion begins when food in the mouth is mixed with **saliva,** a viscous liquid produced by the salivary glands (Fig. 8-2). Saliva contains an enzyme named **ptyalin*** (Greek, spittle) which can catalyze the splitting of starch (a large carbohydrate) into smaller molecules of maltose (a sugar). We may state this fact thus:

$$\text{Starch} + H_2O \xrightarrow{\text{(ptyalin)}} \text{maltose} \qquad (2)$$

This is the first example of the hydrolytic digestion of foods that takes

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* Ptyalin, like many of the digestive enzymes, was discovered and named many years before the systematic way of indicating enzymes by the suffix *-ase* was developed (§ 49).

place in the G-I tract. We may generalize (2) into a formula that will describe the action of every digestive enzyme:

$$\text{Large organic molecule} + H_2O \xrightarrow{\text{(digestive enzyme)}} \text{smaller organic molecules} \quad (3)$$

It will be noted that the above equation says nothing about any energy changes. This omission was deliberate. Although there are energy changes involved in hydrolysis, they are negligibly small. We omit mentioning them in order to emphasize the fact that, practically speaking, *we derive no energy from the digestion of food.* The utility of digestion lies in the breaking down of large organic molecules into small organic molecules that can be more easily taken into the body.

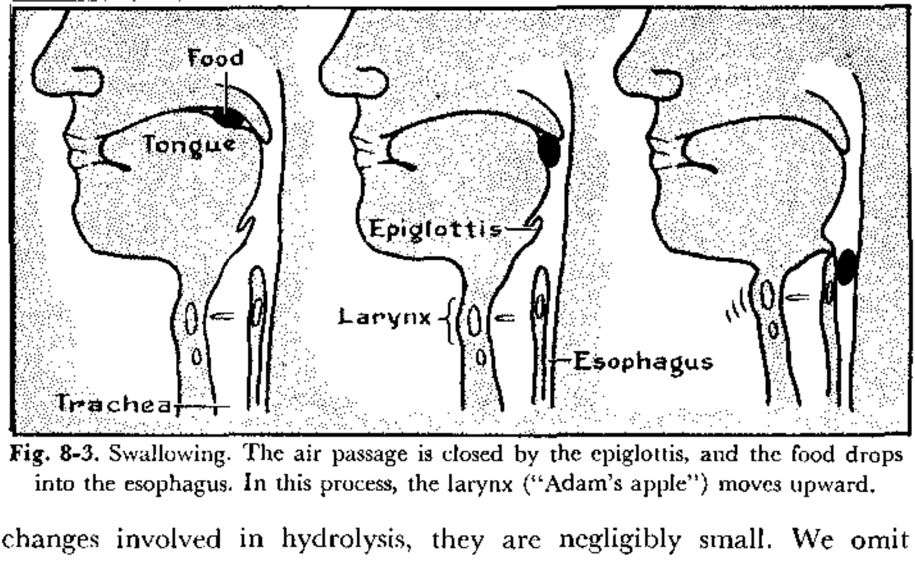


Fig. 8-3. Swallowing. The air passage is closed by the epiglottis, and the food drops into the esophagus. In this process, the larynx ("Adam's apple") moves upward.

52. Swallowing: Peristalsis

Saliva contains more than water and ptyalin; it also contains **mucin,** a slick material which covers the food particles, making them easier to swallow. After the food has been masticated suitably, a small lump of it called a **bolus,** (Latin *bolus,* lump) is moved to the back of the tongue and then swallowed. The process of swallowing is a complex one which we shall only partly describe. In Figure 8-3, it will be noted that a bolus coming off the back of the tongue has two paths open to it, the esophagus and the trachea. To insure its getting into the right opening, the entrance of the trachea needs to be closed. This closure is effected by a complex series of movements, the most prominent of which is the upward movement of the larynx, which can be observed readily from the outside. By its upward movement, the larynx crowds the opening against the epiglottis and other structures and thus prevents food from entering the windpipe—usually.

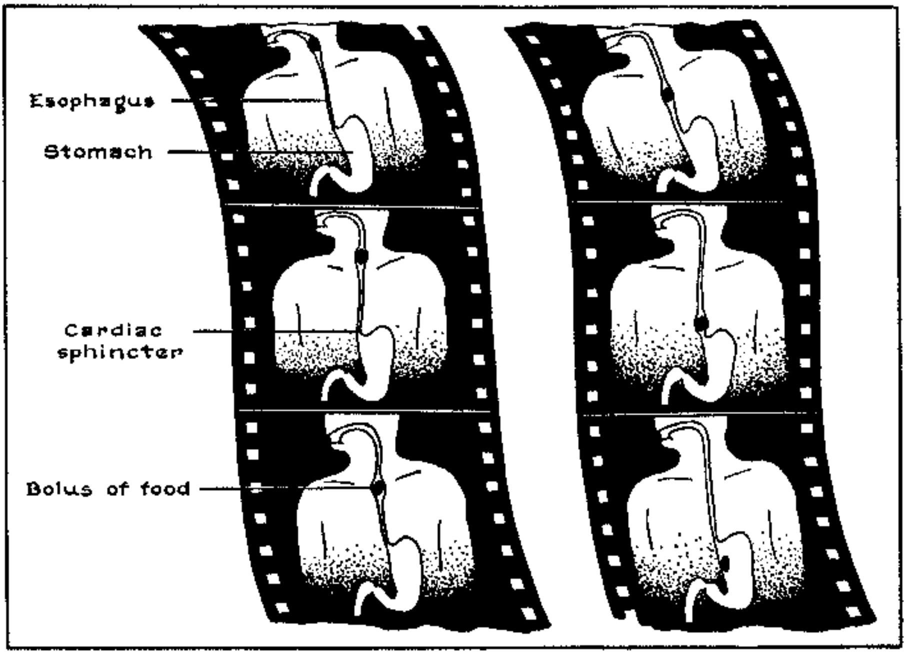


Fig. 8-4. Peristalsis. The circular muscles in the wall of the digestive tract (esophagus in this case) relax in front of the bolus, while the muscles behind the bolus contract. Thus is the lump squeezed along.

Once in the esophagus, the food moves rapidly to the lower end. Fluids move passively under the influence of gravity, but solids are helped along by a process called **peristalsis** (Greek *peri*, around; *stalsis*, constriction). The process can best be understood by studying Figure 8-4. Put into words, the process of peristalsis may be described as the movement of a wave of muscular relaxation along a tube (the G-I tract), followed by a wave of contraction. Since the bolus of food is just in front of the contracted area, it is moved along the tube in the same direction. The total time taken for a bolus to go from the upper to the lower end of the esophagus is, at most, a few seconds.

The esophagus produces no digestive enzymes.

53. Digestion in the Stomach: The Specificity of Enzymes.

From the esophagus, the food passes into the stomach. Here, slow churning movements mix the food with the **gastric juice** (Greek *gaster*, stomach) produced by cells lining the walls of the stomach. Gastric juice is a watery mixture of several substances among which the following should be noted:

Hydrochloric acid.

Pepsin, an enzyme that partially digests a miscellany of proteins.

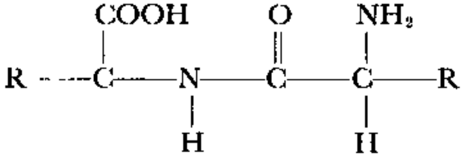
Rennin, an enzyme that partially digests, or at least alters, milk proteins.

An important characteristic of enzymes is their sensitivity to changes in acidity. Each enzyme works best at a particular acidity or alkalinity; if the environment changes markedly in this particular, the enzyme will no longer be active. Ptyalin, the salivary enzyme, works only in neutral or alkaline solutions. At the acidity of the stomach juice, ptyalin can no longer digest starch. Since food is so quickly swallowed, one might wonder if ptyalin has a chance to act. However, though the food is soon in the stomach, it is not immediately thoroughly subjected to the action of the stomach juice. It takes the acid, and other substances, some time to penetrate to the center of the mass of food, during which time the alkaline ptyalin does its work.

Another important characteristic of enzymes is their specificity. An enzyme is specific in two senses: it will act only on a specific substance or type of substances; and it carries out a specific breakdown of those substances. The substances an enzyme acts upon is called the substrate; the substrate of sucrase is sucrose, of ptyalin, starch.

The substrate of pepsin is proteins. There is an almost countless number of different proteins but, apparently, the similarities among them are great enough so that this one enzyme can attack most proteins. In a sense, one might say that this enzyme is not completely specific since it can attack so many different kinds of proteins; however, it is probable that the particular part of each protein attacked is the same in all cases. If so, we may say that this enzyme is specific.

As a result of proteolytic action, substances called peptides are produced. A carbon-to-nitrogen-to-carbon bond is called a **peptide bond,** or peptide linkage. Two amino acids united in this way make a compound called a *dipeptide.** As an example of such a compound:



$$\mathrm{R}{-}\overset{\overset{\displaystyle \mathrm{COOH}}{|}}{\mathrm{C}}{-}\underset{\underset{\displaystyle \mathrm{H}}{|}}{\mathrm{N}}{-}\overset{\overset{\displaystyle \mathrm{O}}{\|}}{\mathrm{C}}{-}\underset{\underset{\displaystyle \mathrm{H}}{|}}{\overset{\overset{\displaystyle \mathrm{NH_2}}{|}}{\mathrm{C}}}{-}\mathrm{R}$$

When many amino acids are thus united, the substances are called *polypeptides.* Polypeptides are the products of gastric digestion. Not until these substances are digested further, to amino acids, are the products of protein digestion absorbed into the body. Such complete digestion does not take place in the stomach.

Meat is largely protein. The stomach produces protein-digesting enzymes. The stomach, being meat, is itself protein. *Why does it not digest itself?* If, in asking, "Why," we are referring to purpose, the answer is obvious; it would be disadvantageous for the stomach to destroy itself. But if by "why" we mean, "What is the mechanism that prevents the stomach from digesting itself?", we must reply that we do not know. That this is more than an academic point is evidenced by the great frequency of stomach **ulcers.** An ulcerous stomach is one that, in one or more restricted places, *has* started to digest itself. The ulcer seems to be the result of the secretion of too much enzyme or of enzyme at the wrong time as, for instance, when the stomach is empty. The primary cause of an ulcer is not, however, to be sought in the stomach itself, but elsewhere, in the environment and the nervous disposition of the individual himself. Ulcers typically afflict individuals constantly subjected to "nervous tension," e.g., New York taxicab drivers.

54. The Eliciting of Pancreatic Juice by Secretin, a Hormone

The length of time food stays in the stomach depends on a number of factors: the kind of food, the quantity of food, and, perhaps, individual differences. Only a few substances, notably alcohol, are absorbed through the stomach wall into the body. The bulk of the food,

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* The student may find it an interesting exercise to see how the dipeptide could be derived through the union of two amino acids with the loss of a molecule of water.

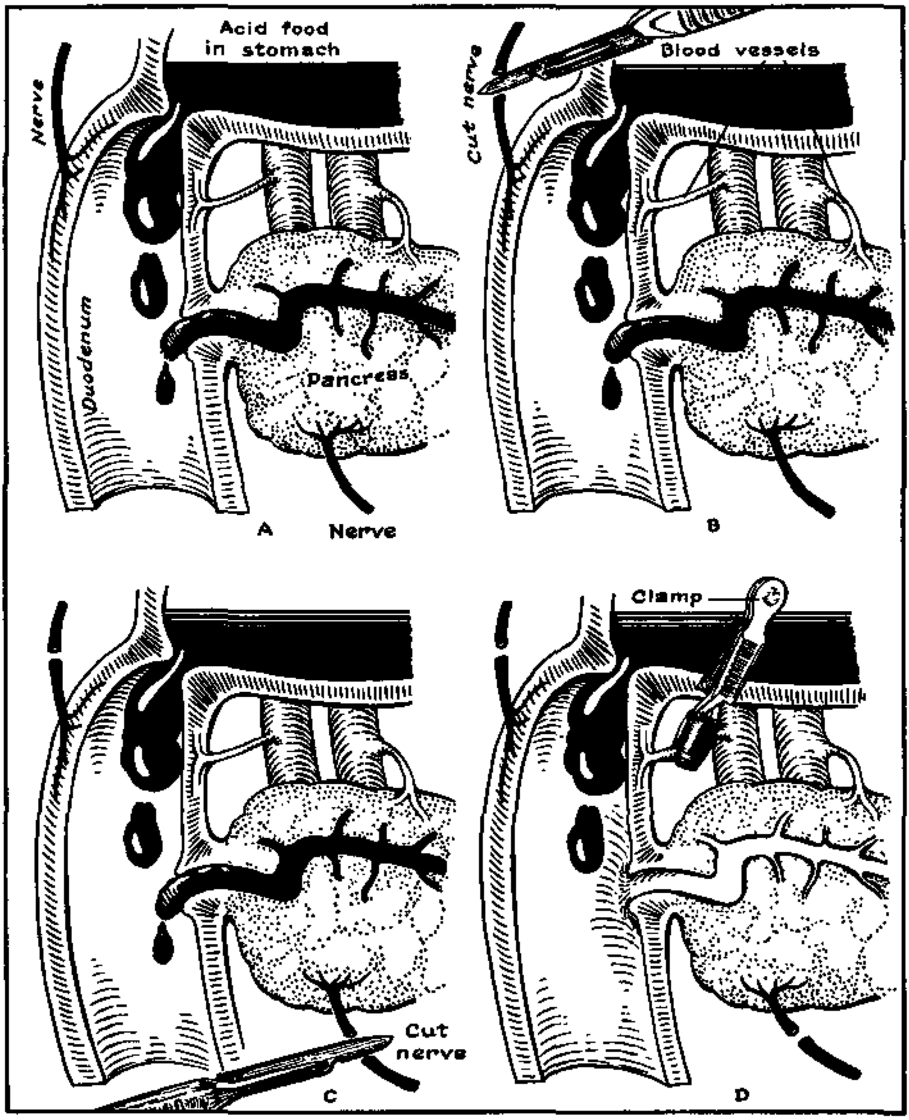

Fig. 8-5. Diagrammatic illustration of the experimental evidence for the hormonal stimulation of pancreatic secretion. When acid food from stomach enters duodenum (A), the pancreas secretes pancreatic juice. Cutting nerves attached to duodenum (B), or to pancreas (C), does not alter the response. But stopping the exit of blood from the duodenal wall prevents the passage of the "message," i.e., the hormone secretin, from the duodenum to the pancreas.

after being reduced to a uniform consistency by peristaltic and other movements of the stomach, passes on to the small intestine.

The lower end of the stomach can be squeezed closed by a ring of muscle. This closable region is called the **pyloric sphincter** (Greek *pyloros*, a gate keeper; *sphincter*, that which binds tightly). During much of the time that the food is in the stomach, the pyloric sphincter is closed tightly but, after an hour or so, it opens periodically and lets a squirt of fluid food enter the small intestine. This process continues until the stomach is emptied.

The first part of the small intestine is dignified by a special name, the **duodenum,** (Latin *duo*, two; *decem*, ten; so-called because in man the duodenum is about twelve finger-widths long). It is in this region that pancreatic juice, perhaps the most important of the digestive juices, is added to the food. The course of events leading to the addition of this juice is worth recounting.

It was early observed in experimental animals that when food moves from the stomach into the duodenum, the pancreas soon starts to secrete pancreatic juice which enters the duodenum by way of the pancreatic duct. It would be natural to assume that a message is sent by way of the nerves from the duodenum to the pancreas, "telling" the pancreas to begin secreting its juice (see Fig. 8-5A). However, a very simple experiment shows that this cannot be the case; when all the nerves leading to the pancreas are cut, the pancreas still secretes when food passes from the stomach to the duodenum (see Fig. 8-5 B,C). Clearly, messages are still getting through from the duodenum to the pancreas, but how? Under the conditions of the experiment, the only visible connection of the pancreas with the rest of the body is by way of the blood vessels. The most reasonable assumption is that some sort of message is being carried by the blood stream from duodenum to pancreas. That this is, in fact, the case can be shown by simply preventing the passage of blood from duodenum to pancreas, which can be done either by stopping the flow of blood *away* from the duodenum (Fig. 8-5D), or stopping the flow of blood *to* the pancreas.* Either experiment leads to the failure of the pancreas to respond to the presence of food in the duodenum. Evidently, the blood stream does, normally, carry a "message" from one organ to the other. Such a message-carrier, really a

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* The former experiment is the better one. Why? If you cannot answer this question now, you might keep it in mind to tackle later, after reading § 63.

substance dissolved in the blood stream, is called a **hormone** (Greek *hormao*, to stir up, to excite).

The full story is this. The food mass which comes from the stomach is strongly acid. The duodenum and small intestine are alkaline. The acid coming from the stomach stimulates certain cells which line the walls of the duodenum to produce a hormone called **secretin.*** This hormone enters the blood stream and is carried to all parts of the body. In most of the body, the hormone has no effect so far as we know. But the pancreas responds to the presence of secretin brought to it in the blood by secreting its pancreatic juice at an increased rate.

55. The Enzymes in Pancreatic Juice

The foodstuffs that we eat are made up of substances belonging to three different chemical classes: proteins, carbohydrates, and fats. Pancreatic juice contains enzymes which attack all three.† It contains several proteolytic enzymes, one of which is called **trypsin**; a carbohydrate-splitting enzyme often called **amylase**; and a fat-splitting enzyme, **lipase.**

The pancreatic enzymes continue the work begun by the enzymes of the stomach and mouth. Trypsin splits proteins into polypeptides which are later split by intestinal enzymes into amino acids which can be absorbed into the body. Amylase duplicates the action of saliva, digesting starch to disaccharides (C_{12} compounds like maltose, $C_{12}H_{22}O_{11}$) which will later be broken down to monosaccharides (C_6 compounds like glucose, $C_6H_{12}O_6$) by enzymes produced by the intestinal wall.

Lipase, the fat-digesting enzyme, is aided by other juices. One of the many functions of the liver is the production of **bile** which enters the small intestine via the bile duct. Bile helps in the digestion of fats, but *it is not an enzyme.* It has a soaplike action; it causes the large fat globules, consisting of many molecules, to break down into very small ones in which, however, the constituent molecules are unchanged. These

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* We cannot too strongly urge the necessity of careful reading; secret*in* and secret*ion* are not synonymous terms. The careless reader often confuses them.

† The word pancreas is derived from Greek *pan*, all; *creas*, flesh; the reference is presumably to the fact that this organ is all flesh, with no bone in it. In view of what we now know about its secretion, the name seems doubly apt for its secretions attack all three kinds of flesh or food.

small globules can remain suspended in water. Bile is said to *emulsify* fats. When fats are thus finely dispersed, they are more susceptible to the action of the pancreatic enzyme lipase.* The end products of lipolytic action are glycerine and fatty acids (R-COOH) which can be absorbed through the intestinal wall.

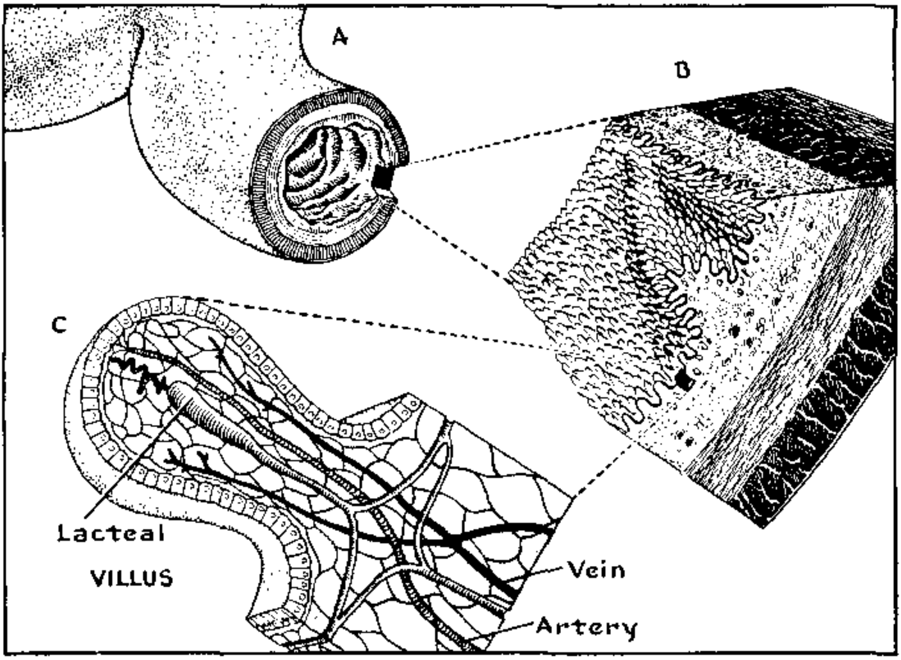

Fig. 8-6. The wall of the small intestine (A) is lined with thousands of tiny villi (B), each of which has the structure shown in C.

56. Other Digestive Enzymes

The cells of the small intestinal wall produce various enzymes which hydrolyze proteins and carbohydrates, although, apparently, lipolytic enzymes are not produced. The large intestine, as far as we know, produces no enzymes at all.

In trying to assign credit for the breakdown of foodstuffs in the intestines, the presence of millions of bacteria complicates study. Bacteria produce hydrolytic enzymes, too, and these unquestionably play a role

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* It is possible that the stomach also produces a lipase, but this is not yet firmly established.

in the breakdown of organic material in the gut. In man, digestion could take place perfectly well without bacteria, so far as we know. In some other animals, however, intestinal bacteria seem to be essential. Cellulose, the woody material of plants, is a type of carbohydrate almost completely indigestible by man. Cows, horses, and termites, however, get an appreciable portion of their nutriment from cellulose. It has been shown that the gut of these animals swarms with bacteria and other microorganisms that produce cellulose-hydrolyzing enzymes. The host animals (as well as the microscopic guests) benefit from the action of these enzymes.

57. Absorption of Food

The wall of the small intestine (Fig. 8-6A), when examined under a microscope (Fig. 8-6B), is seen to be composed of millions of little fingerlike projections pointing into the cavity. These tiny fingers are called **villi** (singular *villus*, Latin, shaggy hair). The villi, when cut lengthwise, exhibit the structure shown in Figure 8-6C. It should be noted that each villus contains vessels designated by two different names: blood vessels and lacteals. The function of the blood vessels will be taken up first.

The end products of protein digestion are amino acids. The end products of carbohydrate digestion are monosaccharides, simple sugars. Products of both these classes are soluble and readily pass through the walls of the villi to the blood vessels. In the blood vessels, of course, the blood is in continuous motion due to the pumping of the heart. Dissolved in the blood stream, the amino acids and sugars are carried to other parts of the body, a process which we will follow in Chapter IX.

The absorption of the products of fat digestion is a different story. If a fasting animal or one fed a low-fat meal is killed and opened, the lacteal vessels are rather inconspicuous. If, however, an animal which has recently been fed a meal rich in fats is opened, the lacteals are readily seen as swollen, milky channels. The name **lacteal** is derived from Latin *lactis*, milk, and refers to its appearance, not to its contents. Microscopic examination of the contents reveals small droplets of material which can be chemically identified as fatty in nature.

How do fatty materials get into the lacteals? There appears to be no fat in the epithelium of the intestinal villi. Following a fatty meal, the presence of fatty acids and glycerine, produced by the hydrolysis of fats by lipase, can be demonstrated in the intestine. Concomitantly, fat droplets appear in the lacteals of the neighboring villi. Presumably, fatlike materials pass through the villous epithelium in the form of fatty acids and glycerol and, once inside, are resynthesized into fats which are carried away by the lacteals. This seems to be a reasonable presumption, though it has not been completely proved.

The lacteals are part of a second circulatory system, the so-called **lymph system** (Latin *lympha*, clear water). This system has no well-developed pump (such as the heart) but depends on the squeezing movements of the surrounding tissues for the movement of the fluids. Microscopic examination of living intestine shows the villi to be in constant motion, weaving back and forth and pumping up and down. The movement of the villi probably helps in stirring the intestinal contents, thus aiding absorption; it undoubtedly helps to alternately squeeze and relax the lacteals, thus forcing the contents on. Ultimately the lymph system joins with the blood system, the lymph entering the blood stream by a vein near the heart.

58. Purposes of Digestion

At this point, it might be well to ask, "What is the purpose of digestion?" The most obvious purpose of digestion is to make molecules more soluble so that they can diffuse through the wall of the intestine and so enter the body. But there is another function which digestion serves, a function hinted at previously.

Every kind of organism contains a great many specific chemical compounds that are found nowhere else. *This is particularly true of the proteins.* The cells of a cow are made up of proteins, some of which are found in no other animal; we might call them cow proteins. Similarly, a horse is made of specific horse proteins and a human of specific human proteins.

Proteins themselves are made up of amino acids which, with rare exceptions, are not peculiar to particular kinds of organisms. The amino acids of a horse are the same in kind (though not in proportions) as those of cows, men, monkeys, worms; or, for that matter, trees, mosses, and bacteria.

In general, one kind of organism cannot use the proteins of another to build up its own substance. A human cannot use cow protein to build up human flesh. But the amino acids from hydrolyzed cow proteins are the same as those that compose human proteins. Cow amino acids can be used to make human flesh. The proportions of the various kinds may not be quite right, but that does not matter. The surplus amino acids can be burned as fuel or discarded as waste.

Cow proteins, injected directly into a human's blood stream, would cause a violent reaction, perhaps death. Cow amino acids, on the contrary, would furnish him food. In fact, the injection of pure amino acids is used as a method of feeding invalids when conventional methods of feeding are impossible or inadvisable.

Amino acids are the most important building blocks of all animals and plants. One of the principal purposes of digestion is to reduce the buildings of other animals and plants to their building blocks to the end that the eater may build up his own tissues from the disassembled building blocks of the eaten.

Exceptionally, some proteins may be absorbed in their original state. Such absorption evidently contributes to food sensitivities. To take but one example, some people are sensitive or *allergic* to eggs; that is, when they eat eggs, they develop any of a number of unpleasant symptoms ranging from hives to complete prostration. It can be shown that the egg substance that evokes such allergic responses is protein in nature. The constituents, amino acids, are not harmful. This must mean, then, that such egg proteins diffuse *as proteins* through the intestinal wall, contrary to our general picture of digestion and absorption. The tendency to show allergic reactions is unquestionably inheritable and *may* depend partly on inherited differences in the intestinal epithelium, though undoubtedly other factors are involved, too.

59. Function of the Large Intestine

The intestinal food mass enters the large intestine in a fluid state; when it leaves, by way of the rectum and anus, it is solid. The change in state is brought about by absorption of water through the walls of the large intestine into the body. Since much of this water originally came from the body, we speak of the *re*absorption of water.

Reabsorption of water is the principal function of the large intestine. There is undoubtedly some absorption of food materials here, but it is probably of secondary importance. There is no evidence of the production of enzymes by this part of the gut.

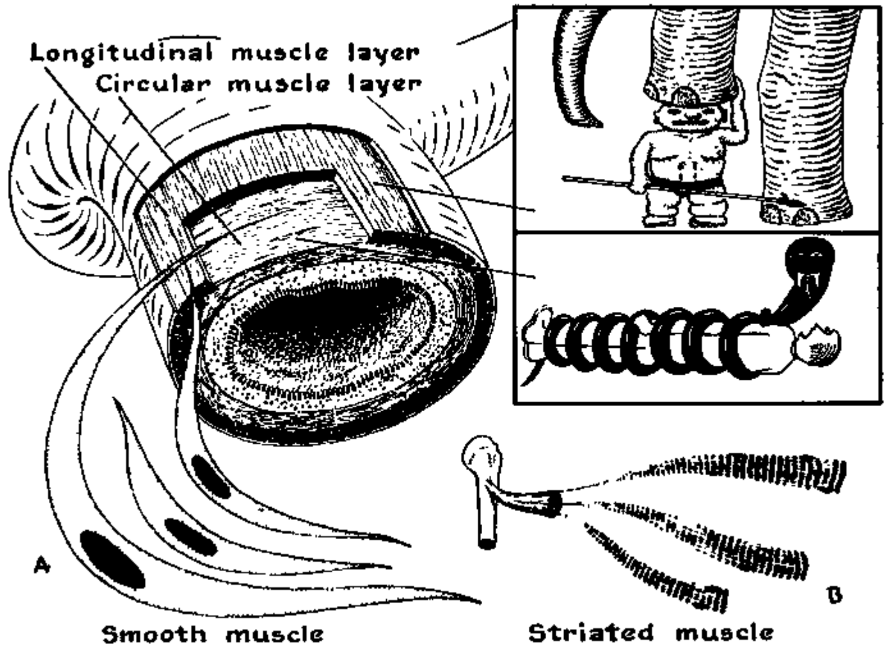

Fig. 8-7. The muscles of the gut are composed of smooth muscle cells (A), in contrast to the striated muscles (B) present in all the skeletal (voluntary) muscles. The figure shows how the contraction of the circular muscles will lengthen the intestine and contraction of the longitudinal muscles will shorten it.

At the end of its journey through the large intestine, the mass is now fairly solid and is known as dung or **feces** (Latin *faeces*, dregs). This material is passed at intervals into the last part of the G-I tract, the **rectum.** The presence of feces in the rectum leads to characteristic sensations and the desire to defecate.

Infrequent* or difficult defecation is called **constipation.** The causes

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* "Normal" rate of defecation is once a day. But there is great individual variability. For some, one evacuation in two or three days may be normal. More important than the infrequency are the other symptoms of constipation: foul breath, headache, depression, irritability, etc.

are many; poor health, poor diet, and "nervous tension" are chief among them. At least one adult in five in the United States experiences constipation most of the time, and about half of these take laxatives regularly. Laxatives, however, when repeatedly taken, tend to lose their efficacy and, hence, are a questionable, or even dangerous, solution to the problem of constipation, which is better attacked by partaking of a sensible diet or by changing one's way of life so as to remove the source of nervous tension.

60. Intestinal Movement: Smooth Muscle

Earlier, we mentioned the phenomenon of peristalsis as it occurs in the esophagus. Peristaltic movements, as well as other movements of a more random sort, occur throughout the digestive tract and serve to churn the food and mix it with the digestive juices.

Movements of the intestine are made possible by the action of two different muscle layers to be seen in Figure 8-7A. The muscle fibers in both layers are oriented in a helical fashion; but the muscle cells of the outer layer are oriented almost parallel to the length of the intestine, and this muscle layer is, therefore, called the **longitudinal muscle layer.** Bearing in mind that when muscle fibers act, they shorten their length, it will be seen that the contraction of longitudinal muscles will shorten the length of the intestine. The inner layer is composed of cells oriented almost at right angles to the axis of the intestine; this layer is called the **circular muscle layer.** Contraction of this layer will constrict the diameter of the gut and, hence, increase the length. By the varied cooperation and antagonism of these two layers, a variety of movements can be imparted to the intestine.

The muscles of the intestinal wall are different from the skeletal muscle discussed earlier (§ 24). One of the conspicuous features of skeletal muscle is the presence of striations (Fig. 8-7B); these are absent in intestinal muscle. In fact, the muscles of most of the **viscera** (Latin, entrails) are of this kind, called **smooth muscle.** Smooth muscle has no striations and cell membranes definitely delimit each cell, each of which has only one nucleus.

Physiologically, there are great and significant differences between smooth and striated muscle. Striated muscle is capable of very rapid contraction but it fatigues easily; smooth muscle is slow to contract and slow to relax and it can remain contracted for long periods of time without fatigue. Striated muscle does its owner's bidding—it is "voluntary muscle"; smooth muscle almost seems to have a mind of its own and is called "involuntary muscle."

Bearing these differences in mind, one can predict with almost complete accuracy where each kind of muscle will be found on the gratuitous and unjustified assumption that need determines presence. All the muscles which move the bones of the body are striated, for movements of the skeleton must be quick and subject to voluntary control. On the other hand, we need not concern ourselves with the movements of the viscera. Quite often, such movements must be long continued. The intestinal muscles, for instance, are almost constantly at work. Correlated with these needs, we find that visceral muscles, with few exceptions, are smooth muscles.*

61. The Length of the Gut, and the Function of Blind Ends

Earlier (§ 50), we urged that, as regards the structure of the gastrointestinal tract, man can be regarded as an elongated doughnut (Fig. 8-8A). Yet, it is clear that this view of man is oversimplified. The gut is not a straight tube running from mouth to anus, a distance of only about two and one-half feet. The representation of Figure 8-8B is more nearly correct, the length of the gut being twenty-five or more feet. There is considerable individual variation. Why this great length? What use is a G-I tract that is ten times as long as it needs to be to reach from one orifice to the other?

Recall that digestive juices are secreted by the walls of the stomach and intestine (neglecting, for the moment, the special secretions of the liver and pancreas) and that absorption takes place through the wall of the small intestine. One would suspect, therefore, that the more wall, the greater the opportunity for the secretion of enzymes and for the absorption of food products. A gut which ran straight from mouth to anus would be too short to allow much digestion and absorption of food. At least, so much seems reasonable, although there is no experimental proof of it.

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* The heart, however, is made of yet a third type of muscle called *cardiac muscle.*

The idea that the shape of the gut may be adapted to the purpose of allowing enough time and surface for digestion and absorption helps explain another phenomenon, the existence of blind ends. The gut of a rabbit (Fig. 8-8C) has a very large blind end called a **caecum** (Latin *caecus*, blind). Material that enters this blind alley undoubtedly takes longer to traverse the entire tract; it is, therefore, longer subject to the process of digestion. It has been observed that caeca are most common and best developed in those animals that live on the most difficult-to-digest food, such as grass and other roughages, which contain much cellulose, a material considerably more resistant to digestion than starch.

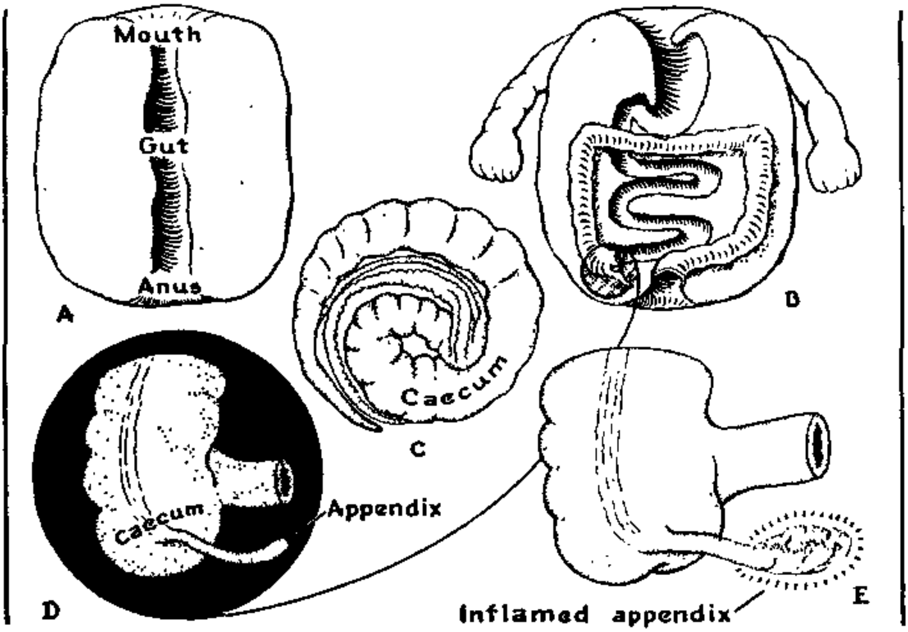

Fig. 8-8. Man's form is essentially that of a doughnut (A), but with the central tube lengthened (B), thus furnishing more surface for absorption. The gut of herbivorous animals has a conspicuous blind end called a caecum (C); the caecum of man is small, but it has an appendix (D), which frequently becomes irritated by bacteria which have stagnated therein (E).

Man has a rudimentary caecum (Fig. 8-8D) indicating, perhaps, his evolutionary descent from earlier beings which fed more on herbs. Noteworthy is the smaller continuation of the caecum, the **appendix.** Just as it does in other blind ends, food often stagnates in this one with consequent increase in bacterial action. Sometimes, the bacteria "go too far" and attack the wall of the appendix itself, inflaming it (Fig.

8-8E); this we call **appendicitis** (from the Greek *itis*, inflammation). *Clinical* records indicate that, at one time or another, about one per cent of the population suffers from appendicitis. *Post mortem* examination of many appendixes reveals that scarcely ten per cent are what the histologists would call normal, indicating that about ninety per cent of the population have a "*subclinical*" (Latin *sub*, meaning under, below, or almost) case at some time. Only about one in ninety inflammations reaches the clinical level of seriousness. Frank cases of appendicitis tend to occur in some families more than in others. The why is not known. An occasional fortunate individual has no appendix at birth.

62. The Nutrition of Man

Man seems to thrive best on a varied diet. Analyses of healthful diets show that they include materials that fall into the following categories:

1. Water.
2. Inorganic salts.
3. Roughage.
4. Carbohydrates.
5. Fats.
6. Proteins.
7. Vitamins.

Although the above categories are not all mutually exclusive, they are convenient ones to adopt for further discussion.

How necessary are the various types of foodstuffs? Everyone knows that water is the most essential of them all and can be least safely omitted, even for a short period of time.

Inorganic salts are also indispensable but need not be taken in everyday. A dozen or more elements are required for normal health, among them being phosphorus, potassium, sulfur, magnesium, calcium, iron, iodine, and copper. The function of some of these is known in part. Iron is a component of the hemoglobin molecule of the red blood cells (§ 69); copper is required in the production of hemoglobin; calcium and phosphorus are needed to make bone, and iodine is required for the normal function of the thyroid gland. Many of the inorganic salts are required because their elements are constituents of organic enzymes. In general, the quantities of the elements required are so slight that almost any diet made of natural foods supplies all the inorganic salts needed. To this generalization there are a few exceptions. Calcium, the principal constituent of bone, is required in rather large quantities, especially in growing children, hence, the importance of milk. Iodine is deficient in the soils of certain regions, e.g., the Great Lakes region of the United States, and hence, the plants and animals (including fish) of the region do not supply enough of the element for man's needs. This deficiency is easily made up by the intake of "iodized salt."

A varied diet composed of natural foods includes adequate "roughage." By roughage, is meant food that is relatively indigestible. Such food passes all the way through the alimentary canal unabsorbed. In the large intestine, it acts, by virtue of its bulk and mildly irritating action, to stimulate peristalsis and, thus, to prevent constipation. Vegetable products which contain much cellulose and other large and indigestible molecules are the principal sources of roughage. Whole wheat bread and bran are good roughages. In passing, it might be noted that the intake of this class of foods can be overdone; too much bran, for instance, may be irritating to the delicate membranes of the intestinal tract.

Most of the food that we consume serves the purpose of furnishing us with energy (recall the equation of respiration). The organic foods that supply this energy can be divided into carbohydrates, fats, and proteins (see § 46). Their breakdown products are sufficiently similar and our synthetic abilities are sufficiently great, so that, for the most part, these substances are interchangeable in our diet. However, only one of them is theoretically capable of supplying the large majority of man's food needs, namely, protein. This is the only one that has nitrogen in it. All living material is composed of proteins, which contain nitrogen bound in organic molecules. To maintain our cell proteins, we must continuously take in organic nitrogen in the form of proteins or their breakdown products, amino acids. Proteins (or amino acids) are, therefore, the only one of these three types of foodstuffs that are completely indispensable.

In addition to these kinds of foodstuffs, there is one other class which, as everyone now knows, is essential to life, namely, the vitamins. If an animal is fed a "synthetic diet" of highly purified carbohydrates, amino acids, water, and inorganic salts, the animal languishes and

TABLE 8-1

VITAMINS OF THE GREATEST PRACTICAL IMPORTANCE IN HUMAN NUTRITION, AND THE CONSPICUOUS MANIFESTATIONS OF THEIR DEFICIENCIES

NAME	GOOD SOURCES	EFFECTS OF SEVERE DEFICIENCY IN MAN
*Vitamin A	Fish liver oils, butter, eggs, yellow vegetables	Night blindness
Thiamine (Vitamin B_1)	Yeast, whole grains, meats	Beriberi, a nervous disease
Riboflavin (Vitamin B_2)	Approximately as above	Various skins ailments, and photophobia
Pyridoxin (Vitamin B_6)	Approximately as above	Not certain in man. (Anemia in dogs and pigs.)
Niacin (Nicotinic acid)	Approximately as above	Pellagra
Ascorbic acid (Vitamin C)	**Fresh** fruits and vegetables, particularly citrus fruits	Scurvy
*Vitamin D	Fish liver oils, eggs, irradiated milk	Rickets. Abnormal calcium and phosphorus metabolism
*Vitamin K	Widely distributed in plants	Prolonged clotting time of blood

* Indicates fat-soluble vitamins, that is, ones that are soluble in fat solvents such as ether, alcohol, chloroform, and toluene. All other vitamins are water-soluble.

perishes, even though it has been given enough food to supply all its energy needs. The addition to the diet of minute amounts—less than one-hundredth of one per cent by weight of the total food—of the substances we call vitamins renders such a highly purified diet adequate to sustain health and life. What do the vitamins supply that the rest of the diet lacks? Why do we need them? How can we plan our diet so as to include them?

Anticipating what will later be treated in more detail, we may point out that vitamins are part of cell enzymes. We need them because the enzymes are important. Most of our enzymes we ourselves can easily make from simple foods. But for a few of our enzymes, we must take in large, prefabricated units of the enzymes; these are the vitamins.

There are four different ways in which we might discuss vitamins: from the point of view of—

a. The medical man.
b. The biological researcher.
c. The professional nutritionist and dietitian.
d. The housewife and layman.

The medical man views vitamins primarily as things the absence of which causes specific, conspicuous illnesses, such as night blindness (vitamin A), neuritis (the B vitamins), scurvy (vitamin C), rickets (vitamin D), and failure of blood to clot (vitamin K). (See Table 8-1.) The research man looks upon vitamins as crucial building stones in the cells' architecture and tries to find out what they are doing there. The dietitian's concern with vitamins is a detailed quantitative one; the man or woman in charge of making up menus for a hospital or other large institution must weigh and count and consult tables that give the vitamin content of various foods, while keeping one eye on the budget, in order to make sure of getting enough vitamins into the regimen without running over the monetary allowance.

We will put aside all of these viewpoints for the present and, instead, adopt that of the housewife or other layman. What should the man in the street know about vitamins? What can he learn that he can carry with him and use in his daily life? Detailed tables of vitamin-content-per-pound for various foods are not for him or for the housewife because our daily life is not run on such a quantitative basis. What most of us need are a few simple generalizations to guide us. The following statements are suggested as things worth remembering.

1. *Vitamins are required for normal health.* An **avitaminosis***, if profound, may cause conspicuous symptoms—such as night blindness. A slight avitaminosis, however, may cause only slight symptoms, not always the same. The cause of such slight derangements can be deduced only by medical men skilled in diagnosis. Since a slight avitaminosis is much more common that the decided ones, the layman had best play safe by trying to make sure that his diet is adequate, without attempting any diagnosis.

2. *From a practical point of view, we need remember the facts only about vitamins A, B, C, and D.* Any natural diet sufficient to sustain life at all is almost certain to furnish plenty of the other vitamins, so we need not concern ourselves with them.

3. *Vitamin A is a breakdown product of an orange-colored plant pigment, carotene.* This pigment is present in all green plant tissues, its color being masked by the green pigments. The most likely place to look for it in abundance is in plant tissues that are yellow, orange, or red, e.g., in carrots and in the skin of tomatoes and apples. Color is not a proof of its presence, for carotene is not the only orange plant pigment; but, in the absence of a chemical laboratory, color is a fair indication. Animals that feed on fresh green plants may accumulate vitamin A and transmit it through such products as eggs and butter. Margarine naturally has none in it, but the manufacturers add it in copious amounts. (Incidentally, vitamin A itself is colorless.)

4. *The B vitamins are particularly abundant in high-protein foods.* Meat, liver, yeast, nuts, and whole grains are good sources. There are many distinctly different chemical substances, e.g., thiamine, niacin, collectively referred to as the B vitamins or the B complex. The chemist distinguishes them, but the layman need not; food that is rich in one is usually rich in the others.

5. *Vitamin C (ascorbic acid) is abundant in fresh, acid fruits.* Citrus fruits are particularly good sources. Vitamin C is also found abundantly in many fresh, uncooked vegetables. It is very readily destroyed by

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* Greek *a* means not, lack of, negative. Greek *osis* is a suffix used to indicate a disease, or condition.

heat. Vegetables lose most of their ascorbic acid within a few days after picking.

6. *Vitamin D is found in irradiated fats.* When animal fat is exposed to ultraviolet light (present in sunlight that hasn't had to pass through window glass or heavy smoke), some of the fatty chemicals are changed to vitamin D. One may get one's supply by exposing oneself to the sun or by consuming milk or other food that has been exposed ("irradiated") to ultraviolet light. Vitamin D is one of the few vitamins for which there is a practical danger of overdosage. Medical council should be sought in case of doubt.

7. *Daily intake is better than sporadic intake.* This is particularly true for ascorbic acid which apparently is not stored to any appreciable extent. Vitamin D, however, needs to be supplied only infrequently, particularly to adults.

8. *The more food eaten, the more vitamins required.* This is particularly true for the water-soluble vitamins. Under starvation conditions, the vitamin needs decrease.

9. *Tissue formation requires more vitamins than tissue maintenance.* New tissue is being formed very rapidly in children of all ages. Consequently, children and pregnant women have high vitamin needs. Following injuries or operations, the vitamin requirements may increase for the same reason.

All of this information can be summarized in a brief bit of advice: We should "go easy" on the carbohydrate foods (bread, potatoes, etc.) which supply many calories and few vitamins; and eat as much fresh fruits, fresh vegetables, and fresh meats as our situation and our pocketbook allow.

QUESTIONS AND PROBLEMS

8-1. Trace the path of food from mouth to anus, naming the parts of the G-I tract in order, telling what enzyme acts in each region, where the enzyme is produced, what sorts of food it acts upon, and what the digestive products and their route of absorption into the body are. It may be convenient to organize this information into a table.

8-2. When a man eats, his "Adam's apple" bobs up and down at intervals. Explain the significance of this laryngeal agitation.

8-3. From the knowledge of etymology already gained, the student should be able to deduce the meaning of the following words at sight: gastritis, laryngitis, colitis, tonsillitis.

8-4. Maltose, $C_{12}H_{22}O_{11}$, and sucrose, $C_{12}H_{22}O_{11}$, are both called disaccharides. Glucose, $C_6H_{12}O_6$, and fructose, $C_6H_{12}O_6$, are monosaccharides. By putting together various bits of information found in the text, the student should be able to deduce the molecular formula of a trisaccharide.

8-5. What is a polysaccharide?

8-6. How is lymph kept circulating through the villi? How is blood circulated?

8-7. What is an enzyme? What are its characteristics?

8-8. How does the anatomical construction of the gut make for a large absorptive surface?

8-9. *Achlorhydria* is an abnormal condition in which the stomach fails to secrete any hydrochloric acid. As a consequence, the food mass in the stomach is usually alkaline. As further consequences, what enzyme would fail to work, and what other enzyme should be active for a longer time than usual?

8-10. In *obstructive jaundice*, the bile duct is plugged with gallstones and, consequently, bile cannot reach the small intestine. As a result, the digestion of one of the three great classes of foodstuff is interferred with. Which one? Why?

8-11. Consider these two statements:

a. The blood stream carries secretin from the duodenum to the pancreas where it stimulates the production of pancreatic juice.

b. The blood stream carries secretin to all parts of the body including the pancreas which it stimulates to produce pancreatic juice.

Which is the better statement? Why?

8-12. An oxidizable organic compound with few oxygen atoms per molecule yields more energy on oxidation than does an oxygen-rich compound. Neglecting all dietary considerations except that of energy needs, *if* a pound of lard and a pound of potatoes cost the same, which would be the better bargain? (If stumped, see § 46.)

8-13. Why is a change of occupation often of more value than the taking of medicine in the treatment of ulcers?

8-14. What chemicals, or classes of chemical substances, should be included in a complete and well-balanced diet for man? Which classes supply the energy needs of man?

8-15. What role does "roughage" play in man's diet?

8-16. What are the principal vitamins needed in the human diet? Give some simple, easy-to-remember rules that should help a man keep alive and healthy under conditions of disaster.

Chapter IX

The Circulatory System

63. Its Primary Function: Transport

Recall once more the equation of respiration:

$$\text{Food} + O_2 \longrightarrow CO_2 + H_2O + \epsilon \qquad (1)$$

The process of respiration takes place in all the cells of the body, but the raw materials required for respiration enter only at certain portals. To get these materials from the lungs and the gut to all parts of the body, some method of transport is required. Such transport is accomplished by what we call **the circulatory system** of the body, which consists of the heart, the blood vessels (arteries, capillaries, veins), and blood, the fluid circulated through these channels. The lymph and lymph channels may also be considered part of this system (see § 71).

At the outset, it is important to realize that, with but few exceptions, the blood flows in definite channels and in a definite direction, whatever part of the body it is in. The blood does not simply ooze and slosh around between the cells. A circulatory system of this sort is called a **closed circulatory system** and is characteristic of all the so-called higher animals.

A closed circulatory system is made up of three types of vessels: arteries, capillaries, and veins. These vessels differ significantly in structure, but of primary importance are their functions.

By definition, **an artery is a vessel that carries blood away from the heart; a vein is a vessel that carries blood toward the heart.**

And what of the capillaries? To understand their relation to the other vessels, let us follow the blood as it circulates through the system as diagrammatically represented in Figure 9-1. The blood leaving the heart is at first enclosed entirely in one large artery, the **aorta,** but this soon divides into smaller arteries; these subdivide further repeatedly until finally the blood is flowing in vessels so fine that they can be seen only with a microscope, though only moderate magnification is needed. These tiny vessels are called **capillaries** (Latin *capillaris*, hairlike). The multitude of them is scarcely imaginable. Every cubic inch of the body is penetrated by a network of thousands of these tiny vessels. Their role in the final stages of getting oxygen and food from the blood to the body cells will be discussed later (§ 69 and § 71; Fig. 9-6B).

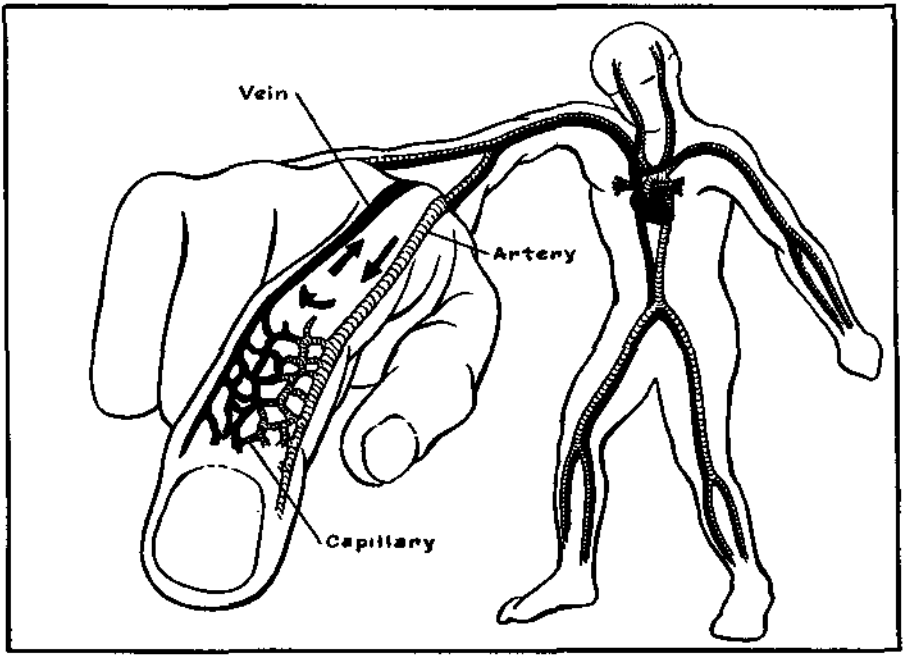

Fig. 9-1. The relations of arteries (light), capillaries, and veins (dark).

The length of an individual capillary is not very great; perhaps one-fiftieth of an inch would be typical. The capillaries, which might be regarded as the final divisions of the arteries, themselves unite to form the first small veins (Fig. 9-1). These veins in turn unite repeatedly to form larger veins until, in man, the blood returning to the heart is all in two veins—the **superior vena cava,** bringing blood from the upper regions of the body, and the **inferior vena cava,** coming from the lower.*

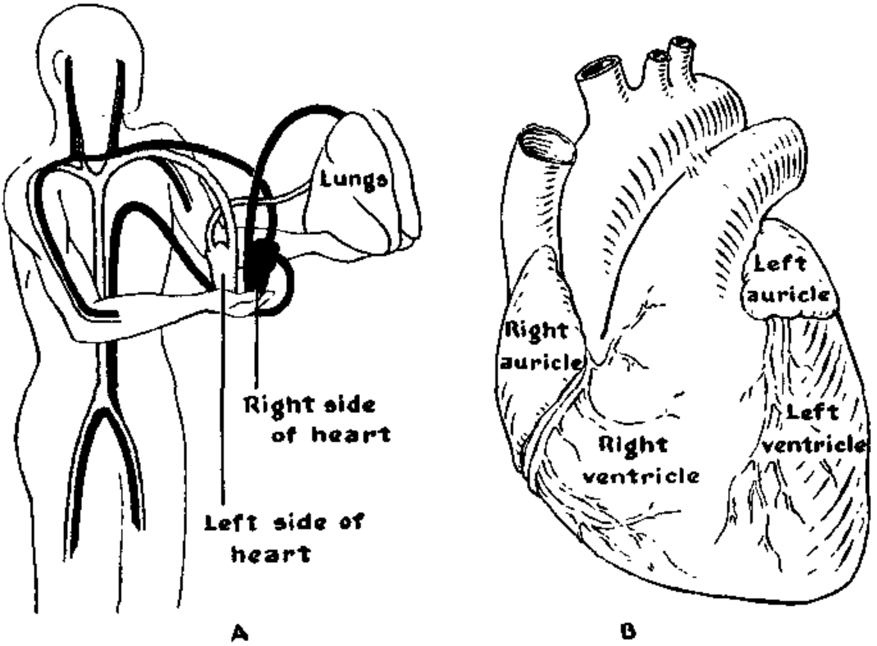

Fig. 9-2. The heart is really two pumps (A), the right one of which supplies the lungs with blood, while the left one supplies the rest of the body. Vessels carrying oxygen-poor blood are dark; vessels with oxygen-rich blood are light. In B is a realistic view of the heart.

64. The "Circulations" of the Body; Systemic and Pulmonary

The threefold system, arteries-capillaries-veins, is often spoken of as a "circulation system" or, more briefly, as a "circulation." There are several such systems in the body. The one which involves most of the body is called the **systemic circulation.** Implicitly, it is the one de-

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* Latin *cava,* cave, or hollow place; Latin *vena,* vein. *Superior* and *inferior* mean higher and lower, respectively; in anatomical use, these terms carry no implication of being better or worse.

scribed in the preceding section. But there are other systems as well, less extensive, but equally important. One of these is the **pulmonary circulation** (Latin *pulmo*, lung), which supplies the lungs with the capillaries that surround the alveoli.

There are other "circulations" too, but discussion of these can be deferred for the present. With the pulmonary and systemic circulations in mind, we are in a position to understand the functioning of the heart.

65. The Heart: A Double Pump

In man and other mammals, the heart is, in a sense, a double organ. The two parts of it have separate functions but they work together. The diagram in Figure 9-2A should make this point clear. The right side of the heart is a pump for the pulmonary circulation system. The left side of the heart is a pump for the systemic circulation. There is no direct channel connecting the two sides. Contraction of a common set of muscles works both "pumps" at once but, in other respects, they might be regarded as two separate organs.

It is worth while to follow the course of blood going through the heart. If we start with blood being returned from the systemic circulation by the large veins, the venae cavae, we find that the blood first goes to the **right auricle.** This chamber is so named (Latin *auricle*, little ear) because externally it is an ear-like flap appended to the rest of the heart (Fig. 9-2B). From the chamber of the auricle, the blood goes to the **right ventricle** and, from there, out the **pulmonary artery** to the lungs where it flows through capillaries surrounding the alveoli. These capillaries unite to form veins which unite repeatedly to form ultimately the **pulmonary vein** which brings the blood back, this time to the left side of the heart, to the **left auricle** first, then to the **left ventricle** and then out by way of the **aorta** which feeds all the arteries of the body except those in the pulmonary system.

In the above account, the movement of the blood was spoken of as though it occurred spontaneously. This is, of course, not the case. The blood is a purely passive fluid which must be moved. The principal moving force is the heart. The way in which the heart moves the blood can be understood by careful study of the series of diagrams in Figure

9-3. Contraction of the muscles of the heart reduces the volume of the chambers. Blood, being a fluid, is incompressible; hence, when the heart contracts, the blood must go somewhere. Where it goes is determined by the valves. It will be noted in the figure that each **valve** (Latin, leaf of a door) is so constructed that it permits passage of blood in only one direction. When the ventricles contract, for instance, the increased pressure of the blood forces the valves between the auricles and ventricles to close, thus preventing backflow of blood into the auricles. The valves leading to the pulmonary artery and the aorta are so arranged, however, that the same pressure opens them, thus permitting blood to flow out to the lungs or the rest of the body. This phase of the heart's action, in which blood is forced out of the ventricles, is called **systole** (a Greek word for contraction).

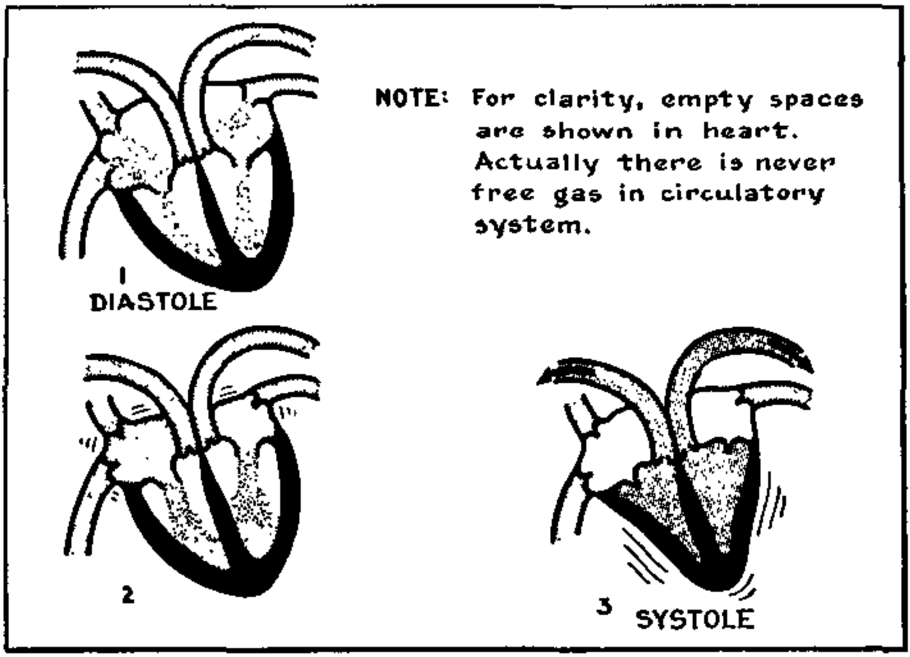

Fig. 9-3. How the arrangement of the valves of the heart determines the direction in which blood is forced by the heart's contraction. Systole (contraction) begins in the auricles (2) and spreads to the ventricles (3).

The opposite phase of the heart's action, in which relaxation of the heart muscle results in expansion of the chambers, is called **diastole**

(Greek, expansion). The role of the valves during this phase should become evident from a study of Figure 9-3.

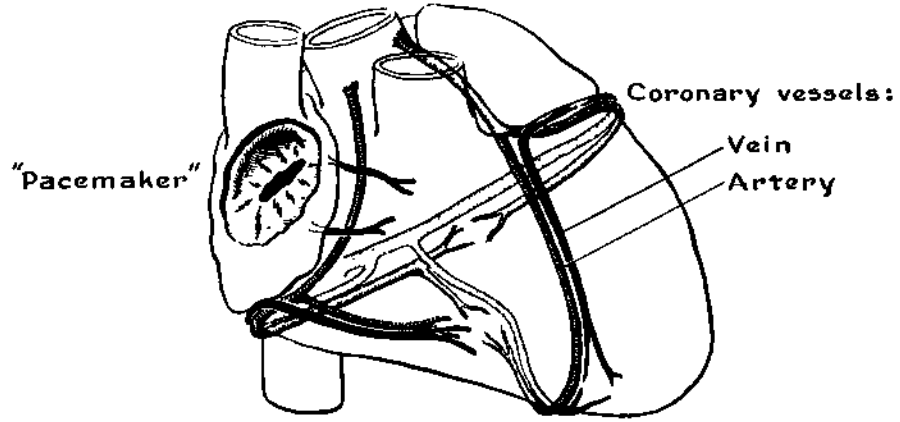

Fig. 9-4. The circulatory system of the heart. Also shown is the region known as the "pacemaker" from which the wave of cardiac contraction extends outward in systole of the heart.

66. Peculiarities of Heart Action

Anticipating material to be presented later, we may point out that most of the muscles of the human body act only when they receive stimuli from other parts of the body, either through the nervous system (brain, spinal cord, etc.) or through hormones (recall secretin, § 54). The heart, however, is a remarkable organ. When a living heart is removed from the body and kept at normal temperature and supplied with suitable food, it will keep beating for a considerable length of time, though clearly it is not subjected to nervous or hormonal stimulation when separated from the body. The heart of a turtle, a "cold-blooded" animal, is especially hardy and can easily be kept beating for hours after removal from the body.

It is noteworthy that not only does the excised heart continue contracting but that its beat is regular, and observation shows that the pattern of its contraction is the same as that of an unexcised heart. Or, as the situation is often summarized, both the automaticity and the rhythmicity of the heart are intrinsic. This does *not* mean that the heart is indifferent to outside influences. In humans, sudden fear is accompanied by a marked slowing of the heartbeat, an effect caused by stimulation of the heart by certain nerves.

Observation shows that the heart does not contract all over at the same time; rather, a wave of contraction starting from one small area spreads throughout all the heart muscle. The area which contracts first is located near the juncture of the systemic veins and the right auricle (Fig. 9-4). Depressant drugs or cold applied locally to other parts of the heart do not affect the rate of heartbeat but, when they are applied to the above-mentioned region, the heart beats more slowly. Because the activity of this region determines the activity of the whole heart, the region is often called the **pacemaker** of the heart.

67. The Coronary Circulation

The heart muscle, like all the muscles and tissues of the body, must be supplied with food and oxygen, and its wastes carried away. These functions must, of course, be performed by the blood stream and, as always, the actual exchange of materials between blood and cells can take place only through the walls of the capillaries, not through larger vessels. From this, it follows that, although gallons of blood flow through the auricles and ventricles in a day, the blood in these great chambers furnishes the heart with no food at all. There are no small vessels to transport blood from the heart chambers to the heart muscle. Instead, there is a separate circulatory system for the heart muscle, and this system is called the **coronary* circulation** (Fig. 9-4). Its principal arteries, the right and left coronary arteries, take off from the aorta near its base and supply all the heart with blood. Like all other circulation systems, this one consists of arteries-capillaries-veins. In keeping with its importance and continuous activity, **heart muscle is more richly supplied with capillaries than any other tissue**; indeed, it is said that there is one capillary for every cardiac muscle fiber.

68. The Constituents of Blood: The Mechanism of Coagulation

In the folklore of primitive peoples, blood plays a role of mysticism and importance. Curiously enough, in the light of modern knowledge, the importance of blood seems not to have been overestimated, though

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* From Latin *corona*, a crown, perhaps because the principal vessels encircle the heart like a crown.

some of its supposed functions, most notably that of carrying hereditary characteristics*, prove not to exist. But blood still performs many functions, many of which are not yet well understood. Some of these functions will now be considered.

Blood can be said to be made up of two parts: a liquid part which is called *plasma* or **blood plasma;** and various bodies which are suspended in the plasma and can be seen with a microscope, which are referred to as the **formed elements** of the blood. Among these formed elements, are the *red blood cells* or **erythrocytes** (Greek *erythros*, red, plus *cyte*) which give the blood its color.

Whole blood is about 80 per cent water and 18 per cent proteins with 2 per cent of various other dissolved chemicals. The proteins here, as elsewhere in any living organism, are of primary importance. Many of the major properties of blood are dependent on the particular proteins it contains.

One of the most important of the properties of blood is its ability to *clot*, or **coagulate,** that is, to turn from a liquid to a firm solid. A few minutes after normal blood is shed from a blood vessel, it clots. Clotting at the site of the wound closes the openings and prevents further loss of blood. Were it not for this property of blood, the slightest wound might result in loss of so much blood as to cause death. This danger is a very real one for certain rare individuals who suffer from a disease known as **hemophilia** (Greek *hemo*, blood, plus *philos*, loving; not very aptly named). The blood of hemophiliacs, though it will clot, clots so slowly that any tiny cut constitutes a genuine threat to life.

The value of the ability of blood to clot, once it is outside the body, is obvious. Equally obvious, should be the utility of the failure of the blood to clot within the blood vessels. However, a clot does occasionally form internally and may act as a plug or **thrombus** (Greek *thrombus*, from *trepho*, thicken) which stops the flow of blood in the vessel where it lodges. The seriousness of such **thrombosis** is determined by the importance of the vessel or vessels plugged. Coronary thrombosis sometimes causes immediate death.

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* Consider such phrases as "blue blood," "royal blood," "tainted blood," "blood will tell." There is no evidence of any difference between the blood of kings, commoners, criminals, white, black, yellow, or red men. The vehicle of hereditary characteristics is quite different, as will appear in Part IV.

The vital importance of clotting has stimulated research into the mechanism of clotting. The principal and more easily understood facts that have been uncovered are presented below.

First of all, it is important to realize that the entire blood does not solidify. This can be shown easily by vigorously stirring some freshly drawn blood with, say, some broomstraws. After a few minutes, the broomstraws will be found to be covered with a solid, rubbery material. The remainder of the blood will still be red and apparently unchanged. If the stirring is vigorous enough and sufficiently prolonged, all the clottable material will be gathered on to the stirrers. The remainder of the blood will remain fluid indefinitely. The clotted material is called **fibrin** because it appears to be a mass of interwoven fibers. The remainder of the blood is called **defibrinated blood.**

Fibrin is a protein. It has been shown that this insoluble protein is not present, *as such*, in the blood stream, but rather that there is normally present another protein, very little different from it chemically. This protein is soluble in watery materials like blood. Since, under certain circumstances, it gives rise to fibrin, it is called **fibrinogen** (*fibrin* + Greek *genos*, race, kind, descent; hence, that which gives rise to). So we may write:

$$\text{fibrinogen} \xrightarrow{\text{(under certain circumstances)}} \text{fibrin} \qquad (2)$$

But what makes the fibrinogen turn to fibrin? It does not normally do so, or clots would occur in the intact circulatory system at any time. Something must "set off" reaction (2). It has been found that the presence of another substance **thrombin** is the stimulus which sets off this reaction. We can amend the above equation as follows:

$$\text{thrombin \& fibrinogen} \longrightarrow \text{fibrin} \qquad (3)$$

The reaction between thrombin and fibrinogen is probably not a simple addition of one to the other in the sense that iron + oxygen ⟶ iron oxide. The thrombin modifies fibrinogen in such a way that fibrin is produced; at the end of the reaction, thrombin or some derivative of it may be left over. In other words, equation (3) is not a complete or exact chemical equation. To indicate that fact, the two reactants are connected by an ampersand (&) rather than by the plus (+) that is used in true and complete chemical equations.

But where does the thrombin come from? By the argument used before, it cannot be present as such in the blood stream or the blood would spontaneously coagulate. Experiments and observations have shown that thrombin is indeed normally absent, but there is present a *precursor* (Latin *prae*, before + *curro*, run), called **prothrombin,** from which thrombin is derived. That is:

prothrombin ⟶ thrombin (4)

What are the circumstances that set off this reaction? Again, we have experimental facts which partly explain it. For one thing, calcium must be present; for another, some other type of material which has been called **thromboplastin** (Greek *plastos*, molded, formed) must be available, too. The sort of reaction between these substances and prothrombin is not thoroughly understood, so again we will use ampersands:

calcium & thromboplastin & prothrombin ⟶ thrombin (5)

Calcium is normally present in the blood plasma; thromboplastin is not, normally. Where does it come from? One source is apparently **blood platelets,** tiny bodies present in the blood which are believed to liberate thromboplastin when they break up, as they do (for reasons that are not completely understood) after the occurrence of a **hemorrhage** (loss of blood from blood vessels). "Thromboplastin" is probably not a unitary substance, but rather the name of a class of substances present in blood platelets and in various body tissues. Little is known of the chemical nature of these substances.

We can summarize the above information by the following series of equations:

hemorrhage ⟶ release of thromboplastin (6)

calcium & thromboplastin & prothrombin ⟶ thrombin (5)

thrombin & fibrinogen ⟶ fibrin (3)

Before leaving the subject of the coagulation of blood, it might be well to make certain points. In investigating "the cause" of any natural phenomenon, we may be looking for nonexistent simplicity. There may be many causes or "causal factors." Quite frequently, these causal factors are related to each other in chainlike fashion, as we have seen in the example just considered. Continued analysis adds one link after another to the chain, and we sometimes wonder if there *is* any first link with which the process starts.

In the case of coagulation, we still are not in possession of all the links. Even our present incomplete knowledge, however, has led to some control of coagulation. To extend the link of causal factors further, it may be stated that a fat-soluble substance called **vitamin K** is required for the synthesis of prothrombin by the body. When the bile-duct is obstructed by gallstones, bile (§ 55) does not get into the intestine; hence, fats are incompletely digested; hence, vitamin K is not released from the food to be absorbed by the body. As a result, the patient's blood does not coagulate readily, and an operation performed to remove the offending gallstones is doubly dangerous. The danger can be decreased by giving the patient extra vitamin K before the operation, a practice that is now routine in such cases.

In recent years, the technique of blood transfusions has been developed to such a high degree that it is now possible to store human blood in "blood banks" for use in transfusions as needed. Even under the best conditions of storage, blood can be kept for only a few weeks. Fortunately, over-age blood need not be wasted, for from it can be separated many medically useful materials for which there is no other source. Thrombin extracted from blood is widely used in surgery to bring about the clotting of blood at cut surfaces. The thrombin is frequently applied by means of a sponge made of blood fibrin. Such a sponge, composed entirely of natural materials, can be left in the body at the conclusion of an operation, for it will eventually be dissolved and absorbed into the patient's system.

69. The Functions of Erythrocytes

Unquestionably, one of the principal functions of the blood is the carrying of oxygen to all parts of the body. Oxygen is, of course, soluble in water and watery solutions like blood, but it can be readily shown that a volume of arterial blood contains many times as much oxygen as can be dissolved in a corresponding volume of water. This great oxygen-carrying capacity is due to the presence of the chemical substance **hemoglobin** which is contained in the red blood cells, the erythrocytes. Hemoglobin is the material that gives the blood its red color; when the hemoglobin-containing erythrocytes are removed (as by a centrifuge), the remainder of the blood (plasma) is light yellow in color.

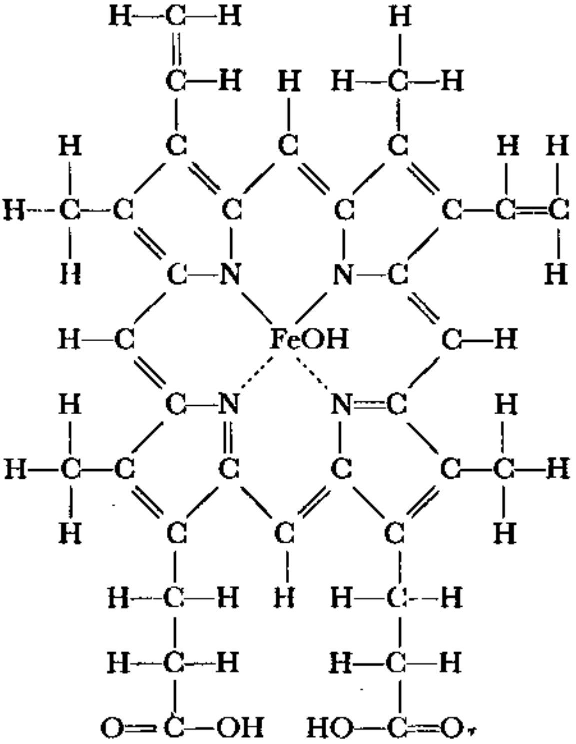

Fig. 9-5. The structure of hematin.

Hemoglobin is a very complex molecule composed of two parts: a massive protein part, the composition of which is not known, of course*, and *hematin* which is much simpler in composition but still scarcely a simple substance (see Fig. 9-5). Determining the structural formula of the latter substance involved years of work, for which its principal investigator, the chemist, Hans Fischer (1881-1945), was awarded the Nobel prize in 1930.

Although the structure of hemoglobin is not known, much is known of the chemical reactions into which it can enter. The reactions that are

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* Why "of course"?

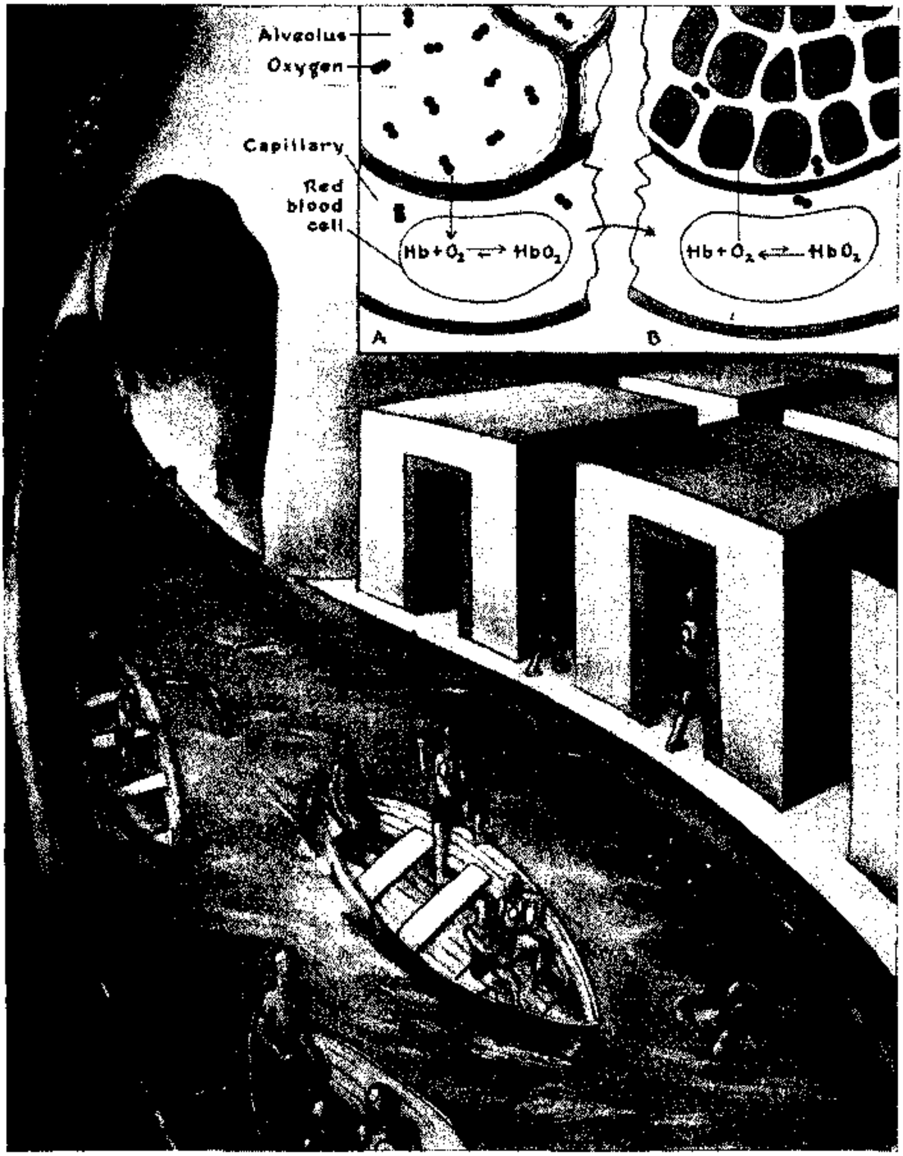

Fig. 9-6. Transport of oxygen to the tissues—pictorial analogy. The boats, "RBC," represent red blood cells, which carry most of the oxygen in the blood stream. Some carbon dioxide molecules are carried by the RBC too, but, for simplicity, this fact is ignored. Only the *net* movement of oxygen between blood and tissues is shown.

of greatest physiological interest will be described below. To symbolize compounds of hemoglobin, the symbol *Hb* will be used. *Hb* is not, of course, hydrogen boride or a new element; it is merely an abbreviation of hemoglobin.

Erythrocytes take up oxygen by virtue of a chemical union of hemoglobin and oxygen to form a new chemical compound called *oxyhemoglobin.* In symbols:

$$Hb + O_2 \longrightarrow HbO_2 \tag{7}$$

The principal reaction is not one of simple solution of oxygen in the blood plasma or in the erythrocytes. Some oxygen is so dissolved but the quantity involved is relatively negligible. Most of the oxygen is carried in chemical combination with the hemoglobin. It has been calculated that if it were not for this chemical transport, the human body would require about 75 times as much blood as it now contains.

HbO_2 is a definite chemical compound which has the very convenient property of being easily decomposed. It decomposes whenever it is surrounded by fluid in which there are few O_2 molecules; it re-forms whenever the O_2 concentration of its surroundings rises above a certain level. Reaction (7) is then a reversible one and should be rewritten thus:

$$Hb + O_2 \rightleftarrows HbO_2 \tag{8}$$

We are now in a position to understand the role of hemoglobin in oxygen transport. Figure 9-6 is a highly diagrammatic representation of the structures and processes involved. At (A), an erythrocyte squeezing along through a capillary surrounding an alveolus of the lungs finds itself in a region of high oxygen concentration. As a result, oxygen molecules enter the erythrocyte, raising the concentration inside. With more oxygen available, reaction (7) tends to proceed from left to right, a fact we have indicated by making the right-pointing arrow the longer of the two inside the erythrocyte of Figure 9-6A. The end result is that as erythrocytes pass through the pulmonary circulation they pick up oxygen.

Now notice what happens as erythrocytes go through a systemic capillary (Fig. 9-6B). This capillary is surrounded by cells that are actively using up oxygen all the time. As a result, there is a low concentration of oxygen in all the adjacent fluids. When a red blood cell comes along, it loses oxygen to the low-oxygen fluid around it. The dissolved oxygen content inside the erythrocyte being low, the unstable

HbO_2 compound breaks up, releasing more O_2 which is first *dissolved* in the erythrocyte. This oxygen then passes through the erythrocyte membrane to the blood plasma, then through the capillary walls (which, of course, are made up of cells—a fact not indicated in our figure) into the fluids surrounding the body cells, and ultimately into the cells themselves, where it is used. In brief, as erythrocytes pass through systemic capillaries, they lose oxygen to the cells of the body.

Respiration, which takes place in all the cells of the body, involves the use of oxygen and the production of carbon dioxide. The method of transport of carbon dioxide closely parallels that of oxygen, with the necessary reversal in direction; that is, the tissues which contain much CO_2 give it up to the blood which in turn eventually gives it up to the lungs. The CO_2, like the O_2, is capable of combining with hemoglobin:

$$CO_2 + Hb \rightleftarrows HbCO_2 \qquad (8)$$

but this compound accounts for only about 20 per cent of the CO_2 carried by the blood; the rest is carried in the plasma, mostly in the form of substances known as *bicarbonates*, compounds which contain the HCO_3^- ion. The bicarbonates easily decompose to yield CO_2.

70. The Manufacture of Erythrocytes

We have several times stressed the artificiality of separating the body into "systems" for discussion, inasmuch as the systems interact and interpenetrate in various ways. A good example of such an interrelationship is found in the origin of the erythrocytes. These characteristic blood cells are formed in the marrow of the long bones of the body. Bone marrow of freshly killed animals, especially young animals, is decidedly red because of the great stores of erythrocytes in all stages of formation. The red bone marrow is the only place in the body where red blood cells are formed, hence anything that injures the bone marrow may also affect the blood system. Salts of the "heavy metals," e.g., mercury and radium, when taken into the body, accumulate in the bone marrow and seriously interfere with the formation of erythrocytes. Such molecules can be readily deposited in the bone marrow but can be removed only with difficulty. As a consequence, continuous exposure to nonlethal concentrations of these substances may result in their accumulation in the bone marrow until they reach lethal concentrations. Such poisons are called **cumulative poisons.** Industries in which these substances must be used present difficult problems in health legislation.

Red blood cells have a relatively short life in the blood stream—about 120 days on the average. Erythrocytes are being continuously broken down in the liver and spleen. Some of their breakdown products are used to form bile; others are kept in the body and utilized in the formation of new red blood cells.

In many animals, e.g., frogs and salamanders (*Amphibia*), the red blood cells are typical cells in that they contain a nucleus. In man and other mammals, however, mature erythrocytes have no nucleus. This condition is a secondary one. Examination of the cells in the red bone marrow reveals many cells with well-formed nuclei and others with nuclei that appear to be in various stages of decomposition. Observation and deduction have led to the conclusion that erythrocytes without a nucleus are derived from red cells with a nucleus. These juvenile, nucleated cells are called **erythroblasts.***

Normally, the rate of formation of mature red blood cells is exactly equal to the rate of their destruction. However, following an extensive hemorrhage, the oxygen content of the blood stream falls because of the low absolute number of erythrocytes. The low oxygen-level stimulates the red bone marrow to pour more red blood cells into the blood stream. If there are not enough erythro*cytes* to make up the deficit, erythro*blasts* will be released into the blood stream. Under the microscope, the erythroblasts can be readily recognized by their nuclei. The condition described is called **erythroblastosis.** We will have occasion to refer to it again when we discuss the "Rhesus factor" in humans (§ 186).

71. Lymph

One of the important links in the chain of transport of materials to and from cells is the fluid found in the spaces between and around the cells of the body (see Fig. 9-6B). This fluid is called **lymph.** All the cells of the body are surrounded by it. Material is never transferred directly

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* Greek *blastos*, a germ or bud. Immature cells, from which more mature cells are derived, are frequently identified by the suffix *-blast*.

from blood to cells but always through this intermediary, lymph. Oxygen, being more concentrated in the blood of the capillaries, diffuses from the blood through the walls of the capillaries into the lymph and from the lymph into the cells. This diffusion takes place continuously in this direction because the cells are continuously using up oxygen, thus setting up a *diffusion gradient* from the high level in the blood, through the intermediate level in the lymph, to the low level in the cells. A similar gradient exists with respect to the various foodstuffs which are also being used up by the cells.

The various waste products of the cells, CO_2 and nitrogenous wastes, also move along a diffusion gradient, but in the reverse direction—from the cells into the lymph of the intercellular spaces, and then into the blood which carries them away, thus maintaining the gradient.

Lymph is derived from blood. Blood, under pressure, constantly loses some of its fluid through the walls of the capillaries. This fluid has substantially the composition of the plasma but is called lymph; the principal difference between the two is in the protein content; lymph has only about half as much protein as plasma.

What is the ultimate fate of the lymph? Surprisingly enough, it has a sort of circulation of its own. It is not a completely closed system like that of the blood but it includes some definite vessels of its own, though many of these are not easy to find. The general path is this: lymph is squeezed through the walls of the capillaries into the intercellular spaces; it moves somewhat at random among the cells, ultimately coming to lie in definite, though tiny, channels called *lymphatic vessels*, or simply **lymphatics.** The lymphatics unite with one another and ultimately with blood vessels, thus returning this material once more to the general circulatory system. There is no heart to move the lymph; its movements are principally due to the squeezing action of the muscular tissues it interpenetrates. Lymph circulation is, consequently, slow and uncertain; exercise increases its rate of circulation.

The process by which lymph is formed is a filtration process in which the pressure involved is blood pressure and the filter is the wall of the capillary. Normally, the rate of formation of lymph is equal to the rate of return of lymph, but this equilibrium is sometimes upset, resulting in the formation-rate exceeding the return-rate. When this happens, the increased volume of fluid around the cells causes a puffiness called *edema* (Greek, swelling). The immediate cause of this condition may be any of several: increased capillary pressure, increased permeability of the capillary membrane, or decreased rate of return of lymph due to increased pressure of blood in the veins. The permeability of the capillaries to passage of fluids is especially easily altered. For instance, the bacteria in an infected wound apparently release chemicals that increase the permeability of the capillaries in that region, resulting in local swelling of the region infected. Even a noninfected, but injured, tissue

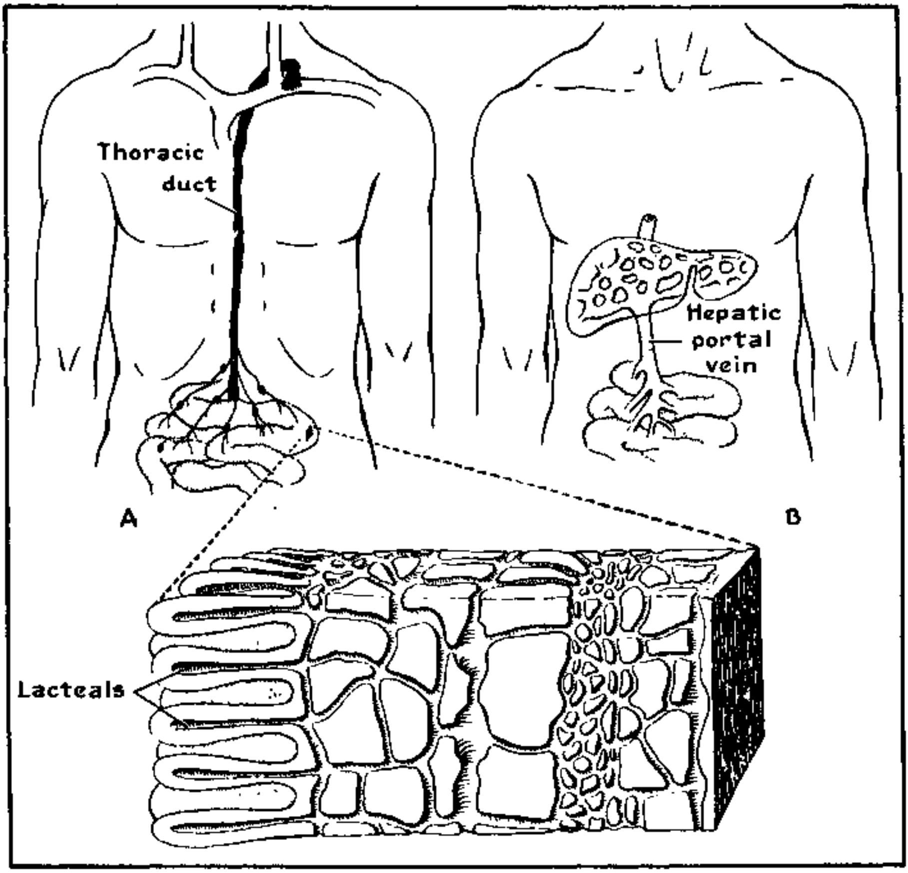

Fig. 9-7. The products of fat digestion enter the body by way of lymph vessels called lacteals (A). The lymph ultimately joins the blood stream via the thoracic duct. The products of carbohydrate and protein digestion enter the blood stream directly, going into blood vessels which enter the liver via the hepatic portal vein (B).

may somehow affect capillary permeability; anyone who has "caught" a baseball on the end of his finger can think of an instance. These are both examples of local alteration of capillary permeability. A general alteration may also occur, for instance, in "starvation edema" or "prison-camp edema," in which the underfed victim develops a deceptively bloated appearance. In such cases, it is believed that vitamin deficiencies are the cause of the change in capillary permeability.

72. Transport of Food

Recall (§ 57) that food absorbed through the intestinal wall passes into two different circulatory systems, the products of fat digestion going into the lacteals which are part of the lymphatic system, and the products of protein and carbohydrate digestion passing into the blood system.

The lacteals from the intestine come together to form larger vessels, the ultimate vessel being a large lymphatic, called the **thoracic duct,** which pours its products into one of the large veins near the heart (Fig. 9-7A). Although fat is first digested by the intestine to fatty acids and glycerine, these digestion products are recombined during the process of absorption (in large part, at least) to form microscopic globules of fat suspended in the blood.

The route followed by the products of protein and carbohydrate digestion is different. These products are absorbed directly into the blood vessels. These blood vessels unite (Fig. 9-7B) to form the **hepatic portal vein** which subdivides into capillaries in the liver. The contents of the blood from the intestines are considerably modified in the liver. A large fraction of the carbohydrates is stored as **glycogen** ("animal starch") by the liver. Various natural but toxic (poisonous) products of protein digestion are modified by the liver into nontoxic substances. This detoxifying action is one of the important functions of the liver.

73. Transport of Hormones

A hormone is any chemical substance produced by one part of the body that, carried in the blood stream, affects the actions of another part of the body. One example, secretin, has already been discussed (§ 54). Other examples will be discussed later.

74. Protection Against Disease

Not the least of the functions of blood is its protective role. Among the formed elements of the blood, are some *white blood cells* or **leucocytes** (Greek *leukos*, white, + cyte), some of which can ingest bacteria and other foreign bodies. The white blood cells that are capable of this action are also called **phagocytes** (Greek *phago*, to eat). These phagocytes can push their way through the wall of a capillary. When bacteria invade the tissues of the body, the phagocytes in the blood squeeze through the capillary walls into the tissue spaces and wander around consuming the invaders.

The blood also contains some chemical substances called **antibodies** which help protect the body against bacteria and foreign proteins. These protective substances are discussed at length in Chapter XXX.

QUESTIONS AND PROBLEMS

9-1. Trace the course of blood through the heart.

9-2. During prenatal life, the human heart has an opening between the two auricles. Occasionally, this opening persists into adulthood. What effect would you expect this persistence to have on the athletic abilities of the individual? Explain in detail.

9-3. Blood flow, like all flow of liquids in pipes, has to work against a resistance. Drawing upon common knowledge, can you predict whether the resistance would be greater in the small vessels or in the large? When the capillaries are partially constricted, does the heart have to work harder, or not so hard, in order to force blood around the system at the same rate?

9-4. The right side of the heart is not so large and muscular as the left side. Assuming that each side is as powerful as it needs to be, can you suggest a reason for this difference?

9-5. What is a coronary thrombosis? Why should it sometimes be immediately fatal and at other times be merely incapacitating?

9-6. By definition, venous blood is poor in oxygen. Name an artery that carries venous blood and a vein that carries arterial blood.

9-7. The volume of blood in an adult human amounts to about 5 liters. The number of erythrocytes per cubic millimeter is normally around 5,000,000. From these facts and another fact mentioned in the text, it is possible to calculate the approximate number of erythrocytes destroyed per day. How many are destroyed per minute? Where are they destroyed?

9-8. How many red blood cells are formed per minute? Where are they formed?

9-9. If blood contained no hemoglobin, how great would the volume of blood have to be, in an adult man, in order to carry as much oxygen as the present volume of normal blood carries? Would this volume suffice for the transport of CO_2?

9-10. The footnote to § 54 presented a question. If you could not answer it at the time, try again.

9-11. What is edema? What may be its causes?

9-12. The citrate ion of sodium citrate has the ability to combine with calcium ions so that they are not available for other reactions. In making blood transfusions, sodium citrate is routinely added to the blood that is being transferred from one person to another. Why?

9-13. When sweet clover spoils, it sometimes produces a substance known as *dicumarol*. If cattle eat this, they develop a disease known as "spoiled sweet clover disease." Dicumarol apparently prevents the synthesis of prothrombin. What will be the consequence of this action?

Chapter X

Nerve Impulses, Consciousness, and Reflex Action

75. Action at a Distance?

It is a matter of common knowledge that our conscious decisions are made in the brain. Suppose I decide to wiggle my toe; instantly, my toe wiggles. The toe-wiggling muscles are found in the foot; the decision-making organ is in the cranium more than a meter and a half away. How does my toe know what my brain wants? How is the news of the decision transmitted over nearly two meters of space in so short a time?

The problem seems even more difficult when we recall that the entire body is composed of microscopic cells, more or less boxlike in shape and generally packed one against the other for the length and breadth of the body. A "typical" cell—a meaningless term, really, since there are so many types—is perhaps about fifty microns* in diameter. Within a distance of a meter and a half, there are about 30,000 cells. Does the message from brain to toe have to be passed from cell to cell through 30,000 cells? That would be a very inefficient communication system and, one would suspect, a slow one. By way of analogy, suppose a message from Smith, at the north end of a large city, had to be relayed to Jones at the south edge, by being passed through 30,000 sets of mouths

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* One micron is 0.001 mm. A micron is symbolized by the Greek letter μ (mu).

and ears. This would certainly be a cumbersome method of transmission, not to mention an inaccurate one. How fortunate it is that there are telephone and telegraph wires, slender elements that pierce, as it were, the mass of seething humans and carry the message directly from Smith to Jones, past all the intervening and unknowing thousands of individuals.

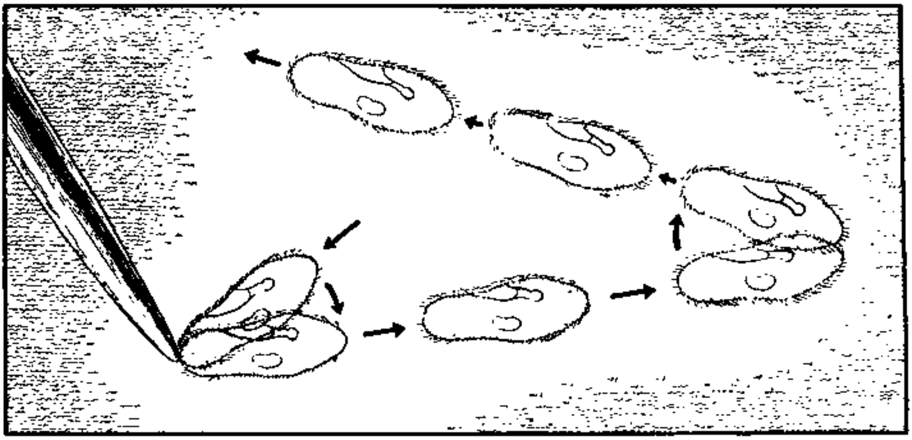

Fig. 10-1. Avoiding-reactions of a *Paramecium* involve the coordinated activity of the cilia of the entire body, implying a system of communication within this single cell.

The brain and the toe are similarly connected by message-carrying cables called **nerves.** The largest of them are easily seen by the naked eye as shiny, tough, white cords that interpenetrate all parts of the body. They carry messages from one part to another, by-passing all the intervening body cells. They are the telephone cables of the body.

But what are these nerves? What are they made of? When we answer this question, the analogy of the telephone cable breaks down. Examination with the microscope shows that *nerves themselves are made of cells*, cells of a definite shape and limited function. We must know more of these *nerve cells*, or **neurons** as they are called.

76. The Responsiveness of the Neuron

Responsiveness is one of the fundamental characteristics of living things (§ 10). All cells are responsive to at least some stimuli. This characteristic is most important of all in a neuron.

It is worth while to observe the responsiveness of a cell that can be more readily studied than a nerve cell—a *Paramecium*, for instance. Paramecia (see Fig. 10-1) are single-celled animals to be found in most fresh-water ponds. The animals are small—about 0.1 mm in length—and are moved by minute, hairlike appendages called **cilia** (Latin singular, *cilium*, an eyelash or little hair). These cilia usually move too fast to be seen by daylight but, by an interrupted light (produced by a machine called a "stroboscope"), their movement can be determined. Sometimes, the periodic variations in the intensity of an incandescent lamp operating on alternating current permit watching the movements

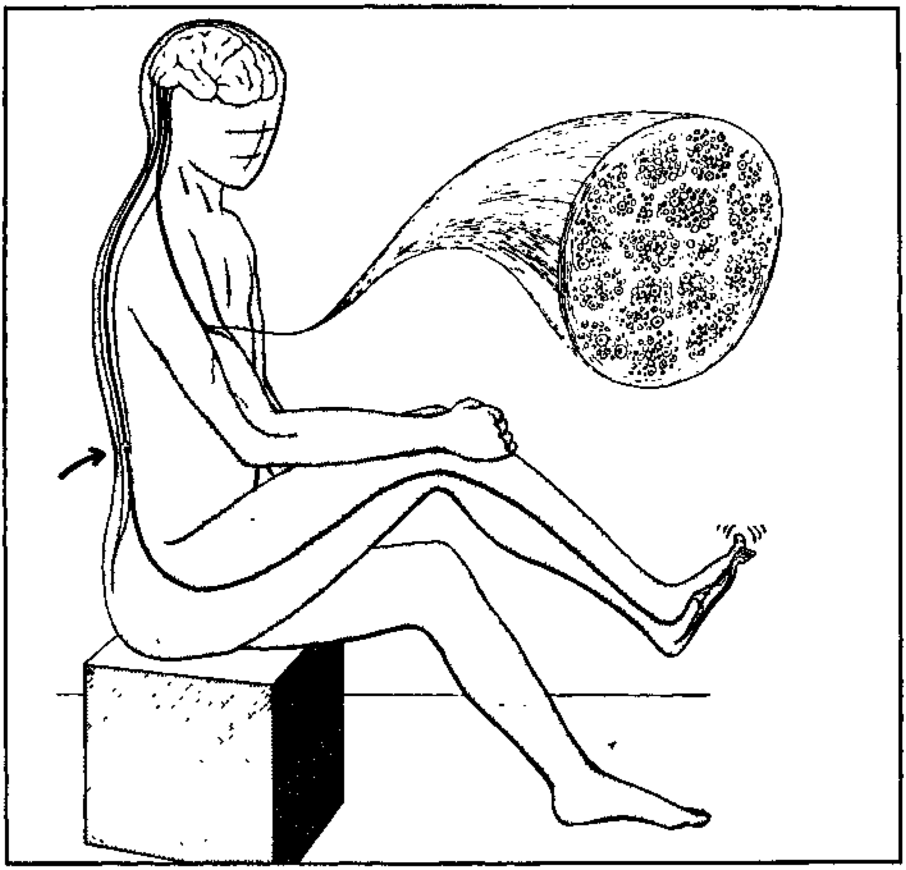

Fig. 10-2. The nerve fiber which delivers a stimulus to a toe is an extension of a cell whose nucleus is located in the mid-region of the body (see arrow). Thousands of nerve fibers are bound together into a macroscopic nerve. A magnified cross section of a nerve is shown above right.

of the cilia. Studies made in this manner show that the cilia move in an organized way. A wave of movement passes along the animal, successive cilia beating in sequence. When an actively swimming animal bumps into an object, it abruptly reverses its direction of motion for a short distance and then starts out again in a new direction. Careful observation of the cilia shows that all of them change their direction of beat, though only the front end of the animal has been touched. This shows that there must be some sort of communication within the animal which keeps all of its parts moving in a useful fashion.

Communication within the cell is undoubtedly possible to every kind of cell; thus are the activities of the various parts of a cell integrated. A nerve cell is, one might say, but an ordinary cell elongated so that when one extremity communicates with another, a very great distance is involved. To comprehend this, let us return to the example of the man who decided to wiggle his toe. A number of chains of nerve cells are involved; we will consider only the last link of such chains. The greater part of the nerve cell that gives the final stimulus to a muscle fiber of his toe is more than a meter away from the muscle, being situated well up in the vertebral column (Fig. 10-2). A neuron is truly microscopic and yet it may be very long; in this case, one thin projection (as small as 1 micron is diameter) is more than a meter in length. What we call a *nerve* is made up of many such projections or *processes** organized into a bundle reminiscent of a telephone cable (Fig. 10-2). It takes a great many nerve processes, or **nerve fibers**†, to move a single muscle, and one nerve usually supplies many muscles with nerve fibers.

77. Communication Between Nerve Cells: The Synapse

The path from brain to toe involves more than one neuron; how many we do not know, but certainly several. We have accepted without question the fact of communication within a cell. What about communication between cells? Clearly this must occur, too.

Communication between cells is not a general phenomenon; only

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* Note this uncommon definition of process, as a structure rather than an occurrence. This usage is common in anatomy.

† Synonyms: a short nerve process = nerve process. A long nerve process = nerve fiber. A nerve cell = a neuron.

some cells exhibit it, the most notable of which are nerve cells. Every nerve cell connects with at least one other nerve cell to which it gives, or from which it receives, messages. The nature of this connection can be understood by the diagram in Figure 10-3. The juncture (region D-E) of the processes of two neurons is called a **synapse** (Greek *syn*, together; *apsis*, mesh). Experiments have shown that *at a synapse* a message can travel from one neuron to the next but *in one direction only*. For example, in the figure, a message (detectable by electrical instruments) might travel from C to E but not from E to C. Within a single neuron, a message can go in either direction; for instance, from A to C or from C to A. In other words, the synapse acts as a one-way valve in the communication system. Messages from head to toe travel over one system of neurons and from toe to head over another system.

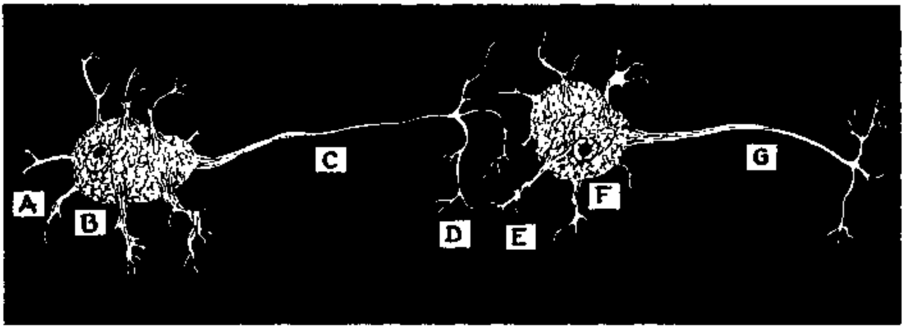

Fig. 10-3. At the synapse (D-E) between two neurons, the message can travel in only one direction, from neuron B to neuron F, in the example. Processes A and E are afferent fibers; C and G are efferent fibers.

The nerve fibers are identified according to the direction in which they ordinarily carry messages. A fiber which carries a message *to* the main body of the cell (B) is called an **afferent** fiber (A, in Fig. 10-3). One which carries the message *away* from the cell body is called an **efferent** fiber (C). A synapse consists of the juncture of the efferent fiber of one neuron with the afferent fiber of another.

78. The Nature of the "Message"

So far, we have been speaking glibly of the "message" that travels along a nerve. What is this message? Elucidation of the nature of this message is one of the basic problems of modern physiology, a problem not yet completely solved. The partial solution achieved at present offers a rather complex story which we shall simplify.

Whenever a neuron is stimulated at one end, an electrical impulse travels rapidly to the other end. This electrical impulse is not quite the same as that which travels along an electrical wire when a telegraph key is closed. For one thing, the speed of this impulse is much slower—only about 260 miles per hour (at the fastest) in a nerve, as compared with 186,000 miles per second in an ordinary copper wire. This difference in speed stems from a fundamental difference in the source of the current. The impulse in an electric wire can be spoken of as a "simple" electric current. That of a nerve fiber is a by-product of a complex chemical reaction which results first in the modification of the electric charge on the surface of the nerve fiber and then in its restoration. The site of these two successive chemical reactions moves from one

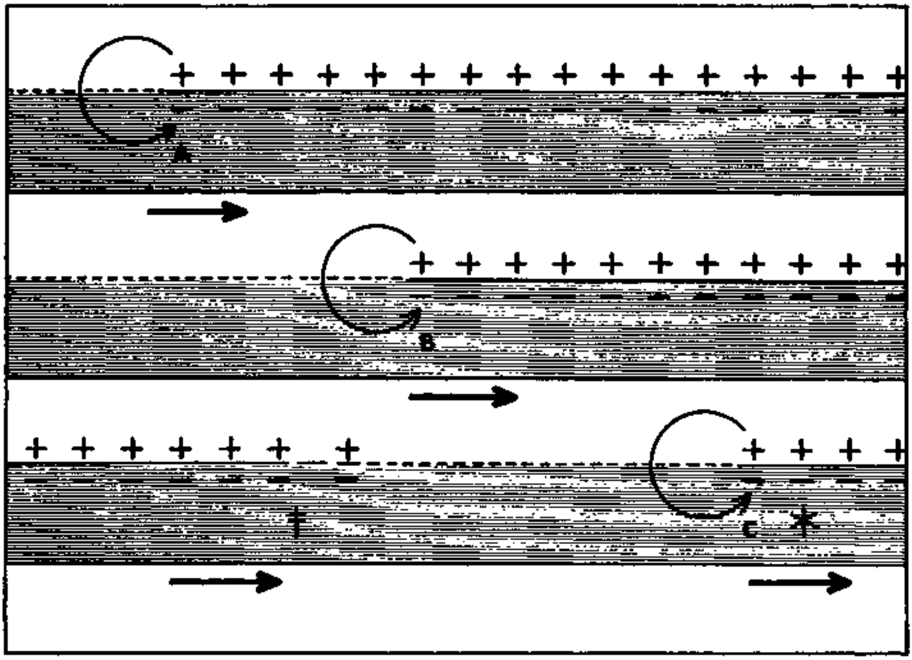

Fig. 10-4. The resting nerve fiber is polarized, i.e., the outside is positively charged relative to the inside. A stimulus passing along a fiber involves a change in the cell membrane and a loss of polarization, indicated by * above. One one-thousandth of a second after *, the membrane reverts to its normal state, the nerve fiber becomes polarized again (at † above), and the fiber is ready for another stimulus to pass along it.

point to another, just as the site of the chemical reaction involved in a powder fuse moves along the fuse.

Figure 10-4 will perhaps help to clarify the picture. The breakdown chemical reaction taking place at region A causes two things: (1) a loss of charge in the internal membrane of the nerve fiber at A, and (2) an initiation of the same chemical reaction at region B. The reaction at B in turn causes a similar reaction to occur at C and so on from one region to the next. Thus, the impulse travels from region to region at a velocity of about 100 meters per second.

If this chemical reaction, indicated by * in Figure 10-4, were the only one to occur, a given neuron could carry only one impulse and then no more. There is, however, a recovery reaction, indicated by † in the figure, which takes place soon after the breakdown reaction. As soon as the recovery reaction is complete, the nerve is ready for a second impulse, or "message," to pass along it. The time between the breakdown reaction (*) and the recovery reaction (†) is about one one-thousandth of a second. The chain reactions diagrammed can pass along the neuron, † behind *, in either direction. If we deliberately stimulate the nerve fiber at the middle of its length, the impulse will travel in both directions until it comes to the extremities where it will either stop or will go across the synapse, depending on which way the "valve" is oriented. Normally, of course, stimulation at the middle of a nerve fiber does not occur.

The nature of the chemical reactions referred to as "breakdown" and "recovery" reactions is not well understood. We do know, however, that *they are chemical reactions*. These reactions can occur only in living neurons, so they may be spoken of as metabolic reactions. It has been shown that when a neuron is stimulated, it uses up an increased amount of oxygen and produces an increased amount of carbon dioxide and heat; hence, it appears that respiration is involved in nerve action. The complete elucidation of the physics and chemistry of nerve action will no doubt present as many difficulties as the understanding of the nature of life itself.

79. The Passage of the Impulse from Cell to Cell

The problem of the transmission of nervous impulses can be analyzed into two problems: the transmission of the impulse within a neuron;

and the transmission of the impulse from one neuron to another, or from a neuron to a muscle fibril. The first problem has been discussed in the preceding section; the second will be briefly discussed here.

The chemical reaction that accompanies the nerve impulse is *intra*cellular. The best evidence indicates that the cell membrane of a neuron is intact at all points, i.e., that there is complete separation of the cell material of two neurons whose fibers touch in synapsis, and of a neuron and the muscle fibril with which it is connected. How, then, does the impulse pass between two cells?

Two theories have been put forward to account for the *inter*cellular transmission of the nerve impulse:

1. The electrical theory, which holds that the only impulse transmitted from one cell to another is an electrical one, which in turn sets off the chemical reaction in the second cell.
2. The chemical theory, according to which the stimulated neuron releases a chemical substance at the end of its efferent fiber, a substance which serves as the stimulus for the reaction of the adjoining neuron or muscle fibril.

The difficulties of experimentation in this field are such that it is not possible to say at the present time which theory is true. There is increasing evidence for the chemical theory; in certain instances, the evidence is quite good. But the general problem of intercellular transmission cannot yet be considered solved.

80. Consciousness and Animal Experimentation

All of man's reactions to his environment involve his nervous system. Every movement, every thought, is possible only because of his possession of this remarkable integrating system. A skilled pianist runs through a *presto* passage faultlessly; every individual movement of his fingers and arms involves a multitude of nervous impulses. An ice skater performs the "school figures" to perfection; again, his movements are brought about by thousands of the most perfectly timed nervous impulses. Not only are the skilled movements of all sports and physical arts made possible by the extremely intricate organization of the nervous system, but all thinking, as well, is carried out by this remarkable system. What structure and functioning can explain the skilled accuracy of the movements of the musical performer and the athlete? What parts and what organization can explain the frightening inventiveness of man's mind? Can we—using the mind itself—understand our own mind and nervous system?

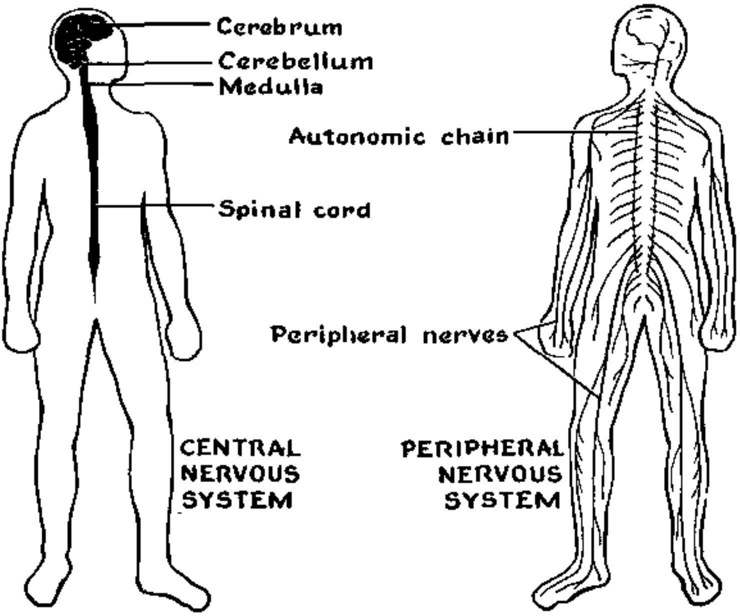

Fig. 10-5. Analysis of the nervous system.

At present, only in part. Of the simpler actions, we have a fair comprehension. The more complex activities we understand at best only vaguely, "intuitively," and uncertainly. This is, however, no reason for surrendering to a mystical feeling of helplessness, however delicious such a feeling may be. When one considers that it is only a little more than a hundred years since the first great advance was made* in the understanding of the nervous system, subsidence into the sensuality of mysticism seems a bit premature.

Before discussing the organization of the nervous system, it is necessary to formulate some definitions. These definitions can best be made clear by reference to Figure 10-5. The **central nervous system** consists of those parts of the nervous system that are entirely surrounded by the

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* By Bell and Magendie, in the elucidation of the "reflex arc"—to be described in § 81.

bone of the vertebrae and skull. The **peripheral nervous system** consists of the nerves that connect the central nervous system with the periphery of the body—with the legs, arms, viscera, etc.

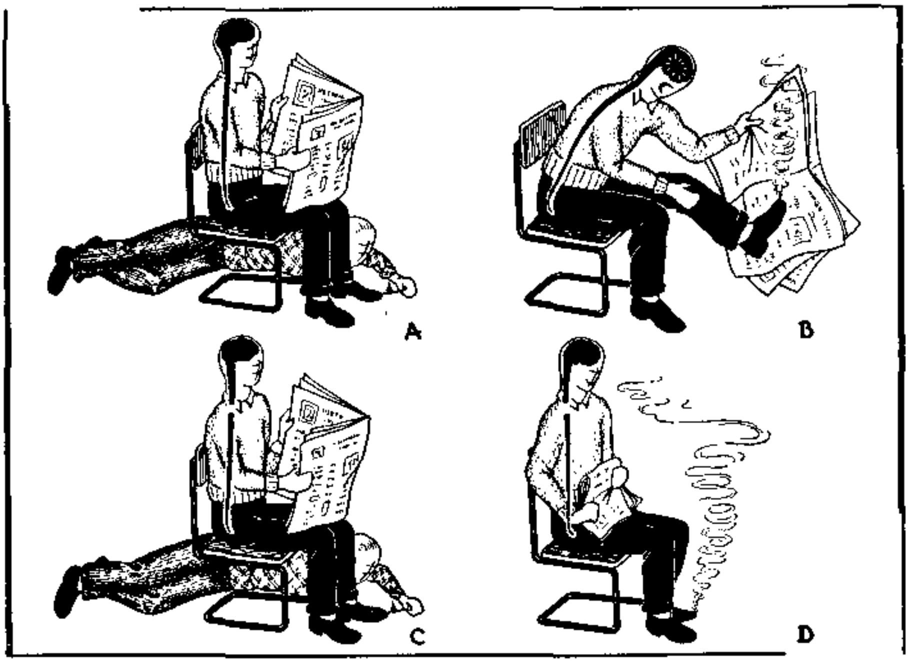

Fig. 10-6. When a "hot foot" is given to a normal man (A), he not only reacts, but *feels* (B). Sometimes, nervous connections between brain and spinal cord may be destroyed; note break in cord indicated in C. In such cases, stimulation of the foot may lead to reflex withdrawal (D), but the victim reports no feeling from the affected part.

To lay the groundwork for an understanding of the nervous system, we shall consider first a simple experiment and a simple question. A man is sitting in a chair. We apply a hot object to his foot. His foot moves suddenly away from the hot object. *Why does his foot move away from the stimulus?*

"Because," someone volunteers, "he feels the heat and moves his foot to get away from the objectionable stimulus." This reply raises two questions, one of which we will consider immediately.

Does he move his foot "because he feels the heat"? If we say so, we imply that consciousness of the sensation is the cause of the movement or, at least, that there must be consciousness before movement will be initiated. *This is not so.* We can make this denial with confidence as a result of the observation of the reactions of certain, fortunately rare, types of injured individuals. It occasionally happens, owing to war or accidental injuries or to disease, that the upper part of the spinal cord is more or less completely cut across. If the injury is extensive enough, the results diagrammed in Figure 10-6C and D can be obtained. When the injured man's leg is stimulated, it may be withdrawn, just as was the leg of the normal man, but the injured man maintains that *he doesn't feel a thing*. We may, of course, doubt his statement. (Consciousness is such a thing that *I* can never really know what anyone but *I* feels.) But those who work with such individuals for long always come to the conclusion that the subject really does not have any sensations coming from the region in question. Putting together the results of many such "spontaneous experiments," physiologists have found that only if a part of the body is connected by intact nerve fibers with the uppermost part of the central nervous system, the *brain* or **cerebrum,** is a man conscious of stimuli applied to the part in question. From this, it is concluded that "consciousness"—whatever we mean by that word—is centered in the cerebrum.

From this analysis, there follow two conclusions of importance:

First, when we ask, "Why does an animal's limb move thus and so in response to a stimulus?", we must *not* reply, "Because the animal feels." We do not *know* that the animal feels; and, more important, human data show us that feeling is not a necessary precursor of a response.

Secondly, because in humans the cerebrum is the seat of consciousness and because so many similarities have been found between humans and other animals, we do not hesitate to say that an animal with its cerebrum missing or not functioning has no sensations of pain or any other stimuli. This means that we can, with a clear conscience, experiment with animals that are *decerebrated* or that are under the influence of an anesthetic such as ether or chloroform, substances that, as human data tell us, stop the functioning of the pain-perceiving centers. Experiments with such animals cause no more pain than operations on humans, pain to which humans willingly subject themselves. Indeed, if the experimental animal is destroyed after the experiment without being brought back to consciousness, the experimental animal suffers far less pain than an operated-upon human, for the animal is not subjected to the postoperative pains, the only ones worth considering.

81. Reflex Action

Complex phenomena are best attacked bit by bit, reduced, if possible, to easily understood elements. With regard to the nervous system and its functioning, the simplest functional unit is what is called a *reflex action* or **reflex.** We are now in a position to understand this unit.

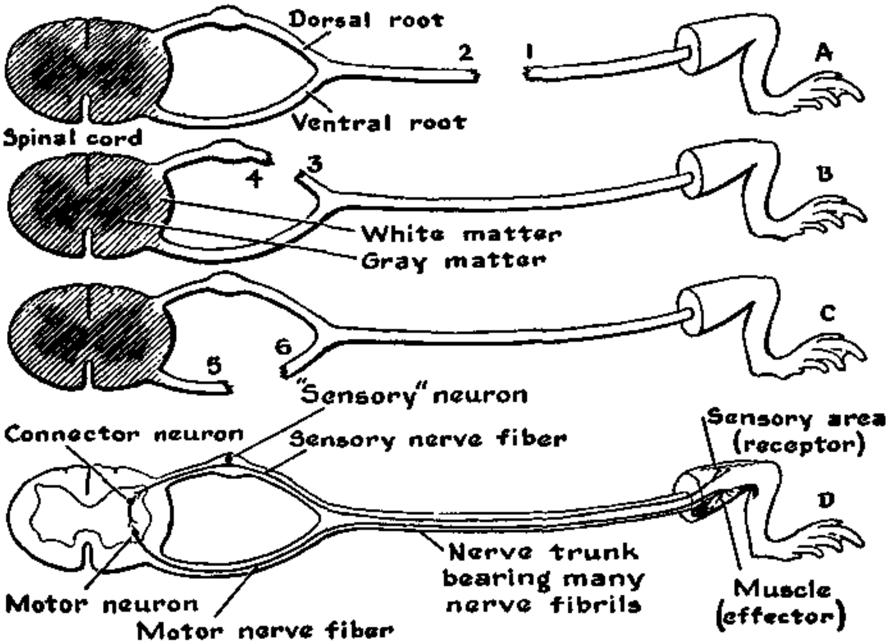

Fig. 10-7. In D, is diagrammed the reflex arc, the simplest unit involved in nervous reaction. Figures A, B, and C, together with the text, give the evidence for the existence of the reflex arc.

A reflex action consists of a simple response (e.g., the contraction of the leg muscle) following a simple stimulus (e.g., the application of heat to the sole of the foot). How much of the central nervous system is required for such a simple reflex? Experiments carried out with various animals show that only a small part of the central nervous system is required for such a reflex. Not only is the cerebrum unnecessary, but most of the spinal cord may also be discarded without destroying a given reflex. There is required only the small part of the spinal cord at the level where the nerve from the leg joins the cord. Close observation shows that the nerve is divided into two parts, one of which **(the ventral root)** is attached to the ventral part of the spinal cord, the other **(the dorsal root)** being attached to the dorsal side.* The function of these two "roots" is made clear by the following experiments (see Fig. 10-7):

Cut the main nerve trunk in front of the fork or bifurcation (Fig. 10-7A). Stimulation of the *distal* cut end (No. 1) with an electric current causes the leg muscles to contract. Stimulation of the **proximal** cut end (No. 2) causes no visible effect.

If, however, the cut is made through the dorsal root only of the bifurcated nerve (Fig. 10-7B), the results are different. Stimulation of the distal end (No. 3) causes no visible effect; stimulation of the proximal end (No. 4) causes the leg muscles to contract.

In another experimental animal (Fig. 10-7C), the ventral root of the nerve is cut. In this case, stimulation at point No. 5 causes no effect; at point No. 6 causes the muscles to contract.

From these and other experiments and observations, it has been deduced that **the dorsal root contains only "sensory" fibers,** nerve fibers that normally carry impulses from sensory areas (in the skin, for instance) to the spinal cord; and that **the ventral root contains only motor fibers,** nerve fibers that normally carry impulses only from the spinal cord to a muscle or gland.

Within the cord, there is evidently some connection between a "sensory" fiber and a motor fiber. The connection is not a direct one but always involves at least one other neuron called a **connector neuron.** This is the simplest possible mechanism involved in a reflex action and is called a *reflex arc.* The minimum elements involved are diagrammed in Figure 10-7D.

It must be emphasized that the diagram greatly simplifies the actual situation. One "sensory" neuron has contact with many connector neurons. Some of these connect with other levels of the spinal cord, ultimately with the brain itself. The impulse carried by a "sensory" neuron is, in part, transmitted to a nearby motor neuron and, in part, shunted to the sensory area of the brain. Only if this latter impulse can get through to the appropriate region of the brain, is any sensation

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* The adjective ventral is derived from the Latin *ventris,* belly. The ventral side is the belly side. Dorsal is from Latin *dorsum,* the back. *Distal* means away from, or farther from, the center or midline of an organism; *proximal* means close to, or closer to, the center of the organism.

experienced. It is for this reason that we have repeatedly enclosed the adjective *sensory* in quotation marks. The message carried by a "sensory" neuron results in a sensation only if many other neurons are also present and their connections intact.

82. Teleological vs. Mechanistic Explanations

We are now ready to return to the question asked in § 80, namely, *why* does an animal move his foot away from a hot object? An answer suggested there was: "He moves his foot to get away from the objectionable stimulus." Is this a satisfactory answer? It depends on what we mean by *why.*

By *why,* we may imply, "What purpose does the action serve?" or "What is the goal of the action?" This kind of *why* we may call the **teleological why,** the adjective being derived from the Greek *teleos,* end or goal. When we answer that the animal moves his foot *to get away from* the stimulus, we are giving a *teleological explanation.* Such an explanation is completely satisfactory to most laymen, though seldom acceptable to scientists. To understand why not, let us consider a different example:

"Why do the wheels of a car turn around?" Suppose, in reply to this, someone said, "The wheels of a car turn around in order to take the passengers somewhere." Teleologically, this might be a correct answer, yet everyone will grant that there is a sense in which it may be deemed a false answer. "The wheels of a car turn around because the combustion of gas in the cylinders moves the pistons, thus moving the connecting rods which cause the driving shaft to revolve which causes the wheels to turn." This is a better answer; it gives us an idea of the *mechanism* behind the movement of the wheels. It is a *mechanistic answer.*

Generally, when a scientist asks *why,* he implies a **mechanistic why.** Why does an animal move his foot away from a hot stimulus? "Because the stimulus causes an impulse to pass along sensory neurons into the spinal cord and then through connecting neurons to motor neurons which stimulate muscles which contract, thus causing the leg to move." This is a mechanistic answer. It is usually a better answer. The mechanism must be there for the action to take place. The existence of the

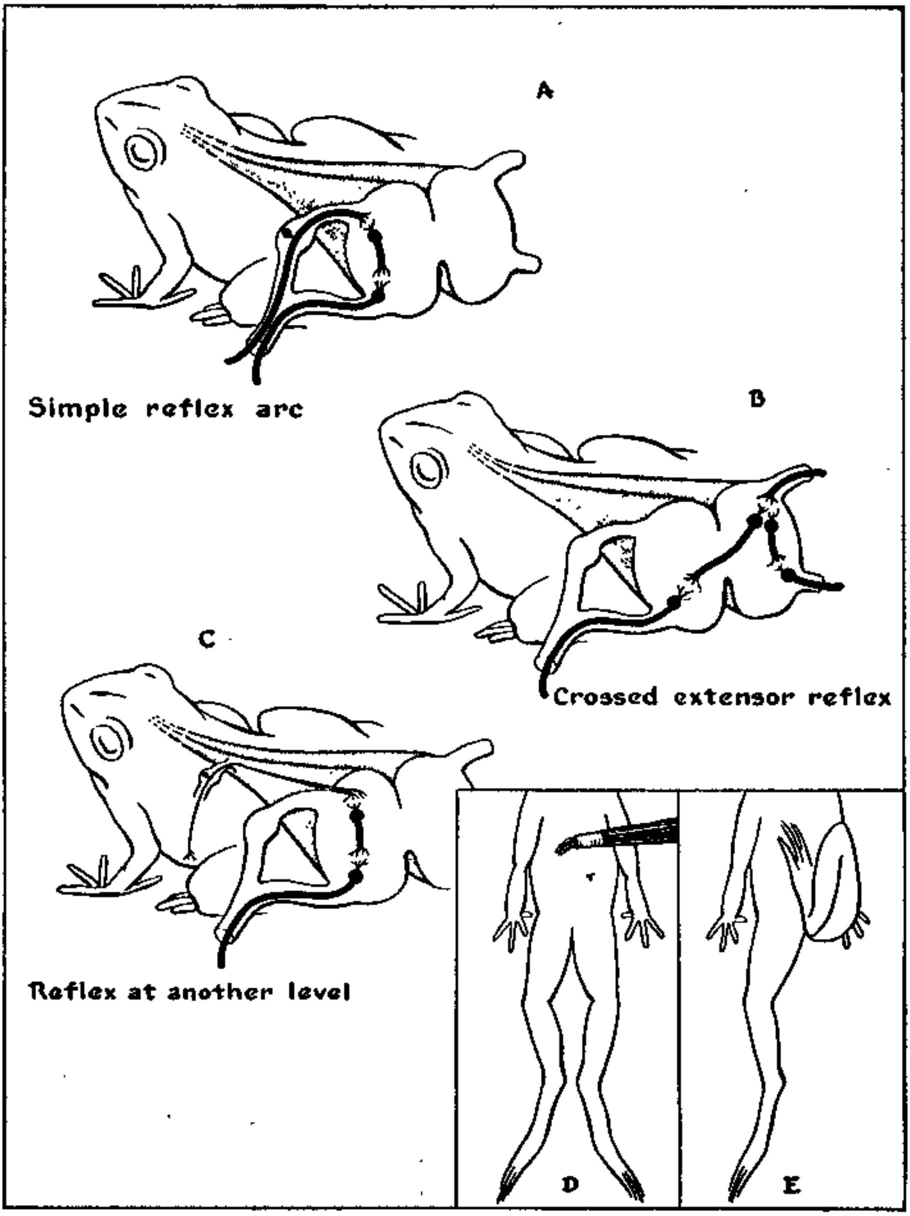

Fig. 10-8. These diagrams show only the neurons in use in each case. In A, the minimum elements of a simple reflex. In B, the minimum elements involved in a crossed extensor reflex, which usually involves motor impulses going to both sides of the body. The action indicated in E, following the stimulus shown in D, can be explained by the nervous connections shown in C.

slowly, the opposite leg may *extend*. The mechanism of a crossed extensor reflex is diagrammed in Figure 10-8B. The crossed extensor reflex is more complicated than the simple reflex in that it must involve synaptic connections between neurons on opposite sides of the spinal cord.

Another stage of complexity is made possible by connections between neurons *at different levels* of the spinal cord. If, using a frog that has been deprived of its brain, we apply dilute acid to the skin of the belly, a very remarkable thing happens. The hind legs of the frog rise and scratch at the belly *as if* the frog were trying to remove the noxious stimulus (Fig. 10-8D,E). Since all evidence points to the conclusion that the debrained frog has no consciousness or conscious aims, the apparent purposiveness of the action is most striking. This action is but another of the many innate reflexes. The teleology is obvious. The mechanism is indicated in Figure 10-8C.

The nervous pathways indicated are probable paths. The precise course followed by an impulse and the exact neurons involved are seldom entirely certain. The postulated pathways exist; but so do too many others. How can we be sure which pathway is the one actually taken? The trouble is not that we can't see enough pathways, but that we can see too many (Fig. 10-9). **Directly or indirectly, every neuron of the central nervous system is connected with every other neuron.** In each reflex act, however, only a small fraction of the possible connections are utilized. The central problem of neurology is to ascertain what determines which few of the many possible connections are utilized in a given action and why.

QUESTIONS AND PROBLEMS

10-1. Define: synapse, neuron, nerve fiber, connecting neuron.

10-2. Define the following pairs of terms so as to distinguish between the members: distal, proximal; afferent fiber, efferent fiber; sensory neuron, motor neuron; central nervous system, peripheral nervous system; stimulus, response.

10-3. Is the fiber attached to a sense organ an efferent or an afferent fiber? What about the nerve fiber that stimulates a muscle fiber?

10-4. Why is ignition of dynamite by means of a powder fuse slower than setting it off with an electrical firing system?

10-5. In what sense is a powder fuse a good analogy to a nerve fiber? Where does the analogy break down?

10-6. What are the two theories of the mechanism of intercellular transmission of impulses?

goal alone will not cause the action. The mechanism may subserve an end, but *the action is brought about by the mechanism, not by the goal.*

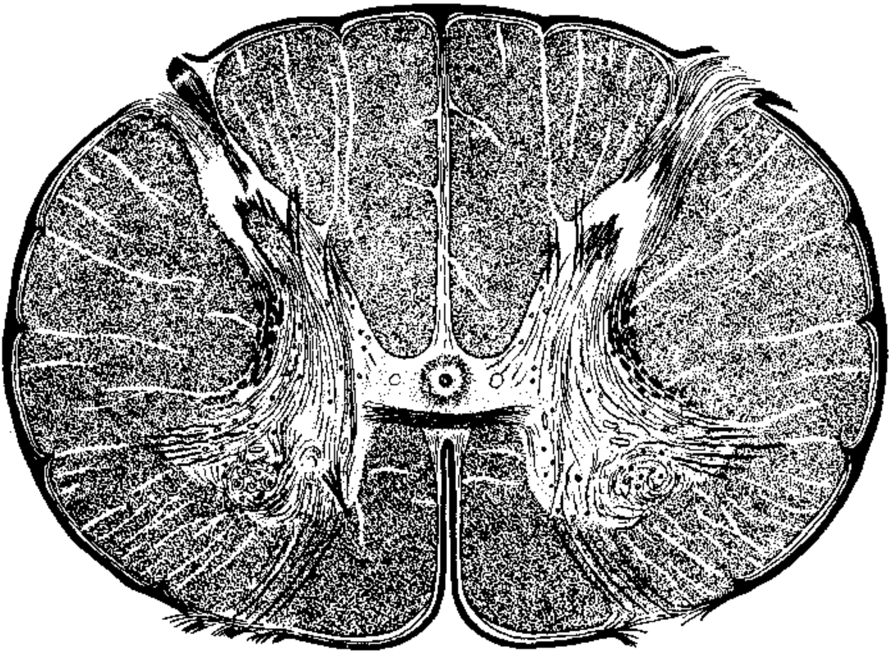

Fig. 10-9. The complexity of the central nervous system. Drawn from a thin cross section of the human spinal cord. Because nerve fibers do not, except by chance, lie always in a horizontal plane, no complete reflex arcs of the sort diagrammed in Figure 10-8 are to be seen here. Because the section is a thin one, the true complexity is minimized.

83. Innate Reflexes

A simple reflex action of the type just discussed does not have to be learned. It is either present from birth or develops later without learning. It is an **innate reflex.** A specific example of such a reflex is the well-known knee-jerk reflex. The stimulus in this case is the sudden stretching of a tendon by a sharp blow; this stretching affects specific sorts of nerve endings that are buried in the tendon. The message from these receptors, passing through a reflex arc, causes the contraction of certain muscles. We do not have to learn this reflex. (See Fig. 10-8A.)

But there are other innate reflexes that are not so simple as this. The **crossed extensor reflex** is an example of a slightly more complicated innate reflex. Under certain conditions, when one leg of, say, a frog, is strongly stimulated, not only does this leg *flex* (draw up), but, more

10-7. For other discussions of the problem of vivisection read:

(1) The preface to G. B. Shaw's *The Doctor's Dilemma*. New York: Brentano's, 1911.

(2) Hughes, Helen MacGill, "The Compleat Antivivisectionist." *The Scientific Monthly*, 65:503-507, Dec. 1947.

Although these two authors are in opposing camps, in what regard do you detect essential agreement between them?

10-8. From the information given in the text, from the general proposition that all mammals are constructed pretty much alike, and from examination of Figure 10-10, you should be able to answer the following question: "How long is the longest cell in a giraffe's body?"

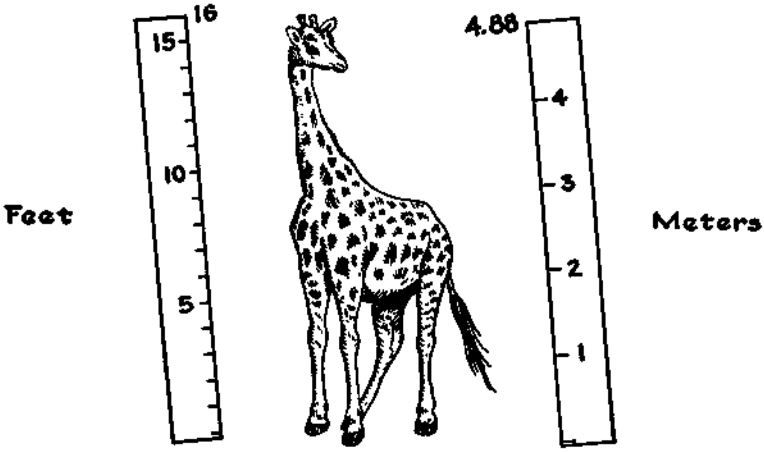

Fig. 10-10. A giraffe, looking for the answer to problem 10-8.

Tell how you arrived at your answer.

10-9. When whole neurons degenerate in an adult, there is no recovery. Assuming that we are dealing with a case of neuron degeneration, the degeneration of what neurons could account for the following cases?

Case 1. The individual's legs are without feeling. He can move them but he can't feel anything with them, not even their own movement.

Case 2. The individual's legs are paralyzed. Feeling is present but no movement is possible.

10-10. By definition, distinguish between teleological and mechanistic explanations.

10-11. One of the two types of "whys" mentioned in the text (§ 82) can frequently be replaced by the word "how." Which one?

10-12. The present chapter ended with a "why." Do you think this was intended to be a mechanistic why or a teleological why?

10-13. De Maupassant's often reprinted story, "Moonlight," is built around a "why." What is the "why" and to which class of "whys" does it belong?

10-14. Science is usually concerned more with which sort of "why"? What other fields of human endeavor are concerned with the other sort?

Chapter XI

The Senses

84. The Sense of "Touch"

It is a matter of popular belief that there are five senses: touch, smell, taste, sight, and hearing. How inadequate this analysis is becomes apparent when we analyze the so-called sense of touch.

A simple experiment which the reader can perform on himself (or better, have someone else perform on him) will demonstrate the multiple nature of the so-called sense of touch. With a little care, one can rule a grid of squares on the back of a hand (see Fig. 11-1A), with the lines two millimeters apart. Then, if one uses some sort of stylus, a metal instrument with a tip a bit smaller than a pin's head, one can explore the area systematically for sensitive spots. If the stylus is at "room temperature," it will be colder than the skin and one can use it as a test for cold-sensitive spots. Some spots will easily detect the coolness of the stylus, others not at all. A record can be made on crosshatched paper of the distribution of "cold spots."

A similar record can be made of warm-sensitive spots, using a stylus gently warmed in a flame. When this record is compared with the preceding one, it is discovered that the "cold spots" and the "warm spots' sometimes coincide and sometimes do not. In other words, the sense of cold and the sense of warmth are two different senses.

In carrying out this test, the experimenter will have noticed that a cold stylus placed on a cold-sensitive spot feels cold only momentarily. Why is that? Does the stylus warm up? Or does the spot respond only to change in temperature?

The stylus undoubtedly warms up; one could, by a suitably elaborate apparatus, eliminate this difficulty. However, popular experience would allow us to predict that, even with a thermostatically controlled stylus, the skin would soon become insensitive to a particular temperature for we have all noticed how a slightly-warmer-than-normal or slightly-colder-than-normal temperature soon feels normal to us. A simple experiment that dramatically illustrates the point is diagrammed in Figure 11-1B,C. Three buckets are filled with water, one with warm, one with medium, and one with cold water. The experimenter immerses his right hand in the warm, his left in the cold and leaves them there for perhaps a minute, at the end of which time the sensations of hot and cold have almost disappeared. Then he places both hands in the center bucket at room temperature. Although both hands are subjected to the same temperature, the left hand reports that the water is warm, and the right hand

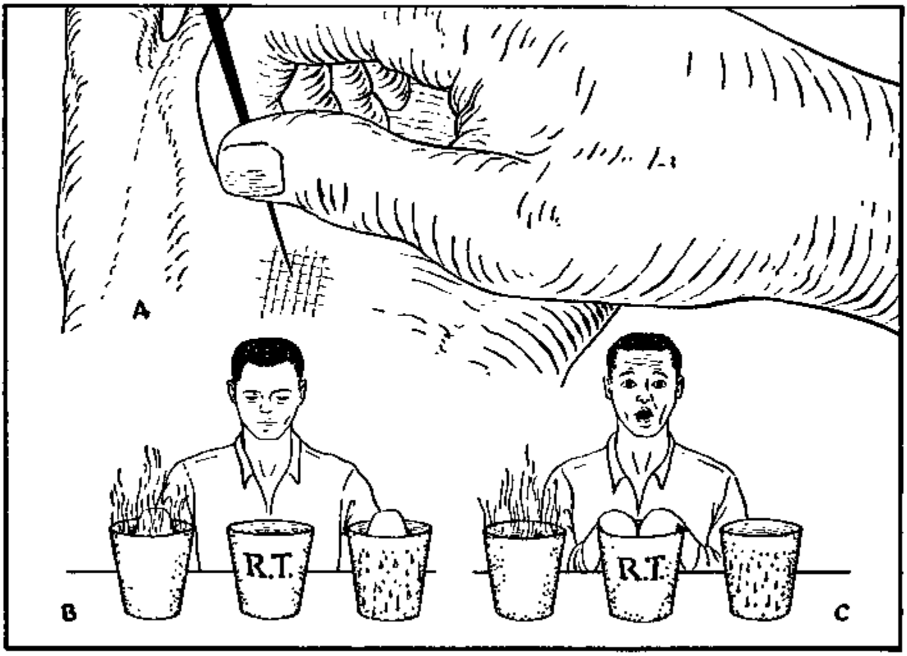

Fig. 11-1. A, a simple way to analyze the sense of touch into its component senses, as described in the text. B and C, a simple experiment which proves that one's senses report changes in stimulating conditions rather than absolute values.

that it is cold. From this, we learn that the cold spots and warm spots are not sensitive to cold and warmth as such, but to changes. Sensitivity to *change* rather than to *absolute state* is a characteristic we shall find in the other senses.*

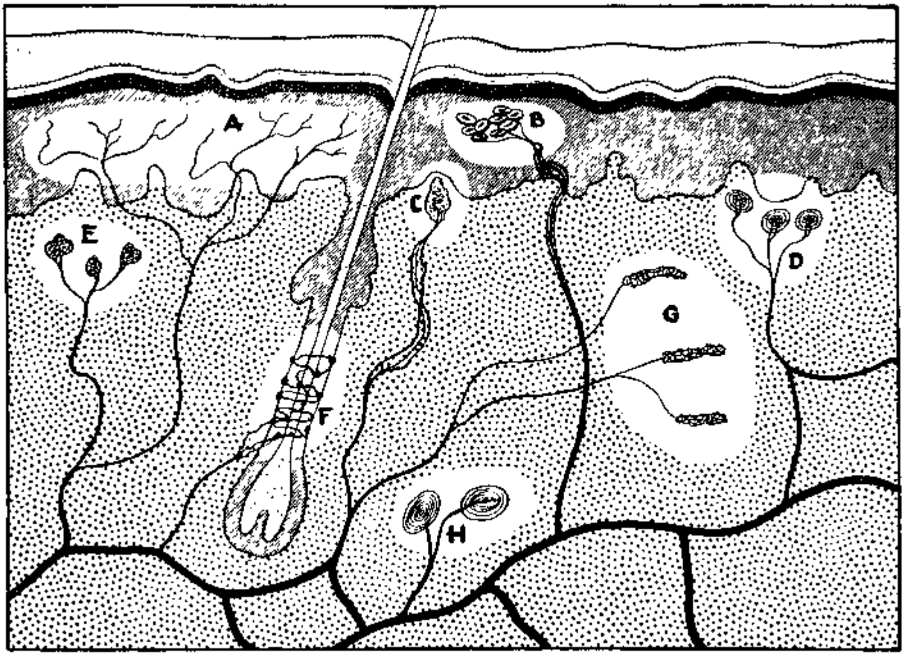

Fig. 11-2. Distinguishable nerve elements in or near the skin. The names and probable functions follow: A, free nerve endings: *pain.* B, Merkel's discs: *touch.* C, Meissner's corpuscles: *touch.* D, Krause's end bulbs: *cold.* E, Ruffini's end organs: *warmth.* F, follicle nerve plexus: *touch of hair.* G, endings of Ruffini: *pressure.* H, Pacinian corpuscles: *pressure.*

It should be noted that most of these structures are named after men. Such naming is typical in a new field of study, or when structures are difficult to observe and have been seen by only a few men, or when the exact structure and function are matters of dispute. However, the histology of the senses of touch is not a new field.

Sensitivity to cold and warmth are part of what is popularly called the sense of touch. There is also sensitivity to touch in the strict sense. To test this, the experimenter uses a single bristle mounted in a holder. A bristle of a given diameter will exert only so much pressure before it bends, and

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* These temperature receptors are extraordinarily sensitive to change. A rise in temperature—at the level of the sensitive nerve endings under the skin—of only 0.001° C per second, continued for three seconds, will give a sensation of warmth. The cold spots are only one-fourth as sensitive.

never more; consequently, it can be used for administering a standard stimulus. With such a bristle, one can map the touch-sensitive spots, and it is found that they are distributed independently of the warm and cold spots.

Yet a fourth sense constitutes a part of the sense of touch—the sense of pain. This can be readily tested with a needle-sharp instrument. The map of pain-sensitive spots once more shows independent distribution. Pain-sensitive spots are more closely spaced and more widely distributed over the body than are any of the other spots, a fact which is, no doubt, of value in insuring the survival of the individual in a dangerous world.

What is the structural basis for the different touch sensations? Microscopic study of sections of skin shows a number of recognizably different nerve endings (Fig. 11-2). It is natural to guess that the different kinds of nerve endings subserve different sensations. It is difficult to prove this. One can readily appreciate why it is difficult when one recalls the nature of the phenomena we are investigating, namely, phenomena called **subjective**—phenomena known only by the subject himself, and not identifiable in external objects as are **objective** phenomena. The sensations of warmth and cold can be reported only by a human, so animal experimentation is ruled out. Obviously, the curious experimentalist must use himself as the experimental animal, and this a few courageous men have done, first mapping the distribution of various spots on the skin and then having the section of skin sliced off and examined microscopically for the distribution of the various types of end organs and trying thus to correlate sensitivities with presence of end organs. Unfortunately, the results of such experiments have not always been consistent. The most widely held theories are indicated in the legend of Figure 11-2.

Only one type of end organ has had its function established for certain—the so-called **free nerve ending**—which subserves the sensation of pain. Establishing this fact was made possible when it was observed that the central area of the cornea (the transparent, central outer surface of the eye) perceives only pain. Since this was true for all men, it was not necessary for the experimenter to sacrifice his own eye, since the eye of any deceased person would do. Examination of this region of the eyes of cadavers disclosed the presence of free nerve endings only. As would be demanded by the ubiquitous distribution of pain spots over the body, free nerve endings are also ubiquitously distributed.

In this account, the nature of touch sensations has been somewhat simplified. For one thing, many students believe that there is another skin sense, one of pressure, distinct from touch in the strict sense. The nature of the hypothetical organs sensitive to this stimulus is shown in Figure 11-2. Moreover, we experience many sensations that are not easily identifiable as any of these simple sensations, e.g., stinging, burning, or itching sensations. Consider also the sensations caused by tickling and by an electric shock. It is possible that these sensations are curious mixtures of several of the fundamental sensations.

One must realize also that a sense spot of a named type may be sensitive to more stimuli than its name would indicate, provided the stimulus is great enough. For instance, a very hot object will be *painfully* so, due in part to its affecting the spots that we ordinarily regard as pain-receptors rather than heat-receptors. Heat may also affect the cold-receptors, paradoxical as this may seem; recall the shiver that often accompanies one's sudden immersion in a tub of hot water. The shiver and the sensation of cold come before the sensation of warmth; notice in Figure 11-2 that *Krause's end bulbs*, the supposed mediators of the sense of cold, are closer to the surface of the skin than are the *Ruffini organs*, the probable mediators of the sense of warmth.

Another paradox of sensation is the observation that pain itself may sometimes be enjoyable, in a sense. Who does not recall, from the days of his childhood, at least, the irresistible desire to remove the scab from a superficial wound, painful though it was. Again, the mild pain of muscles, "stiff" the day after unwonted exercise, is at the same time an enjoyable sensation to many people. Not all observers will agree to this statement, and it may be that there are differences among individuals. In this connection, one wonders about the sensations of the Indian fakir reclining on his bed of nails. Is he merely relatively insensitive to pain (as American Indians and successful pugilists are purported to be), or does he actually enjoy his prickly couch?

85. Subjective Characteristics of Exteroception

The various touch senses are among those that are sometimes referred to as the **exteroceptive senses** (exterior perception), the senses which give us information about the exterior world, as contrasted with other senses, to be discussed subsequently, which give us information about our own interiors.

It should be noted that even these exteroceptive senses do not really give us information about the external world, but only about our own insides very close to the surface. A warm spot does not tell about external warmth, but only about the temperature changes taking place in the sensitive end organ itself, which is buried under our skin. Subjectively, however, we refer the feeling to the outside and say, "This room is hot," though it would probably be more accurate (though more pedantic) to say, "My Ruffini end organs detect an increase in temperature." Upon contemplating this situation, we may give intellectual assent to this point of view, but it is doubtful if our feelings about the matter will change.

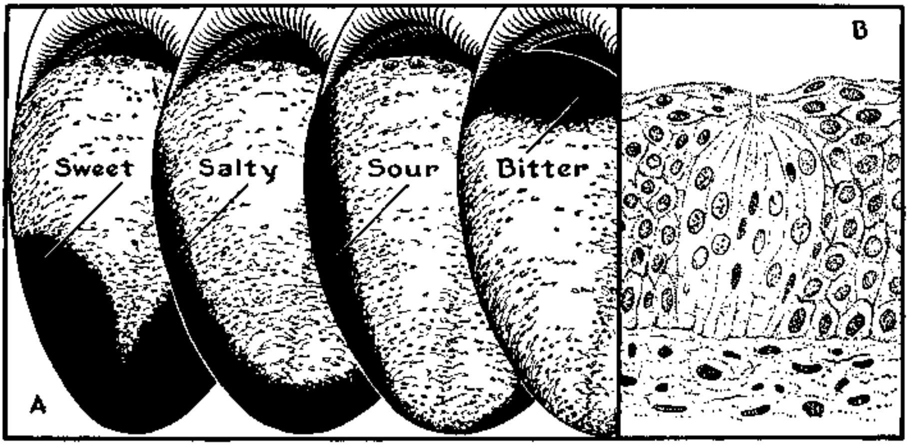

Fig. 11-3. In A, the areas most sensitive to the different taste qualities are indicated as black areas on the surface of the tongue. In B, a magnified section of a taste bud.

The sense of touch operating through the hair follicles gives a striking example of our false localization of the source of a stimulus. When the hairs of the arm are lightly moved with a pencil, without touching the skin, one gets a distinct impression of feeling the pencil with the hair itself. Yet, all the hair which protrudes from the skin is dead. It can be cut without pain. And if we hold the basal portion of a hair steady with some tweezers, movement of the distal portion gives rise to no sensation. The hair itself is not sensitive. The sensation arises when the shaft of the hair, moving in its *follicle* (sheath) touches the nerve net that surrounds it (see Fig. 11-2). This mechanism is a convenient way of extending the sense of touch beyond the limits of the living body by means of nonliving tissue. An exaggerated instance of such a mechanism is seen in the long "whiskers" of a cat which serve as a sort of short-range radar to enable the cat to get around in tight, dark places. No doubt, if we could interview a tomcat, he would maintain stoutly that he felt at the end of his whiskers.

86. The Sense of Taste

Much of what we call taste is actually smell, as we learn on those rare occasions when a really severe cold completely plugs up the nasal passages. When so afflicted, we discover that we can still taste a few things: **sweet, salt, sour,** and **bitter.** All the various "tastes" that we ascribe to food are made up of combinations of these four primary tastes plus, most importantly, odor detected by the nose. Deprived of our sense of smell, we have difficulty distinguishing an onion from an apple.

The various taste sensitivities are differently distributed over the surface of the tongue. If one uses the least strong solution (of sugar, salt, citric acid, or quinine) that will elicit taste sensations, it has been found that the areas sensitive to the various substances are as shown in Figure 11-3A. This does not mean that the substances cannot be tasted everywhere on the tongue—they can—but that the sensitivity varies. The sensitivity to quinine, for instance, is six times as great at the back of the tongue as it is at the tip. This helps explain, of course, the frequent experience of noticing a bitterness in some food or drink only as an "aftertaste," that is, after swallowing. Also involved in this experience may be a slower response to the sensation of bitterness.

Research has disclosed that there are considerable differences between individuals in their sensitivity to taste, as one would predict from common knowledge. More striking, is the discovery that these differences are not merely of a *quantitative* sort, but are also sometimes *qualitative.* The chemical substance, phenylthiocardamide (PTC, for short) tastes bitter to about 7 persons out of 10; to most of the others, it has no taste at all; a few report it as sweet or salty. The uncommon sugar *mannose* tastes sweet to only about 20 per cent of our population; 10 per cent find it bitter; and 55 per cent experience a sweet taste followed by a bitter taste. The remainder say it is tasteless.

Using pure chemicals, a number of other taste differences have been found. Undoubtedly, differences in taste reactions to pure chemicals are among the factors contributing to differences in judgments of the palatability of various foodstuffs and dishes. The old saying, "There's no disputing tastes," has been given new support, though conscientious gourmets will be the last to admit it.

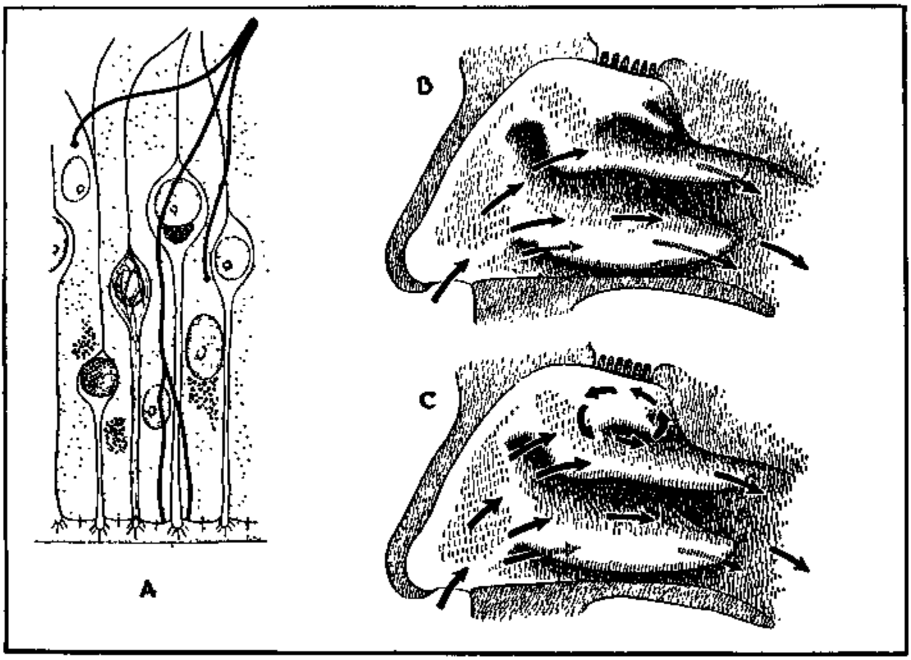

Fig. 11-4. The olfactory nerve endings (A) are so placed high up in the nasal passages that a gentle inspiration carries little air past the olfactory tissue (B). A vigorous sniff (C) brings a good sample of air past the sense organs.

The end organ responsible for the ability to taste is the **taste bud,** a cluster of cells sunk in the surface of the tongue (Fig. 11-3B). Taste-localization experiments suggest differences in these sensory organs. Microscopic examination fails to reveal such differences.

87. The Sense of Smell

The four taste sensations are evoked by substances that are, for the most part, nonvolatile, that is, substances not present to an appreciable extent as vapor in the air. The nose, however, is sensitive to a multitude of volatile substances. For that reason, the sense of smell, or *olfaction*, is unquestionably the more important of the two for most animals. With it, one can detect danger or delectation at a distance and react accordingly.

The amount of substance that can be detected is extremely small. Measurements have shown that as little as 0.000000000002 of a gram of a nauseous chemical called mercaptan will affect the nose. However, it is worth pointing out that even this weight, which seems small by everyday standards, contains more than 200,000,000,000 molecules of the garlicky-smelling substance.

The nose is sensitive to many more different qualities than is the tongue. There is unquestionably some correlation between chemical structure and quality of odor, though the relations are not simple enough to permit predicting the one from the other with complete accuracy. A good organic chemist, however, finds his nose invaluable in cutting down the amount of his analytical work.

Are the multitudes of smells reducible to combinations of some simple, unitary odors? Many attempts have been made to develop systems of odor elements analogous to the four primary taste sensations, but without very convincing success. One of the systems proposed recognizes four primary odors: fragrant, vinegary, burnt, and rancid, with 0 to 9 being used to represent various degrees of each odor quality. According to one observer, the odor of a rose would be represented as 6423 in this system, the 6 standing for the amount of fragrance, 4 for the amount of vinegariness, and so on.

The end organs of the sense of smell are nerve endings modified as shown in Figure 11-4A. The placing of the **olfactory tissue** is remarkable. There is only about 2.5 sq. cm. of sensitive tissue in each nostril, and it is placed high up in the breathing passages, so that an ordinary, gentle breath causes very little air to go past the sensory cells (Fig. 11-4B). A vigorous breath (Fig. 11-4C) will, however, develop a turbulence that will carry some air past the olfactory tissue. Hence, the importance of *sniffing* when we suspect we are in the presence of something worth smelling.

88. The Fatigue of a Sense, as Illustrated by the Olfactory Sense

In discussing the sensitivity of the temperature receptors of the skin, it was pointed out that the receptors are really sensitive only to *changes* in temperature, that when an area is long exposed to a constant temperature, it ceases to be "aware" of that temperature. Another way of verbalizing the same phenomenon is to say that the sense of temperature becomes *fatigued.*

The development of fatigue is characteristic of all the senses, to a greater or less degree, except possibly the sense of pain. (Though one can become *accustomed* even to pain.) The phenomenon of fatigue of the olfactory sense is both conspicuous and practically important.

When we first step into a bakery shop, the olfactory experience is, for most people, one of pure delight. But, if there are many customers ahead of us, by the time we are waited on our perception of the odors has diminished almost or quite to the vanishing point. After perhaps ten minutes' sojourn in the bakery, we might just as well be in a machine shop for all the pleasure we get from the odor. This fatigue of the olfactory sense, it can be shown by experiments, is not a general fatigue. Subjection to the bakery odor does not dull the nose to other, fresh odors. Though there are exceptions, olfactory fatigue is usually specific for each odor. This fact, together with the fact that most of what we call "taste" is actually smell, explains many of the practices of the gourmet, e.g., the preference given to the multicourse banquet over the one-dish meal.

Fatigue to *un*pleasant odors is probably a fact of greater importance. It is common practice for domestic gas companies to add malodorous substances to the gas supply. These substances are detectable in very small quantities and serve to warn the home-owner when a leak has developed in his gas lines. However, if the leak develops slowly and steadily while he remains at home, the fatigue of the olfactory sense may keep pace, so to speak, with the increase in concentration of gas in the room and, as a result, he may be asphyxiated without his nose ever warning him. However, before the dangerous level is reached, should a friend visit him, he might be warned by the friend, whose nose would be subjected to a sudden increase in concentration of odor.

The fatigability of the olfactory sense may even have international consequences. Some white Occidentals speak disparagingly of the odors of humans of other racial groups, the implication being, "Of course, *we* don't smell." However, white people who have spent much time in China sometimes learn to their horror that the Chinese consider them distinctly odorous in an objectionable way. This is a fact that a man can never discover about himself because of the phenomenon of olfactory fatigue. How can one smell the body he has lived with all of his life? There is probably nothing white people can do about their affliction—though frequent baths may help minimize the offense*—but it is a fact that they should always keep in mind in their dealings with other peoples.

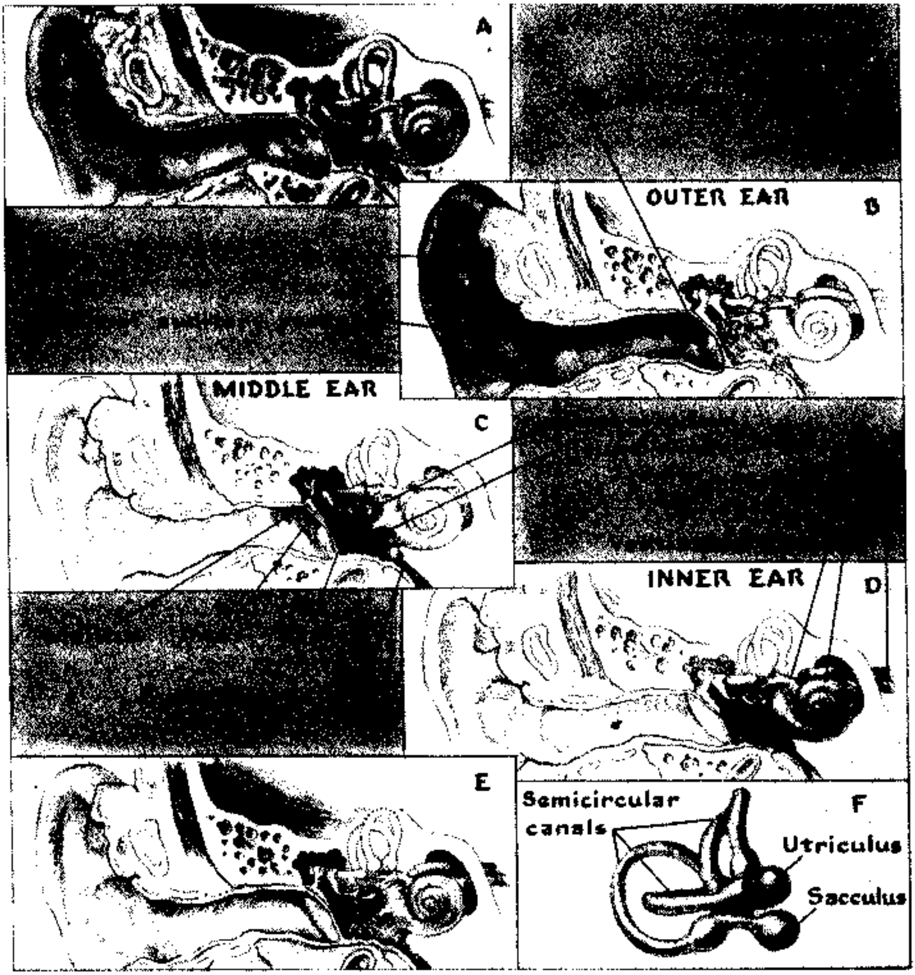

Fig. 11-5. The parts of the ear.

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[*] It has also been suggested that the odor of Occidentals is due to their diet, which is different from that of the Chinese, containing proportionately more meat and fewer vegetables. This is a question requiring more research.

Satisfactory international relations require more than good will; self-awareness is also a necessity.

89. The Sense of Hearing

That which is the primary function of the ear, we shall ignore for the present, namely, its function as an organ of equilibrium. In the primitive vertebrates, the ear was only an organ of equilibrium; the auditory function was assumed much later in evolutionary development. In man, the ear serves both functions. The parts concerned with equilibrium, the semicircular canals, may be seen in Figure 11-5D. For the present, they will be ignored and only the auditory structures and functions will be considered.

For convenience, the ear is considered as consisting of three portions called the outer, middle, and inner ears (see Fig. 11-5). The **outer ear** consists of the decorative flap on the outside of the head, called the *pinna* (Greek, a kind of mussel, evidently because of the resemblance between a mussel half-shell and our ear), and the **external auditory passage** leading inward. In so-called lower animals, the pinna serves as an admirable trumpet to collect and concentrate the sound waves. In most animals, it can be moved or turned so as to be most favorably oriented toward the source of the sound. Recall, for instance, the mobile pinnae of horses and mules. Among men, only a few virtuosi can move their ears at all, and then to little or no acoustic advantage. To achieve the sound-gathering effect of a large animal pinna, a man may cup his hand behind his ear and aim the concavity at the source of a sound. This act is especially useful to the hard of hearing.

The problem of hearing is one of concentrating and transmitting vibrations. What we call *sound waves* consist of alternate regions of concentration and rarification of air molecules. These waves move at a speed of about one-fifth mile per second (though the individual molecules often move very little—just as the particles of water in a pond move very little as waves pass over the pond). The pinna concentrates the waves somewhat and directs them down the external auditory passage at the end of which they strike the **tympanum** or eardrum. In this way, wave motion of the air is translated into vibratory motion of the solid material that constitutes the tympanum (Fig. 11-5B).

Following the route of this vibration, we are taken next to the middle ear cavity, an air-filled space in which repose three bones hinged together, the **malleus**, the **incus**, and the **stapes** (i.e., the hammer, the anvil, and the stirrup, from their resemblance to these objects). The first bone, the malleus, is attached to the tympanum; the last bone, the stapes, is attached to a similar membrane at the other side of the middle-ear cavity, the so-called **oval window.** The path of the vibration so far is this: air waves striking the tympanum move it; the tympanum moves the malleus, which moves the incus, which moves the stapes, which moves the membrane of the oval window. What does the oval window move?

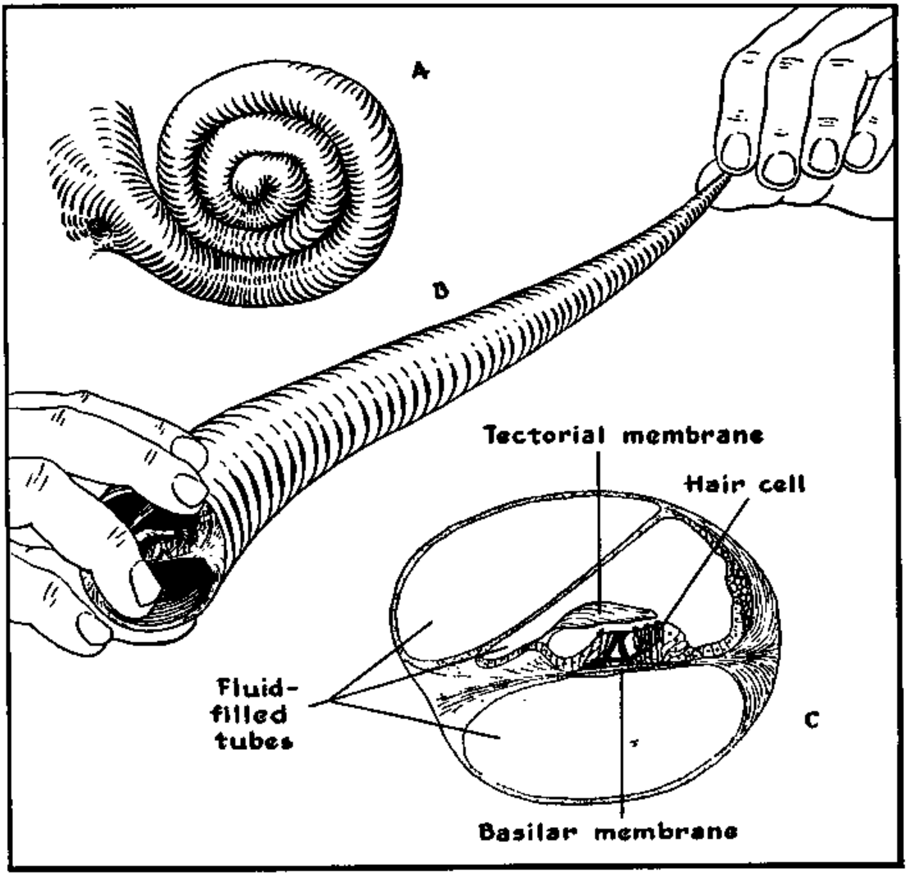

Fig. 11-6. The cochlea (A) of the ear. Imagine the cochlea to be much enlarged and uncoiled (B); a cross section of it shows the structures shown in C.

The oval window forms the boundary of the inner ear. The inner ear is the actual organ of hearing*; it is here that mechanical vibrations are converted into nerve impulses. All the rest of the machinery of the outer and middle ear is merely for the purpose of conveying the vibrations to this region.

The inner ear is filled with fluid. When one recalls that fluids cannot be compressed (hence the effectiveness of hydraulic brakes), it will be realized that the pressure exerted by the stapes against the oval window must somehow be relieved. The relief mechanism is the membrane called the **round window.** Vibration of the oval window causes the fluid within to vibrate, which in turn vibrates the round window. The round window apparently has no other function.

The part of the inner ear concerned with hearing is called the **cochlea** (Latin, snail). How does the vibration of the fluid in the cochlea give rise to sensations? We can understand the mechanism better if we, in imagination, straighten out the cochlea (Fig. 11-6B), then, slice across it and examine the slice under the microscope (Fig. 11-6C).

A section of the cochlea shows more detail than we need assimilate in our first observations. The most important part for the present discussion is in the center and consists of a flexible ledge called the **tectorial membrane** (Latin, *tectorium*, a cover) which overhangs hairs attached to nerve cells. Observation with experimental animals shows that when sound waves reach the ear, nerve impulses pass along the nerves which come from the hair cells below the tectorial membrane. How can a sound stimulate these cells?

At this point, we must enter the realm of hypotheses. Experimentation presents so many difficulties that we have not yet proved the mechanism of hearing. The picture presented below is supported by considerable evidence of an indirect and involved nature, even if it is not completely established.

The **basilar membrane,** on which the nerve cells rest, is flexible. It seems reasonable to suppose that vibration of the fluid of the cochlea will cause vibration of the basilar membrane. Vibration of the membrane will move the hair cells up and down; this movement of the hair cells

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* Also, part of it is concerned with equilibrium—but we are ignoring that for the present.

will press them against the tectorial membrane, thus stimulating the hair cells and causing a nervous impulse to travel along the nerve. (Notice that if this theory is true, the sense of hearing is only a highly modified sense of touch, evoked by touching the cochlear hair cells.)

There are many phenomena for which any adequate theory of hearing must account. One of these is pitch discrimination. We can tell the difference between a high note and a low one. How do we do it? The evidence clearly indicates that different parts of the cochlea are sensitive to tones of different pitch. The basal region, i.e., the region nearest the middle ear, is sensitive to the highest tones; the apical region, to low tones. This difference in sensitivity is apparently determined by the *tension* of the basilar membrane in different parts, the membrane being stretched tighter in the basal region and, hence, *resonating* to higher notes in this region.

That, in brief, is the present theory of hearing. In broad outlines, it seems to fit the facts well. In details, it is incomplete. The above theory regarding the mechanism of tone discrimination is reasonably convincing. A theory of hearing must account for some very remarkable facts. For example, the normal human ear can discriminate several thousand pure tones. Moreover, when two or more pure tones are sounded simultaneously, our ear can detect the fact and, with training, can analyze the mixture into separate components.*

The adult human ear can distinguish tones ranging from that produced by 20 vibrations per second (a low note) up to 12,000-15,000 per second (high notes). There is much variation in the upper limit, and children can commonly detect higher tones. Many animals can detect much higher notes, and use is made of this fact in the design of "silent dog whistles" which produce a note that is inaudible to the human ear but audible to the canine ear.

90. Types of Deafness

Three types of deafness are distinguished: *transmission deafness*, *perception deafness*, and *central deafness*. The salient features of these can be best

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* At least, most people can do this by a matching procedure. Persons gifted with "absolute pitch" can *name* the component notes without recourse to matching.

understood by again referring to Figure 11-5. By deafness, we mean any degree of deafness from slight to complete.*

Transmission deafness is caused by some obstruction or fault in the transmitting apparatus of the outer and middle ears. The simplest cause is accumulated wax in the external auditory passage, sometimes found in uncared-for children. The remedy is obvious. More serious is it when there is damage to the middle-ear machinery. This is a not uncommon aftermath of a serious infection of the breathing passages. The route of the infection can be seen from the diagram. Disease germs in the throat region can pass up the **Eustachian tube** to the middle ear where the invaders set up an infection. This infection may result in the accumulation of pus in the middle-ear cavity, exerting pressure on the tympanum, causing pain. In such cases, the physician may make a tiny puncture in the tympanum and drain the cavity. A small hole in the eardrum will almost always heal rapidly and completely. If this operation is not performed, the infection may destroy the middle-ear bones or the eardrum. In either case, there will be considerable impairment of hearing. Fortunately, hearing aids are of great benefit in cases of transmission deafness.†

Perception deafness might better be called *inner-ear deafness*, as it refers to deafness resulting from defects in the cochlear apparatus, e.g., in the basilar membrane, the hair cells, or the nerves. Frequently, only part

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* Considered here are only those forms of deafness that may be called **organic** deafnesses, i.e., ones due to determinable defects of organs. Besides organic types of deafness, there are also **functional** deafnesses, conditions in which no organic defect is present, though the individual nonetheless cannot hear. A functional ailment is part of a psychological difficulty. There are functional diseases imitating every organic disease known, including deafness, blindness, and paralyses. A few words bearing on the causes of such conditions will be found in § 95 but, for thorough discussions, the student is referred to textbooks of psychology and psychiatry.

† The use of hearing aids is, fortunately, increasing rapidly—fortunately, because there are so many people who need them but who hesitate to use them out of mistaken pride. It is a curious fact that social acceptance of hearing aids has lagged so far behind that of seeing aids. A generation ago, the use of spectacles was very unpopular among young females; today, due to clever design and advertising, wearing certain models is not only permissible, but is almost *de rigeur* in certain circles. In recent years, more thought and effort have been applied to the design and advertising of hearing aids with the good result that their use is spreading. This is fortunate because the psychological effects of poor hearing are at least as important, if not more so, than the effects of poor seeing. Poor hearing is all too frequently accompanied by a gnawing feeling that *other people are talking about me.*

of this apparatus is damaged, and as a result, only part of the perceptive ability is lost. A small region of the cochlea may be injured and, concomitantly, the perception of pure tones in a certain region of the scale

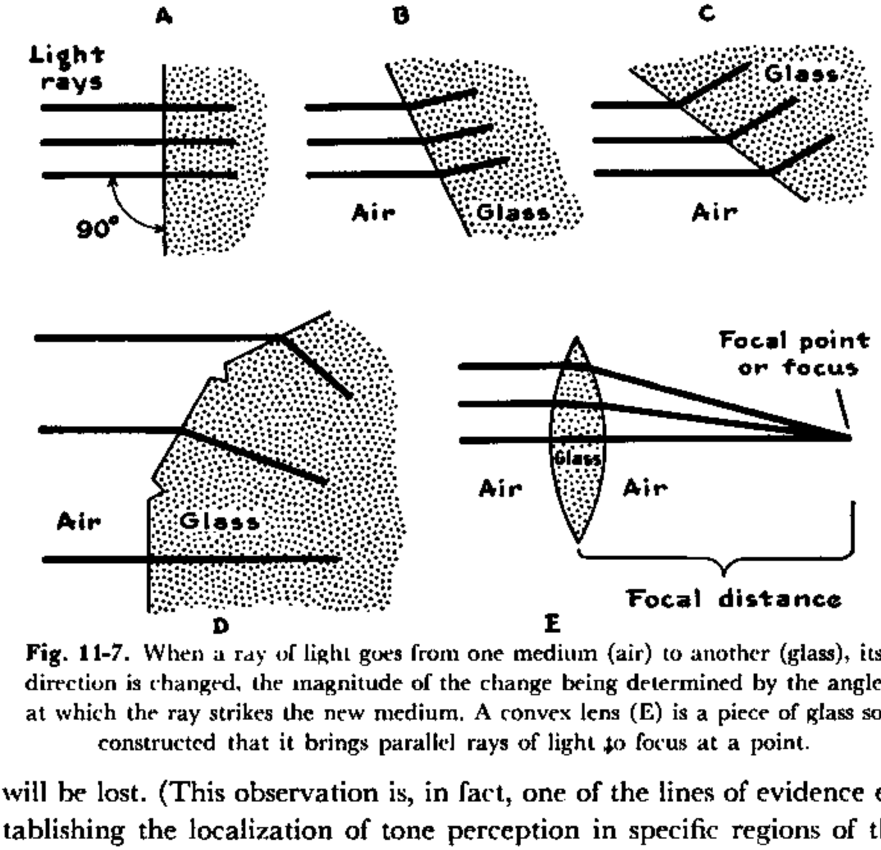

Fig. 11-7. When a ray of light goes from one medium (air) to another (glass), its direction is changed, the magnitude of the change being determined by the angle at which the ray strikes the new medium. A convex lens (E) is a piece of glass so constructed that it brings parallel rays of light to focus at a point.

will be lost. (This observation is, in fact, one of the lines of evidence establishing the localization of tone perception in specific regions of the cochlea.) Normal aging results in progressive loss of perception of high tones. Hearing aids are of no benefit for any type of inner-ear defect.

Central deafness is the term applied to deafness in which there is no defect in the outer, middle, or inner ear. Such deafness is due to some deficiency in the part of the central nervous system with which the auditory nerves are connected. Hearing aids are of no use.

91. The Sense of Sight

Probably the best way to understand the eye, the organ of sight, is to compare it with a camera. To do this, we must understand a few simple physical facts about light.

Light travels in a straight line (Fig. 11-7A) as long as it does not change from one "medium" to another, i.e., from air to water, air to glass, etc. The straightness of a beam of light is easily seen in a shaft that enters a darkened, dusty room through a small hole. Since light travels in a straight line, one can never see a beam of light from the side unless there are floating dust particles, which act as tiny reflectors, to reveal the path of the beam.

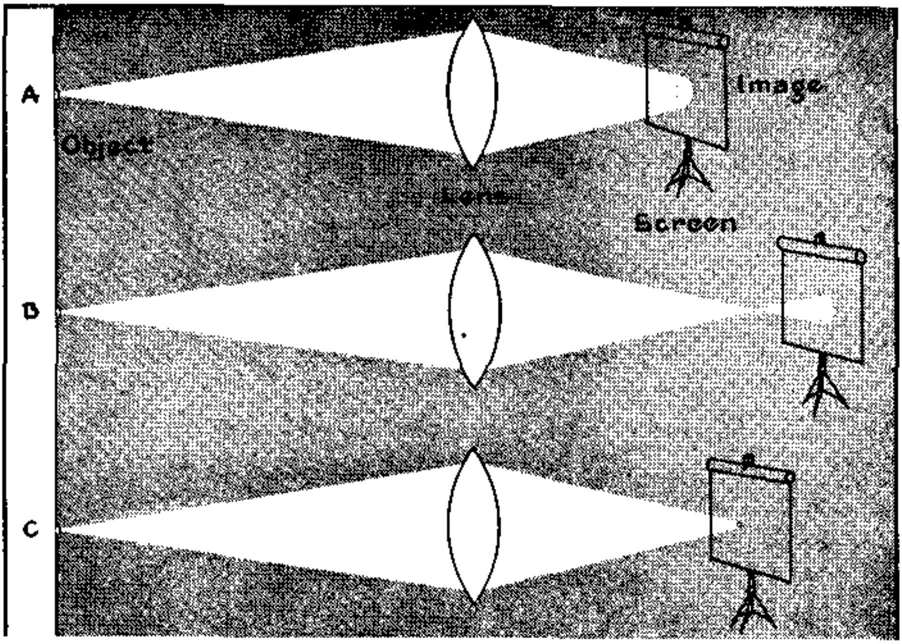

Fig. 11-8. Only when the screen is at the proper distance is the image well defined.

When light passes from one medium to another, its direction is almost always altered. The direction and the extent of the alteration are dependent on the kinds of media and on the angle at which light strikes the boundary of the new medium. When light rays pass from air to glass, their direction is changed (Fig. 11-7B). The magnitude of the change depends on the angle the surface of the glass makes with the light rays (Fig. 11-7B,C). If the surface of the glass is a single flat plane, all parallel rays will remain parallel (Fig. 11-7B,C). But if the surface is not a single flat plane, parallel rays will be bent by different degrees (Fig. 11-7D). With a glass surface that is properly curved, it is possible to cause all parallel rays of light that strike it to be brought to a focus at one point

(Fig. 11-7E) which is called the **focal point,** or simply the *focus.* The distance between the focal point and the lens is called the **focal distance** of the lens. A lens of the sort figured, thicker in the middle than at the edges, is called a **convex lens.** It is with this kind of lens that we are principally concerned in our study of the eye, so we will discuss it further.

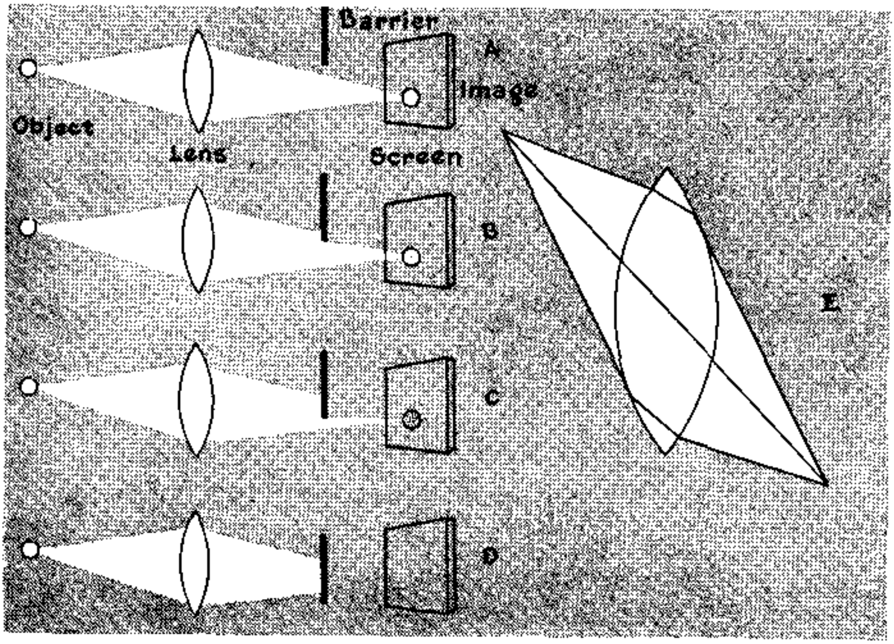

Fig. 11-9. If a barrier is partially interposed between lens and screen, it will *not* cut out part of the image but will merely make the image less bright, showing that the light rays that fall on each point of the image come from all parts of the lens. For simplicity, we shall hereafter represent no more than three rays from a single point, as in E.

Consider a point of light sending out beams in all directions. A convex lens is fixed in position facing the point of light, at a considerable distance from it (Fig. 11-8). Now, let a diffusely reflecting screen (a piece of ground glass or a movie screen) be moved back and forth behind the lens. When it is very close (Fig. 11-8A), a large circle of light that has a diffused ("fuzzy") edge will be seen on the screen. Also, when the screen is quite distant (Fig. 11-8B), a large circle of light appears. But, at a certain intermediate distance (Fig. 11-8C), the image will be a sharply defined point of light. This is the focal distance of the lens. When the screen is in this position, we say the image is in focus, that is, the image is smallest, brightest, and most clearly defined.

With the screen placed at the focal distance, let us interpose an opaque barrier between the lens and the screen (Fig. 11-9A). When the barrier blocks off only part of the lens (Fig. 11-9B,C), there is no change in the shape of the image but *there is a change in the intensity of it.* The greater the degree of the blocking (B,C,D), the dimmer the image becomes. This shows that *the light that makes up the image comes through every part of the lens and that every beam of light from the object that goes through the lens falls on the same spot (the image) on the screen* when the screen is at the focal distance from the lens. To represent *every* beam would be impractical but it may help if we depict the path of three of them through the lens (Fig. 11-9E). Note that only one beam goes straight through the lens, the one that goes through the center. Notice, also, that though the object on the left side is high, the image on the right is low. The consequence of this fact appears in the following paragraph.

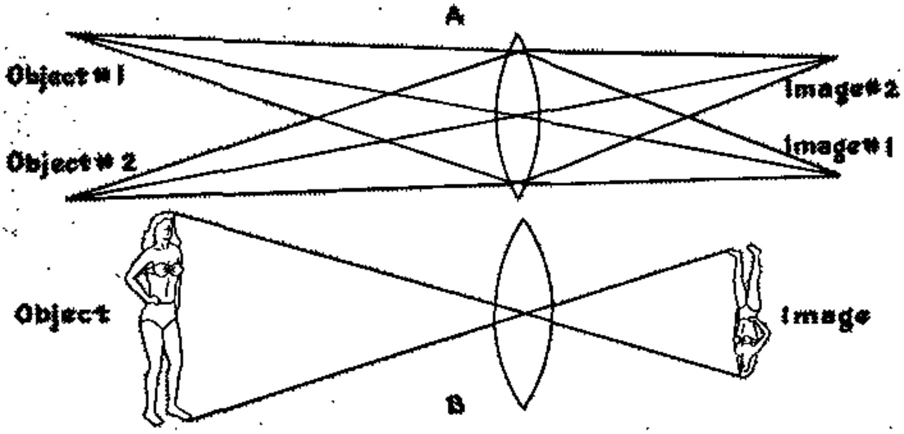

Fig. 11-10. All the rays of light that come from one point (on the left) and pass through a convex lens come to a focus at a single point (on the right). For simplicity, only three rays are shown coming from each object in A. Notice the relative reversal in position of points #1 and #2. This action of the lens results in the reversal of the entire image, as shown in B. In B, only the rays which pass through the center of the lens are shown.

What will happen if, instead of one object and one point of light, we have two points of light? In Figure 11-10A, we see that the relative position of the objects is reversed in the images—the high is now low, the low high. If, instead of two points, we have a large object (which may be considered to be made up of many separate points of light), the position of the image will be the exact reverse of the position of the object (Fig. 11-10B). *The image formed on a screen by a convex lens is always a reversed image.*

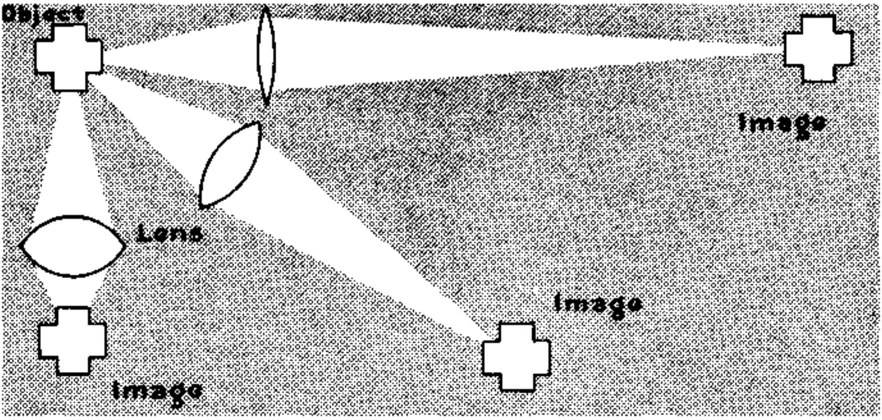

Fig. 11-11. The more convex the lens, the shorter is its focal distance.

A further property of convex lenses which should be known is made evident by Figure 11-11. *The more convex the lens, the shorter its focal distance.* Or, to put it another way, the more convex the lens, the more it "bends" the rays of light that go through it.

With this introduction, we are in a position to understand the design of the camera and the eye, which are diagrammed in Figure 11-12A. The camera consists of a system of lenses whose net effect is that of a convex lens; a dark chamber* filled with air; and a sensitive screen, called the film, at focal distance from the lens system. There is also a diaphragm between the lenses for modifying the amount of light that reaches the film. Also present, but not indicated in the diagram, is a shutter which is usually closed.

The eye is strikingly similar to the camera. Again, there is a system of lenses—two lenses in this case—one of which is called the **cornea** (Latin *corneus*, horny, perhaps because of its toughness), the other being called the **lens**; the dark chamber filled with fluid; and a sensitive screen called the **retina** (derived, for reasons we will soon appreciate better,

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* *Camera* means vault or chamber in Latin and Italian.

from Latin *rete*, net). Between the lenses, there is a diaphragm called the *iris*. (See Fig. 11-12B.)

There are three conspicuous differences in construction between camera and eye. In the first place, the eye has no shutter like the camera—unless one wishes to regard the eyelid as a shutter. The eye can remain open continuously because—second difference—the sensitive screen (retina) can be used over and over again for "taking pictures" in the eye; whereas, in the camera, the screen (film) can be used for only one picture, unless one doesn't object to "double exposures."

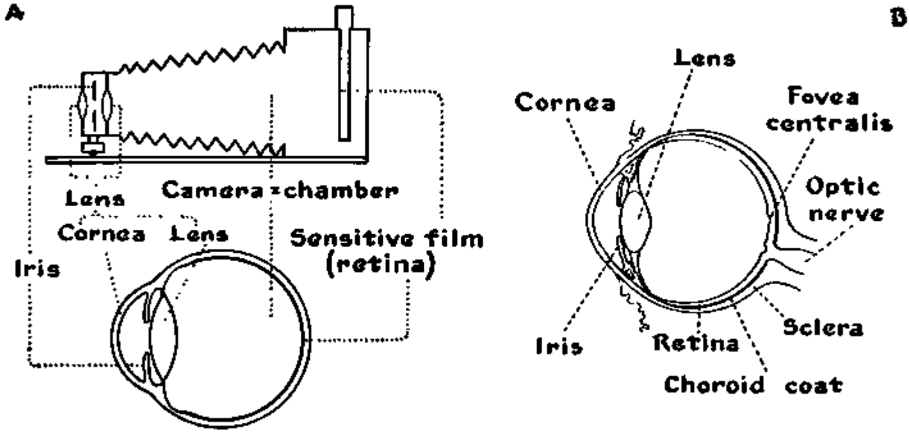

Fig. 11-12. The basic similarities between a camera and an eye are emphasized in A. In B, a larger view of the eye with the more important structures labeled.

The third conspicuous difference lies in the method of focussing. With a fixed convex lens and a movable object, experiment shows that, as the object approaches the lens, the position of the image on the other side moves in the same direction, that is, away from the lens (Fig. 11-13A). Obviously, there is no one focal distance at which all objects, however far from the lens, can be focussed. If a picture-taking system is to work for both near and far objects, one of two modifications of the system must be possible. Either it must be possible to change the lens-to-screen distance (Fig. 11-13A), or it must be possible to change the curvature of the lens (11-13B). In the camera, the first adjustment is made; in the human eye, the second. Interestingly enough, the eyes of many fish adjust after the fashion of the camera.

The lens of the human eye is held in a sheath of transparent tissue which is attached by fibers to the inner surface of the eyeball (Fig. 11-14).

These suspending fibers are normally under tension and, as a consequence, the lens is at its least convexity. Hence, when relaxed, the eye is focussed for distant objects rather than for close ones (recall Fig. 11-13B). Near the point of attachment of the suspending fibers, there is a muscle which is called the **ciliary muscle.** When this muscle contracts, the tension on the suspending fibers is relieved slightly; the lens bulges, and the eye is thus *accommodated* for near objects. Note that **accommodation** to near objects is an active process. When relaxed, the eye is naturally set for distance.

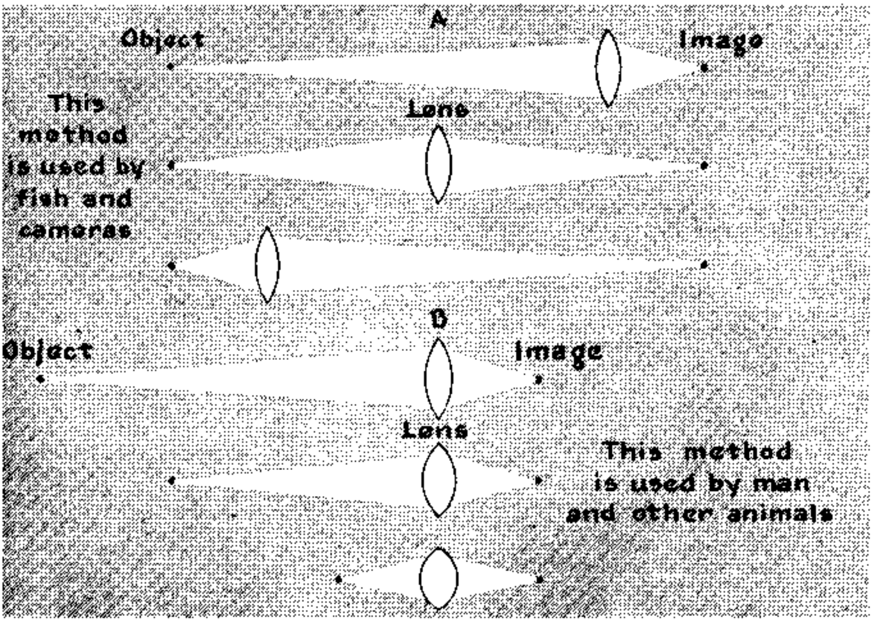

Fig. 11-13. Accommodation to near objects can be made (A) by moving the lens farther from the retina or film; this method is employed in the camera and in the eyes of squids and some fish. Man and many other animals achieve the same end by (B) altering the curvature of the lens.

It may be well to mention once more that the greater part of the lens action of the eye is carried out by the cornea. The "lens" is merely an *auxiliary lens* to permit accommodation. In one form of a disease called "cataract," the lens becomes opaque. Vision can be restored by removal of the lens, and substitution of a corresponding glass spectacle lens outside the eye, a lens which cannot accommodate, of course. In another form of cataract, the cornea becomes opaque. The only remedy for this abnormality is the replacement of the defective cornea with a healthy, living cornea from a living, or recently living, donor. There is a slowly growing tradition of making provision for this laudable use of part of one's body after death, a tradition certainly worth fostering.*

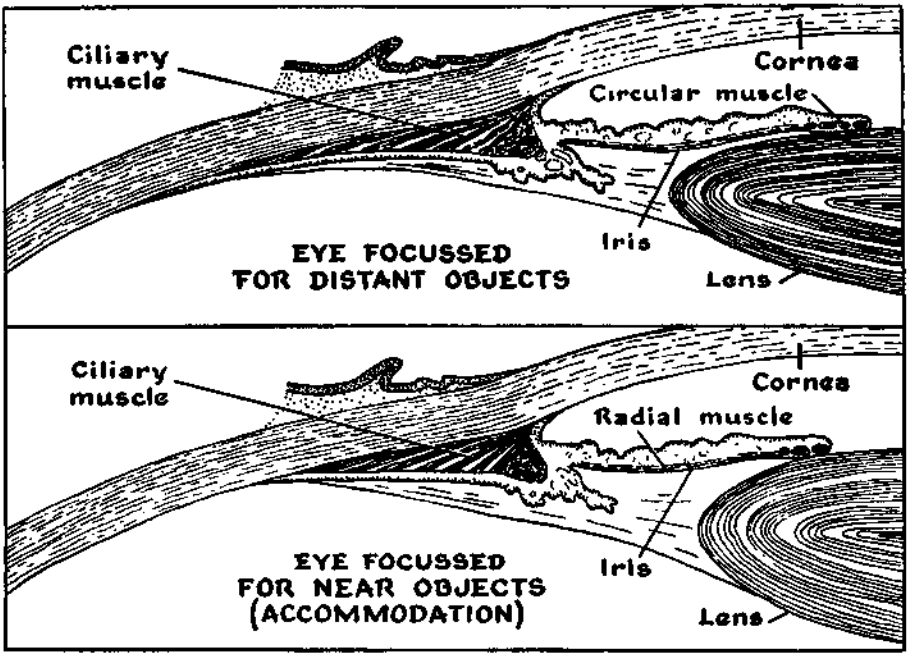

Fig. 11-14. The transparent fibers that hold the lens are normally under tension and, thus, keep the lens relatively flat, thus adapted for seeing at a distance. When the ciliary muscle contracts, the tension on the suspending fibers is relieved somewhat, the lens becomes more convex, and the eye is, thus, accommodated for near objects.

Far more common defects of the lens system are what are collectively called "errors of refraction," i.e., conditions in which the light is refracted (bent) either too little or too much. If the lens system bends the rays too much relative to the particular eyeball, only near objects can be properly focussed, and the individual is said to be **nearsighted;** the remedy is the wearing of a concave lens which spreads the rays of light, thus allowing distant objects to be focussed on the retina (Fig. 11-15). A **farsighted** eye, on the other hand, can see distinctly only far objects. This condition can be remedied by wearing a convex lens. An **astig-**

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* Those interested in providing for this use of their corneas should get in touch with The Eye-Bank for Sight Restoration, Inc., 210 East 64th Street, New York 21, N. Y.

matic eye is an eye that is curved differently in different planes. In this case, one must use a lens that also has different curvatures in different planes.

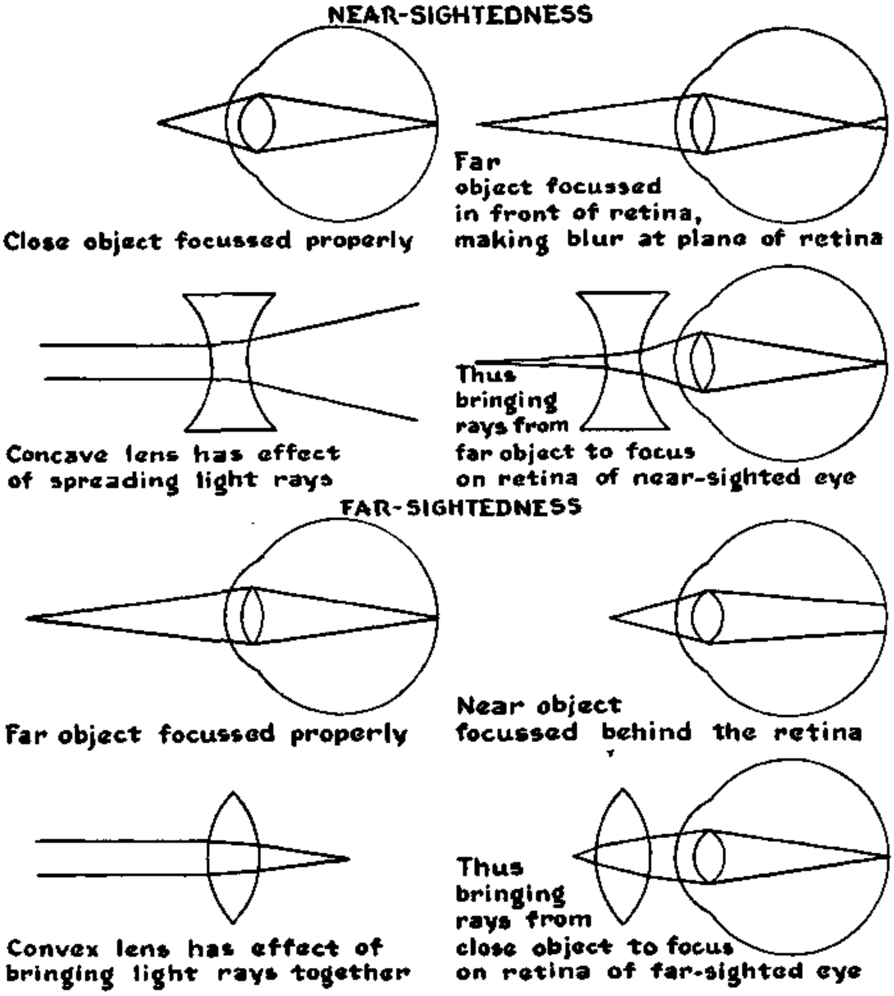

Fig. 11-15. Errors of refraction of the eye and their correction by lenses. Read left to right, top to bottom.

In taking a picture, it is important to control the amount of light reaching the light-sensitive screen. In the eye, light control is effected by the iris, the structure we ordinarily refer to when we describe the color of the eye. The hole in the middle of the eye is called the pupil. It is only a hole, and it appears black because the light that goes in is almost completely absorbed by the structures at the rear of the eye. From Figure 11-14, it can be seen that contraction of the radial muscle of the iris will dilate the iris; contraction of the circular muscle will constrict the iris. These muscles cannot be voluntarily controlled but are under involuntary control of the nervous system and respond to the amount of light entering the eye.

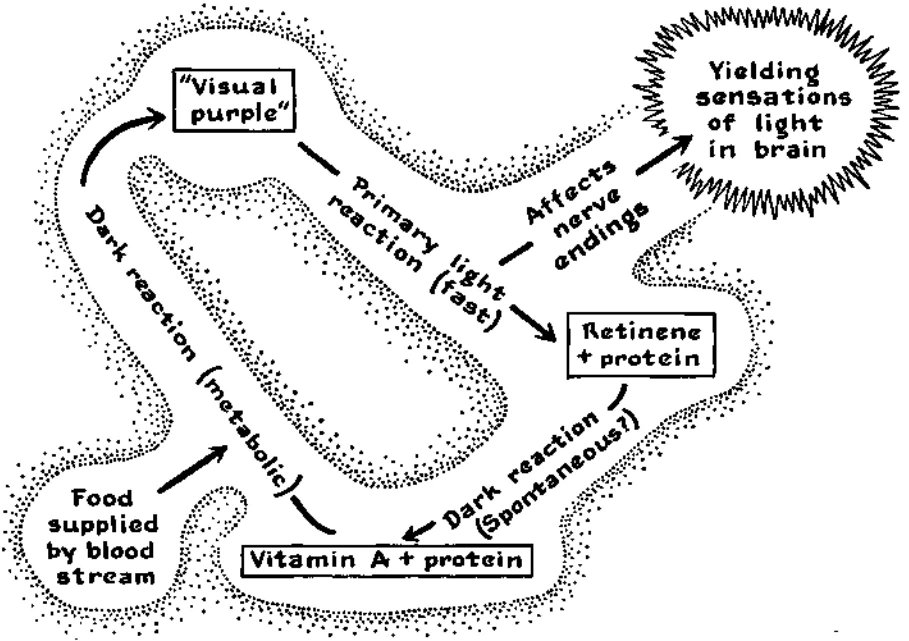

Fig. 11-16. Diagram of the chemical changes in the retina and their probable role in vision.

The sensitive screen of the eye is called the retina. There is perhaps no more remarkable or intricate part of the body. It has been an object of intensive study by scores of able scientists for more than a century and the details of its workings are still far from completely known. However, the broad outlines of the visual machinery are pretty clear.

How can light affect a nerve? It is clear that it must if any sensation is to result. But most nerves are not so affected. What is the mechanism involved in the eye? Indirect, and not completely conclusive evidence, indicates the existence of the chemical reactions diagrammed in Figure 11-16.

In the retina of the eye, there is a red-colored chemical compound called **visual purple.** It is made up of two parts: a protein and a simpler compound which gives it its color. Visual purple is unstable in the presence of light; it breaks down to a protein and a substance called **retinene.** Retinene further breaks down to a substance already familiar to us, **vitamin A.** In the presence of living, actively metabolizing cells, vitamin A plus protein can be used to make visual purple once more.

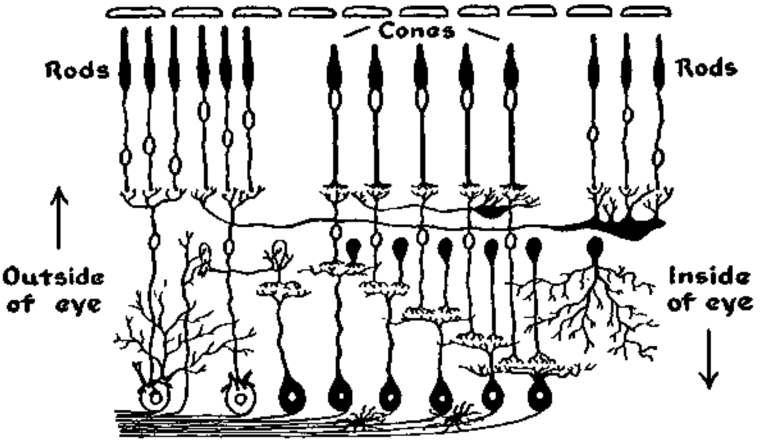

Fig. 11-17. A much simplified diagram of the structure of the retina. As the diagram is oriented, light enters the eye from below. Notice the many structures the light must pass through before it strikes the light-sensitive elements, the rods and cones.

The reaction which results in a sensation of light is the one called the "primary light reaction." This causes the production of chemicals (perhaps the retinene?) which affect the endings of the nearby nerve fibers, thus stimulating them. In other words, the basic reaction of vision is a chemical one and, as such, falls into the same class as those responsible for taste and smell.

The function of vitamin A should be noticed. Most vitamins are required because they serve some purpose in the chemistry of the body. Elucidating their roles has been a long, slow process and one that is still going on. Vitamin A was the first vitamin to be firmly tied to body chemistry. One of the clinical signs of vitamin A deficiency is "night blindness" in which the eyes of the sufferer fail to respond to weak light. Consequently, he can see well only by strong light, such as daylight.

The chemical reaction involved in vision takes place in and among the cells of the retina. The retina is an exceedingly complex structure, as Figure 11-17 makes evident. It is composed of many different kinds of cells, only a few of which are identified in the figure. The sensitive cells are called **rods** and **cones.** These, when stimulated by the *photochemical* (light-chemical) reaction, stimulate the nerve cells which send stimuli to the brain.

Measurements made of the minimum images that can be seen show that each rod and cone can give a stimulus independently of its neighbors. Our vision is, in effect, a mosaic vision, made up of extremely numerous individual elements, analogous to the composition of illuminated "spectacular" advertising signs which are made up of many thousands of separate lightbulbs. That we are not aware of its mosaic character is attributable to the fine scale of the mosaic, just as the mosaic character of the "spectacular" advertising sign is not evident several blocks away.*

How fine a line one can see is determined by many factors which fall into two main classes: the quality of the optical system (lens, cornea, etc.) and the fineness of the retinal mosaic. The first varies enormously, as the abundance and variety of spectacles in our society bear witness; the extent of the variation of the second has not been studied, but it probably varies greatly also. It should be pointed out that, in the eye of each individual, there is considerable variation from one region of the retina to another. In the central region (the **fovea centralis** in Figure 11-12B) which contains only cones—a point we shall return to later—the cones are only a third as wide as they are elsewhere in the retina and there are about six times as many cones per unit area as there are cones and rods in other regions. This region is the region we use whenever we give our closest attention; we focus the object on this area of "finest grain." Another factor which contributes to the relatively greater acuity of vision in this region is the relation of rods and cones to nerve cells. In the central region, there is one nerve cell for each sensitive cell, as depicted in Figure 11-17. Elsewhere, there are more sensitive cells than nerve cells, and the more distant the region from the fovea centralis, the greater this ratio. At the edge of the retina, there are as many as 250 sensitive cells to each nerve cell and all 250 sensitive cells act as a unit in the visual mosaic.

What are the functions of rods and cones? What their differences?

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* This account is somewhat simplified. The formation of an image is, in part, a matter of not-well-understood integration of stimuli by the central nervous system.

The answers to these questions have been found by correlating the distribution of rods and cones over the retinal area with observed differences in capabilities of different parts of the retina.

With respect to structure:

1. The centermost part of the fovea centralis contains only cones; and there are very few rods in any part of the fovea.
2. In regions other than the fovea, both rods and cones are present; the greater the distance from the fovea, the more rods and the fewer cones.

With regard to function:

1. Perception of color is excellent in the fovea, poor or totally lacking elsewhere. (With your eye fixed on a point straight ahead, have someone else bring a colored object slowly into your field of vision, moving it from periphery to center. Notice how you can *see* it before you can tell its color.)
2. Perception of dim light is most acute outside of the fovea. (In looking for stars at night, notice that you can see the dimmest of them only "when you don't look at them," i.e., when you don't focus them on the fovea.)

From these two observations, it is reasonable to deduce that perception of color is a function of the cones; and that, though both rods and cones are sensitive to light, the rods are more sensitive.

The natural question to ask next is, how do the cones distinguish colors? Are there different chemical reactions involved? Different cones? Filters? Or what? In spite of a great deal of work and theorizing in this field, we can best summarize the present state of knowledge by saying simply, *We don't know.*

92. WHERE Do We Feel?

Consider our sensations of feeling, tasting, smelling, hearing, and seeing—where do we have these sensations? The natural response is that we feel at our skin, taste in our mouth, and so on. But do we? In a sense, yes; but we know enough of physiology now to bring forward evidence not compatible with this simple view.

Occasionally, as a result of accident, war injury, or required surgery, a portion of the principal part of the brain, the **cerebrum,** is exposed.

Although the membranes surrounding the cerebrum are very sensitive to touch, it has been found that the brain-stuff itself shows no sensitivity and can be touched or cut with the patient not under anesthetic. It is completely insensitive to touch **locally.** When certain spots in the mid-region of the cerebrum are touched, the patient reports a sensation of touch in distant parts of his body. When the brain is touched at one spot, he may report a feeling in his hand; at another, a feeling in his leg. More striking, he may sometimes report that he feels his leg is moving, even though he can see it is not. *Where* is the feeling in this case? In his leg, where he says he feels it, or in his cerebrum which the experimenter knows is being touched?

Whatever the answer to the vexing question, "Where is the sensation located?"*, sensation normally involves the following three elements: a receptor, "sensory" and other nerve fibers, and the sensory area of the brain. Normally, when the receptor is stimulated, it sends a stimulus along a chain of nerve fibers which terminate in the sensory areas of the cerebrum. We know this because with electrical instruments we can detect a current traveling along the nerves coming from the receptor, as well as the current that reaches the brain. Sensation can be elicited in any of three ways.

1. *First*, by stimulation of the receptor—the normal way.
2. *Second*, by stimulation of the nerves. Everyone has experienced the "natural experiment" of striking his crazy bone which is really an exposed nerve trunk in the elbow. Besides the local pain, due to local receptors in the elbow, the blow often leads to a tingling sensation in the finger tips because of the direct stimulation of the sensory nerves coming from the fingers.
3. *Third*, by stimulation of the "sensory area" of the brain. Here again, common experience presents us with an example: a blow in the back of the head produces images of stars, rockets and other pyrotechnics, when none are visible to bystanders.

If the sense-receptor is destroyed, there will normally be no more sensation. If the sensory nerve is destroyed, no more sensations occur, even though receptor and brain are intact. If the sensory area of the brain is destroyed, sensation ceases. Where, then, is the sensation located?

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* There are some who say that this is a meaningless question, i.e., one that cannot be answered.

Interestingly enough, it is not always true that destruction of receptors leads to loss of sensation in the part affected. Frequently, a man who has had a leg or an arm amputated later has recurrent feeling in the nonexistent limb. In this case, the receptors are gone; only the sensory nerves and the sensory areas of the brain are still intact. Probably, some abnormality of the remaining nerve stump causes the stimulation of the nerve and brain. The stimulus is interpreted as coming from the regions that used to be in contact with the nerve, the fingers and hand of a once-existent arm, for instance. Sometimes the pain is quite intense and precisely localized and the patient reports the localization even though he *knows* that the pain cannot be where he says it is. In severe cases, it may be necessary to put the nerve into a long sleep by injecting alcohol or other anesthetic directly into the nerve.

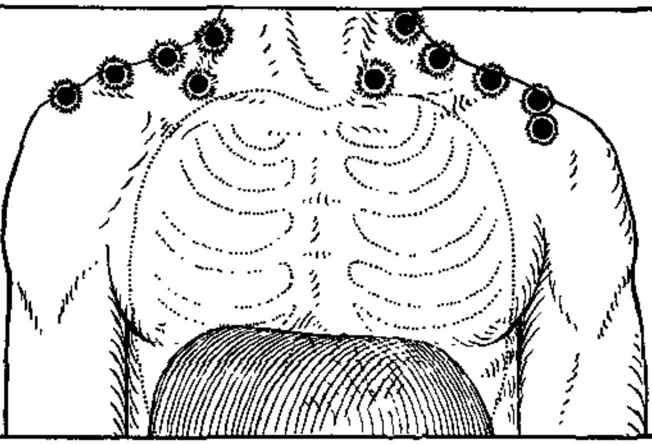

Fig. 11-18. Stimulation of the diaphragm leads to mistaken localization of pain in the shoulder regions.

There are regions of the body in which the supposed *locus* of the sensation cannot be accurately determined. The abdominal cavity is one, a fact of some inconvenience when it is necessary for a physician to diagnose an ailment from some pain vaguely located "somewhere" in the mid-region. Perhaps worse is the fact that the source of the pain may be precisely, but wrongly, located. Some of these mistaken localizations are consistent (which isn't so bad); for instance, stimulation of the central region of the diaphragm causes pain that is positively identified as coming from the shoulders (Fig. 11-18). The same nerve trunk supplies nerves to both regions, and apparently, one might say, we never learn which fibers go to which region. Another and more common example of referred pain is that which follows the ill-advised swallowing of a too-large piece of food. For some time thereafter, we may "feel the lump in our throat." Fluoroscopic or X-ray examination, using a mass opaque to X-rays, shows that the lump is really lodged down against the upper sphincter of the stomach, several inches lower than we "feel" it.

In the preceding paragraph, it was implied that we *learn* to associate the sensations coming from certain nerves with stimulation of a certain part of the body. This is unquestionably true for most sensory functions. As an example of a learned association, consider the way we orient the visual field. A convex lens, such as we have in our eye, inverts the image. Why, then, does not the world appear upside down, like this? The answer is, there is no reason why it should. We have sensations *from* the retina, but no sensations *of* it; it has no "right-side-upness." Conclusive proof of this statement is found in the outcome of an experiment in which a psychologist donned inverting prisms to see how the world would look. As expected, the world looked upside down—at first. But the subject scrupulously looked at the world only through his peculiar spectacles, doffing them only at night in a completely dark room. In a few weeks' time the world came to appear right-side-up and the subject could perform all his accustomed movements with their accustomed delicacy. *The world looked and felt perfectly normal.*

After this period of learning, the subject removed his inverting spectacles and the world once more looked upside down, though the position of the image was what would ordinarily be regarded as normal. It appeared upside down until the subject once more learned how to interpret the visual stimuli in terms of the world of space outside himself. This experiment, and observation of the learning process in infants, make it very probable that we have no *a priori* knowledge of how to interpret the messages that come from the retina. We learn.

Before closing this discussion of sensation, it may be of interest to mention an unproved, and perhaps unprovable, hypothesis of the nature of sensation. Consider the question: what is the objective difference between two kinds of sensations? A well-trained philosopher will say that this question does not make sense. But what we mean is this: what that we know of objectively determines the reported differences between sensations? Take the sensations of seeing and hearing: why are they different? We know that it is not because of the difference in end organs —in receptors—because:

1. If the receptors are destroyed, direct stimulation of the nerves, as by a blow or an electric shock, will still yield the "proper" sensations; e.g., stimulation of the auditory nerve gives rise to a sensation of sound, of the optic (visual) nerve to a sensation of sight, though the stimulus is precisely the same.
2. The messages which normally come along the optic and auditory nerves seem to be of the same sort, as measured by electrical instruments.

If the qualitative character of the sensation is not determined by either the end organ or the nerve, it must be determined by what we call the "sensory area" of the brain. From this deduction, the prediction was made nearly a century ago that if we could cut the optic nerve and the auditory nerve and then join the cut stumps so that the eye now sent impulses to the auditory region, and the ear to the visual region of the brain, we would then be able to *see* thunder and *hear* lightning. This seems a reasonable hypothesis in the light of the facts. No one has succeeded in carrying out this experiment. It is, nonetheless, a fascinating speculation.

QUESTIONS AND PROBLEMS

11-1. Enumerate as many different "senses" as you can.

11-2. Generally, does a sense organ tell us about the absolute value of a stimulating condition or about its rate of change? Evidence?

11-3. What justification could one give for lumping the sense of hearing with the senses of touch? Or the sense of sight with the senses of smell and taste?

11-4. (This question involves some knowledge of the physics of materials.) Why does a cold piece of metal feel colder than a cold piece of wood, even though both are initially at the same temperature?

11-5. A patient who is given a local anesthetic by a dentist finds that, though the pulling of a tooth does not hurt, he can distinctly feel it. Can you explain this observation?

11-6. Mr. Smithers, who had run hard for four blocks, noticed the odor of some flowers in Jones' room the minute he stepped in. Mr. Van Alstyne, who was driven to Jones' door by a chauffeur, did not notice the odor until it was called to his attention. Assuming that the men are equally sensitive to odors, and equally observant, can you explain the difference in their reactions?

11-7. Three families live among the glue factories (see Fig. 11-19). Mrs. O'Riley, Mrs. Murphy, and Mrs. Clanahan have never been known to leave their houses. The town's two glue factories are distinguishable by name but not by odor. From midnight to noon, the wind blows continuously from north to south, and from noon to midnight from south to north. The wind never blows in any other direction and there are never any lulls. One of the housewives never complains of the odor. Which one? Why?

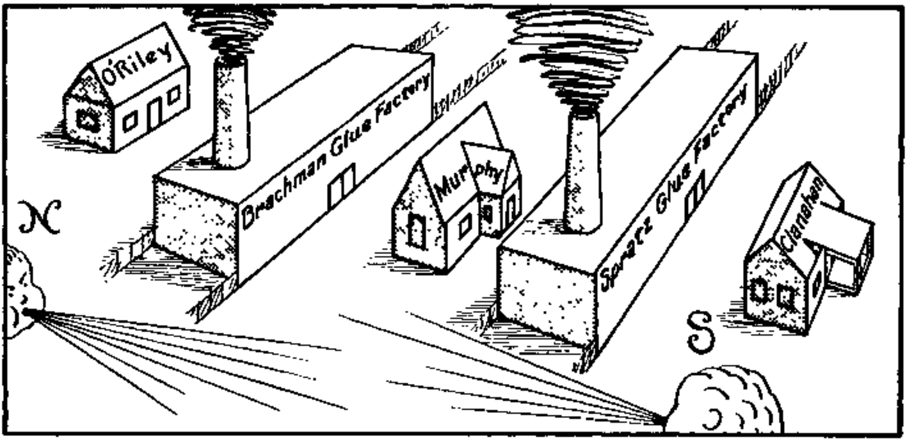

Fig. 11-19. A problem in real estate values.

11-8. At one time, it was believed that infantile paralysis could be prevented in children by frequently spraying the upper nasal chambers with a chemical that hardened the epithelium and temporarily destroyed the nerve endings. While undergoing this treatment, the children complained that they did not enjoy eating as much as usual. Can you explain this reaction?

11-9. What are the three types of deafness? Can they be remedied? If so, how?

11-10. Define, using diagrams freely: convex lens, concave lens, focal point, focal distance, image.

11-11. What are the characteristic properties of concave and convex lenses?

11-12. What in the human eye corresponds to the lenses of the camera?

11-13. How does a fish eye resemble a camera more closely than does a human eye?

11-14. What in the human eye corresponds to the film of the camera? How does it differ therefrom?

11-15. John Doe requires glasses only for reading, preferring not to use them when he is active outdoors. What may be his trouble, and what sort of lenses does he require?

11-16. In speaking of the eye, what is meant by the term *accommodation?*

11-17. As old age approaches, a man's eyes commonly lose the power of accommodation. How will this affect vision and what sort of lenses should be used?

11-18. In some diseases, the pupil of the eye remains permanently contracted to pinpoint size. How does this affect vision?

11-19. Describe two kinds of cataract. Describe the remedial treatments.

11-20. *Some* cases of poor vision in weak light can be helped by a diet that includes large quantities of carrots. Explain.

11-21. What is the evidence that the retinal cones are concerned with color vision? That both rods and cones are sensitive to light but that the rods are more sensitive?

11-22. Where in the body is sensation located? Discuss this problem.

Chapter XII

The Autonomic Nervous System

93. Unconscious Nervous Control

In the discussion of the simple reflex arc, the impression may have been given that the effector is always a muscle. This is not true. Glands, also, may be effectors. However, the nervous mechanism involved in the case of a gland is slightly more complicated, and for that reason discussion was postponed.

Let us take the salivary gland as an example. Although it can be consciously stimulated—we can *will* to increase its flow—the gland is normally controlled unconsciously. We will subsequently (§ 94) examine a complete arc involving both sensory and motor nerves, but for the moment we should focus our attention only on the motor end of the arc. In Figure 12-1, are diagrammed two different systems of control of an organ by the central nervous system, one of the control of a voluntary muscle, the other of the control of a salivary gland. Notice that the muscle is stimulated directly by a neuron which lies within the central nervous system (Fig. 12-1A), whereas stimulation of the salivary gland involves a chain of *two* neurons, one within the central nervous system, connected with a second outside which, in turn, transmits the stimulus to the gland (Fig. 12-1B).

All glands, in so far as they are subject to nervous control, are governed by mechanisms like this, mechanisms that involve *at least* one motor neuron lying outside the central nervous system. Innervated in this way are various glands, such as the salivary glands and the pancreas, and many muscles, including those of the viscera, of the walls of the blood vessels, and of the iris of the eye. The members of this heterogeneous assemblage of organs have one thing in common: they are only slightly, or not at all, subject to conscious control. To a willful human, they may seem to be independent, or autonomic, in their actions. For this reason, the part of the nervous system which is concerned with their activity is called the **autonomic nervous system.** Notice that the adjective "autonomic" refers to a (superficial) aspect of the things controlled rather than to the system exercising the regulation, for the autonomic system is definitely guided by impulses from the central nervous system.

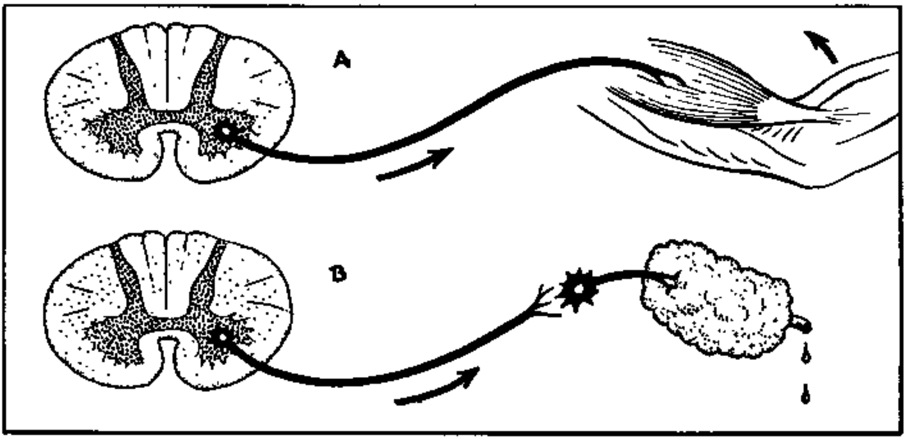

Fig. 12-1. Innervation of a voluntary organ (A) compared with innervation of an organ controlled by the autonomic nervous system (B). In the latter, note the extra motor neuron lying outside the central nervous system.

The autonomic nervous system is, in part, identifiable in gross structures visible to the naked eye. Along either side of the spinal cord, outside the vertebral column, there is a knotted cord of nervous tissue (Fig. 12-2). The knots of this cord are composed of thousands of neurons. Each of these neurons is the second neuron of the chain diagrammed in Figure 12-1B. When many neurons are massed in bunches like this, the bunch is called a **ganglion** (Greek, a swelling; plural, *ganglia*). These ganglia are autonomic ganglia.

Not all the autonomic ganglia are grouped into macroscopic groups like this. Many of them, particularly those of the extreme upper and extreme lower part of the system, are dispersed, each ganglion being found close to or imbedded within the organ it controls. All these dispersed ganglia (and their associated fibers) are referred to as the **parasympathetic system,** in contrast to the more centrally located system, the **sympathetic system,** the ganglia of which are visible in Figure 12-2.

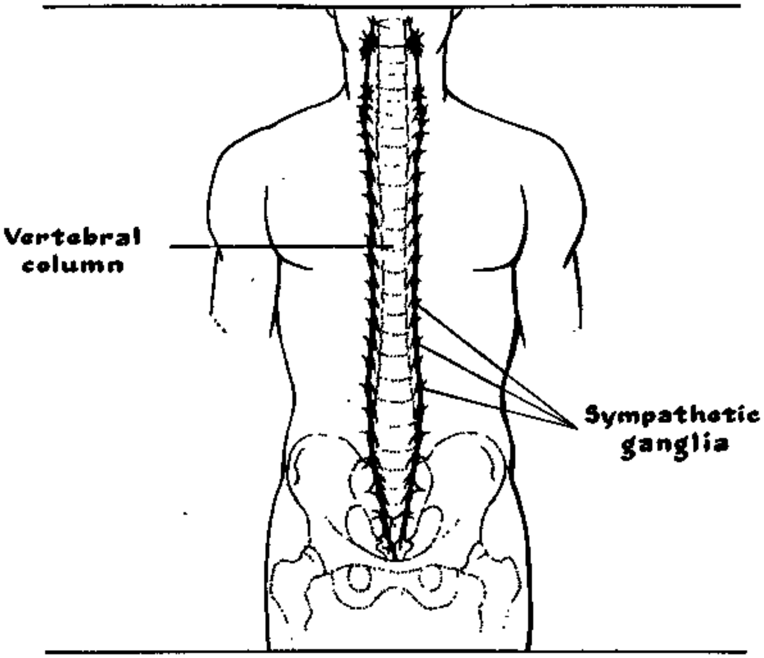

Fig. 12-2. The autonomic ganglia lying outside the central nervous system.

Perhaps the most important fact about the separation of the autonomic nervous system into two subsystems is that it is based on real differences in physiology. Figure 12-3 shows the contrasting effects of these two systems on various organs. Notice that, whereas the parasympathetic system constricts the pupil of the eye, increases the flow of saliva, increases the lumen of the small intestine and decreases that of the large intestine, the sympathetic has the opposite effect in each case. The student cannot predict, in advance, the effect of one of these two systems on a particular organ but, knowing the action of one system, he can predict the action of the other. The sympathetic system and the parasympathetic system are always mutually antagonistic.

The antagonism of the sympathetic and parasympathetic systems results in some cases from the fact that they innervate antagonistic muscles, for instance, the circular and longitudinal muscles of the intestine. However, in other cases, the antagonism is due to *different effects on the same effector.* This is something new. Skeletal muscle is either stimulated by the nerves to contract; or, lacking stimulation, it relaxes. There are no nerves that stimulate skeletal muscle to relax. But smooth muscle and cardiac muscle both have a certain amount of intrinsic activity and can be either stimulated to contract more than usual (by nerves of one division of the autonomic nervous system) or to relax more than usual (by nerves of the other division of the autonomic nervous system).

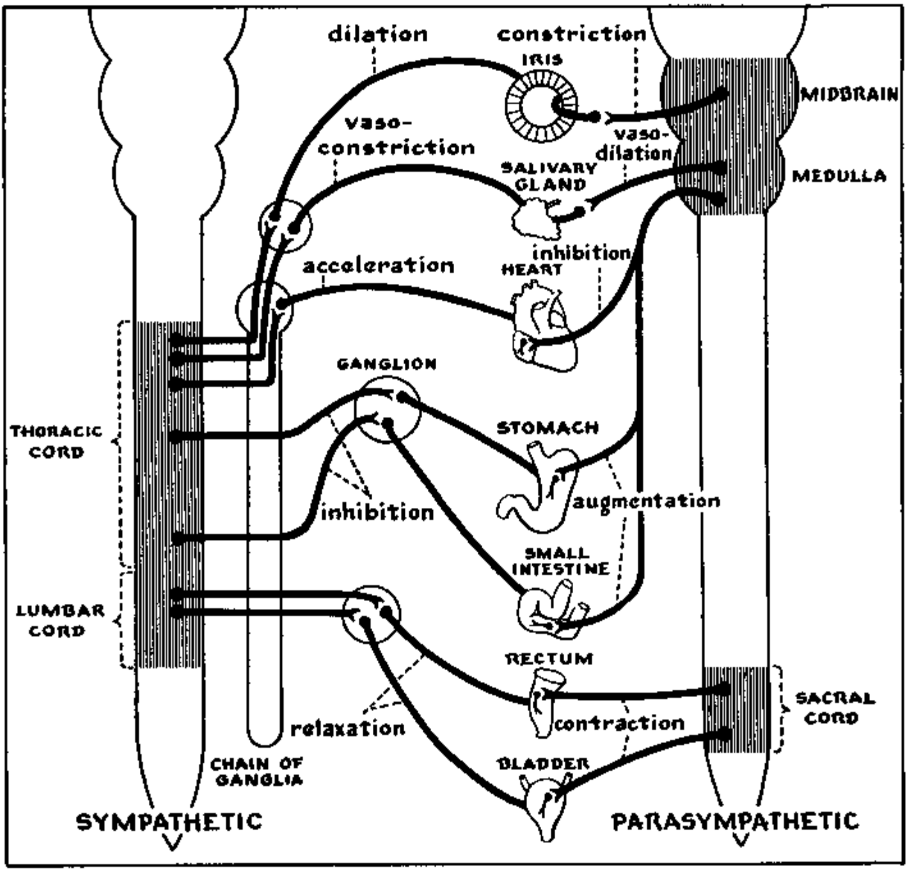

Fig. 12-3. The two divisions of the autonomic nervous system drawn separately. Note their antagonistic actions.

Besides motor neurons, the autonomic system contains some sensory fibers. Sensory innervation of the viscera does not, however, seem to be very extensive; this is evidently one of the reasons why sensations from our viscera are not frequently experienced. Some of the viscera do, however, send in frequent "reports" of their doings; but these reports merely activate innate reflexes involving only the lower part of the nervous system and seldom reach the conscious level. The heart, for instance, is continually influenced by reflexes operating through the autonomic nervous system but the heart's owner remains unaware of the control.

QUESTIONS AND PROBLEMS

12-1. Define the autonomic nervous system in terms of: (a) its anatomy; (b) its function.

12-2. The drug pilocarpine stimulates the parasympathetic nerve endings. What will be the effect of this drug on: the iris, the salivary glands, and the rectum?

12-3. Atropine causes acceleration of the heartbeat, decrease in the flow of saliva, and dilation of the iris. What part of the nervous system does atropine stimulate?

12-4. In extreme fear, men and other animals are likely to defecate and urinate regardless of their surroundings and their previous training. In addition, the heart beats faster and the mouth becomes dry. Can you give a simple explanation for all these phenomena? What would you predict to be the appearance of the eyes in fear?

12-5. What is blushing? What part of the nervous system controls it? Would you call it a voluntary or an involuntary activity?

12-6. An occasional unusual individual can willfully stop the beat of his heart. What part of his nervous system has he learned to control?

12-7. Would you consider the usual lack of willful control of the autonomic nervous system a fortunate or an unfortunate state of affairs? Why?

Chapter XIII

The Biological Background of Mental Phenomena

94. The Establishing of the Conditioned Reflexes

If man's behavior were composed only of innate reflexes, he would be unable to exist in the modern world or, indeed, in any world that we know. Some of the simplest animals survive by virtue of innate reflexes only. Even some fairly complicated animals, notably the insects, exhibit behavior that is made up almost entirely of reflexes. We call their behavior "instinctive." Even the behavior of insects, however, is subject to modification by experience. A bee can be taught to associate a certain color with the presence of sugar.

Among mammals, particularly man, the ability to make new associations is conspicuous and important. This fact has been known more or less intuitively for thousands of years. The systematic investigation of the phenomena of association-formation was begun, however, only in the last century by the Russian physiologist, Ivan Pavlov. To this field, he contributed a technique of experimentation which has permitted a step-by-step analysis that has contributed greatly to our knowledge of mental processes.

If food is placed in the mouth of a dog, the dog salivates. This is true only if the sensory nerves from the taste buds and the motor nerves (part of the parasympathetic system) to the salivary glands are intact. The salivation is a reflex act that does not need to be learned. The probable path of the reflex arc is indicated in Figure 13-1A.

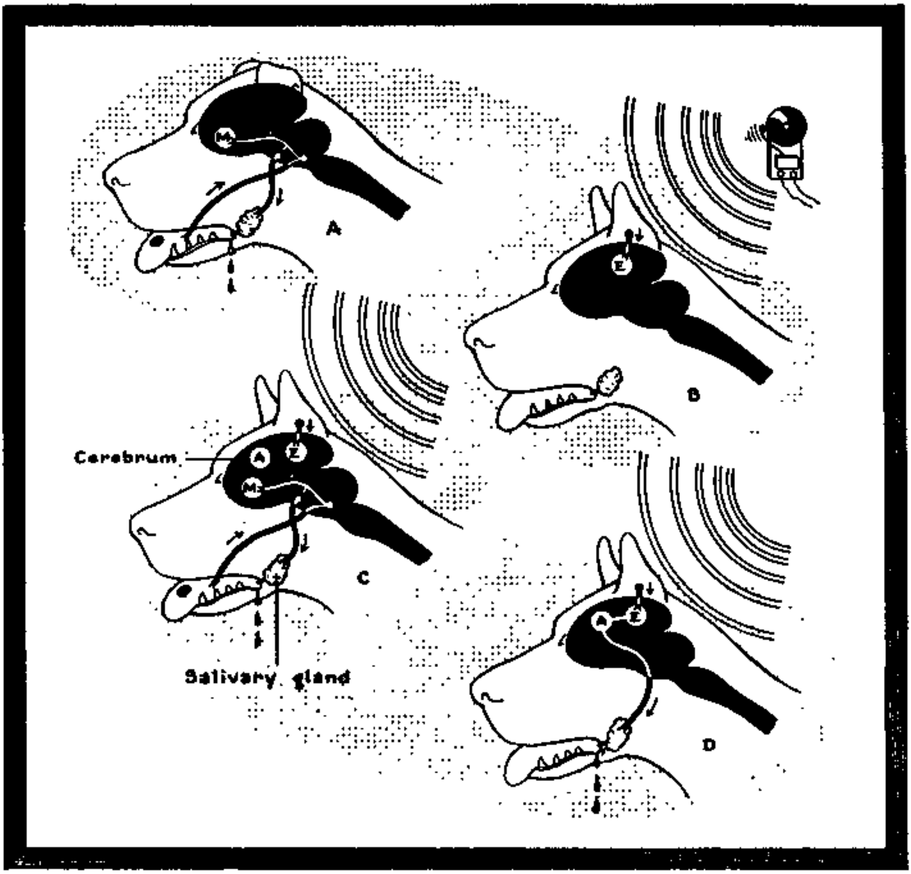

Fig. 13-1. Establishment of a conditioned reflex. Taste of food evokes salivation (A). Sound of bell (B) does not. When taste and sound are presented simultaneously (C), somehow an association is made in the cerebrum between sensations from ear and mouth. Once this association exists, sound alone will evoke salivation (D).

If a bell is rung, the dog's salivary glands do not react (Fig. 13-1B). If, instead, we ring the bell and then present the dog with food, salivation follows the presentation of food. If we repeat this act many times: sound of bell—food, sound—food, sound—food, the dog will be somehow modified so that the mere sound of the bell will cause him to salivate. It is as if there were a reflex involving the sensory nerves from the ear and the motor nerves to the salivary glands. Innately, there is not.

But, evidently, under suitable conditions, such a reflex can be set up. Such a learned reflex is called a **conditioned reflex.**

How are we to visualize a mechanism for a conditioned reflex? Figure 13-1C,D is an attempt to do so. Somehow, the fact that the innate salivating reflex is being activated at the same time that the auditory center is receiving stimuli from the ear results in establishing a connection between the two. *How* is this connection made? We do not know. There are, of course, abundant nerve-fiber connections already existing between them, as there are between all parts of the central nervous system. But what determines that these pathways, not previously used, shall now be put into operation? Why should the simultaneous, or near simultaneous, activity in two different parts of the brain result in a functional connection between the two? The anatomical connection always exists. It is as though the process of conditioning opened the switches, so to speak. Do the synapses in the connecting pathways initially have high resistances, and does the conditioning process result in a permanent lowering of these resistances? We can think of the process in this way, though we cannot prove this hypothesis.

We know little about the exact nervous pathways involved in the process of conditioning and learning. We do know, however, that, regardless of the kind of stimulus used, if a conditioned reflex is to be established or maintained, the cerebrum must be present. **There is no learning or remembering without the cerebrum.**

The ringing of the bell need not be simultaneous with the presentation of food; the sound can precede the food. The longer the period between the unconditioned stimulus (the sound) and the innate stimulus (the taste), the more repetitions will be required to set up the conditioned response. This is as we would expect. We easily associate two events that happen simultaneously, but not so easily do we "see" the connection of events that are separated in time.

Developing the clear-cut, explicit concept of the conditioned reflex was Pavlov's initial contribution to this field. With this simple concept as a tool, he and his coworkers were enabled to carry out many enlightening experiments. They used dogs but it will be obvious that the significance of their findings is not confined to the dog world.

It will be readily appreciated that a bell-sound is not the only stimulus which can be developed into a conditioned stimulus. Any stimulus can be so developed. An animal can be conditioned to react to a sight, a sound, a touch, or any other perceptible stimulus. As a matter of fact, the mechanism of the conditioned stimulus permits us to determine what stimuli the dog can perceive. Can a dog see ultraviolet light? We cannot ask him but we can see if ultraviolet light can be established as a conditioned stimulus. It cannot; therefore, we conclude that a dog cannot see ultraviolet light. (Neither can we.) Similar experiments tried with bees showed that they *can* perceive ultraviolet.

Since we have learned how to establish conditioned reflexes in other animals, a door hitherto closed to us has opened. It is hard for us to penetrate the mind of an animal that does not speak. But, with the mechanism of the conditioned reflex, we can pry into the minds of other animals—the more "intelligent" ones, at any rate. Can a dog tell the difference between red and green? We cannot ask him. But we can condition him to salivate when a red light is flashed on. After he is conditioned, we can then condition him not to salivate when a green light is shown. When we have succeeded in doing this, we can try different intensities of colored lights and if we can find a particular intensity of red that he cannot distinguish from a particular intensity of green, we must say then that he cannot distinguish red and green, which is indeed the case. Studies of this sort indicate that dogs cannot distinguish any colors; they can merely distinguish intensities.

Any perceptible stimulus can be made into a conditioned stimulus, even a noxious one. Pavlov found that he could condition dogs to salivate on being given an electric shock. By first using mild shocks and gradually increasing their strength, he found it was possible to train dogs to react to strong, and probably painful, shocks by salivating, instead of fighting or running away. One can easily think of similar instances among humans. Consider, for instance, the punishment the stooge of a slapstick comedian may take, all for a bit of money, that is, for the wherewithal to stimulate his salivary glands. This is a striking example but it is not fundamentally different from a sort of learning to which all of us are exposed. For the sake of anticipated pleasures yet to come, we daily put up with unpleasant experiences and abjure momentary delights. In his ability to act in the light of distant and subtle goals, rather than to react thoughtlessly to evanescent and momentary pain or pleasure, man is without peer among living things.

95. "Unconditioning" and the Experimental Study of Neuroses

Conditioned stimuli can be "unconditioned." A simple way to do this is to present the conditioned stimulus, e.g., the sound of a bell, many times without the "reward" of the innate stimulus, e.g., the taste of food. If, to use the example suggested, the bell is rung a number of times and food is *not* presented, the dog no longer salivates on hearing the bell. Does this mean that the dog has *forgotten* the connection between the two? It does not seem likely. Moreover, if the ringing of the bell is once more followed by the presentation of food, the conditioned reflex is reestablished almost immediately. The second time it takes only one or two sound-food presentations to establish the association, instead of the dozen or so originally required. Extinguishing a conditioned reflex is itself a conditioning process, rather than a lapsing-for-want-of-payments process . . . . In this connection, it is not without interest to learn that there is abundant psychological evidence to prove that a great part (perhaps all?) of what we call "forgetting" in humans is an active, positive process. We forget because we want to. This seems to be frequently true, a fact which every student should remember and think about in connection with his personal problems.

Related to the phenomenon of "unconditioning" or extinction of conditioning is the phenomenon of **differential inhibition.** This may be illustrated by the following example:

A tone of a fixed pitch is set up as a conditioned stimulus. Then a note *one-half tone lower* is sounded, and no food is given. This routine is repeated a number of times until the animal has learned to salivate for the higher note but not for the lower. Then a normal rate of secretion of saliva for the higher note is determined and is found to be, say, 12 drops. Now:

Sound lower tone once. Result: 0 drops.
Sound higher tone once. Result: 12 drops.
Sound lower tone four times. Results: 0, 0, 0, and 0 drops.
Sound higher tone. Result: 1 drop.

The dog "should" have produced 12 drops in response to the last stimulus but produced only one drop, apparently because the repeated presentation of the "negative" stimulus (the lower tone) had resulted in a "spreading," so to speak, of the negative response. Or, we might say that repeated stimulation by the negative stimulus *inhibited* the action of the positive stimulus.

Out of such studies of inhibition, came another discovery. Under some conditions, the "spread" of inhibition would be greater, extending, for instance, to conditioned tones which were more distant than a semitone from the negative stimulus or even to conditioned stimuli of different qualities, such as sight stimuli. In extreme instances, dogs subjected to inhibition *went to sleep*. This observation led Pavlov to postulate that sleep is essentially a widely spread inhibitory state and that every inhibition may be regarded as a partial, localized sleep. That sleep may vary in its *extension* is known to everyone who has been faced with the problem of attending to something while he sleeps. The mother of a sick child or the soldier who must be on the lookout for certain sorts of warning sounds may sleep and yet may respond to the slightest stimulus of the significant sort. With practice, one finds that such partial sleep can give fairly satisfactory rest.

Using the mechanism of the conditioned reflex to explore the discriminatory capacities of dogs, Pavlov made other observations that throw light on important human problems. A dog was conditioned to salivate at the sight of an ellipse, but not at the sight of a circle. Then, it was presented with ellipses that were more and more nearly like circles. When the ratio of the two axes of the ellipse was about 9:8, the limit of canine ability was reached. At this stage, a dog would give one of two reactions: either it would bark and yelp meaninglessly, straining wildly at its harness; or it would go into a sort of trance, refusing to attend to anything for a long period of time. Pavlov pointed out that these reactions resemble two well-known **neuroses** in humans, *hysteria* (the former) and *neurasthenia* (the latter). Which reaction was produced seemed to be less a function of the particular experimental set-up than it was of the temperament of the dog. After the upsetting experience, the dog had to be given a long rest from the experimental set-up before it could be used again. Its retraining period was prolonged and necessarily involved much exposure to easily-solvable problems.

This is only one of the ways in which neuroses can be caused in experimental animals. Many other procedures have been followed, but whatever the details, the experiments boil down to this: the experimenter in some sense "double-crosses" the subject, either by demanding too much in the way of discriminatory ability or by deliberately changing the conditions of reward or punishment in a manner that is unpredictable from the subject's viewpoint. When the subject must make a choice, and it has no certain guide to action, it frequently, and in a sense, logically, retreats into neurotic behavior.

Experimentation of this sort is still in its relative infancy but it shows promise of ultimately yielding great benefits. It is not carried out from sadistic motives; watching neurotic dogs or rats* is not pleasant. But it must be done, whatever the cost, for the stakes are high—man's own mental health. The price of mental ill-health is incalculable, but the few available figures may give some idea of the magnitude of the problem. It is estimated that every psychological casualty of World War I cost the government $30,000 from beginning to termination by cure or death. Figures from World War II will not be available for a long time. Fifty per cent of the hospital beds of the United States are occupied by mental patients and the cost of caring for these patients is estimated at $175,000,000 per year.

But hospitalized patients are probably only a minor part of the problem. Nonhospitalized patients, of all degrees of ill-health, are much more important. What these cases cost all of us is inestimable†, even in dollars and cents, which is only the lesser part of the cost. The greater part of the price we have paid is not in money but in waste and suffering, costs which devolve upon all of us. These costs will continue to be paid by society as a whole until our clinical and anthropological studies of man and our experimental studies of other animals give us the certain knowledge we need to insure the mental well-being of individuals and communities. This is one of the great frontiers of science.

QUESTIONS AND PROBLEMS

13-1. The German mathematician and philosopher, *Leibnitz*, in 1714, wrote: "Memory provides the soul with a kind of consecutiveness which resembles reason, but which is to be distinguished from it. Thus we see that when animals have a perception of some-

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* Dogs are not very satisfactory because of their initial expense, the cost of the large equipment required, and the lack of sufficiently pure breeds. Only mongrels are within the budget of a research laboratory. Even dogs with a pedigree are not *very* pure by laboratory standards. Highly inbred rats offer ideally uniform psychological material, thus making possible adequate controls.

† What, for instance, did Adolf Hitler cost the world?

thing which strikes them, and of which they have formerly had a similar perception, they are led by means of representations in their memory to expect what was combined with the thing in the previous perception, and they come to have feelings similar to those they had on the previous occasion. For instance, when a stick is shown to dogs, they remember the pain it has caused them and howl and run away."

In modern terminology, what is Leibnitz talking about?

13-2. Define and describe a conditioned reflex.

13-3. How does the mechanism of the conditioned reflex explain the traditional practices of the professional animal-trainer?

13-4. Many red-green color-blind men have no difficulty in distinguishing between red and green traffic lights. How do you explain this fact?

13-5. If a man cannot distinguish between reds and greens, what color does he see them as? All as shades of red? Or of green? Can one use the mechanism of the conditioned reflex to answer this question? If this is possible, describe the experimental procedure.

13-6. That mental health, like all health, is only partly an individual matter and largely a consequence of community structure, is only gradually being recognized. A good introduction to this point of view can be gained by reading:

Benedict, Ruth, *Patterns of Culture*. Boston: Houghton-Mifflin Co., 1934. (Paper-bound edition, New York: Penguin Books, Inc., 1946.)

Mead, Margaret, *And Keep Your Powder Dry*. New York: Wm. Morrow & Co., 1943.

13-7. Conditioned reflexes cannot be established in an animal that lacks the cerebral cortex (the surface of the largest part of the brain). Yet, as the American physiologist, Lashley, has shown, once a conditioned reflex has been established in a rat, a single cut through the rat's cortex, regardless of the plane of the cut, will not destroy the conditioned reflex. In the light of this fact, reexamine Fig. 13-1. Is the mechanism of conditioned reflex formation, as there illustrated, to be understood as an exact image, or as an analogy? Explain.

Chapter XIV

Reactions of the Organism as a Whole

96. A Synthetic View of the Organism

In § 15, it was stated that, in order to keep our heads above water in this complex subject of human physiology, it would be necessary to develop first an analytical view of the body, speaking now of one system, now another. However, it was also pointed out that such a view has its shortcomings; the body never acts by isolated systems, one system at a time, but always acts as a unit with almost every "system" more or less involved in even the simplest of actions. Fortunately, it is possible to speak of the functions of some of the systems as if they were isolated from the others without too great a misrepresentation of the facts. Other activities, however, can hardly be discussed in so disarticulated a fashion; for instance, the activities connected with maintaining equilibrium, or with reproduction. In discussing these, a more synthetic viewpoint is needed, one in which the different roles of the various component systems are brought together in discussion, as they are in their functioning in the body.

97. Control of Movement: Proprioceptive Senses

We can make a good beginning toward understanding the complexity of even apparently simple functions by reconsidering the problem of movement. We tend to think of movement as a simple thing. I wish to move my arm; I move it. *Presto!* That's all there is to it. But, when we see the difficulty that an infant has in performing even the "simplest" act, such as reaching out and grabbing a rattle, we begin to wonder if the simple is simple after all. It takes a child weeks to learn to grab, and months to learn to walk. What is so difficult about these movements? What is it that has to be learned?

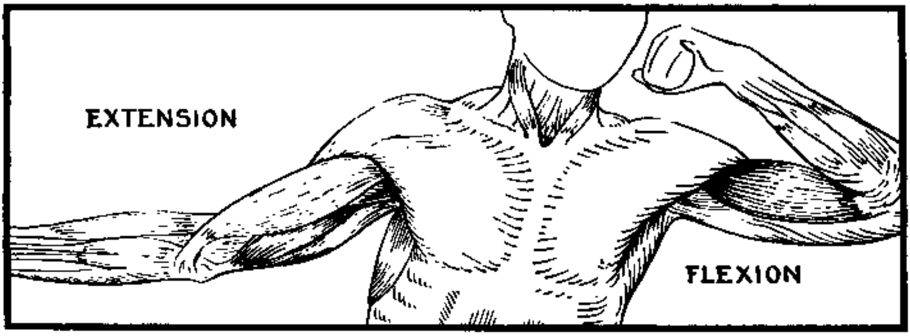

Fig. 14-1. The extension and flexion of a limb by muscles.

Let us return to the basic anatomy of a limb (see Fig. 14-1). Two bones, connected by a flexible joint, can have their relationships to each other altered by contraction of an extensor muscle which will increase the inner angle made by the bones, or of a flexor muscle which will decrease this angle. This, in simplest outline, is the mechanism of movement of a bone.

But it is too simple. No bone is moved by only two muscles. It takes six muscles to give the forearm its various movements, and many more to carry out the multiple movements of the hands and fingers. One anatomist has estimated that no less than fifty-four muscles are involved in a "simple" forward movement of one leg, as in walking. The complexity of the muscular system is clearly evident in Figure 14-2. It seems not unreasonable to conjecture that a rather complex system of control will be required for managing all these muscles.

As stated earlier, every motion of the skeletal system involves the simultaneous contraction of antagonistic muscles; change in position of the part occurs because one of the antagonists contracts more strongly than the other. To make a successful movement—say, reaching out and grasping a bottle of ink on the desk before you—you must not only

(1) be able to cause the muscles to contract in the right amount, but you must, at every moment, (2) know just where your arm is and what it is doing. *Vision is not necessary for this knowledge.* Close your eyes and reach for the bottle; you can still reach it with almost complete accuracy and efficiency. Your knowledge of where your limbs are and what your muscles are doing does not depend on vision. You can "feel" where they are and what is going on.

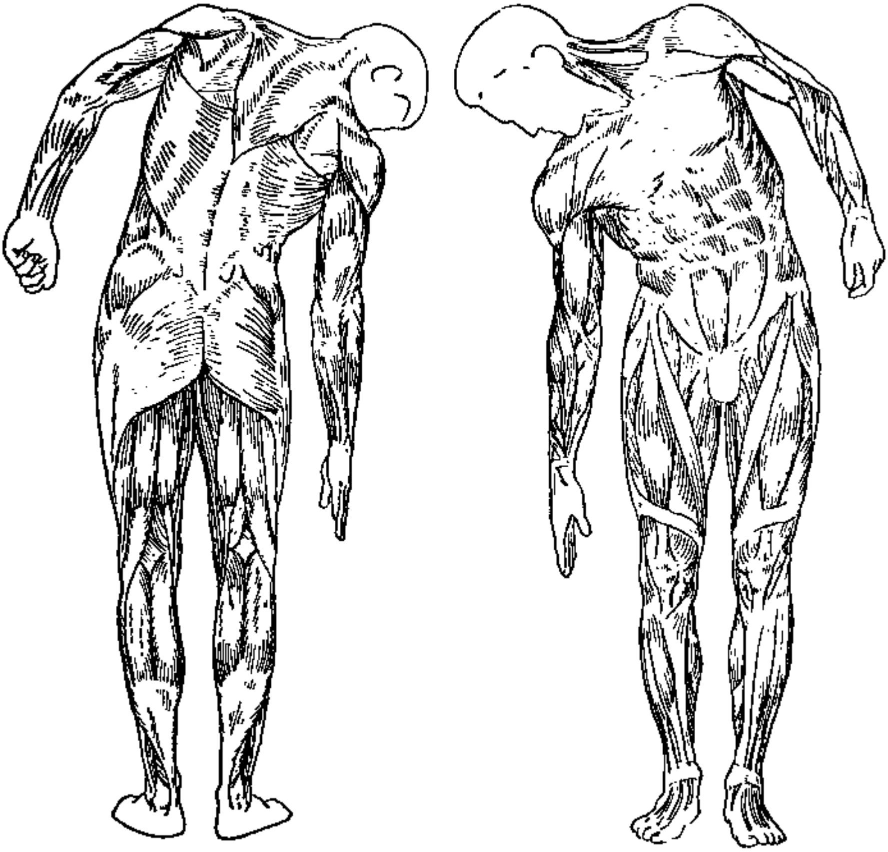

Fig. 14-2. The complex muscular system of man.

What sort of feeling is this? Touch, warmth, cold? It is none of these. These senses of touch are all exteroceptive senses, that is, senses that tell us of the exterior world. The sort of feeling that we are investigating now is based on senses that have been called the **proprioceptive senses** (Latin *proprius*, one's own), i.e., the senses that tell each of us about the doings of his own body. That there must be such senses follows as a strong probability from such a simple observation as we have just made, yet it was not until about a century ago that physiologists realized this, and called this sense the "sixth sense."* Actually, further analysis has shown that it is a complex of several senses.

One of the elements of the "sixth sense" is *muscle sense.* Imbedded in every muscle, are numerous nerve endings which are stimulated by the changing pressure of the surrounding muscle fibrils. When these receptors are stimulated, they send messages to the central nervous system, thus keeping it continuously informed of what the muscle is doing. We think of a muscle as an effector, which it is primarily, but the great English physiologist, Sherrington, estimated that 40 per cent of the nerve fibers attached to a muscle are *sensory* fibers. One might call a muscle a sense organ, though it is a rather self-centered one, reporting information only of its own affairs.

Another of the elements of the "sixth sense" is *tendon sense.* Every muscle is connected to bones by some sort of connective tissue which, when in the form of a long strip, is called a tendon. Imbedded in the tendons are nerve end organs that inform us when the tendon is on a stretch, thus adding to our knowledge of what our muscles and bones are doing. Tendons cannot expand or contract, but are moved passively. They are, therefore, not effectors but receptors only.

Continuous knowledge of the position of our muscles and the tension of the muscles and tendons permits us to know where our muscle-moved parts are, in what direction they are moving and how fast, and what opposition they are encountering, i.e., how hard the muscles are having to work to effect movement. For instance, we make our estimates of the weight of objects using these proprioceptive senses.† If, for instance, we are asked to say which of two melons is the heavier, we "heft" them in our hands, noting, however unconsciously, how much stretch the muscles and tendons of our arms are put to, and on this basis deliver a judgment. The more nearly equal are two weights, the more difficult

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* One reason for the belated discovery of this sense was probably the ease with which proprioceptive knowledge could be ascribed to other causes, for instance, to the sense of touch affected by the pressure of clothing or by the wrinkling of one's skin at the flexion of a joint—feelings which clearly *do* give information of the position of body. These sensations may contribute to our information but they are not necessary.

† Do any other senses aid?

it is to distinguish them. One can easily distinguish between two pounds and three pounds, but not between two pounds even and two pounds one ounce. However, one can distinguish between a one-ounce letter and a two-ounce one. How does it happen that one can detect a one-ounce difference in the latter case and not in the former? Obviously, because the *relative* difference in weights of the two objects is not great in one case, and is in the other. Two ounces are twice as heavy as one ounce, but two pounds one ounce is only 3.1 per cent greater than two pounds. Numerous experiments make it clear that it is the *relative difference* that is important in determining distinguishability of two stimuli. For what we might call the "hefting sense," an ability to distinguish a relative difference of about 1 part in 30 is normal.

The doctrine that it is relative differences in stimuli that are perceived is embodied in what is called the Weber-Fechner Law. It holds not only for stimuli arising from the proprioceptive sense, but also for those from most of the other senses.* For each sense, there is a smallest relative difference that is perceptible, and this is true for a wide range of stimuli. The law holds only over the middle region of perceptibility, however. When stimuli are very slight, or very great, we are less able to distinguish small relative differences. Moreover, the magnitude of this "smallest perceptible relative difference" will vary widely in different individuals, and such differences undoubtedly contribute to the diversity of individual aptitudes for the various vocations.

98. Control of Movement: The Semicircular Canals

When the structure and function of the inner ear were first discussed, an important portion of this organ was deliberately ignored: the fluid-filled portions that are illustrated in Figure 14-3A,B. The time has come to remedy this omission.

Occasionally, the inner ear is completely destroyed by disease. If both ears are so affected, the individual becomes stone deaf, of course†, and, in addition, his sense of equilibrium is seriously affected. When in a completely dark room, he is unable to stand or move upright because he has lost all sense of "down-and-upness." He still has the

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* From your experience would you say it holds for the sense of pain?

† Could his hearing be partially restored by hearing aids?

proprioceptive senses from his tendons and muscles and sense of touch and pressure in his skin, and these help him slightly in perceiving his

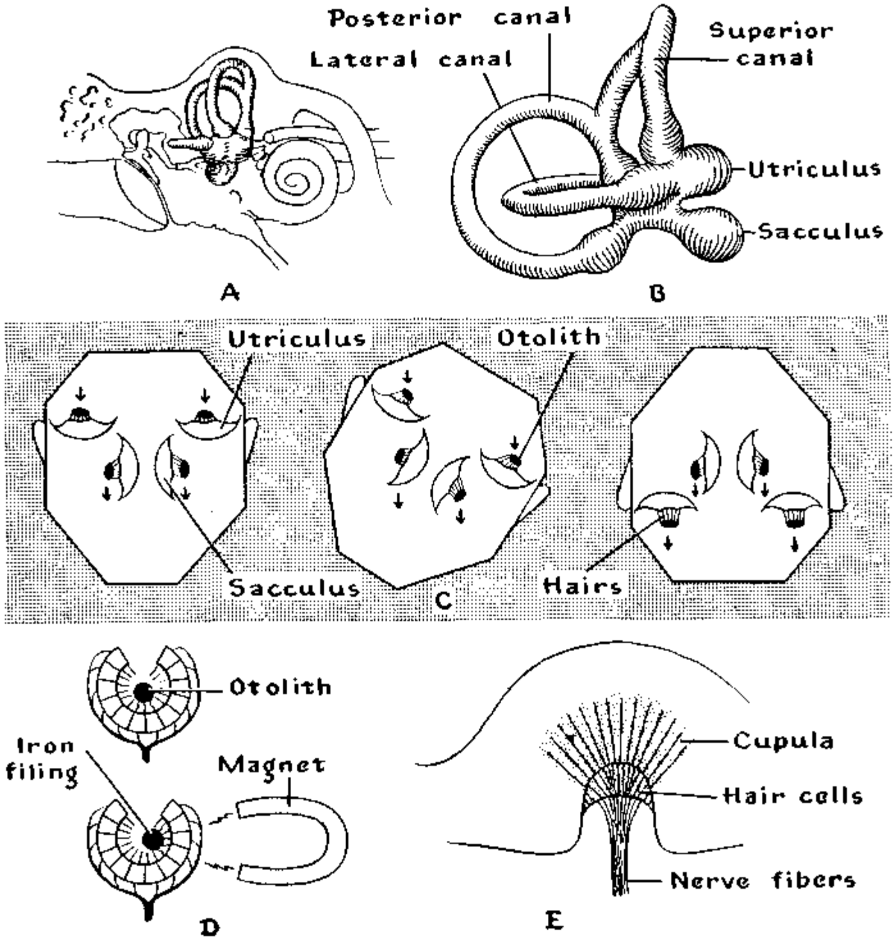

Fig. 14-3. A, B, the utriculus and sacculus, the organs of static equilibrium; and the semicircular canals, the organs of dynamic equilibrium. C, effect of position of body upon the position of the otoliths. D, otolith of crayfish, in which function can be experimentally proved. E, sense organs within semicircular canals.

relations to his surroundings (he can feel the pressure of his body on the floor through the soles of his feet, for instance), but this aid is not enough to enable him to move around without danger to himself. If the light is turned on, he can successfully move around, using his eyesight to tell him which way is up.

Most of our orientation to our surroundings is brought about through three kinds of senses: the proprioceptive senses of muscles and tendons, vision, and the middle-ear senses. The middle-ear senses are of two sorts, static and dynamic. The static sense tells us the position of the head with respect to gravity, and the dynamic sense tells us of change in rate of movement or change in direction of movement of the head.

Experiments with animals and observation of natural anomalies in man have shown that the organs of static sense are the swollen bulbs, the **sacculus** (Latin, little sack) and **utriculus** (Latin, little bag), seen in Figure 14-3B. Inside of these bulbs are to be found the structures seen in Figure 14-3C, sensitive cells with flexible hairs supporting an **otolith** (Greek *otos*, ear; *lithos*, stone), a tiny pebble of calcium carbonate. Since the otoliths are not rigidly fixed in position, different positions of the head will result in unequal stimulation of the sensitive hair cells. Perception of this inequality is believed to be the means by which we know of the position of the head with respect to gravity.

This theory of the mechanism of static equilibrium in humans has not been proved but it receives strong, though indirect, support from experiments that have been carried out with crayfish. A crayfish has a similar equilibrium organ (Fig. 14-3D) which, at certain stages in the life history, is easily accessible from the outside. An ingenious experimenter made use of this convenient situation by replacing the stony otoliths with iron filings. Then, when he brought a strong magnet close to the crayfish, the animal oriented itself to the face of the magnet instead of to the gravity of the world, thus proving, *in the case of the crayfish*, the correctness of the theory of otolith function. In mammals, the minute otoliths are almost inaccessible to operative procedure, so it seems doubtful if the theory will be tested in them.

Knowledge of change of movements of the body is apparently derived from the **semicircular canals.** Notice (Fig. 14-3B) that these canals are oriented at right angles to each other so as to correspond to the three planes of Euclidean space. Inside the semicircular canals, are sense organs of the sort diagrammed in Figure 14-3E. The canals are filled with fluid, and movement of fluid past these sense organs, which must occur during acceleration, causes sensation of movement.

It is interesting to compare man's reactions to movements in the various planes of space. Changes in movement in the horizontal plane, to which we are fully accustomed, cause little or no discomfort; whereas, changes in movement in a vertical plane may cause anything from slight discomfort, as in the "sinking" feeling in the pit of one's stomach when the elevator starts to descend rapidly, to the extreme nausea that may be experienced in an airplane that is being thrown up and down in rough weather. It is difficult to imagine any teleological reason why sensations proceeding from the inner ear should affect the stomach so. There are great differences between individuals, and experience may, fortunately for most of us, ameliorate the reaction.

99. Control of Movement: The Cerebellum

It was mentioned earlier that over fifty muscles are used in making a simple forward movement of a leg in walking. It will be readily appreciated that the sequence and strength of the contractions of these various muscles must be finely and intricately organized if the foot is to go where and when we want it to. When we recall that a walking movement is not the only movement possible; that we may run, hop, skip, or jump at will; that all these movements entail different patterns of muscle contractions; and, that while we are moving, we may be carrying on a conversation, or thinking about something else—then, do we appreciate how marvelous is the unconscious control of our complicated movements. Where is this control exercised? What is the *central* organ involved?

Extirpation experiments show that the **cerebellum** (Fig. 14-4) is the organ essential to the fine control of movements. When it is removed, the animal becomes, for a time, completely incapacitated. After some weeks, it manages to move about slowly and awkwardly. It sways and falls frequently; when it tries to extend a limb to a certain place, it is very likely to overshoot the mark. Tremors of the muscles are frequent. Voluntary movements are achieved with difficulty, and the gait of such an animal is said to resemble that of a drunken man.*

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* Humans suffering natural damage to the cerebellum exhibit a similar "drunken" gait. This has led to the suggestion that some of the effects of alcohol may be explained by its anesthetic effect on the cerebellum.

Humans sometimes suffer partial loss of cerebellar functions due to localized tumors or other degenerative diseases. The extent of the injury can be estimated by careful determination of the parts of the body, whose accurate movements are affected. Frequently, the affected parts are flabby because the muscles are usually completely relaxed. This raises a point we have not made before: *in the normal animal, the skeletal muscles are never completely relaxed even in sleep.* At all times, the muscles are under some tension; we say they possess **tone*** or **tonus.** *All the muscles of the body are continuously receiving slight nervous impulses* that keep them contracted just enough to be firm but not enough to cause any movement of the associated skeleton. When the nerves to a muscle are cut, the muscle immediately assumes a flabbiness never observed in a normal animal except, possibly, in a very deep sleep or drunken stupor or in cases of cerebellar injury.

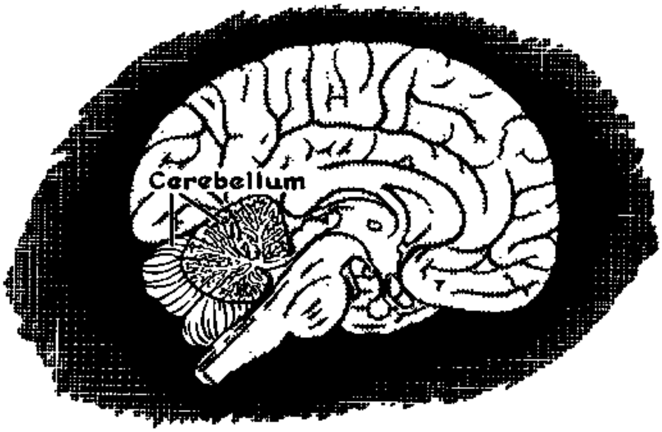

Fig. 14-4. The brain's executive secretary.

It is important to realize that, in the complete absence or destruction of the cerebellum, voluntary movements are still possible. But, for accurate execution of them, the cerebellum is essential. The *cerebrum* is responsible for making the decisions; the *cerebellum* is responsible for carrying them out. This relationship has led to the statement that the cerebellum is the "executive secretary" of the central nervous system.

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* This use of a musical term may seem surprising but its origin is enlightening. It is derived from the Greek *teino* meaning *stretch*. The musical use of the word *tone* is a secondary one, probably derived from the fact that stretched strings produce musical notes.

This figure of speech may help the student to remember and understand its functions.

100. Blood Flow: Mechanical Factors

The circulatory system, like all the systems of the body, must be able to make adjustments to meet varying conditions and needs. A man writing a letter does not have nearly as much need of food and oxygen as does a man swimming in a race. Since the mechanism for transporting foodstuffs to the tissues is the blood stream, it is clear that increased activity will necessitate increased flow of blood. How may this be brought about?

The various mechanisms involved may be understood by referring to the simplified diagrams of Figure 14-5. Here, the heart is represented as a single mechanical pump and the arteries, capillaries, and veins as pipes of varying diameters. (See Fig. 14-5A.)

Increase in blood flow through the system may be brought about in two ways: (1) by increasing the rate of heartbeat; or (2) by increasing the amount of blood pumped per beat. In our mechanical analogy, the second possibility is represented by an increased length of stroke of the piston. In the heart, this effect is achieved by an actual increase in size of the heart at its maximum volume and a more complete emptying of it. In most normal adjustments to tissue demands for more blood, both means (1) and (2) are used. That the heart beats faster is a matter of common knowledge; that it pumps more blood per beat can be shown experimentally.

The means described above will cause blood to flow faster through all parts of the body. However, the tissue needs often vary in different parts. How can the relative volumes flowing through various parts be modified?

The "pipes" of the body differ from nonliving ones in that the bores of some of them can be changed in size. This is particularly true of the smallest of them, the capillaries. Fluid flows more readily through a large pipe than through a small one; therefore, if the capillaries in region Y expand (Fig. 14-5B), more blood per second will flow through this region.

Increase in the rate of flow of blood through Y can be achieved by another means, by *decreasing* the rate of flow through other parts of the body. If the capillaries at X are constricted (Fig. 14-5C), the result will be to force more blood per unit time through region Y.

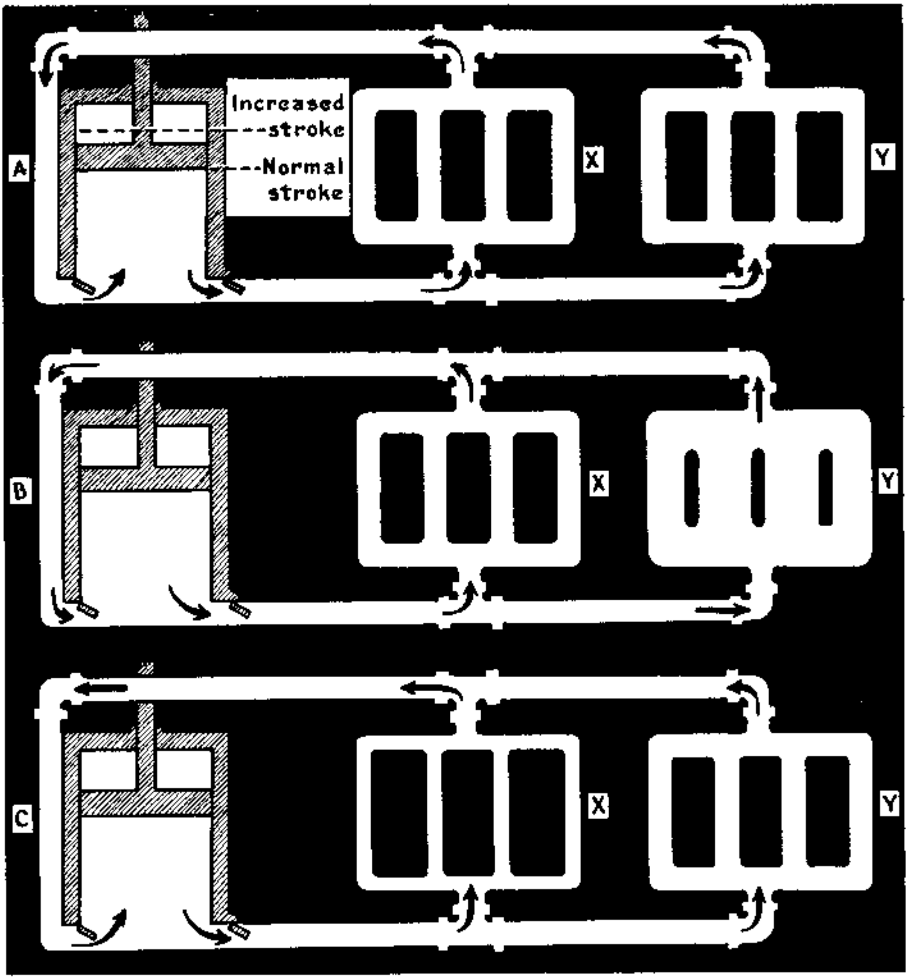

Fig. 14-5. Mechanical analogy to the circulatory system. The amount of blood flowing through region Y can be increased by increasing the amount of blood pumped by the heart (A); or (B) by opening more widely the capillaries in region Y; or (C) by narrowing the capillaries in other regions, represented by X.

101. Blood Flow: The Means of Control

The rate of flow of blood through the various parts is determined by the rate and extent of heartbeat and by the contraction or expansion of the blood vessels. But what *tells* the heart and blood vessels what to do? This is a rather complex story, part of which we shall relate now.

The contraction and expansion of the smaller arteries (called **arterioles**) and the capillaries are effected by muscles in their walls (Fig. 14-6). These muscles are smooth muscles, hence, not usually under voluntary control. They are innervated by autonomic nerves. There are two layers, a layer of circular muscles and one of longitudinal muscles. Contraction of the former will decrease the diameter of the vessel, of the latter will increase it. Most of the changes in bore seem to take place, however, largely through the contraction, or absence of contraction, of the circular muscles. In the absence of contraction of these muscles, the vessel will automatically tend to enlarge because of the pressure of the blood inside.

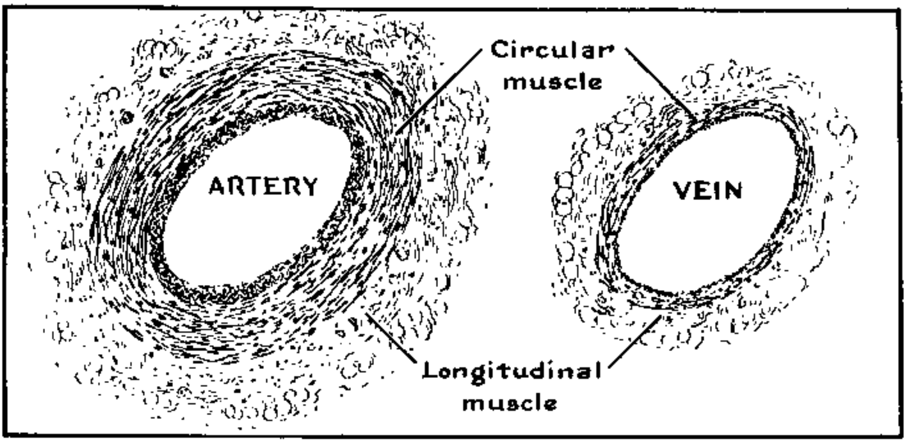

Fig. 14-6. Blood vessels in cross section, showing the muscles which regulate their diameters. Notice that the muscular layer of an artery is thicker than that of a vein of the same internal diameter.

The autonomic nerves that control the blood vessels are controlled largely by the **medulla** (Fig. 14-7). For this reason, the medulla is referred to as the **vasomotor center** of the body (Latin *vas, vasculum*, a vessel). This region of the central nervous system has many other important functions, as we shall soon learn.

The musculature of the blood vessels can also be directly affected by chemicals. Carbon dioxide causes the circular muscles to relax, thus increasing the flow of blood through the capillaries. This is undoubtedly important in causing local vasodilatation in response to increased activity of a part of the body. More widespread effects are caused by another chemical, **adrenin,** a hormone produced by the central portion, called the adrenal medulla* (Fig. 14-8B), of the *adrenal gland* (Fig. 14-8A).

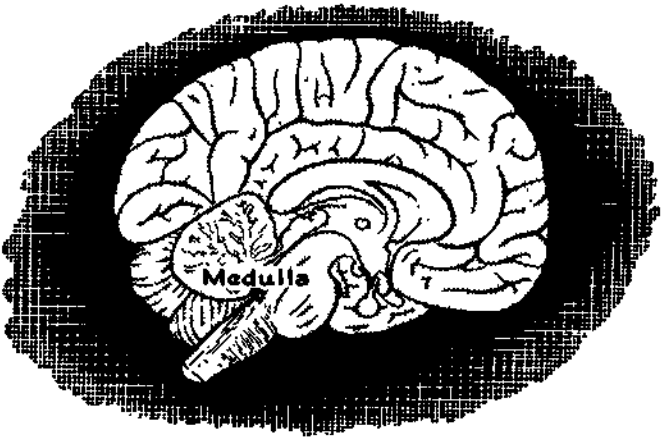

Fig. 14-7. The unstippled region is the medulla, the vasomotor and respiratory center.

Adrenin causes a constriction of the arterioles of the viscera and a relaxation of the arterioles of the skeletal muscles. This action—a combination of the two diagrammed in Figure 14-5B and D with X representing the viscera and Y representing the skeletal muscles—has the effect of shunting blood from the viscera to the muscles. There is evidence that adrenin is released in increased quantities at times of stress, e.g., during fear, anger, flight, etc. (See Fig. 14-8C.) The adaptive value of furnishing more blood to the muscles which need it at those times, at the expense of the viscera whose needs are not urgent, is obvious. The adrenal medulla is innervated by fibers from the autonomic system, and it is probably through these that the activity of the gland is coordinated with the emotional state of the individual.

It will be worth while to describe the chain of circulatory events that takes place whenever the body becomes more active. Increased activity is accomplished by increasing the rate of burning foodstuffs.

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* What does *medulla* mean? Does its etymological meaning help explain why it is applied to two such different regions as the medulla of the nervous system and the medulla of the adrenal glands?

Increased food-burning produces increased CO_2. Locally, the CO_2 causes dilatation of arteries as previously explained. Carbon dioxide is carried to the vasomotor center of the medulla which then sends impulses along the autonomic nerves to the vasoconstrictor muscles of the blood vessels. This action is contrary to the *direct* action of carbon dioxide on these muscles and the net result is to constrict the capillaries in those regions that are not entering into greater activity while allowing the capillaries in the more active region to expand, a useful reaction that is enhanced by the action of adrenin. The medulla is also the

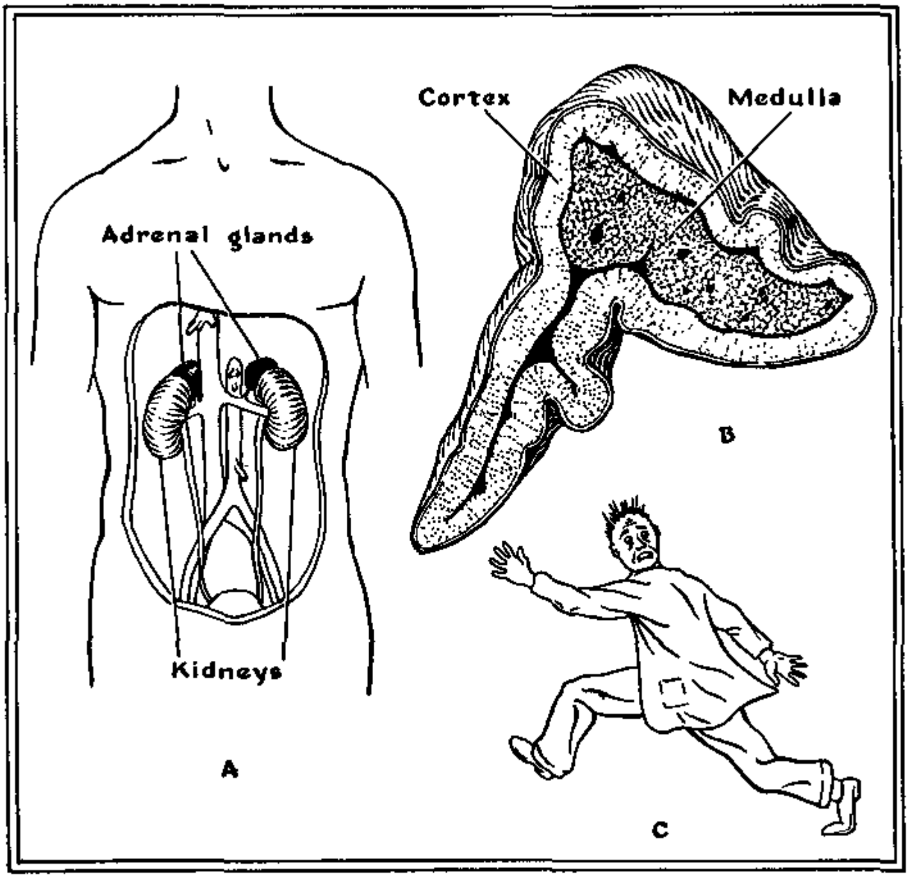

Fig. 14-8. The adrenal glands, which just happen to lie next to the kidneys (A) but have no connection with them, are divided into cortex and medulla. The medulla (B) produces a hormone, released in times of fright, that constricts the arterioles of the viscera and relaxes those of the skeletal muscles—a useful reaction in times of fear (C).

cardiac center. Stimulation by carbon dioxide causes this center to stimulate the heart to greater activity, the stimulus being carried by nerves belonging to the autonomic system.

This outline of the nervous control of vasoconstriction also helps us understand the well-known fact that rapidly repeated forced breathing causes dizziness. The greatly increased rate of breathing results in lowering the concentration of CO_2 in the blood; because of this, the medulla is not stimulated as much as normally; consequently, the vasomotor center sends out fewer impulses to the vasoconstrictor muscles; consequently, the capillaries of the body expand. With most of the capillaries of the body dilated, there is a greater volume available to the blood, and consequently, the blood pressure falls everywhere. The fall in blood pressure results in slower movement of blood; slower-moving blood brings less O_2 to the brain than it needs; hence, the individual develops a feeling of dizziness and may even faint.

102. Temperature Regulation: Animals With and Without Thermostats

It is common knowledge that animals can be divided into two groups: "cold-blooded," such as reptiles and fish; and "warm-blooded," including the birds and mammals. The terms for these groups are not well chosen, however, for "cold-blooded" animals sometimes have a body temperature higher than the "warm-blooded" forms. A lizard sitting on a rock in the sun of a warm summer day has been found to have a body temperature as high as that of a man with a very high fever. The same lizard at night, however, will have a temperature far below that of man. In the same environment, man's temperature will be almost invariable. The real difference between the two groups lies in the variability of temperature. They are, therefore, sometimes referred to as the **homothermal** (constant temperature) and **poikilothermal** (variable temperature) animals. Or, one might call them animals-with-thermostats and animals-without-thermostats.

Man belongs to the homotherms, the animals-with-thermostats, and this is one of the factors that has been instrumental in bringing about his rise to dominance in the animal world. One of the basic generalizations of chemistry is that *chemical reactions proceed faster* at high temperatures than at low. Metabolism, recall, is the name we give to the complex of chemical reactions of the living body. As the body temperature rises, metabolism speeds up; as it falls, metabolism slows down. A nonthermostated animal lives at a fast pace at high temperatures, at a slow pace at low.

More important is the fact that **different chemical reactions are affected to different degrees by changes in temperature.** What we call metabolism is a complex of precisely interconnected chemical reactions. If some of the reactions go too slowly or too fast, relative to the others, the whole system is thrown off balance, often with serious, even fatal, results. In this fact, we see the real importance of a thermostat to an organism; it permits a more intricately organized complex of chemical reactions, greater complexity of structure and function. Installing a thermostat in a fish would probably do the fish no immediate good, because its metabolic system is already organized on a *relatively* simple basis that is not very temperature-sensitive. However, once a species is equipped to keep its temperature constant, it can then afford, so to speak, to evolve a more elaborate metabolic system which will permit it to get along better in the world. This more elaborate system may be more easily thrown out of balance by temperature changes. A rise of ten degrees Fahrenheit or a fall of twenty degrees in a man's temperature may be fatal, whereas the slower-moving, less intricately organized lizard will be but little affected by such variations. The price of specialization is vulnerability.

103. Temperature Regulation: Adaptation to Heat

How does a man in a hot room keep cool? The principal means is that afforded by the activity of the sweat glands. How does this cool the body?

To understand this, we must recall once more our picture of the molecular structure of matter (see Chap. V). All matter is made of molecules that are in continuous motion. At any given instant, different molecules are moving at different rates. *What we call the temperature of a substance is a measure of the average speed of its molecules.* If the average molecular speed is great, the temperature is high. Low average speed, low temperature.

Now consider the oversimplified diagram of Figure 14-9. The skin is covered by millions of molecules of water (part of the *sweat*) of which we have shown only a few for simplicity. These molecules are bouncing around. At the instant we "look" at them, their speeds are as recorded by the figure written inside each diagrammed molecule. The average speed of these water molecules is, say, 100. (Never mind what the units are.) An instant later, every molecule is somewhere else and, because of collisions, the speeds are different; but, in the absence of outside influences, the *average* speed of the molecules remains the same.

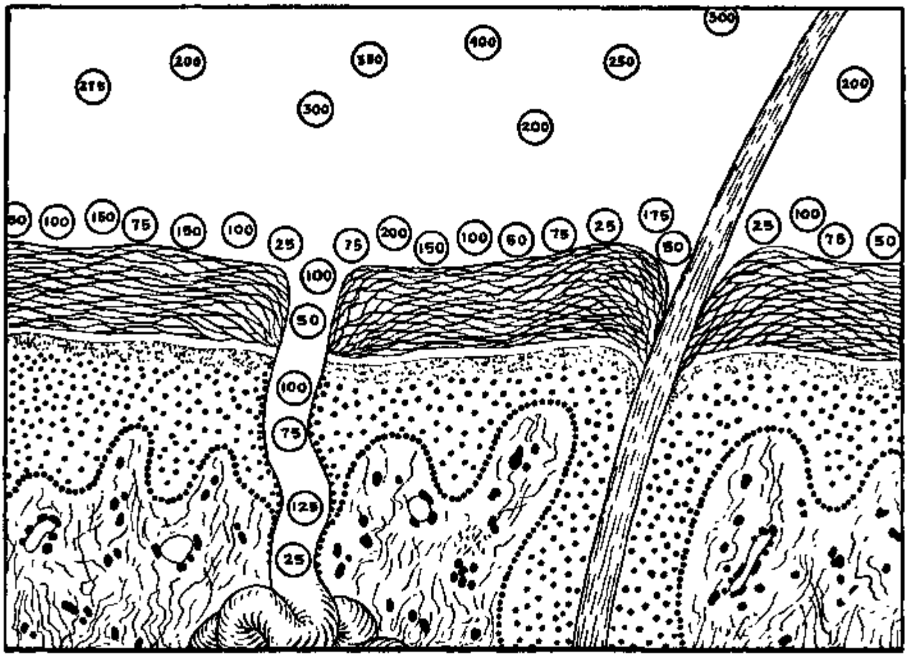

Fig. 14-9. When some of the water molecules of sweat reach a high enough speed to "take off" the surface of the skin, the average speed of the molecules left behind is necessarily reduced somewhat, hence, the cooling effect of the evaporation of sweat.

The molecules of a gas have a greater average speed than the molecules of a liquid at the same temperature. If we have liquid of a certain kind (water) in contact with a gas containing molecules of the same kind (e.g., air containing water molecules—"water vapor"), every now and then, one of the molecules in the water layer will have a speed great enough to jump out and become one of the gaseous molecules. Referring to our diagram, suppose 200 is the speed needed for a molecule to move out of the water layer into the gas above. There are a few molecules of water on the surface of the skin that have this necessary speed. These fast molecules have a high probability of leaving the water layer. When they do, *the average speed of the molecules remaining in the liquid layer will necessarily be decreased. Since average molecular motion determines what we call temperature, the temperature of the remaining liquid will drop.* The escape of molecules from a liquid into a gas is called **evaporation.** We see why evaporation has a cooling effect.

The human skin does not exude water at every point; water is secreted locally by specialized glands called **sweat glands** (Fig. 14-9). The secretion of these glands, called **sweat***, is not pure water but contains in it a number of other substances, principally sodium chloride or common salt. Sweat is secreted continuously at all temperatures but its rate of secretion is greatly stepped up under conditions of heat and physical exertion. In one experiment in which a man worked very hard in a hot, dry atmosphere, measurements showed that the loss of water by evaporation amounted to nearly one-half gallon per hour.

That sweat is not pure water is a matter of considerable practical importance. The concentration of various salts in the body is of great importance; if their concentration falls too low, prostration and even death may occur. Since sweating removes salts from the body, profuse sweating may desalt the body to a dangerous extent. This is the principal cause of the "heat prostration" and "sunstroke" that may afflict workers in hot places such as deserts, deep mines, boiler rooms, and steel mills. It would be more accurate to refer to it as "salt stroke" or "low salt prostration." It may be avoided by increasing the intake of salts, particularly sodium chloride. It is now standard practice in many industries to place salt tablets alongside the water tap with instructions for their use. In this connection, it is interesting to note that desert burros secrete a sweat that is almost pure water, much purer than the sweat of man. These animals are very tolerant of heat. One wonders to what extent differences in human susceptibility to heat might be explained by differences in composition of sweat.

Besides evaporation from the skin, there is also evaporation ("insensible perspiration") from the exposed surface of the lungs, and this, too, tends tc cool the blood. Some animals, dogs, for instance, possess

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* "Perspiration" in some circles; always called sweat by physiologists.

no sweat glands and, hence, must cool themselves in hot weather by increased evaporation from the lungs, breathing passages, and tongue. (Recall the "panting" of a heated dog.) Among humans, an inheritable absence of sweat glands is rarely encountered; for such humans, hot weather presents a very serious problem.

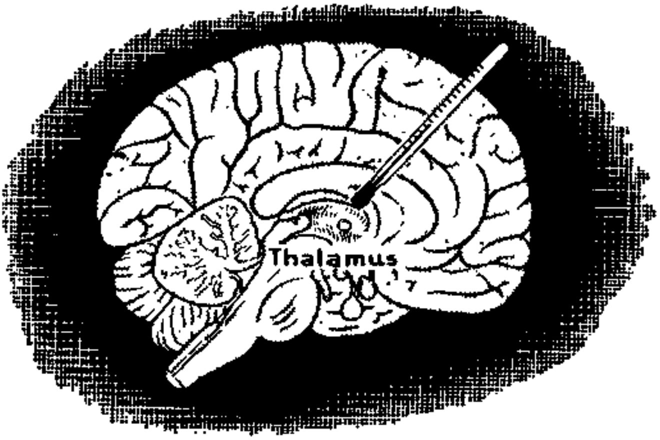

Fig. 14-10. The unstippled region is the thalamus, the temperature-regulating center.

The activity of the sweat glands is under the control of the central nervous system. When the nerves to the glands are cut, these glands no longer function. It has been shown that the part of the central nervous system known as the **thalamus** (Fig. 14-10) acts as the temperature-regulating center or thermostat. Activity of the sweat glands is stimulated reflexly when the heat-receptors of the skin are stimulated.

104. Temperature Regulation: Adaptation to Cold

Heat is lost from the body by three means: evaporation of water, convection, and radiation. We shall now consider how the body controls these means of heat loss.

Evaporation can be decreased by lessening the activity of the sweat glands. This is done by reflex action, upon stimulation by cold. However, evaporation is never completely zero for the sweat glands are always slightly active even under the coldest conditions. Furthermore, evaporation of water from the exposed surface of the lungs and breathing passages is always taking place and, for obvious reasons, this cannot be stopped.

Convection is a term that refers to the gross movements of unequally heated portions of a liquid or gas. Figure 14-11A will perhaps make the idea clear. Hot water is lighter than cold water; consequently, it will move up away from the heating object and will be replaced by cooler which, when heated, will . . . . and so on. The movement is called convection; we refer to the convection currents of the fluid. A warm man in a cold room (Fig. 14-11B) will similarly cause convection currents in the air which will increase the rate of heat loss from his body.

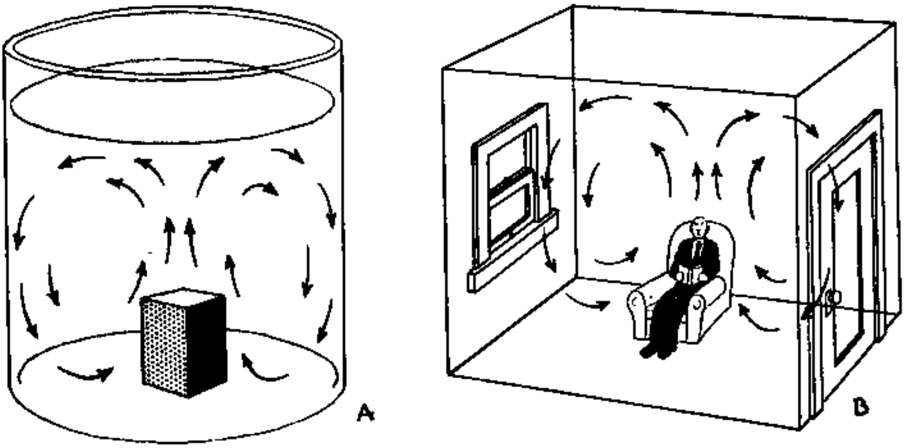

Fig. 14-11. In A, convection currents in beaker of water, caused by warm object on the bottom (B): warm man in cold room causes convection currents and loses heat to air of room.

Convection losses can be decreased by having a dead air space next to the hot body, in which air can circulate only with difficulty. Birds achieve this with feathers, most mammals with hair; but modern man, poor creature, must resort to clothing. When the weather gets colder, the feathers of birds and the hairs of mammals stand out more from their bodies, thus increasing the amount of dead air space. Man, being a mammal, attempts to do this, too, but the result is little more than ludicrous goose-pimples formed by the contraction of tiny muscles at the base of insignificant hairs. So, he puts on another sweater or turns the electric blanket one notch higher.

Radiation must be distinguished from evaporation and convection. All bodies send out heat rays in all directions. These heat rays are like light rays: they travel in a straight line and can travel through a vacuum.

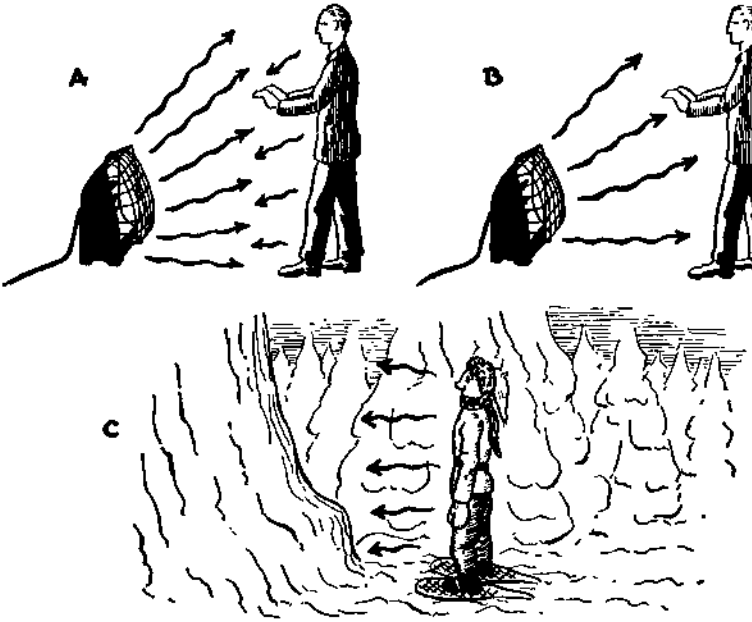

Fig. 14-12. All bodies radiate heat rays in all directions, but since an electric heater sends more heat rays to a man than the man does to the heater (A), the *net* effect is one of radiation from heater to man (B). A man standing near a glacier (C) loses heat to the glacier by radiation.

The filament of a light bulb sends out both light and heat rays, which we can feel or see even though the filament is surrounded by a vacuum.

Objects at different temperatures will radiate heat to each other. (Fig. 14-12A.) But a hot object sends out more heat rays than does a cooler one (Fig. 14-12B,C); consequently, the *net effect* will be that the hot object loses heat and the cooler one gains it. In a shorthand way of speaking, we may say that the hot object radiates heat to the colder one.

A man facing a snow bank or a glacier is aware of his loss of heat to the cold object by radiation (see Fig. 14-12C). Convection currents in the air, of course, cool him, but over and above this, he is cooled by his radiation. It *feels as if* the glacier were radiating cold to him, which is physical nonsense.

How is the problem of heat loss by radiation controlled? It should be apparent that the hotter the surface of a man, the more heat he will radiate. How can the surface temperature be controlled? By controlling the rate of flow of warm blood to it. If the blood flows fast, it will keep the surface warm; if it flows slowly, the surface will become cooler. The control of blood flow is effected by the arterioles and capillaries *through reflex action*. The sensation of heat, originating either locally in the heat-receptors or centrally, stimulates the heat-control center which, in turn, sends fewer stimuli through the nerves to the circular muscles of the blood vessels. The blood vessels then expand; more blood flows through the capillaries per unit of time, and more heat is radiated away from the body. The sequence of adjustments to the sensation of cold can be readily predicted. The final adjustment of the size of the surface capillaries causes a change in appearance that is readily observable to the naked eye. The face of a man on a hot day becomes quite ruddy; on a cold day, he becomes very pale and "blue" on account of the change of color of his blood as it stagnates in the vessels.

105. Temperature Regulation: Indirect Control

So far, we have been discussing means of increasing or decreasing the rate of heat loss from the surface of the body. Body temperature, however, will be affected also by the rate of heat production.

Recall once more the fundamental equation of respiration:

$$\text{food} + \text{oxygen} \longrightarrow CO_2 + H_2O + \text{energy} \qquad (1)$$

By increasing or decreasing the rate of respiration, we can increase or decrease the amount of energy produced. No matter how we make use of this energy, whether for muscle movement, growth, or what, a large part of it always appears as heat. Therefore, changes in the amount of respiration effect corresponding changes in heat production.

Everyone has had the experience of shivering in a cold room. At first glance, such a reaction might appear to be nonadaptive, since it unquestionably increases the loss of heat by conduction and convection. However, recalling the consequences of respiration suggests a different answer. Shivering is brought about by the strong contraction of antagonistic muscles. The result of any muscle action can be written:

$$\text{muscle contraction} \longrightarrow \text{motion \& heat} \qquad (2)$$

Usually, the motion is the main product and heat is only an unavoidable by-product. In the present instance, however, the situation is reversed, and heat may be regarded as the principal product required by a cold man, with motion as a by-product, a by-product largely avoided by the simultaneous contraction of antagonistic muscles.

The rate of respiration is affected by other factors as well. Respiration occurs not only in the muscles but in all parts of the body. Every cell respires. The rate of respiration is affected by many factors, among them the amount of food supplied, the kind of food, and various hormones.

The maximum amount of respiration possible is obviously determined by the amount of food taken in (equation 1). As might be expected, people in cold countries eat more food than people in hot. This may be partly a matter of custom, but experiments have shown that, when allowed to eat freely, both men and animals eat more when they are in a cold environment than when they are in a warm one.

The kind of food also influences the rate of heat production. Proteins, for some reason, stimulate respiration. Intake of 500 calories of proteins causes a greater immediate increase in the rate of heat production by the body than does intake of 500 calories of carbohydrates. Correlated with this is the natural tendency for people in cold climates to eat heavily of meat when given free choice.

The influence of hormones on respiration and heat production is easy to establish but hard to explain. Hormones affect not only respiration, but also many other of the chemical processes that we lump, with respiration, under the term metabolism. The hormone of the **thyroid gland,** often called **thyroxin,** has a marked effect. Patients with a thyroid gland that is not secreting enough hormone into the blood stream have a much lower metabolic rate than normal, even as much as 40 per cent lower. Consequently, such individuals may suffer abnormally in a cold environment. Such individuals are said to be suffering from **hypothyroidism** or *hypofunctioning* (*hypo,* Greek, under) of the thyroid. On the other hand, individuals suffering from *hyper-*

thyroidism produce much more heat than normal and, therefore, may suffer in the summer.

It is of interest to note that one form of *hypo*thyroidism is caused by a diet too low in the chemical element iodine. When not enough iodine is available, the thyroid gland enlarges (*as if* it were trying to make up for the deficiency by harder work), producing the characteristic lump seen in Figure 14-13. The development of such a **goiter** (derived from Latin *guttur*, throat), as it is called, can be prevented by adding iodine to the diet.

Fig. 14-13. Simple goiter. (From Arthur E. Hertzler's *Diseases of the Thyroid Gland*. New York: Paul B. Hoeber, Inc. Courtesy of Dr. Irene A. Koeneke.)

In most regions of the world, there is enough iodine in the soil to furnish plants with the iodine man and other animals need for their thyroids to function properly. In some regions, however, the soil is deficient in iodine. In Derbyshire, England, for instance, this is true; as a result, the term "Derbyshire neck" was early applied to this sort of goiter. There are similar regions in Switzerland; and considerable areas in the middle part of the United States, especially around the Great Lakes, have low-iodine soils.

Since diet can affect a goiter and, hence, can affect metabolism, one might regard this as but another example of the effect of diet on heat production. However, it should be pointed out that there is no one "cause" of "simple goiter," as this kind of goiter is called. In the "Goiter

Belt" of the middle United States, only a small proportion of the population ever suffer from goiter. There seems to be a hereditary predisposition to simple goiter. There is a sex difference; women are far more liable to the disease than are men. Moreover, there is evidence that suggests an infectious agent may be involved, possibly a virus. The people of Derbyshire, England, for instance, did not exhibit their celebrated neck until after 1717 when Italians from Piedmont, Italy, were brought in to start up a silk industry. Many similar instances that suggest infection are known.*

Other glands also affect the rates of metabolism and heat production by the body. The mechanisms by which they produce their effects are not well understood. In general, any effect of a hormone on heat production will be a slow one, several days being required for an injection of thyroxin to take effect. (Adrenin is exceptional.) The abnormal functioning of *any* gland will probably cause, directly or indirectly, some disturbance of metabolism and heat production.

106. Control of Breathing: The Mechanism

A man can deliberately stop breathing for only a short period of time. After a few minutes, no matter how "strong" his "will power," he starts to breathe again. Following a period of no breathing, the impulse to breathe is so strong it cannot be denied. No man can resist the impulse; no man can wilfully commit suicide in this way. Why is this?

The teleological "why?" is obvious: the fact prevents individuals from stupidly taking their own lives. But what of the mechanistic "why"? That is, what is the *mechanism* that controls breathing?

A little thought about what must go on during suspended breathing will suggest possible answers. *Respiration* (recall the definition, § 36) goes on all the time. If *breathing* is stopped, that is, if exchange of gases between the body and the outside world is stopped, it is apparent that inside the body the *concentration of carbon dioxide will increase and that of oxygen will decrease*. Will either of these changes be effective in causing breathing?

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* Simple goiter is only one of many types known. Another well-characterized type is called "exophthalmic goiter" and involves *hyper*functioning of the gland. From an etymological analysis of the name, the student should be able to deduce one of the symptoms of this goiter.

Simple experiments with a human (or other mammal) who is breathing freely reveal that *either* low oxygen or high carbon dioxide content in the inspired air can cause an increase in the rate of breathing, but that *high carbon dioxide content is by far the more effective factor*.*

How does carbon dioxide exert its effect? Anatomical observation reveals that the motor nerves going to the breathing muscles (diaphragm, rib muscles) are connected with the medulla. Physiological experiments show that varying the concentration of carbon dioxide in the blood circulating through the medulla will affect the rate of breathing; when the CO_2 concentration is high, breathing is rapid; when CO_2 is low, the rate of breathing slows or stops. The medulla is, therefore, spoken of as the *breathing center* of the body.

This method of control is rather interesting from several points of view. To begin with, if one guessed in advance of the experiments, one would probably guess that oxygen would be the more important factor for it is oxygen, after all, that we need. Carbon dioxide is a waste product. Yet the mechanism is tied to carbon dioxide. In the second place, this observation broadens our viewpoint regarding the significance of "waste products." A substance may be waste material, produced in excess and requiring to be disposed of. Yet, it may still fulfill important functions: witness, carbon dioxide. In a sense, CO_2 may be said to be a hormone produced by all the cells of the body and having a stimulating effect on the medulla.

Although carbon dioxide is the most effective agent, careful experiments have shown that a fall in O_2 can also act as a stimulating agent. In this case, however, the stimulation is a reflex one. The receptor nerves are located in the walls of some of the principal arteries coming from the heart. When the oxygen content of the blood flowing through these arteries falls, the *chemoceptors* located in the vessel walls are caused to send impulses to the breathing center which, in turn, stimulates the breathing muscles. Ordinarily, this mechanism is probably of little importance. In general anesthesia, however, the medulla, anesthetized, may fail to respond to the stimulus of high CO_2 but may still respond to

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* The experimental details are not given. By this time, however, the student should be able to reconstruct the probable experimental details from bald textbook statements like this.

sensory impulses sent from arterial chemoceptors which have been stimulated by a low concentration of O_2.

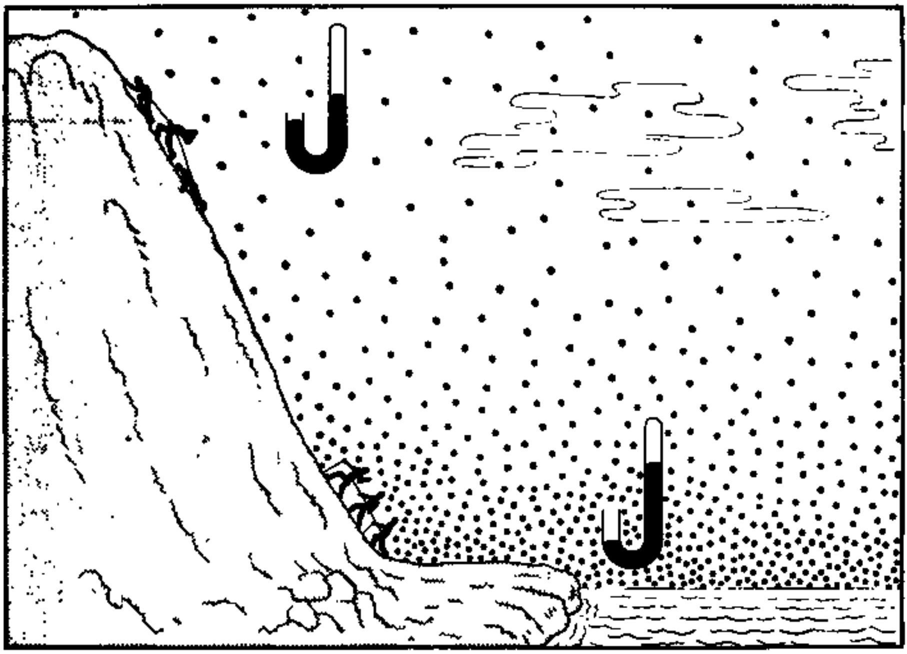

Fig. 14-14. Air is compressible. At sea level, the concentration of molecules is great, the barometric pressure is high, and men work easily. On mountain tops, the barometer is low and men faint easily because the concentration of oxygen molecules (as well as that of other kinds) is low.

107. Control of Breathing: Some Characteristics of the Mechanism

The mechanisms of the body have been evolved to meet the "natural" situations in which man may find himself, that is, the situations that man's body has faced during the millions of years in which it was evolving. It is not surprising, therefore, that when confronted with a new problem, man's body may not always achieve a thoroughly satisfactory solution. As an illustration, we may consider the new problems posed by air travel.

Gases are compressible. Consequently, a given volume at the bottom of a tall column of gas subjected to the influence of gravity will contain more gas molecules than will the same sized volume near the top of the column. The pressure will also be greater at the bottom than it will at the top. The pressure is, therefore, a measure of the concentration of molecules.

The atmosphere surrounding the earth, under the influence of gravity, packs itself so that the concentration of molecules is greater near the earth than far from it (Fig. 14-14). This is true of all of the several kinds of molecules that compose the atmosphere so that the *relative composition* of the air is approximately the same at all places.

From Table 14-1, it can be seen that, at greater altitudes, the barometric pressure is less than at lower altitudes. Moreover, the concentration of O_2 and CO_2 in the alveoli of a man, as measured by their partial pressures, decreases correspondingly. As a consequence, what will happen when a man goes to higher altitudes? Clearly, with the same rate of breathing, he will get less oxygen into his body than at sea level; at the same time, however, since the pressure of CO_2 decreases and since CO_2 is the principal agent affecting breathing, he will not breathe more, as he needs to, but *less*. As a result, his brain gets less O_2, and he may faint. At sufficiently high altitudes, of course, he will die for lack of oxygen.

TABLE 14-1

The relation between altitude, barometric pressure, and partial pressures of oxygen and carbon dioxide in the alveoli of humans. Experimental data gathered from humans in an altitude chamber.*

Altitude (Feet)	Barometric Pressure (mm Hg)	Partial Pressure of Gases in Alveoli in mm Hg	
		Pressure of O_2	Pressure of CO_2
0	760	103	40
4,000	656	84	37
8,000	560	66	36
12,000	480	53	34
16,000	410	43	31
20,000	352	35	30

There are great differences between individuals in reactions to altitude, that is, to reduced barometric pressure. Many people are, apparently, almost entirely indifferent to decreased oxygen pressure;

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* From Lutz and Schneider, *Amer. Journ. Physiol.*, 50: 280, Dec. 1919.

apparently, their arterial chemoceptors are not sufficiently sensitive. A person of this sort, on ascending, will faint without ever breathing faster. On the other hand, a man with sensitive arterial chemoceptors will react to lower oxygen concentration by breathing faster. Differences of this sort are important in determining suitability for altitude flying.

The consequences of altitude can be partly avoided by changing the composition of the air breathed. It is not the air pressure *per se* that is important, but the partial pressure of oxygen. Oxygen makes up about 21 per cent of normal air; by increasing the concentration to nearly 100 per cent, it is possible for man to fly at altitudes where the pressure is only about one-fifth as great as would be required if unenriched air were breathed. When normal air is breathed, 16,000 to 20,000 feet is about the highest practicable limit for flying. When one breathes nearly pure oxygen (to which a little CO_2 has been added*), the upper limit is raised to around 38,000 feet.

From these considerations, one can see why an oxygen mask is an aid in flying only up to a certain altitude. Above 38,000 feet, pure oxygen is not enough because the pressure is too low in any airplane that is open, or essentially open. The only solution to the problem of very high altitude flying is to use a plane that can be hermetically sealed from the outside and then to increase the pressure inside. With such a plane, there is no limit to the height that can be achieved, as far as the passengers inside are concerned, so long as no leaks occur. The building of a safe, hermetically sealed plane is easily accomplished by modern technology. However, under battle conditions, flying in such a plane at great altitudes is clearly risky if there is serious danger of puncture. Not only would a hole in the plane's fuselage immediately subject the inhabitants to too low an oxygen pressure but, at elevations exceeding 63,000 feet, the total air pressure is so low that the water of the body would literally boil away.

108. Control of Breathing: Adaptation to High Altitudes

A coastal man transported to a moderate elevation, say 10,000 to 14,000 feet, cannot do as much work as a native of the region. The

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* Why is it desirable to add carbon dioxide to the oxygen supply?

slightest effort may cause the lowlander to experience shortness of breath and a feeling of weakness.

One of the principal causes of this weakness is the inadequate oxygen-carrying capacity of the blood. Erythrocytes are too few in the lowlander's blood to absorb sufficient oxygen from thin, highland air. As an immediate reaction to decreased oxygen pressure, the spleen contracts, forcing its store of red blood cells out into the blood stream. This immediate reaction only partially takes care of the new needs. If an individual remains for several weeks or more at high altitudes, the hemoglobin content of the blood increases by as much as 50 per cent, largely through increase in the number of erythrocytes per volume of blood. Other changes in physiology also occur.

The physiology of people who live at very high altitudes differs considerably from that of people at sea level in ways that are not understood. Inhabitants of the high Andes (20,000 feet) are unable to survive lower altitudes for any considerable period of time, though why (in the physiological sense) is not known.

109. Maintaining Chemical Constancy: Blood

One of the most conspicuous differences between water-dwelling and land animals is the apparent indifference of the land forms to their environment. Most ocean-dwelling fish and other animals will die within a few days after being transferred to fresh water; fresh-water forms are similarly sensitive to salt water. (There are exceptions, of course; salmon and eels come to mind.) Ocean-dwelling animals are similarly sensitive to slight changes in temperature. Land forms, of necessity, can withstand much greater variation.

The ability of organisms to withstand changes in their environment stems from two sources:

1. Genuine adaptability of the cells themselves. (Most free-living bacteria, for instance, are very adaptable cells.)
2. Adaptability, not of the constituent cells but of the organism as a whole.

The adaptability of higher organisms, including man, is mostly of the latter sort. We have already seen how man can live in temperatures from less than −50° F to more than +115° F. The lower part of the range is possible only because of clothing, though even unclothed man, as Darwin observed among the Tierra del Fuegians, may survive continuous exposure to 32° F. On the face of it, man would appear to be a very adaptable organism.

When one considers the situation of the cells of man, a very different picture presents itself. A fever of 108° cannot continue for long before death intervenes. Similarly, a lowering of the body temperature by a few degrees results in death. Although man as a whole can withstand great changes in the temperature of his environment, his cells can withstand only slight changes in *their* environment. This situation has led to the concept of the **internal environment,** by which is meant the fluids surrounding the cells of the body.

The internal environment of man is extremely constant, not only in temperature, but in chemical composition as well. This constancy is made possible by two sorts of devices:

1. A rapid circulatory system which equalizes conditions in all parts of the body. This system includes the blood, lymph, and the pumping mechanism.
2. Regulatory organs that tend to eliminate any changes in the blood that may develop. Among the regulatory organs, are the sweat glands, liver, and kidneys.

The circulating blood, then, is the means whereby relatively constant conditions are maintained throughout the body. By controlling its composition, the composition of the intercellular fluids everywhere is controlled. How, then, is the composition of the blood controlled, and how close is this control?

110. Maintaining Chemical Constancy: The Kidneys

One of the most important means of regulating the composition of the blood is the selective secretion of different substances into the **urine** which is voided from the body through the passages diagrammed in Figure 14-15A. Urine is formed by the kidneys, large, bean-shaped organs that lie just back of the posterior wall of the body cavity. Urine is secreted by the solid part of the kidney into the kidney pelvis (or renal pelvis; Latin *ren*, kidney; Latin *pelvis*, a basin); thence, it passes down the **ureter** (Latin *urina*, urine). The right and left ureters empty into the **urinary bladder** where urine is stored, to be released from time to time into the **urethra** which carries the fluid to the exterior.

What is the structure of the solid part of the kidney, and what relation does the structure bear to the secretion of urine? If we take a thin slice of the kidney meat and examine it under the microscope, what we see is puzzling; we see various irregular "doughnuts" (Fig. 14-15B). Each "doughnut," it turns out, is a cross section of a long and tortuous tube.

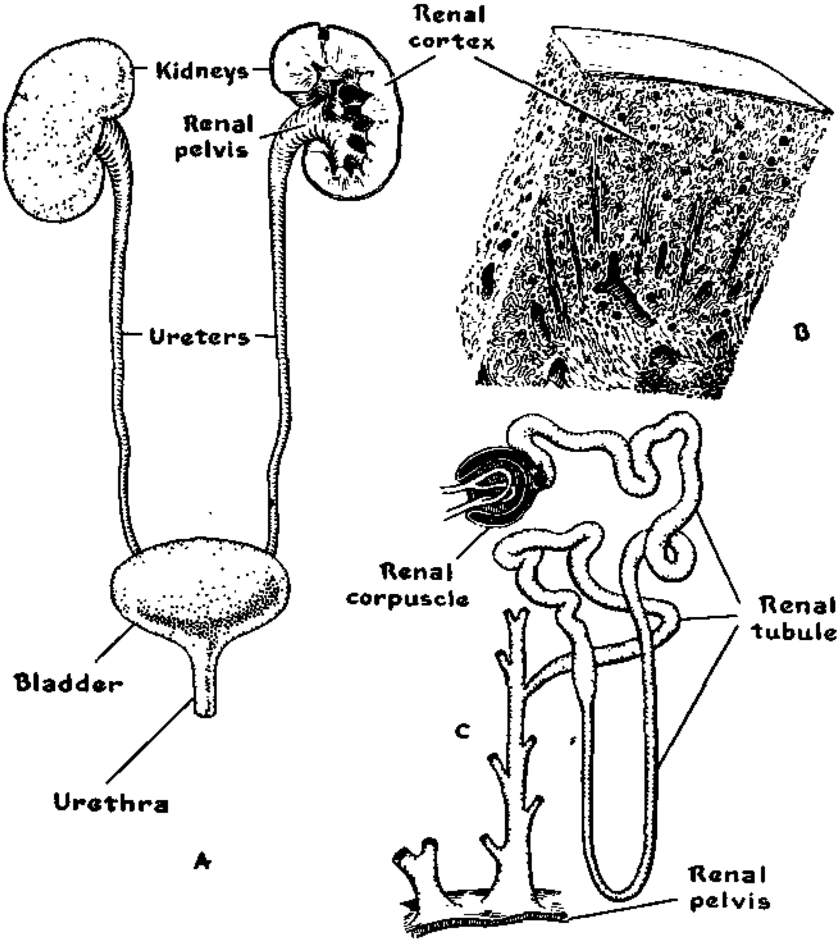

Fig. 14-15. The excretory apparatus. A human kidney is composed of about a million working units like that shown in C. The tuft of blood capillaries is called a glomerulus. Urine begins as a secretion from the glomerulus into the cavity of the renal corpuscle and travels down the renal tubule, ending in the space of the renal pelvis.

By careful chemical treatment, which partially destroys the flesh, and by reconstruction from thinly sliced sections, it has been learned that the kidney is made up of many units like those idealized in Figure 14-15C. Notice the **renal tubules** ("little tubes"); a swelling called a **renal corpuscle** (Latin *corpusculum*, diminutive of *corpus*, body; hence, a little body) is located at one end of each tubule. Inside the corpuscle, we find an aggregation of even smaller "doughnuts," which again suggest the existence of tubules. These tubules are filled with blood; they are, in fact, blood capillaries. The whole tuft of tubules is called a **glomerulus** (diminutive of Latin *glomeris*, a ball, or ball of yarn); it lies within a capsule called the **renal capsule.** The fluid within this capsule and its connecting tubule is not blood but a watery fluid which resembles a very dilute urine. This fluid, which has been filtered from the glomerulus, is called **glomerular filtrate.**

The working unit of the kidney consists of the renal capsule (including the glomerulus) and the attached renal tubule. **A single human kidney is made up of about one million such working units.**

How does this renal unit function? The answer to this question was made possible by a technical *tour de force* performed by A. N. Richards of the University of Pennsylvania a generation ago. Although the renal unit is microscopic, Richards and his coworkers succeeded in inserting a tiny glass tube into the space of the renal capsule of a living frog kidney and drawing out samples of the fluid which were then analyzed chemically. The results of these analyses revealed that the capsule fluid has almost the same constitution as blood plasma except that the proteins are lacking. Fluid collected at the far end of the renal unit—in other words, urine—shows a composition that differs considerably from that of blood plasma, as Table 14-2 reveals. This table shows that many substances, for instance, chloride ion, urea and creatinine, are considerably more concentrated in the urine than they are in the blood plasma or in the glomerular filtrate. How does this come to be? Only two possibilities present themselves: either the walls of the renal tubule secrete these substances into the glomerular filtrate, or they remove water from the glomerular filtrate, leaving behind increased concentrations of such substances as urea.

The latter proves to be the case. The volume of glomerular filtrate has been calculated to amount to 75 to 100 liters a day, but the urine excreted amounts to only about 1 to 1½ liters per day. This means that the renal tubules return to the blood vessels that surround them between 74 and 99 per cent of the water present in the filtrate. They also return other substances to the blood but not in strict proportion to their concentrations in the filtrate. As a result, the concentrations of these other substances are changed as the fluid in the renal tubules is changed to urine. In other words, **the wall of a renal tubule is a secretory tissue;** it is a rather unusual secretory organ since it secretes material that is almost outside the body back into the body. But it is, nonetheless, a secretory tissue.

TABLE 14-2

CONCENTRATIONS OF VARIOUS SUBSTANCES IN BLOOD PLASMA AND IN URINE

COL. A	COL. B	COL. C	COL. D
	PARTS PER HUNDRED		CONCENTRATION FACTOR (APPROX.)
SUBSTANCE	IN BLOOD PLASMA	IN URINE	(COL. C/COL. B)
Water	90-93	95	
Proteins	7	0	
Glucose (sugar)	0.1	0	
Sodium	0.3	0.35	1
Chlorine	0.4	0.6	1.5
Urea	0.03	2	60
Uric acid	0.004	0.05	12
Creatinine	0.001	0.075	75
NH_4 ion	0.001	0.04	40

It is worth while now to look again at the functioning of the kidney unit from the point of view of the *work* done. The first stage of the process, the formation of "glomerular filtrate" by the glomerulus, is a process of simple filtration as the name implies. To carry out any filtration, force is necessary. In the common filtration process of the chemical laboratory, the *force* is furnished by gravity. The *work* of such filtration is performed when the material to be filtered is lifted to the height of the filter paper (Fig. 14-16A). The work of glomerular filtration similarly involves a force and work. The force in this case is the force of blood pressure pushing against the walls of the glomerular capillaries. The work is the work required to develop the force of the pressure of blood, in other words, the work of the heart (Fig. 14-16B). **The work of glomular filtration is performed by the heart.** As one would deduce from this principle, when the blood pressure falls, the amount of glomerular filtrate (also of urine) formed also falls. As the blood pressure rises, the amount of glomerular filtrate increases.

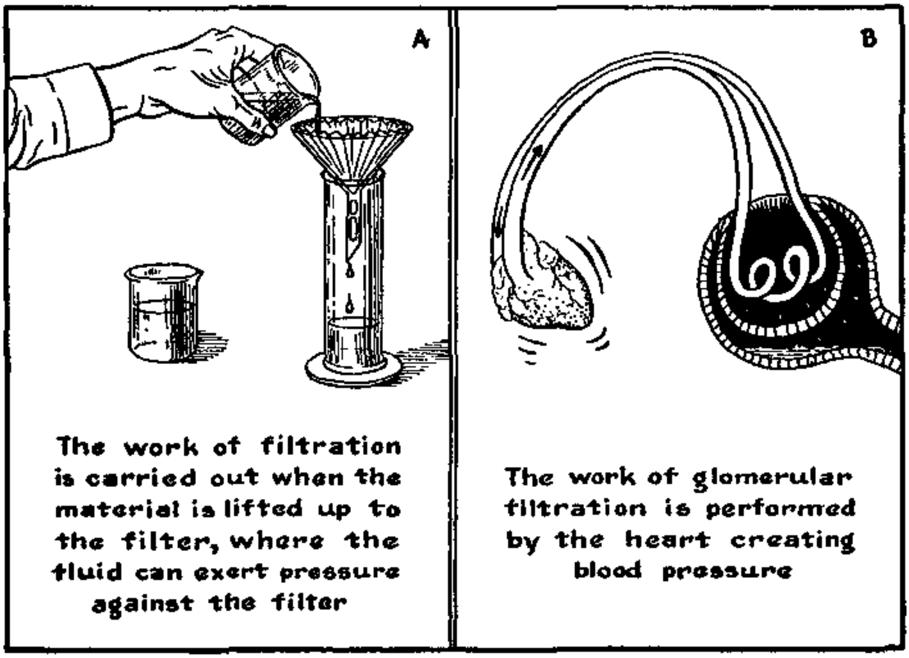

Fig. 14-16. How the work of glomerular filtration is accomplished.

Increase in blood pressure has another consequence. In the common filtration process, if a thin filter paper is covered by too deep a layer of fluid, the weight of the fluid may partially rupture the filter paper, letting through some of the material the paper was supposed to retain. In other words, when the pressure is too great, the filter breaks down. The glomerulus, the filter of the kidney, is similarly subject to overloading. If the blood pressure rises too high, proteins, which are normally held back, may push through the walls of the glomerular capillaries and appear in the urine. The improper functioning of the kidneys is but one of the many undesirable consequences of high blood pressure.

Let us now proceed to the other phase of kidney function, that of the secreting, or reabsorbing, of substances, a process carried out by the

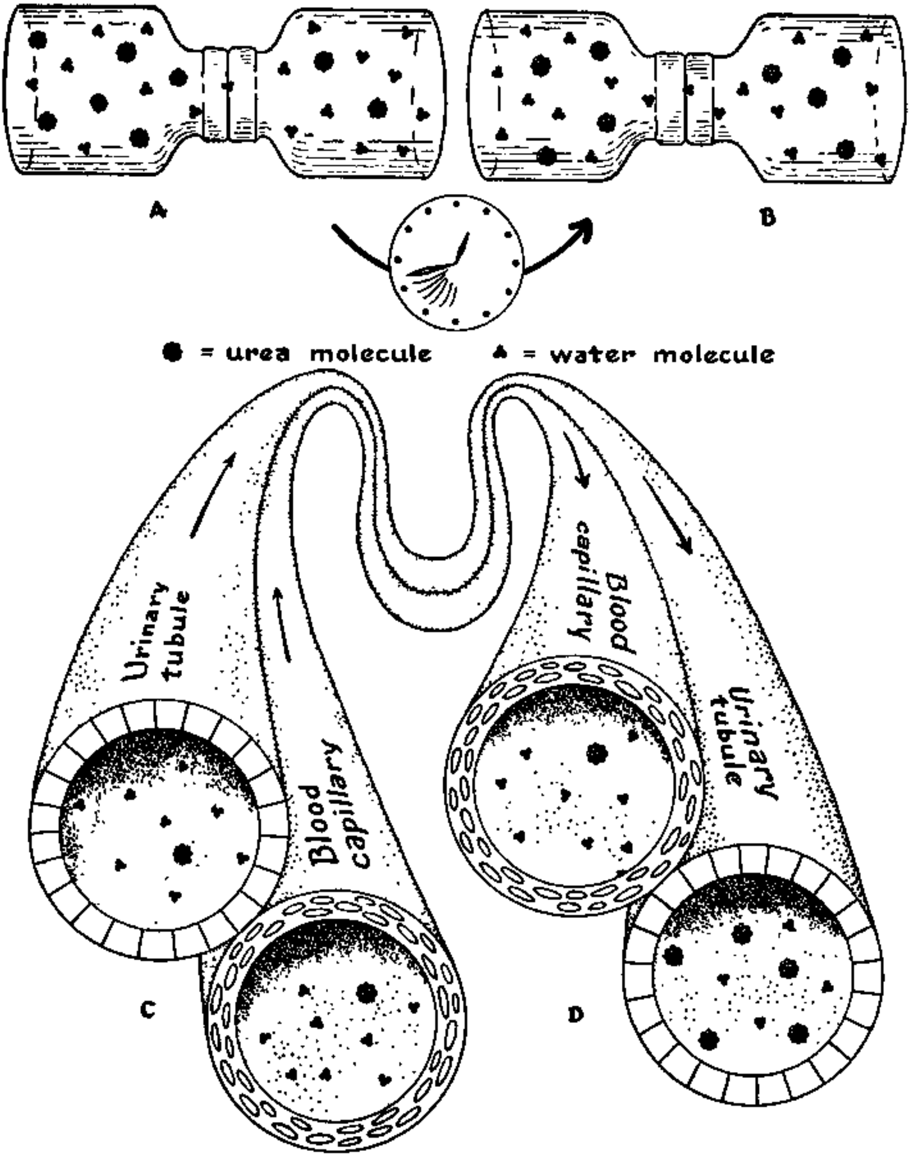

Fig. 14-17. By the laws of probability, an unequal distribution of molecules in connecting vessels (A) cannot long be maintained (B). But in the kidney, an initially equal distribution of water and urea molecules in the renal tubule and blood capillary at the level of the renal capsule (C) is changed to an unequal one as the renal fluid approaches the end of the urinary tubule (D). To achieve an improbable situation like this, work is required. This work is performed by the metabolizing cells of the wall of the urinary tubule.

walls of the tubules. What sort of process is involved here? Is work done? How?

It is necessary to recall our fundamental concepts of molecular activity (Chap. V). If we have, in intercommunicating spaces, two species of molecules (Fig. 14-17A), the concentration of each of these species will ultimately be the same in both compartments and will, thenceforth, remain the same. The movement of the molecules is at random. If, at any time, there were more of species A molecules in the left box than in the right, then the probability of a left-side molecule moving into the right-hand box would be greater than the probability of right-side molecules moving to the left side. Consequently, any inequality of distribution would be automatically erased.

But what happens in the renal tubules? This situation is diagrammed in Figure 14-17C,D, in which, for simplicity, only two species of molecules are shown, urea and water. In the first part of the tubule (Fig. 14-17C), the concentration of each of these substances inside the tubule and in the blood of the capillaries around the tubule is very nearly the same. Later (Fig. 14-17D), the urea is much more concentrated inside the tubule. The change is brought about by the activity of the cells of the tubule wall, which push water into the blood while holding back the urea molecules. By simple molecular movements, such a situation would never develop or, to put it more exactly, this is an extremely improbable situation. **The development of an improbable situation always requires work.** This is the fundamental nature of the work performed by the walls of the renal tubules.

How is this work accomplished? Here, we must admit, we do not know the whole answer. Situations like this have been studied extensively and a great many facts discovered, most of which are too complicated to present without an extensive background of physical chemistry. However, this much can be made clear: the functioning of the tubules is dependent on the metabolism of the cells that line their walls. Dead cells cannot reabsorb materials; anesthetized cells can do so poorly or not at all. It takes living, actively metabolizing cells to develop and maintain an improbable situation.

As one would expect, the functioning of the renal tubule cells is dependent on an adequate supply of oxygen and foodstuffs. It is also dependent on a hormone secreted by the small tab of tissue that hangs down from the brain, the **pituitary gland** (Fig. 14-18). The pituitary is composed of two* distinct parts or *lobes* (Fig. 14-18B). The **posterior lobe** secretes a hormone called **pituitrin** which is required by the kidney cells. When adequate pituitrin is lacking, as may be the case when the pituitary gland is diseased, the renal tubule cells are unable to secrete much water back into the blood stream; consequently, a large volume of watery urine is excreted. This condition is known as **diabetes insipidus**† and can be controlled by periodic artificial injections of pituitary extract. In the absence of such treatment, the individual must sometimes drink literally gallons of water in a single day to make up for his water losses.

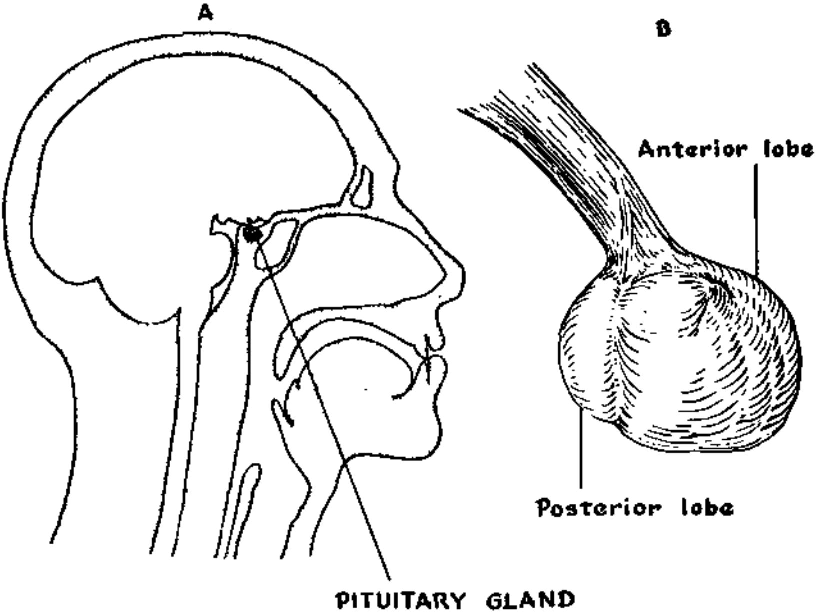

Fig. 14-18. The pituitary gland, the posterior lobe of which secretes the hormone pituitrin which is required for normal function of the renal tubule cells.

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* The anterior lobe produces hormones required for growth and will be discussed in § 194.

† Not to be confused with *diabetes mellitus* discussed in § 111.

111. Maintaining Chemical Constancy: The Fate of Sugar in the Body

Everyone has heard of **diabetes mellitus,** or "sugar diabetes" (Latin *mellis,* honey), a condition in which sugar appears in the urine. What is the cause of this condition?

It will help to explore the normal movements and transformations of sugar in the body. All sugar is ultimately derived from the food consumed. Digestion of carbohydrates produces the simple sugar *glucose* which is absorbed through the intestinal wall into the blood stream. Glucose is transported to all parts of the body and part of it is used immediately in the metabolism of the cells. Respiration of the glucose yields, of course, CO_2 and H_2O, and energy which may be used for muscular movement and other activities. However, immediately after a meal, more glucose is taken into the blood stream than is needed at the time for respiration. The excess must be either stored or excreted. It is normally stored, principally in the muscles and in the liver, in the form of a less soluble carbohydrate called **glycogen,** or "animal starch." That carbohydrates can be so stored is most fortunate or, one might say, necessary. Were it not so, an active man would have to eat continuously.

Glycogen is stored when there is a surplus of glucose in the blood and released when there is a metabolic drain on the blood sugar. Studies have shown that several hormones are involved in this storage and release of carbohydrates in the liver and muscle. Among these hormones, are adrenin, from the central portion of the adrenal gland, and **insulin,** a secretion of the pancreas. The latter is the gland encountered before in the study of digestion (§ 55). It is an organ of both internal and external secretion. Its external secretions are the digestive enzymes, and its internal secretion is insulin which it pours into the blood stream. Insulin aids in the process of storing carbohydrates as glycogen. Adrenin helps change the glycogen back into sugar which can be released into the blood stream. Studies made with carbohydrate molecules containing radioactive or "marked" atoms show that normally both processes are going on. In the period immediately after a large meal, the storage process is in the ascendancy; during vigorous exercise, the release process is dominant. These process-rates are directly determined by the rate of secretion of the hormones, insulin and adrenin.*

The renal tubules secrete sugar back into the blood stream again. However, their ability to do so is limited. When the sugar level of the blood is very high, the sugar level of the glomerular filtrate is correspondingly high and the renal tubules cannot restore all the sugar to the blood; consequently, some of it appears in the urine. This is normal. It may happen after a meal rich in carbohydrates. The high blood-sugar level in diabetes mellitus, however, is to be attributed to the breakdown of the carbohydrate-storage system, due to the lack of pancreatic secretion. Notice that the appearance of sugar in the urine in such cases is not due to "kidney trouble" but to pancreas trouble.

QUESTIONS AND PROBLEMS

14-1. The first section of this chapter is entitled, "A Synthetic View of the Organism." How does this use of the adjective *synthetic* differ in meaning or implication from everyday usage?

14-2. Which of the following occupations could be successfully followed by a man with poor proprioceptive senses: architect, window-washer, painter, potter, mathematician, violinist, public speaker, sculptor, wrestler, gymnast, accountant, physicist? Justify your answers, briefly.

14-3. In the meat market, the butcher picks up a roast. The customer says, "That will weigh 10¼ pounds." The butcher hefts it and says, "No—I'd say 10½ pounds." Assuming that the butcher has normal sensitivity, is he justified in making a correction of this order of magnitude in the estimate?

14-4. What kind of nerves, motor or sensory, innervate the following: muscle; tendon; skin, exclusive of hair follicles and sweat glands; hair follicles and surrounding area; sweat glands?

14-5. An inmate of an institution for the totally blind suffers an infection that completely destroys his inner ears. What sort of life will he lead thereafter?

14-6. What is the function of the cerebellum?

14-7. Name a function of the thalamus.

14-8. Why is it better to call a lizard a "poikilotherm" than a "cold-blooded animal"?

14-9. Describe the sequence of events involved in our adjustment to too great heat; to too little heat.

14-10. On a hot day, would a man keep cooler by sitting still or by moving around? Argue both sides of the case.

14-11. Ideally, how should the diet of a man in summer differ from his winter diet?

14-12. What is iodized salt? For what is it used?

14-13. In reviving a person who has fainted at high altitude, why is a gas mixture of 95% O_2 + 5% CO_2 better than either 95% O_2 + 5% N_2, or 100% O_2?

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* It should be pointed out that other hormones are also involved; for instance, the hormone from the anterior lobe of the pituitary. The role of the other hormones is not yet clearly understood.

14-14. Define, so as to distinguish between, the words *urine* and *urea.*

14-15. When proteins appear in the urine, what may be the trouble?

14-16. What effect will the following have on the amount and composition of urine:

a. A meal rich in carbohydrates?
b. Drinking large quantities of water?
c. A hot, dry day?
d. High blood pressure?
e. Low blood pressure?
f. Ruptured renal capsules?
g. Hypoinsulinism?
h. Death of tubule cells?
i. Destruction of the posterior lobe of the pituitary gland?

14-17. Explain the aptness of the names *diabetes insipidus* and *diabetes mellitus.*

14-18. Name four secretions of the pancreas and tell which are secreted externally and which internally. Justify the use of the adjective *external.*

14-19. Etymologically, what does the word *insulin* suggest? What is the rationale of its derivation? (Answering this may involve recourse to an unabridged dictionary, a medical dictionary, a physiology text, or a histology text.)

14-20. Name a hormone produced by each of the following structures and give its effect: pancreas, adrenal medulla, posterior lobe of the pituitary, wall of the duodenum.

14-21. (A subject for further reading in a physiology text.) What hormones are produced by the anterior lobe of the pituitary, by the parathyroids, and by the adrenal cortex? What are their effects?

Chapter XV

Reproduction

112. The Essential Feature: Union of Gametes to Form a Zygote

To the layman, the reproductive practices of birds, mammals, reptiles, fish, and other animals may appear to vary widely. Biologists, however, who have looked into the matter closely are impressed with the essential similarity of sexual reproduction throughout the plant and animal kingdoms. Among the simpler forms, and occasionally among the more complex forms, of plants and animals, there also occurs a type of reproduction that is not sexual, i.e., *asexual* reproduction. For the present, we will be concerned only with sexual reproduction.

What is the essential feature of sexual reproduction? To answer this, we must recall once more the Cell Doctrine (Chap. III) which states that all living organisms are composed of cells and their products. Observation shows that the cells of a young, small animal are about as large as the cells of a large animal. It follows, therefore, that growth involves an increase in numbers of cells, an increase from few to many. How few? How few cells are there "in the beginning"?

It has been found that every individual begins as a single cell called a **zygote** (derived from the Greek *zygosis*, a joining). The aptness of this term will appear subsequently. The zygote divides and redivides, and the resultant cells, called daughter cells, become organized into the various masses that make up the tissues and organs of the body.

Where does the zygote come from? The zygote, a single cell, is the result of the fusion of two other cells, one of which comes from the male parent, the other from the female. These cells are called **gametes** (Greek *gamo*, a marriage; *gamete*, a wife; *gametes*, a husband). The male gamete, that is, the gamete that comes from the male, is called a **sperm cell** or **spermatozoon** (literally, "seed-animal"); the female gamete is called and **egg** or **ovum** (Latin, egg).

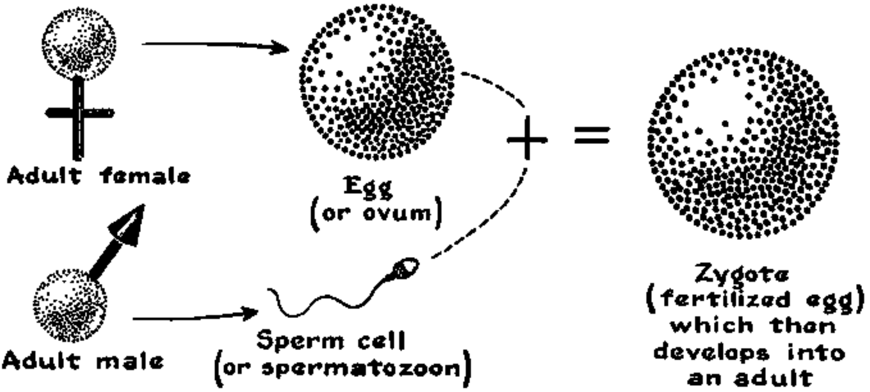

Fig. 15-1. The essence of sexual reproduction. The role of male (♂) and female (♀) in producing gametes which unite to produce a zygote.

The essential process of sexual reproduction consists in the union of sperm and egg. This process of union is called **fertilization;** the result is the *fertilized egg*, or *zygote*, which develops into the adult animal or plant.

The essential facts of reproduction are diagrammed in Figure 15-1. The terms defined above will be used repeatedly in this book and should be learned promptly.

Fertilization may be regarded as the most important event in reproduction. However, it is by no means the whole process. The subsidiary processes may be considered under the following heads:

1. The production of gametes.
2. The bringing-together of the gametes.
3. The care of the helpless, developing offspring.
4. The process of development from zygote to adult.

These four phases will be considered in the following sections; the last one, however, only in a sketchy fashion since a thorough treatment of development is better postponed until some knowledge of genetics and the physiology of cells is acquired.

and sperm may be made possible by the chemical attractiveness of the egg for the sperm. The probability of the meeting of gametes may be increased by the proximity of the parents at the time of the discharge of their gametes, but the gametes are still essentially on their own.

In animals, **fertilization always takes place in liquid surroundings.** This necessity, for such it is, requires that land animals, surrounded by dry air, must somehow surround their uniting gametes by fluids. Furthermore, in "higher animals" (e.g., mammals), the zygote and the youngster into which it develops are helpless for a long period and must be thoroughly protected and nourished by the mother. Logically connected with these two necessities are the organs and structures we are accustomed to think of as specifically sexual, e.g., the uterus, and the breasts.

The spermatozoa that the human male ejects are, then, in a liquid medium, that is, surrounded by fluid. The liquid ejected by the male is called **semen** (Latin *sero*, to sow). Only a small fraction of the semen consists of sperm cells. Most of it is fluid contributed by various portions of the male genital system.

The path of the sperm cells going from the testis to the opening of the penis can be seen in Figure 15-2. During their journey through the epididymis and past the prostate and Cowper's glands, they are mixed with various secretions, the function of which is not completely clear but which apparently serve as nourishment and chemical protection for the spermatozoa after they are deposited in the female vagina.

The discharge of semen occurs as the culmination of the act of copulation. Preliminary to copulation, the penis changes from a flaccid organ to a firm one, a process known as **erection.** Erection is brought about by a constriction of small muscles which slow up the exit of blood from the penis while leaving the entering flow unimpeded. As a result of this process, the spongy tissue of the penis becomes filled with blood under pressure, and the penis erects. When the penis is in this condition, entrance into the vagina can be effected and semen deposited therein.

Copulatory activity is determined principally by the amount of male hormone, or **testosterone,** secreted into the blood stream.* The behavior of domesticated animals can be greatly modified by **castration,** that is, by removal of the gonads. If a male is castrated while still young, it not only is made sterile, but it fails to develop into a typical male.

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* In man, psychological factors are also decidedly influential.

Males are frequently distinguished by **secondary sexual characteristics,** such things as a large comb in roosters, a male-type feather pattern in many birds, and whiskers in man. A castrated male does not develop secondary sexual characteristics. Moreover, the copulatory activity of the adult fails to develop in castrates; the castrated male, with few exceptions, shows no interest in females *qua* females. His interest in males tends also to be impersonal, so to speak. Normal adult males of many species instinctively fight each other. Such fighting, which may result in serious or fatal injuries, is almost completely lacking in castrated animals. Besides this, if castration is performed early, the male tends to develop a body conformation closer to that of the female, often putting on considerable fat. For these reasons, a castrated animal is more valuable to the animal husbandman than the normal one and we find that castration of all but the breeding stock has been carried on by livestock raisers for thousands of years.

Until only a few hundred years ago, castration of humans was extensively practiced in what we now regard as the civilized world, and even now is performed in the remoter parts of the earth. The custom has been justified variously: as a means of warfare, or of judicial punishment; as a method of self-"purification" or self-punishment by some of the early religious mystics; as a means of creating reliable harem-keepers in the Moslem world, or of producing permanent male sopranos—the pitch of the voice is partly a secondary sexual characteristic—for church choirs.

Castration is no longer extensively practiced in any country we would willingly call civilized. However, another operation, called **sterilization,** is frequently performed. Because castration and sterilization are often confused in the mind of the layman, it is important that we carefully distinguish between the two here.

Sterilization, in the male, involves severing the sperm duct coming from each testis. (See Fig. 15-2.) That and nothing more. As a result, spermatozoa can no longer get to the exterior. Semen, however, is still formed. The testes, still in place and unharmed, continue to secrete male hormone into the blood stream. The desire of the individual toward the opposite sex is unchanged, as is his ability to copulate. Indeed, if the operation—which is a minor one—were skillfully performed without the individual's knowledge, he would never know of it unless his lack of children made him suspicious. Sterilization makes an individual sterile, that is, incapable of producing children; but nothing else.

Sterilization is frequently used to prevent the breeding of mental defectives. The morality of its use is still a matter of debate, and will be discussed in Chapter XL. It is not expected that all persons will view the morality of sterilization in the same light. It is important, however, that they understand precisely what it is and what it does.

116. The Release of the Female Gamete

One of the most conspicuous features of female sexual activity is its cyclical nature. Whereas spermatozoa may be released at almost any time, ova are normally released only once a month, and then only one at a time. Coupled with this periodic release of ova is a complicated sequence of events generally spoken of collectively as the *menstrual cycle.*

The word **menstruation** is derived from the Latin word *mensis*, month. The aptness of the name lies in the fact that, on the average, menstruation occurs once a month. Menstruation shows itself externally as a flow of blood and other fluids from the vagina, a flow that continues for several days. What is the source of the menstrual fluid?

Observation of the wall of the **uterus** (the "womb" of poetic literature) shows that it undergoes cyclical change. Immediately after menstruation, the epithelium or innermost layer of the wall of the uterus starts getting thicker, and the blood vessels enlarge, ultimately becoming large, irregular spaces in which the blood may stagnate. Finally, the epithelium with its engorged blood vessels is sloughed off and passed to the exterior; it is this discarded material that constitutes the menstrual flow. This phase marks the end of one cycle and the beginning of another.

The phases of the menstrual cycle are indicated in Figure 15-4. Correlated with menstruation is the process of ovulation or release of ova. The ovary at all times, perhaps from the time of birth, has many ova in it but most of them are inconspicuous because they are not surrounded by a Graafian follicle. Each month, a Graafian follicle matures around one of these eggs. At approximately the fifteenth day of the menstrual cycle (see Fig. 15-4), the follicle breaks, releasing the ovum, which presently starts to move passively down the oviduct. The journey from ovary to uterus may take a day or two. What happens during this time and subsequently depends on whether or not the egg is fertilized. These two possibilities will be treated separately.

If no fertilization occurs, the cycle of events illustrated in Figure 15-4 transpires. The ruptured follicle that is left after ovulation changes in appearance, developing into a structure known as a **corpus luteum** ("yellow body"). When menstruation takes place, the corpus luteum starts to degenerate and disappear. In the meantime, the released, unfertilized, egg has disintegrated in the uterus.

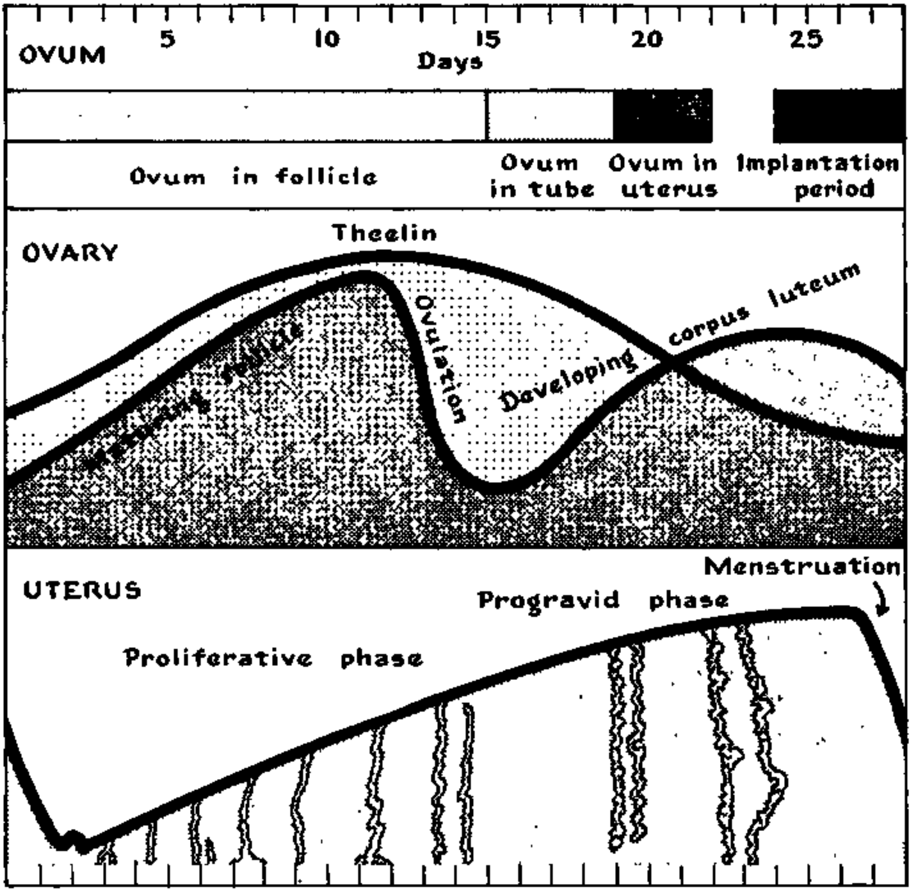

Fig. 15-4. The events associated with the menstruation cycle. The ovum is fertilizable for only a few days after its release from ovary. The timing indicated is typical of, but not universal among women.

If fertilization occurs, the whole menstrual cycle is suspended. The fertilized egg "implants," that is, attaches itself, on the wall of the uterus, and the corpus luteum does not degenerate but remains intact for the full period of pregnancy, during which time further menstruations seldom occur. The corpus luteum is, apparently, a temporary hormone-secreting gland, and functions to prepare the uterus for implantation of the ovum.

Other hormones are involved in the menstrual cycle. The ovary, like the testis, produces both gametes and sex hormones. Castration of the female has consequences analogous to castration of the male. If carried out before puberty, it will produce sterility, lack of sexual desire, and failure of development of the secondary sexual characteristics (feminine breasts and deposition of fat in characteristic female pattern). If castration is carried out after puberty, the result is less predictable; only the loss of fertility is certain. Sexual desire and secondary sexual characteristics are modified to various degrees in different cases. The menstrual cycle is completely absent in castrates.

Sterilization in the female is performed by closing the oviducts. Because these ducts lie within the body cavity, the operation is a more serious one than sterilization in the male but the consequences are in no significant way different.

The amount of hormone, called **theelin,** secreted by the ovary varies with the menstrual cycle, as shown in Figure 15-4. Correlated with this are variations in sexual desire in the female; though, as is always true of desire of any sort, it is affected by many other factors that we can only vaguely refer to as "psychological."

117. The Getting-Together of Sperm and Egg

In all human societies, there have been two acute problems connected with reproduction: how to prevent reproduction when children are not wanted, and how to encourage it when children are wanted. To solve the first problem, various means have been employed, ranging from abstinence from sexual intercourse, through restriction of intercourse to certain portions of the menstrual cycle, to the use of mechanical barriers that prevent the intermingling of gametes and chemical barriers that insure the nonviability of gametes.

The problem of inducing reproduction in cases where children are wanted but seem reluctant to appear has yielded more slowly to solution. Sterility and semisterility have existed for thousands of years, as is apparent from references in the Bible (see, for instance, Genesis, Chap. 16-21). Sterility is still a widespread problem. Its causes are only imperfectly understood. We can get some idea of the problems involved by reviewing the events immediately preceding fertilization.

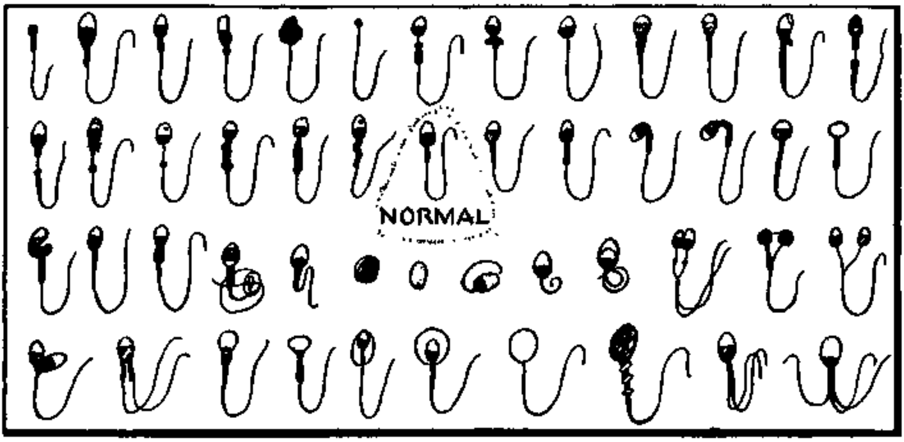

Fig. 15-5. Variety observed among human spermatozoa. When the supposed abnormal types constitute more than 25 per cent of the sperm population, the man is usually sterile. (After Moench and Holt.)

There is considerable experimental evidence indicating that both the sperm and the egg are capable of fertilization for only a very short time, for only a few days in the case of the ova, and perhaps for less than a day in the case of the spermatozoa. The egg's period of fertilizability corresponds to the time that it is traveling down the oviduct; the sperm must reach it in the oviduct and fertilize it there or it is too old. In other words, in a "typical" menstrual cycle, fertilization can occur only between about the 15th and 18th or 19th days. It should be noted that the word typical is enclosed in quotation marks. There is great variation among women, and the cycle in an individual woman may vary from time to time, perhaps in response to psychological factors.*

Most primitive peoples, especially in male-dominated societies, tend to lay the "blame" for sterility on the wife. It is now clear that the source of the sterility can at least as often be properly ascribed to the husband. Physicians who specialize in sterility problems have noticed

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* It is a matter of interest that, in rabbits, ovulation is caused to occur by copulation, apparently through some nervous system reflex action. So far as is known, ovulation in humans is independent of copulation.

that the numbers and kinds of spermatozoa in semen show individual variations. Figure 15-5 shows a few of the many types that have been found; it is believed that only the type of sperm cell, the normal cell, shown in the center of the figure is capable of fertilizing an egg. This type is usually present in the greatest numbers. When the proportion of abnormal types is as great as 25 per cent, the male is usually sterile.

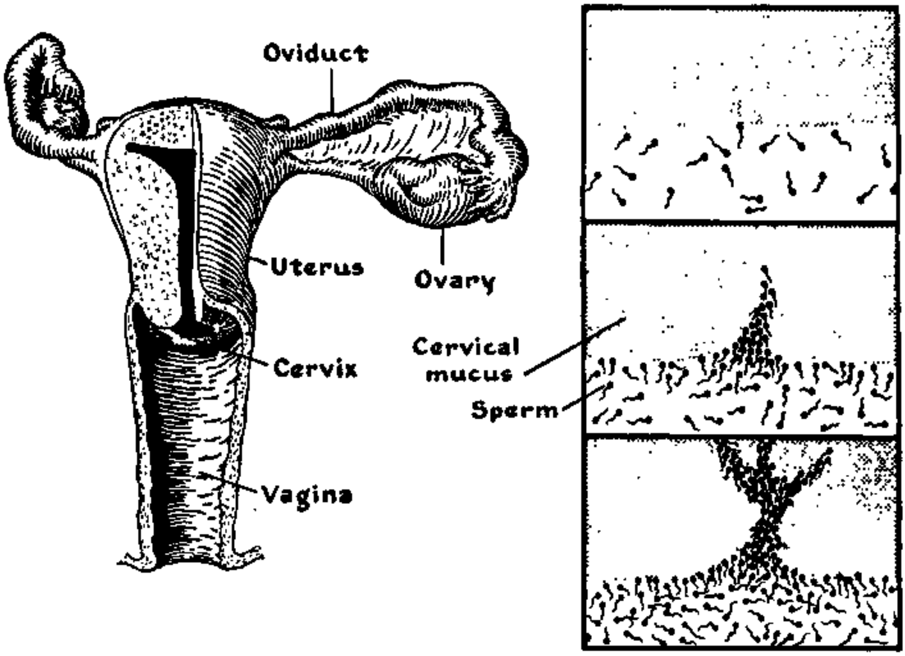

Fig. 15-6. The advantage of numbers: the mucus-dissolving enzymes of many spermatozoa clear a path through the mucus plug of the uterine cervix.

Furthermore, it has been found that when the number of spermatozoa per cubic centimeter of semen is less than 60,000,000, pregnancy is unlikely to be induced. An overwhelming amount of evidence, including direct observation, indicates that in *all* plants and animals only one sperm cell is required to fertilize each egg. There is no question but that this is true for humans, too. Why, then, do millions of spermatozoa appear to be required in copulation when fertilization requires but one cell?

We can give a probable answer to this question. The answer lies perhaps partly in the geography involved. Referring to Figure 15-6, notice that the place where semen is deposited, the upper end of the vagina, is at a considerable distance from the place where fertilization must occur, the oviduct. The distance is at least 7000 times as great as the length of the head of the sperm. It is hardly to be wondered at if a great many of the sperms never get near their goal. Translating the problem into everyday terms, imagine a crowd of men released about eight miles from their goal (that is, a distance about 7000 times the length of one man). It is easy to imagine that a great many of the men, for want of strength, motivation, sense of direction or what-not, might never reach the goal. There might be a minimum number of men that would have to be released to insure that one completed the trip in the allotted time. For similar reasons, a minimum number of sperm might be needed to insure a reasonable probability that one arrived at the ovum soon enough.

There is probably another reason why so many sperms seem to be required. The **cervix,** or neck of the uterus (see Fig. 15-6), is normally filled with a mucus. It has recently been found that the sperm cells contain a specific enzyme which digests the cervical mucus. The thickness of mucus is probably greater than any one sperm cell can digest its way through; the spermatozoa that get through appear to be the ones that move in a crowd, each individual contributing its bit to the process of digestion (see Fig. 15-6). This would appear to be another explanation for the tremendous number of sperm apparently required.

118. The Care and Nourishment of the Young

The fertilized ovum or zygote moves down the oviduct and into the uterus. Here, it sticks to the wall and presently becomes buried by an overgrowth of uterine tissue, a process known as implantation. So far as is known, this never happens to an unfertilized egg. The causal factors accounting for implantation are not known.

Two sorts of development take place during pregnancy. First, the zygote grows and passes through one stage after another until it is recognizably human. The process of development of the **embryo** (Greek *en*, in; *bryo*, swell), which is the name for any unborn individual, forms the subject of study of the science of embryology. Elementary aspects of this subject will be presented in Chapter XXXI; for the present, we shall content ourselves with presenting an exhibit of some of the stages

Fig. 15-7. Human embryos. Top left, at 26½ days after ovulation (×11); top right, at 34 days (×5). Lower left, 43 days (×3); lower right, 56 days (×2). (Courtesy of Dr. G. W. Corner and the Carnegie Institution of Washington.)

through which every human passes in his development from egg to infant.

Quantitatively, prenatal growth amounts, roughly, to a two-billionfold increase in weight of the individual. Qualitatively, the change in appearance is equally striking (Fig. 15-7). It is apparent that, relatively speaking, the greater part of our development takes place in the nine months before we become legally recognized persons. The Chinese show a fine realization of the facts in regarding a newborn child as being already one year old. This is a slight exaggeration, but it is certainly closer to the truth than our own method of reckoning age.

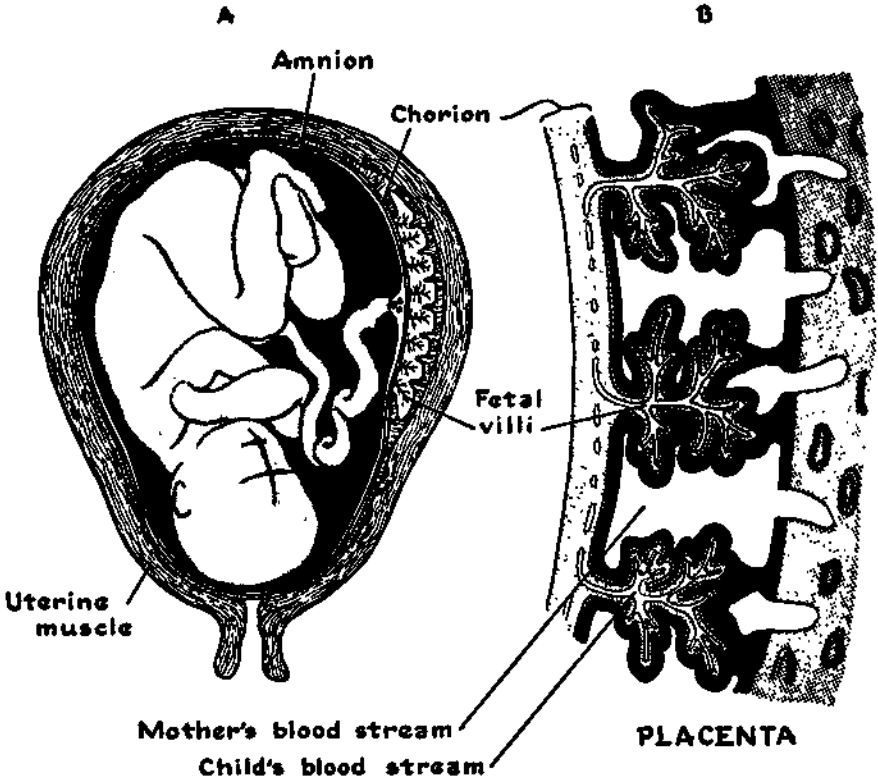

Fig. 15-8. The normal position of the mature fetus in the uterus (A). In B, the placenta magnified and simplified. Notice that, normally, there is no mixing of the blood of the mother with that of the child.

The second sort of development that takes place during pregnancy is the development of a set of extraembryonic structures, which have been simplified in the accompanying diagram (Fig. 15-8). For nine months, the embryo is entirely dependent on its mother for its existence. All its food and oxygen must come to it from its mother's blood stream, and its waste-products must pass from embryo to mother to be disposed of by the latter. The embryo and the mother do not, however, have a common blood stream, a point clearly demonstrated by the fact that a child may belong to a blood group different from that of its mother. Microscopic examination of the region where embryonic and maternal tissues meet reveals the sort of structure diagrammed in Figure 15-8B. Notice that the blood streams of mother and child are separated by a thin wall of tissue. Everything that passes between the two must be soluble and capable of diffusing through this tissue.* The whole region diagrammed in Figure 15-8B, including both embryonic and maternal tissue, is called the placenta. It constitutes the only means of "communication" between mother and child. There is no nervous connection between the two.

119. Some Hormones Involved in Pregnancy

Earlier, it was pointed out that the corpus luteum secretes a hormone that makes possible implantation of the fertilized ovum. Some of the other hormones involved in reproduction will now be described. The hormonal story of reproduction is only partly known but, even so, it is a complicated one which will be only partially presented here. The interrelationships of the elements can best be understood by constant reference to Figure 15-9.

The anterior lobe of the pituitary gland, a source of many different hormones, occupies a central position in this complex of hormonal interrelationships. The development of the Graafian follicle is stimulated by one of the pituitary hormones, the **Follicle Stimulating Hormone,** or **FSH** for short. In turn, the developing follicle itself produces a hormone, called **estrogen,** which stimulates the uterine epithelium to go through the early part of its menstrual cycle and the pituitary to secrete more hormones.

When the follicle ruptures, the egg escapes from the ovary, leaving a mass of follicle cells behind. These now develop into what might be called a new organ, the corpus luteum, the development of which is stimulated by the **Luteinizing Hormone (LH)** of the pituitary. However, the corpus luteum does not develop far unless the egg is fertilized

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* The difficulties occasionally caused by the Rhesus blood factor point to the existence of occasional breaks in this barrier. This problem is treated in Chapter XXX.

and implanted on the uterine wall. If pregnancy takes place, the corpus luteum remains intact during the approximately nine months of the normal "term"; though it is doubtful if it serves a function in humans for, in women, the ovaries, including the corpus luteum, can be removed after the first month of pregnancy without affecting the course of events.

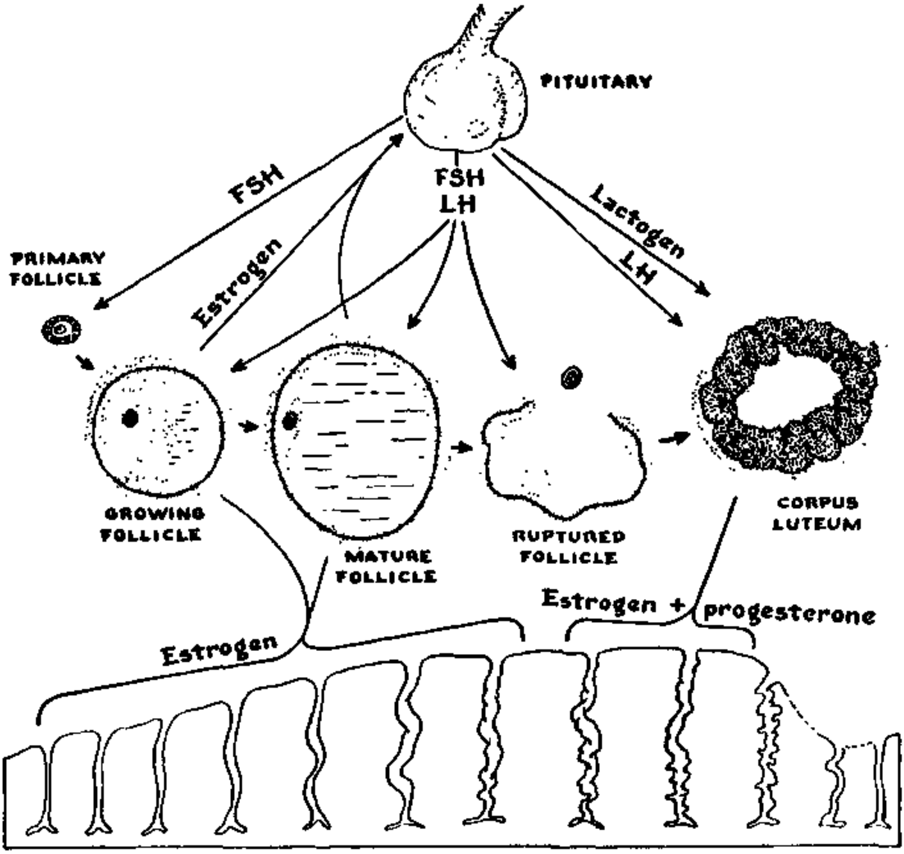

Fig. 15-9. The complex interrelationships between the pituitary, the ovarian follicle and its derivatives, and the uterine wall (below).

The placenta itself produces at least two hormones, **progesterone** and **gonadotropin.** Progesterone, which appears to be necessary for the continued placentation, is secreted by the placenta. Surely this is the physiological equivalent of lifting oneself by one's bootstraps!

The significance of the gonadotropin secreted by the placenta is not clear. The hormone is so named because, experimentally, it can be used to simulate the action of similar gonad-stimulating hormones of the pituitary. Large amounts of it are secreted into the blood stream and excreted in the urine during pregnancy. There are several tests for pregnancy based on the presence of gonadotropin in the urine. In one of them, the Ascheim-Zondek test (or A-Z test), the urine to be tested or *assayed* is injected into a female mouse. If the urine contains significant amounts of the gonadotropin, the ovaries and uteri of the mouse—in mice and most mammals, the female has two uteri—change to the pregnant condition. Such a method of assay, using a biological test, is called a biological assay or **bioassay.** Other bioassays for pregnancy involve the use of rabbits (Friedman test) or a South African toad, *Xenopus laevis.*

The full story of the significance and interaction of hormones in pregnancy is not known, but it is unquestionably a very complicated one. It is just because it is complicated that it is so hard to untangle the constituent threads. During pregnancy, for instance, the mammary glands increase in size—why? It is known that the pituitary secretes a hormone that may have this effect, but the placenta also appears to secrete such a hormone. Or does the placental hormone stimulate the pituitary which, in turn, stimulates the mammary gland?

One hormone may have several effects; the same effect may be due to several different hormones; the same hormone may be produced by more than one organ; and a given effect may be the end result of a chain of hormonal actions of one organ on another. Is it any wonder that we still do not really understand the interaction of causes that insures implantment, placentation, pregnancy, parturition and lactation? Perhaps the wonder is that we have learned as much as we have in so short a time. Soundly conceived and carefully executed experiments should eventually untangle the entire story.

120. Problems of Birth

What factors cause pregnancy to terminate and birth **(parturition)** to begin are not really known. Does the embryo or placenta "keep its own time," so to speak, or is there a change in hormonal balance that causes parturition to take place? Presumably, nervous influences are not required to start off the process but they can have an influence, as is shown by the fact that a severe emotional or nervous upset to the mother can—however directly or indirectly—cause a premature birth.

The process of birth begins by rhythmic contractions of the smooth muscles of the wall of the uterus. Later, these muscular movements are aided by contractions of the muscles of the abdominal wall. At the same time, the exit of air from the trachea may be periodically prevented, increasing the pressure in the entire abdominal cavity and, thus, aiding the expulsion of the child to the exterior. It can readily be appreciated that a highly muscular torso is an aid to easy birth. This one factor is probably the principal one accounting for the easier birth among primitive, i.e., hard-working, women, as compared with "civilized" ones. However, with the increase in the fashionableness of vigorous sports for civilized women, the differential is probably lessening.

The vagina, normally a passage much too small for so large an object to pass through, enlarges sufficiently during the latter stages of pregnancy to permit the child to be squeezed through it. Also, the pubic bones that surround the vagina and meet in front of it have their suture, evidently under the influence of hormones, loosened to the point where the bones can be partly sprung apart at birth. Normally, a child is born head first; when any other part of its body is presented first, the delivery is more difficult and may necessitate the use of instruments.

For the child, being born brings about the most sudden and radical revolution of its entire life. In its mother's uterus, it does not need to breathe, feed, or maintain its own temperature, nor is it required to move around, though it does move, as any mother can tell. The most radical change at birth is that involved in breathing for itself, a change that involves both the breathing and the circulatory systems.

The lungs of an unborn child are in a completely unexpanded condition and contain no gas whatever. He gets his oxygen from his mother; she breathes for him. As soon as he is born, the child must do his own breathing and *do it right*. He has no time to learn; there are no second chances for first failures. Breathing, as we know, means much more than merely filling the lungs with air. It means doing it periodically. The chemical mechanism of breathing has already been described (§ 106-§ 107). The child is born with this mechanism. As soon as the CO_2 in his blood rises, his medulla is stimulated to send messages to the breathing muscles, causing the appropriate motions. Besides the chemical mechanism, there is another factor involved in normal breathing, an inherent tendency in the medulla to send impulses at regular intervals. This inherent rhythmicity is often almost lacking in the newborn child; as a result, its breathing tends to occur in alternating periods of activity, in response to high CO_2 content, and in periods of complete inactivity following the lowering of CO_2 content of blood by heavy breathing. This sort of breathing (called Cheyne-Stokes breathing) is frequently observed during infancy. Usually, the medulla develops its

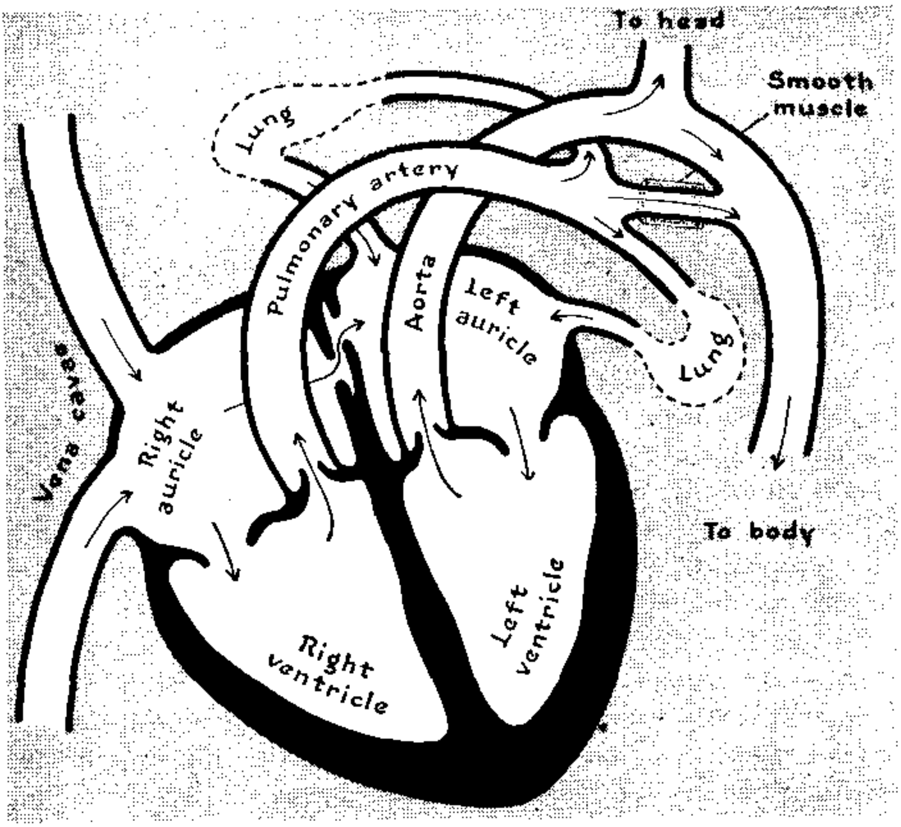

Fig. 15-10. The fetal heart has two short circuits between the two pump systems: (1) an opening between the two auricles, and (2) a special vessel (the **ductus arteriosus**) between the pulmonary artery and the aorta (above, right). The ductus is surrounded by smooth muscle which contracts after the birth of the child. The opening between the auricles also closes at the time of birth.

inherent rhythmicity by adulthood, though there are exceptions. It is noteworthy that even the normal adult may show Cheyne-Stokes breathing in extremely deep sleep.

Recall the double nature of the circulatory system and the reasons therefor (Chap. IX). The need for both a pulmonary and a systemic circulation in the adult does not exist in the unborn child; yet, it must have such a system all ready to go at the time of birth. The means by which the embryo compromises the conflicting needs is extremely neat. The adultlike system of separated circulatory systems is first developed with "short circuits" in the vascular "plumbing" that permit blood to pass from the pulmonary system to the systemic system without going through the lungs. One of these short circuits (see Fig. 15-10) is an opening between the two auricles. It is guarded by flaps of tissue that, during embryonic life, do not interfere with the passage of blood from the right auricle to the left auricle. After birth, because of pressure relationships too complicated to go into here, the flaps close and remain closed. Ultimately, new tissue grows across the opening and the two auricles are thenceforth completely separated—in four out of five persons. The remaining 20 per cent of the population have a tiny opening between the right and left auricles.

The other short circuit is a blood vessel that connects the pulmonary artery with the aorta. This vessel remains open until birth. It is surrounded by a muscle (see Fig. 15-10) that, in response to some unknown stimulus connected with being born, contracts at the time of birth, completely closing the vessel, and thus causing all the blood in the pulmonary artery to go through the capillaries of the lungs before getting out into the systemic circulation. Once the muscle of the short-circuiting blood vessel contracts, it never relaxes and, in some weeks, growth of new tissue occludes the vessel. The muscle degenerates and disappears. A muscle which is destined to contract but once in an individual's life, then to perish! It would be difficult to find a more striking instance of the adaptation of a structure to a specific function.

QUESTIONS AND PROBLEMS

15-1. What is the essential feature of reproduction?

15-2. Define: gamete, zygote, spermatozoon, ovum, fertilization, testis, testicle, ovary, oviduct, womb, uterus, gonad, semen, placenta, pregnancy, lactation, parturition.

15-3. Define, so as to distinguish between, the terms *sterilization* and *castration*.

15-4. In cryptorchidism, the sperm-producing cells of the testes do not function but the hormone-producing cells do. Does this condition resemble castration or sterilization more closely?

15-5. What is the etymology of *cryptorchidism?* Do you know of common words using the same roots?

15-6. Some people have speculated as to whether the prolonged hot baths of the Japanese may not have a tendency to lower their reproductive rate. What physiological facts led to this speculation?

15-7. Why is an expectant mother urged to walk a mile a day?

15-8. Some people believe that the mother can influence the character of her child by "thinking the right thoughts." *If* such prenatal influence exists, what is the route of the "message," nervous or homonal? Do you think it likely that it could be directional and specific, e.g., that a mother could produce a musical child by much listening to symphonies?

15-9. "Blue babies" are babies whose blood (both arterial and venous) appears blue under the skin insteady of rosy. They sometimes grow into adults who are incapable of much exertion.

a. What is the significance of the blue color?

b. What abnormalities of development could account for the babies' condition?

c. Could these abnormalities be remedied surgically and, if so, how?

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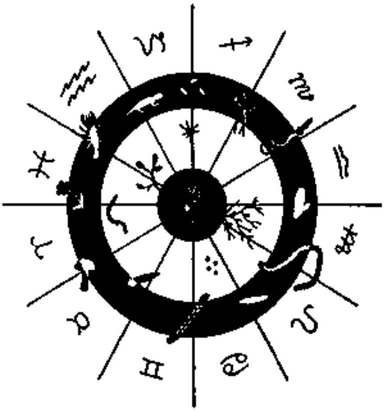
PART III

The Variety of Living Things



Chapter XVI

The Lower Invertebrates

121. The Purpose of Classification

We have considered at some length the structure and physiology of but one organism, man. The justification for this emphasis is twofold: (1) We believe that, to understand organisms in general, we need to study at least one kind of organism intensively; and (2) we are men. However, if we wish to have a more balanced view of the universe, we must consider at least some of the other million or so kinds of plants and animals. Plainly, we cannot study them all in as great detail. We must by some means get an impression of their variety and significance. To this end, we set forth on a rapid survey of the living world.

It is not possible, by even the most rapid survey, to gain useful impressions of millions of things unless these things are somehow organized or classified. How one classifies things is determined by one's interests. St. Augustine, adopting (as was characteristic of his time) an almost exclusively human point of view, divided all animals into three groups: useful, hurtful, and superfluous. We of today take a more objective point of view and try to classify animals and plants according to their structural and functional similarities. The classification we shall present here is modern, not Augustinian. However, there is a certain psychological soundness in St. Augustine's point of view. It is natural, on learning of any other being, to ask oneself, "What is this to me?" The neophyte, especially, wants to know about the "practical" (i.e., human) significance of the organisms he sees. For this reason, in what follows, we shall point out the human importance of many of the organisms. Students who become interested enough in any organism to want to know more of it will find useful bibliographies at the ends of the chapters.

122. Taxonomy: The Art of Classification

The art of arranging living things in groups, according to their similarities, is called **taxonomy** (Greek *taxis,* arrangement; *nomos,* law). The ultimate unit of taxonomy is the **species** (Latin, kind or sort; *species* is either the singular or the plural form). Unfortunately, this basic unit is not easy to define; but a common definition, and one good enough for a first approximation, is this: **two individual organisms belong to the same species if they can mate and produce fertile offspring.** All living men are classified as belonging to one species (*Homo sapiens*) because there is no record of the inability of any one race to interbreed successfully with any other. The horse (*Equus caballus*) and the dog (*Canis familiaris*) are considered to be different species because they cannot interbreed. The horse (*Equus caballus*) and the ass (*Equus assinus*) are also considered to be different species because, although they can be successfully bred together, their offspring, the mule, is not fertile.

It will be noted that each species bears two names, e.g., *Canis familiaris* in the case of the dog. The first name is called the **genus name,** or the **generic** name, and must always be capitalized. The second name is the **species name,** or the **specific** name, and is usually not capitalized. Both names are customarily written in italics, and if the context is such that the reader may be expected to know the genus referred to, the generic name is abbreviated, e.g., *C. familiaris.* The genus is the lowest rank that includes more than one species. In a genus are included organisms which, while bearing obvious resemblances to each other, cannot pass the "species test" of producing fertile offspring. The genus *Canis,* for instance, includes the domestic dog, *C. familiaris,* the jackal, *C. aureus,* and the coyote, *C. latrans.*

Similar *genera* (plural of genus) are placed together in the next larger rank, the **family.** The genera *Canis* (dogs), *Vulpes* (red foxes), and *Urocyon* (gray foxes) are all included in the family *Canidae.* The **-ae** ending characterizes all family names.

The system of classifying plants and animals that we follow today was first developed by the Swedish naturalist, **Linnaeus,** when he was in his twenties, and was published in 1735. The various categories of this system are visible in the table below in which the names of the particular groups that include *C. familiaris* are listed.

RANK	CLASSIFICATION OF DOMESTIC DOG
Kingdom	Animalia
Phylum	Chordata
Class	Mammalia
Order	Carnivora
Family	Canidae
Genus	*Canis*
Species	*familiaris*

Classification being an art as well as a science, it is not surprising that there is not complete agreement in the classifying of organisms. At the species level, it is often impossible for taxonomists to reach accord. For instance, all domestic dogs are commonly considered to be of one species; but it seems probable that they were derived from several wild species of the genus *Canis* and it is certain that, as a practical matter, the Mexican hairless cannot interbreed with the St. Bernard breed. It is futile to argue about such matters; taxonomy deals with questions of definition and one cannot *demand* agreement in definitions. The individual organisms are the primary reality. How we throw them into taxonomic pigeonholes is determined by human judgment which is always fallible.

As a generalization, it may be said that the closest agreement exists on questions of generic identification. As we proceed to more inclusive ranks (family, order, etc.), disagreements become more common. What one man will regard as a class, another will call a subclass or will combine with some other group. With respect to the largest subdivision of the animal kingdom, authorities differ in the number of **phyla** (plural of **phylum**) recognized. Fortunately, there is agreement regarding the more important ones, and it is only these that will be discussed here. The unmentioned phyla include many fascinating animals, some of considerable theoretical importance; but, in order to see the forest, we shall have to ignore some of the trees. The same principle will be adhered to in the discussion of each phylum. In each phylum, only a few examples will be presented, thus greatly minimizing the variety of the group. The student should bear this in mind.

That the present-day kinds of living things have evolved from extinct forms that were unlike them is a matter of common knowledge. The idea of evolution is widely accepted even by people who do not know the evidence for it. Before this book is finished, we intend to present this evidence for critical examination. For the present, however, we propose to exploit the common acceptance of the idea of evolution and to describe, in a comparative way, various plants and animals. We shall discuss different taxonomic groups on the assumption that they are part of an evolutionary series, running from the more primitive to those more recently evolved. The critical reader, however, if he is unwilling to accept tentatively the idea of evolution, may consider the series presented to be merely a logical series, running from "simpler" to "more complex." All of the statements could be reworded to fit this viewpoint. The wording would be more awkward, but the essential sense of the statements would be unaltered.

123. The Protozoa

Any sample of muddy pond water will furnish us with many examples of the **protozoa,** the smallest of the animals. The word *protozoa* is derived from two roots meaning *first animals* (Greek, *protos*, first, and *zoion*, animal). In the evolution of the animals, these were unquestionably the first forms. They are also first in order of complexity, though this by no means indicates that all of them are really simple. **Each individual protozoan is only a single cell,** but within the confines of a cell membrane may be included many structures that remind one of the multicellular animals (see Fig. 16-1). Such complexity is to be found within an amazingly small compass—the majority of the protozoa are less than 100 microns (0.1 mm) in length.*

The cells of protozoa, like all cells, increase in number by cell division or **fission** (Fig. 16-2A). This process has a different significance in the protozoa and in the **metazoa** (multicellular animals). In the latter, cell

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* For expressing the size of small objects, the micron is a convenient unit. One thousand microns equal one millimeter. The symbol for the micron is the Greek letter *mu*, written μ.

division merely results in growth. In the protozoa, however, since the cell is the individual, cell division is a method of reproduction.

Sexual reproduction also occurs in many protozoa. Two cells of the same species come together in **conjugation** (adhere to each other) and exchange nuclei or fragments of nuclei. Following separation, the ex-conjugants, as they are called, multiply by cell division again. In some species, there are different "mating types"; no two members of the same mating type will conjugate.

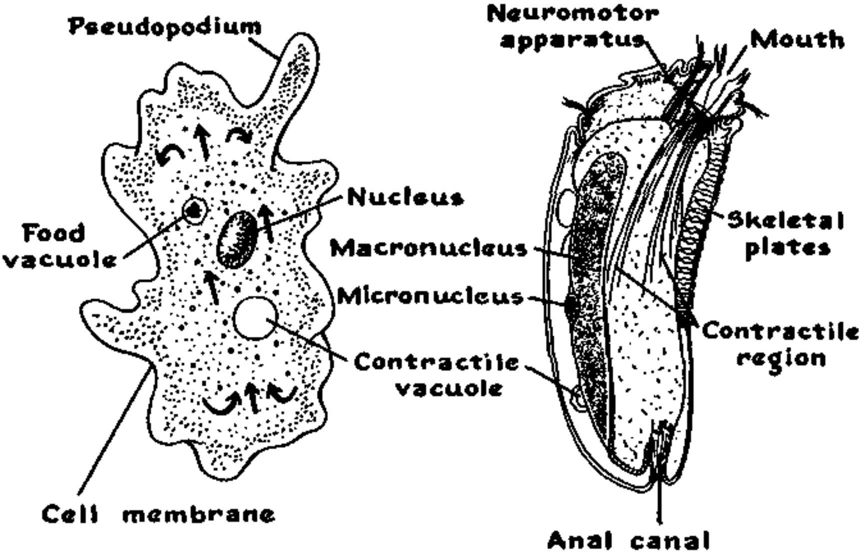

Fig. 16-1. *Left:* an amoeba. The arrows show the direction of movement of the cell contents as the whole animal moves. *Right:* a ciliate found in the intestinal tract of cattle. Notice the complexity possible within the confines of a single cell.

Some protozoa have the ability to develop a thick wall within which an individual goes into a quiescent stage. A protozoon or other organism in this stage is called a **cyst** (Fig. 16-2B). By means of a resistant cyst, some parasitic protozoa manage to survive exposure to the dangers involved in the passage from one host to another.

The protozoa are commonly divided into four classes, as follows:

Flagellata – The members of this class (Fig. 16-3) move themselves by means of thin, flexible whips called **flagella** (singular **flagellum**). The class Flagellata is believed to be the most primitive group of animals both because of the relative simplicity of its members and because many of them (e.g., *Euglena*) are green like plants. The green flagellates are, in fact, studied by both botanists and zoologists. It would seem that they represent a connecting link between the plants and animals, though which evolved from which is still a matter of dispute.

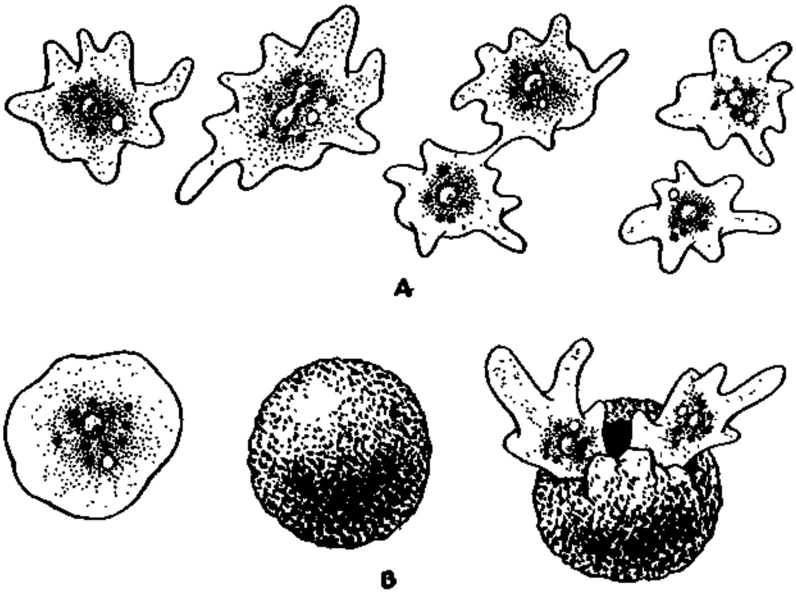

Fig. 16-2. Reproduction among protozoa. A, simple fission of one cell to form two. B, encystment and excystment. In this case, the protozoon divides while within the cyst. In other cases, the process of cystment is not a method of reproduction, but is merely a means of producing a form that can resist some adverse environmental conditions.

Most of the flagellates are free-living, i.e., nonparasitic, and are abundant in soil and water. All species of the genus **Trypanosoma,** however, are **parasites;** that is, they get their nourishment from other organisms in which they live. One species lives in the blood stream of man and causes African sleeping sickness. It is spread from man to man by blood-sucking tsetse flies.

Rhizopoda—The name of this class signifies rootlike feet and is justified by the extensions of the body by which a rhizopod moves. The familiar example, *Amoeba* (Fig. 16-3), varies in its shape as first one part of its body and then another extends as the animal slithers along. Each such temporary extension is called a **pseudopod** (Greek *pseudes*, false; *podos*, foot). There are some organisms that have both a flagellum and pseudopods, thus suggesting a relationship between the flagellates and the rhizopods.

Besides the well-publicized *Amoeba*, the class includes many other forms, among which are the **Foraminifera** which produce microscopic shells that are characteristically different for each species. Since the shells persist after the death of the organisms and may become imbedded in sedimentary rocks in the process of being laid down, Foraminifera

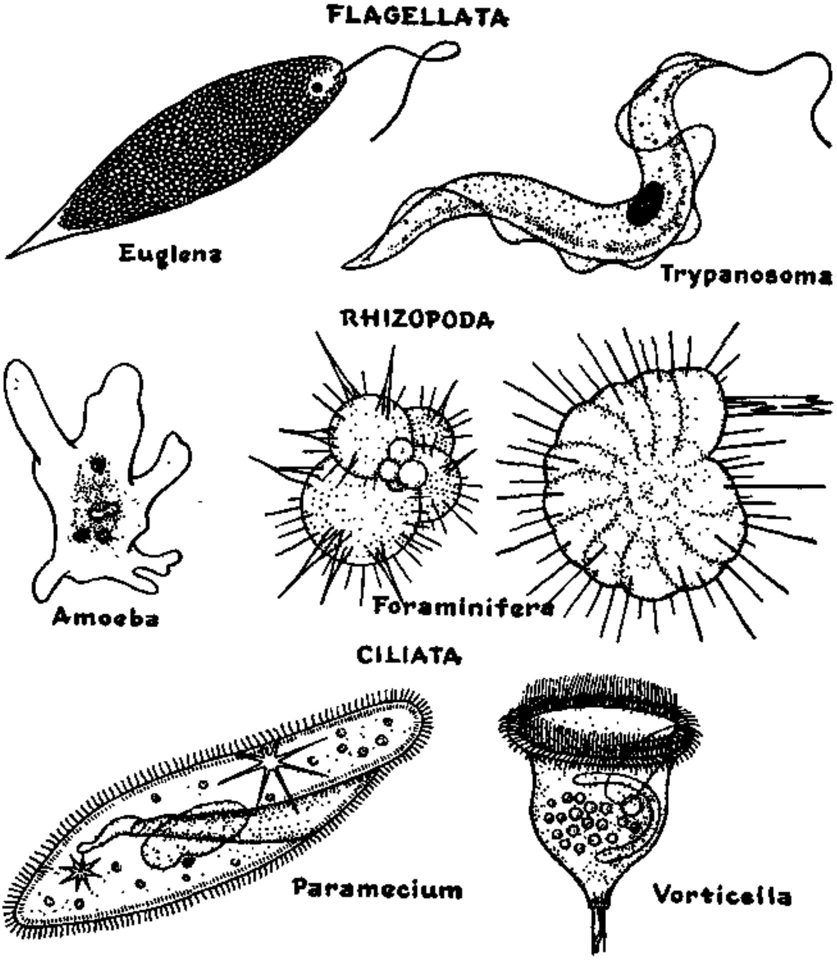

Fig. 16-3. Representative members of three classes of protozoa. All of the forms illustrated are free living except trypanosoma. One of the many species of trypanosomes causes African sleeping sickness in man.

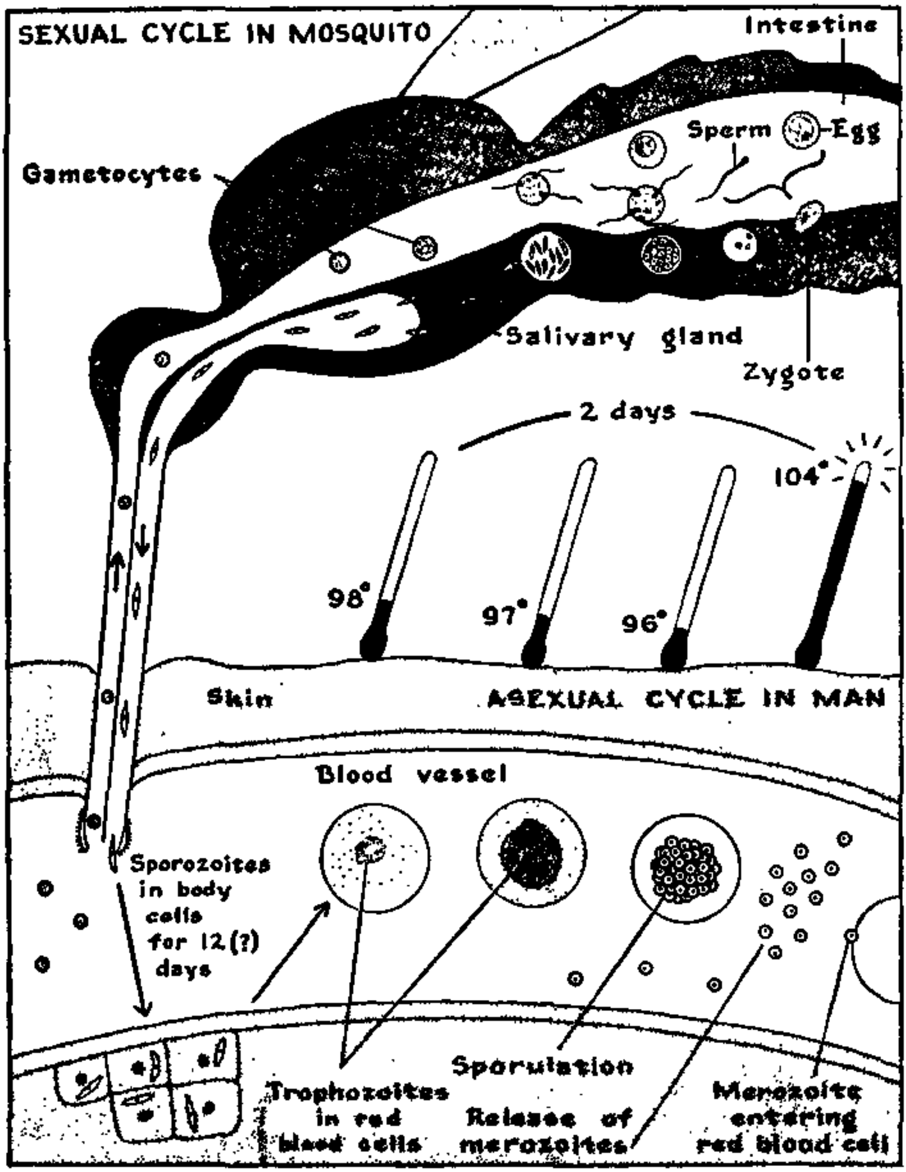

Fig. 16-4. The life cycle of the malaria parasite in its two hosts, mosquito and man.

shells are used to identify rocks that were formed at different geological times when different species of Foraminifera were living.

Almost without exception, the rhizopods are free-living. The best-known parasitic form is **Entamoeba histolytica,** an amoeba that causes an intestinal disease known as **amoebic dysentery.**

Ciliata—The ciliates (Fig. 16-3) are so named because of the possession of numerous small hairlike appendages or **cilia** (singular **cilium,** Latin, an eyelash) by which they propel themselves. The ciliates are perhaps the most spectacular and beautiful of the protozoa and are certainly the least important, falling truly in St. Augustine's third class of the superfluous organisms. Nevertheless, their ready availability and their attractiveness have made them favorite objects of study by biologists, study which has led to some discoveries important in the field of general biology.

Sporozoa—In contrast to the ciliates, the members of this class are short on morphological beauty and complexity and long on practical importance. All the members of this class are parasitic, and there is perhaps not a single species of animal that does not harbor, at times, a sporozoan species that is to be found in no other host. Malaria, man's most important disease—it is estimated that half of the annual deaths in the world are caused by malaria—is caused by a sporozoan. The malaria sporozoan has a complex life cycle. Some of its stages are passed in the body of certain mosquitoes of the genus *Anopheles,* and other stages occur in man. The principal features of the life cycle are indicated in Figure 16-4. As is true of all members of the class, this parasitic organism reproduces by multiple fission or **sporulation,** hence the class name. Fission occurs inside the red blood cells of man and all of the parasitized erythrocytes burst simultaneously, releasing the spores into the blood stream. The fever of malaria appears to be due to decomposition products released by the bursting of the red blood cells.

The attacks of malaria can be controlled with some success by two chemical compounds, quinine and atabrine. A more fundamental line of attack is one directed against the integrity of the life cycle. The malaria-parasite population can be maintained only by continuous transfer from one host species to the other. In the absence of either man or mosquito, the protozoon would perish. Obviously, the real way to eliminate the disease is to eliminate one of the hosts. In the regions of the world where malaria is important, this line of attack is being followed, with man's natural bias determining the host selected for elimination.

124. Porifera

All animals except the protozoa are placed in the subkingdom **Metazoa.** The lowliest of these are the **Porifera** or sponges. The "sponges" with which the layman is most familiar these days are synthetic products of the chemist's art. The natural sponges, which are knobbier in appearance, are still used to a considerable extent. Natural sponges are skeletons of rather simple water-dwelling animals. Most sponges (the animals, that is) are marine organisms that grow in shallow water. They are collected by "sponge-fishers" who use long hooked poles or who dive

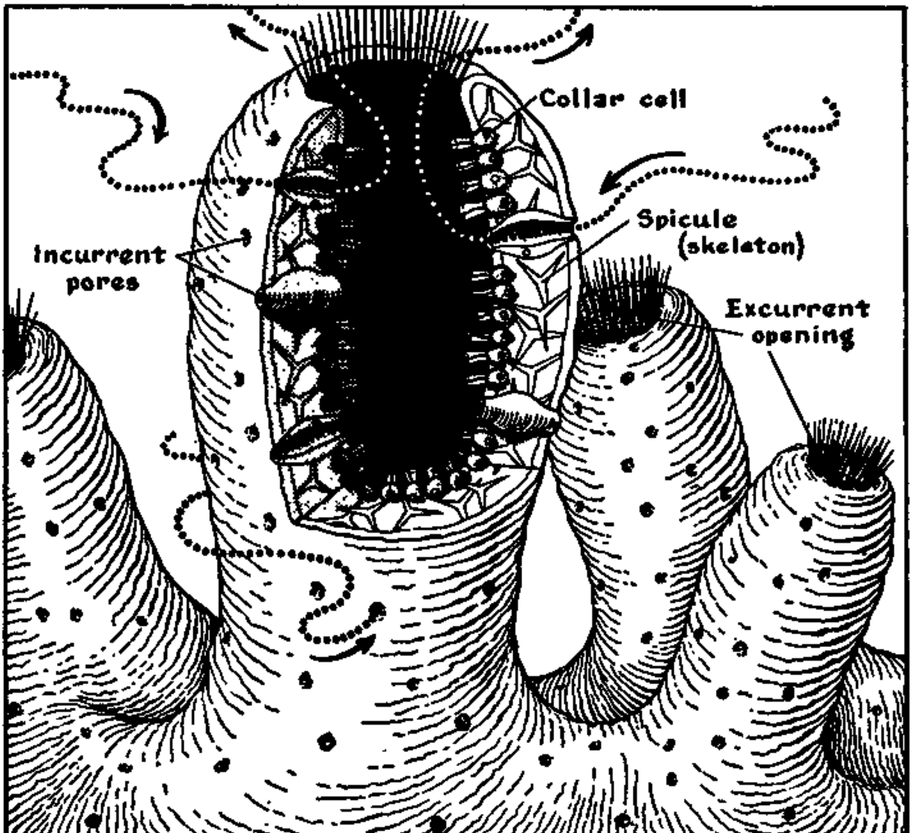

Fig. 16-5. A sponge, a member of the Porifera, the only phylum in which the largest opening is an exit rather than an entrance. The collar cells closely resemble certain specialized protozoa, indicating the probable evolution of Porifera from Protozoa.

for them. After being collected, the sponges are allowed to decay until only their skeletons remain.

At first sight, one would say that the living sponge is an unprepossessing-looking vegetable. A sponge is essentially a hollow sack of living material (Fig. 16-5). The principal opening of the body conducts water out of the body. In no other phylum, is the principal opening an exit opening. Water is taken into the body through many small **incurrent pores;** tiny bits of food are filtered out of the water by the cells that line the cavities of the body, and the waste water is extruded from the large **excurrent opening.** The sponge does not have to move around to get its sustenance from the world; instead, it pumps the world through itself. One investigator found that a single sponge about the size of a small fountain pen moved five gallons of water through its food-gathering passages in a single day.

The skeleton of the sponge consists of interlocking elements called **spicules.** In the case of the bath sponge, these spicules are of organic nitrogenous material. In other sponges, the spicules are of silica (like sand) or calcium carbonate (like limestone). It is obvious why only some natural sponges can be used in the bath.

The collar cells (see Fig. 16-5) of sponges point to the evolution of the Porifera from the Protozoa, among which are found free-living cells of similar shape. The sponges themselves seem to be a dead end as far as further evolution occurs. It is not likely that any higher group arose from their line.

125. Coelenterata

In the coelenterates, we are dealing once more with animals whose principal opening is an entrance, as is true of all the higher phyla. These animals are almost entirely confined to the ocean where they are abundant. Along the shores, are found various sorts of sea anemones and corals, animals that are generally taken for plants by the neophyte because of their sessile habit. In the open waters, are found forms that float or even swim—the jellyfishes.

As different as the stationary coelenterates (the sea anemones) and the floating ones (the jellyfish) may appear to be, examination shows that they are of similar construction. (See Fig. 16-6A,B). In both, a mouth opens into a "gastrovascular cavity" in which the food (caught by the tentacles) is digested. The walls of coelenterates consist essentially of only two layers of cells, one of which is called the **ectoderm,** the other

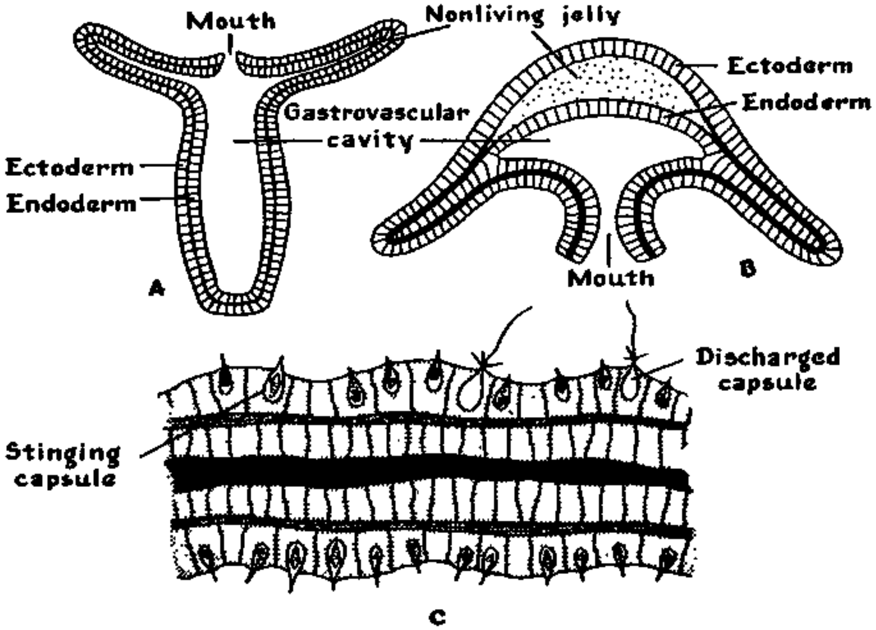

Fig. 16-6. Coelenterata. The fundamental similarity of the polyp (A) and the medusa (B) is evident. C, cross section of the wall of a coelenterate showing the stinging capsules that are produced only in this phylum.

the **endoderm.** Between these two, is a layer of nonliving jelly that is thin in the sessile forms and thick in the floating ones. This jelly, by its relative lightness, aids in flotation.

Coelenterates catch their food by means of minute **stinging capsules** which are clustered in batteries on the movable tentacles (Fig. 16-6C). When suitably stimulated, as by a small living object, a stinging capsule discharges, producing a minute, harpoonlike weapon that can impale small objects. Many of the stinging capsules seem to include some sort of poison that can paralyze the victim. In most coelenterates, the size of the weapons and the amount of poison are too small to hurt humans· but, in the case of a few, e.g., the large jellyfish called the "Portuguese man-of-war," the animals constitute a genuine threat to the life of humans who tangle with them.

Sessile coelenterates are called **polyps**; floating forms are called **medusae.** In most cases, a polyp will be one species, and the medusa another. But there are a number of species in which there is a regular alternation of a polyp generation with a medusa generation.

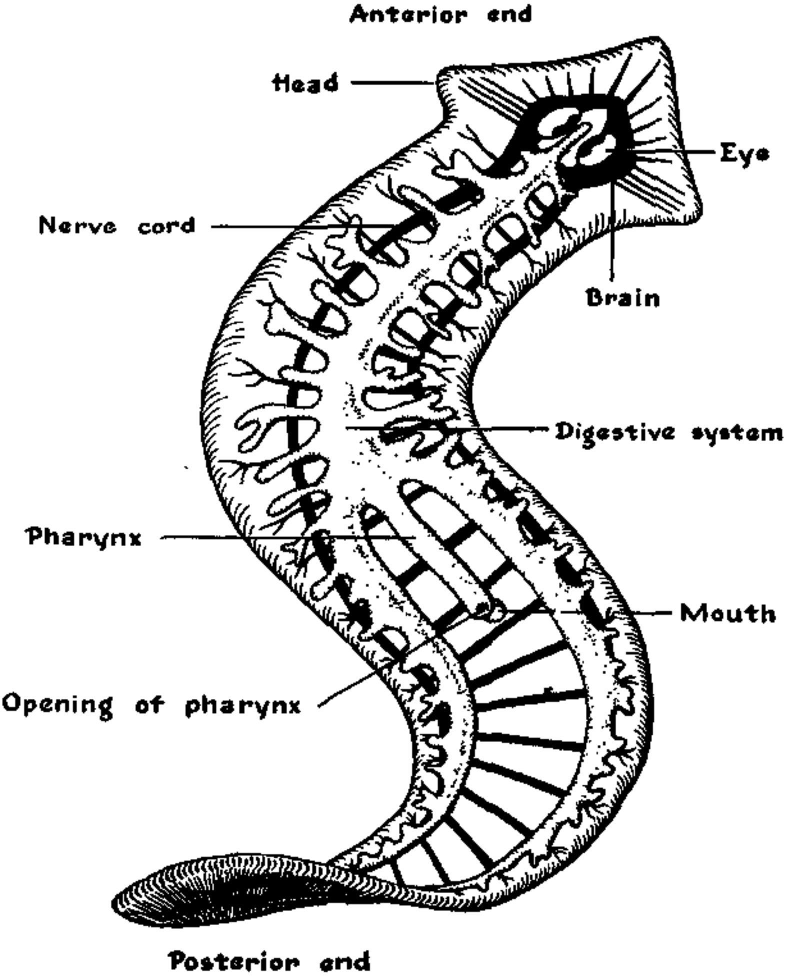

Fig. 16-7. A planarian and its internal structure.

126. Platyhelminthes

Although free-living flatworms, called **planarias** (Fig. 16-7), are ubiquitous, few laymen have seen them because of their small size and retiring habits. They live under rocks and vegetation in fresh-water ponds and streams, are dun-colored, and but a few millimeters in length. Planarias may often be collected by submerging a trap, which consists of a bottle containing a bit of liver, to a stream bottom and leaving it overnight.

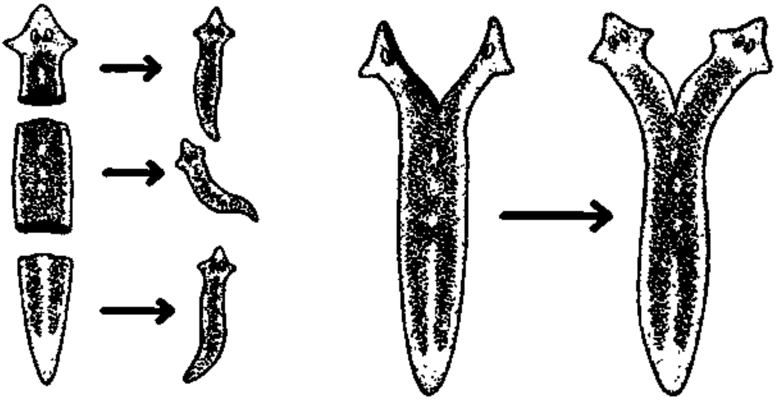

Fig. 16-8. Regeneration of planaria.

In one respect, the flatworms represent no advance over the coelenterates; there is still but one opening (the mouth) into the digestive cavity. In some other respects, they are more advanced. The coelenterates have only two layers of cells, the ectoderm and the endoderm. (See Fig. 16-6.) In the flatworms, and all "higher" animals, there is, in addition to these two layers, a third layer of cells, the **mesoderm,** which is sandwiched between the other two. The body has a definite and permanent front end—which coelenterates do not have—and the nervous coordination of the actions of the parts of the body is more advanced.

With the development of a definite front end, is associated a new type of symmetry. Coelenterates are **radially symmetrical;** any vertical plane passing through the mid-line will cut the animal into similar halves. (A pumpkin is radially symmetrical.) The Platyhelminthes, however, are so constructed that there is only one plane, passing lengthwise of the body, that will produce two similar halves. Platyhelminthes are said to be **bilaterally symmetrical.** Man, in his external features, exhibits bilateral symmetry.

In the economy of nature, planaria do not count for much. In the biology laboratory, they are of more importance. Planaria possess, to an unusual degree, the ability to regenerate lost parts. A single worm may be cut into several pieces (Fig. 16-8), and each piece will regenerate all of its missing parts, thus forming a complete worm. A head that is split lengthwise between the two eyes will regenerate two heads. An operation of this sort may be performed with any sharp knife. The survival rate of the "patients" is high, hence, their popularity as laboratory subjects. The results of a diversity of experiments with planaria have led to general theories of the mechanism of regeneration in all animals.

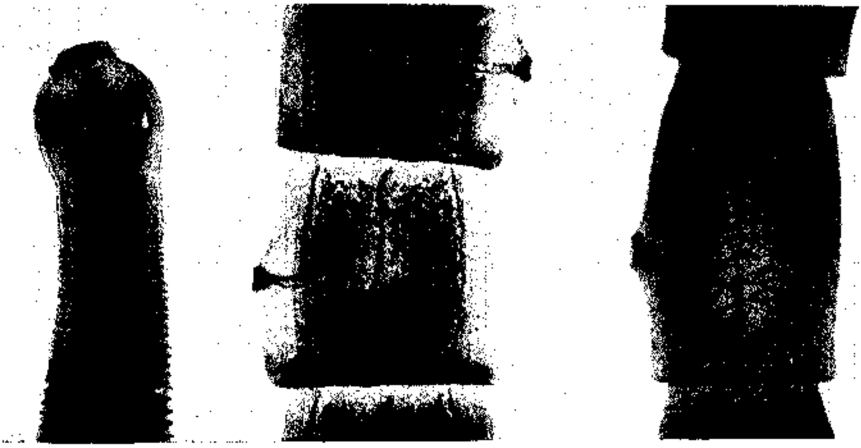

Fig. 16-9. Portions of a tapeworm. At the left, the "head" by which the worm attaches to the intestinal wall. In the middle, one of the hundreds of sections. It consists of almost nothing but ovaries and testes. At right, a mature section, which is little more than a sack full of eggs. Mature sections pass out of the body of the host in the feces. In the absence of medical treatment, the head remains attached and continues to produce more sections. (Copyright by General Biological Supply House, Inc. Chicago.)

Although the free-living platyhelminthes are of little practical importance, it is otherwise with the parasitic species. Millions of Chinese suffer seriously from the effects of the "Chinese liver fluke," a parasitic flatworm. This fluke has three hosts in which it lives in succession: man, water snail, and fish. In the fish, the flukes occur in resting stages and are embedded in the muscles. When a man eats uncooked fish, the flukes come out of their resting stages and turn into active forms. To prevent the spread of this fluke, only one thing is necessary—to cook the fish. This sounds simple enough, but the millions of Chinese who live in the affected localities have neither fuel nor money to buy the fuel with which to cook the fish. This is but one of the many modern medical problems that are not really medical problems at all, in the strict sense, but problems involving economics and the relation of population size to productivity of the land.

Another parasitic flatworm is the beef tapeworm. One stage of its life cycle is passed as a multisectional worm living in the intestine of man. What is ordinarily considered a single adult tapeworm could perhaps better be considered a whole colony of individuals oriented in tandem. Each section consists of almost a complete set of organs, with emphasis on the reproductive (see Fig. 16-9). As mature eggs and embryos develop within, sections break away from the whole and pass out in the feces. If a cow happens to eat grass contaminated with human dung that contains tapeworm embryos, these embryos then pass through other stages of their life cycle leading to the ultimate formation of resting stages reposing within "bladders" in the muscles of the cow. When these bladders are ingested by man, they "hatch" to produce a new tapeworm.

The control of the beef tapeworm can be effected in three ways:

a. By always cooking beef thoroughly.
b. By inspecting beef at the slaughterer's and condemning meat that has bladders in it. (These are easily visible in certain muscles.)
c. By always disposing of human dung in a sanitary manner.

The first form of control can be effected by the individual. Anyone who wishes may prevent tapeworm in himself by refusing to eat rare meat. The other forms of control must be carried out by society, and can, in fact, render the first unnecessary. To put it another way, we can safely indulge in the delight of eating rare beef only so long as we have organized community control of meat inspection and sewage disposal.

We have cited only two instances of parasitic flatworms. There are many other parasitic species of worms, and there is much variety in their life cycles. As a generalization, we may say that the two most common ways in which a parasitic species is passed from one host to another is via feces or by one host eating another. In a society that enjoys a "high standard of living," as Occidentals understand the term, parasitic worms are of negligible importance. If the standard of living goes down, or if the organization of society is disrupted by war or other catastrophe, parasitic worms become an important threat to community health.

Fig. 16-10. Photomicrograph of trichina worm in human muscle. (Copyright by General Biological Supply House, Inc. Chicago.)

127. The Nemathelminthes

The **Nemathelminthes,** besides being round, are distinguished from the flatworms by the possession of two openings to the digestive tract, a mouth and an anus. Included in this phylum, are numerous species of microscopic soil nematodes and plant parasites as well as a number of important human parasites, of which we will mention three.

The **hookworm parasite** is a minute worm that attaches itself by the thousands to the intestinal wall of man. Its fertilized eggs pass out with the feces. The eggs hatch in the soil producing immature worms that live in the dirt for some time, ultimately re-entering man by burrowing through his skin, e.g., through the sole of a bare foot. The immature worms can live only in warm, moist soil, and, hence, the cycle cannot be maintained in cool regions. The control measures needed in warm countries are obvious: the sanitary disposal of human feces, and/or the wearing of shoes. In many impoverished regions of the southern United States, neither measure can be invoked without outside aid or influence. Since hookworm infestation causes a very debilitating disease, its victims are often despised for their "shiftlessness." The sufferers become increasingly less able to afford—or desire—the controls needed, thus setting up a truly vicious circle.

The **trichina parasite** (Fig. 16-10) can infest the flesh of a number of animals (pigs, rats, bears, man), passing from one to another when one animal devours another. It is *not* transmitted through feces. The most important source of infection for man is pork. As in the case of the beef tapeworm, this avenue of infection can be closed by thoroughly cooking the meat. Government inspection measures are of no avail, however, since the resting forms in the meat are too minute to find without a microscopic examination that is so detailed and expensive that, for practical reasons, it cannot be routinely made. The only feasible control measure is thorough cooking of the meat. The rule for pork is: *cook it DONE.*

Filaria worms are another species of minute worm of considerable medical importance. The immature worms are so small that they are transmitted from person to person by mosquitoes of certain species. In humans, filaria cause trouble by blocking lymph passages (§ 71) causing permanent swelling of the part of the body that is normally drained by the particular lymph passages that happen to be blocked. As a result, the affected part of the body swells to a tremendous size; hence, the name of the disease, **elephantiasis.**

128. Mollusca

The phylum **Mollusca** includes the well-known, and often highly edible, clams, oysters, mussels, and snails. Rather surprisingly (to the beginner), it also includes octopuses and squids. Superficially, the alert, speedy squid would seem to have little in common with the sedentary oyster, but the internal anatomy and the embryological development of the two indicate that they are closely related. Throughout the living world, embryology and internal anatomy have proved to be sounder criteria of natural relationships than has external anatomy.

In size, the familiar mollusks are not very large. Some unfamiliar marine forms, however, are of impressive size, some clams weighing hundreds of pounds and some squids as much as two tons. Squids are, in fact, the largest of the invertebrates, i.e., the animals without backbones (vertebrae).

129. Annelida

An immediately striking characteristic of worms that belong to the phylum **Annelida** is their **segmentation.** An earthworm, for example, has an indented ring running around it every few millimeters. The section of the body between two rings is called a **segment.** Except for a few segments at both ends and a short section in the middle of the body, most sections appear to be nearly identical.

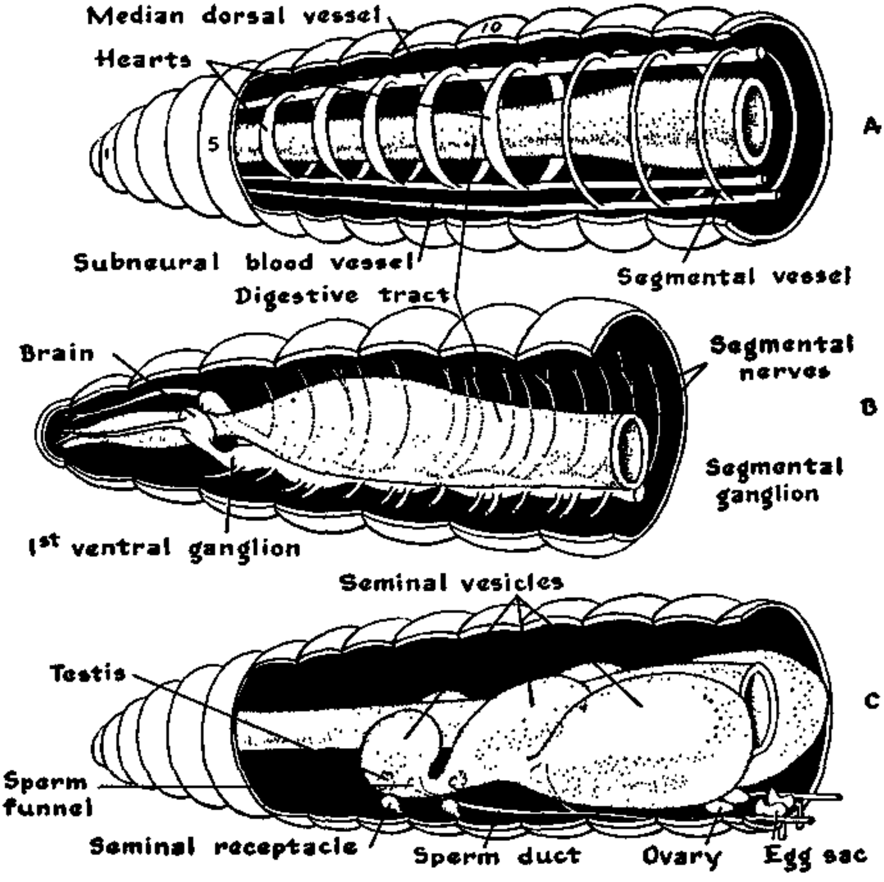

Fig. 16-11. The anterior end of an earthworm, analyzed to show circulatory system (A); nervous system (B); and reproductive system (C).

The segmentation is more than skin deep. The repetitive tendency it implies is evident in the internal anatomy of the earthworm. For instance, an earthworm has five pairs of hearts. (See Fig. 16-11A.) The nerve cord also shows a swelling (ganglion) and repetitive branches in each segment (Fig. 16-11B). Notice that the nerve cord is on the ventral side of the animal, as is true of all the higher invertebrates, in contrast to the vertebrates in which it is dorsally placed.

Not all systems are segmental in arrangement. The intestinal tract is the conspicuous exception. This tube extends continuously from one end of the animal to the other. The earthworm's diet consists of dirt and whatever nutritious remains of plants and animals are in it. This food enters at the mouth at the extreme anterior end and passes the length of the intestinal tract, undergoing digestion along the way. Eating, for the earthworm, is both a means of securing nutrition and an aid in burrowing through the soil. A great deal of material that is of no nutritional value to the earthworm is thus moved around.

The soil, however, is much benefited by the stirring up that it gets. In the course of their activities, earthworms carry much soil to the surface of the earth and deposit it as little coiled lumps of material known as worm castings. Measurements in one worm-rich soil indicated that on each acre in the course of one year there were deposited eighteen tons of worm castings. At this rate, there would be deposited on the surface of the ground about two inches of reworked soil every ten years. How much net increase in soil this represents is not known, but there is no doubt that earthworms are beneficial to the soil. The translocation of soil from below to above has the effect of gradually burying both rocks and man-made structures, if the latter go unattended. Thus have many of man's early edifices been buried and preserved to the delight of archaeologists.

The reproductive system of the earthworm is segmentally arranged, but is confined to the ninth to fifteenth segments inclusive. The earthworm is *hermaphroditic*, i.e., both sexes are found in a single individual. The earthworm does not fertilize itself, however. Two worms come together and fertilize each other. Hermaphroditism is a condition that is found here and there throughout the animal kingdom. It is not confined to any one phylum but rather is characteristic of animals leading a certain kind of life. Though there are exceptions, it is generally found among animals that lead a more or less sedentary life. It seems reasonable to suppose that an animal that does not get around much would be more likely to reproduce itself if it could be sure that the first one of the same species that it encountered would be of the right sex(es) for mating. At any rate, hermaphroditism is frequently found among the relatively slow-moving forms such as the earthworm and parasitic forms such as the tapeworm.

QUESTIONS AND PROBLEMS

16-1. In the following names of organisms, which is the generic and which the specific name: *Homo sapiens; Acer rubra; Lespedeza bicolor; Musca domestica; Hyla versicolor?*

16-2. Closely related genera are combined in a larger group which is called what?

16-3. Define protozoa. Define metazoa.

16-4. The significance of cell division is slightly different in the protozoa and in the metazoa. Explain.

16-5. What is a cyst? What function may it serve?

16-6. Name two diseases caused by protozoa, and tell the sort of organism that causes each.

16-7. What control measures can be used against each of the following diseases: malaria, beef tapeworm, Chinese liver fluke, hookworm, and trichina parasite?

16-8. In the widespread disorder that would follow the breakdown of civilization, which ones of the above diseases would you expect to increase? Which ones could be readily avoided by the individual who had the necessary knowledge?

16-9. Of what practical importance are earthworms?

16-10. Of what value is hermaphroditism to an organism?

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Chapter XVII

The Arthropoda

130. The Jointed-Legged Animals

The phylum *Arthropoda* includes such things as crayfish, spiders, and the insects. The arthropods and the vertebrates are clearly the two dominant groups of animals. Which one might be said to be *the* dominant group is a matter of opinion, in which neither man nor bug may render an unbiased verdict. We think we are; perhaps we are right. But if either numbers of individuals or numbers of kinds of species is to be taken as the criterion, clearly the vertebrates come out second best. The number of individual ants, bees, and flies in a few square miles is greater than the number of humans in the entire world. As for the number of species, an estimate made in 1935 placed the number of described species of vertebrates at less than 60,000, while the number of described species of arthropods was estimated at 640,000. If a modern Noah set out to collect a pair of every species of arthropod for his Ark, and if he could check off one pair per second, it would take him a month to get all the jointed-legged creatures in his boat, assuming that Noah worked a modern forty-hour week. Many authorities think that the total number of species of arthropods, known and unknown, is at least twice as great as the number already described. A modern Noah might be flooded before he could finish entering the beasts in his register.

A conspicuous difference between the arthropods and the vertebrates is in the position of the skeleton. In the arthropods, it is external to the soft parts of the body; hence, its name **exoskeleton.** It is made of a nitrogen-organic compound called **chitin.** When pure, chitin is a soft and flexible material that resembles some synthetic "plastics." In many arthropods, especially the larger ones (for instance, the lobster), the chitin is impregnated with calcium compounds which make it as hard as a rock.

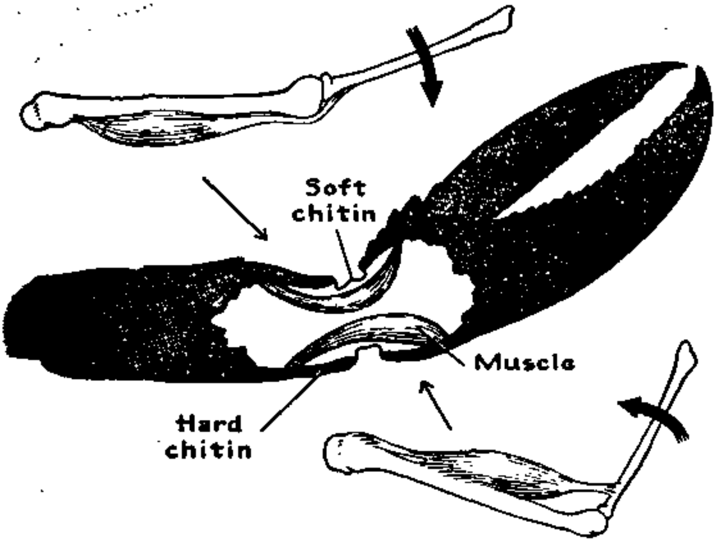

Fig. 17-1. The fundamental mechanics of an arthropod joint. Compare the action of muscles within an exoskeleton, like that of a crayfish, to the action of muscles attached to an endoskeleton, like that of man.

The skeleton being on the outside, the system of muscle attachment is somewhat different from that prevailing in vertebrates, as Figure 17-1 makes apparent. And because hard chitin is not sufficiently flexible, movable hard parts must be articulated by short sleeves of soft chitin.

The chitinous exoskeleton is an admirable system for achieving protection without sacrificing mobility. It constitutes a splendid suit of armor and is undoubtedly one of the reasons why the arthropods have done so well in the world. It has, however, a conspicuous disadvantage: it does not readily permit growth. To increase in volume, an arthropod must first split open his old hard armor, pull himself out of it (still covered by a thin underlayer of flexible chitin), and then swell very rapidly before his new skin hardens into an armor once more. This process of moulting is a complicated one, and the period immediately following a moult is a vulnerable one for the individual. The necessity of moulting has probably set upper limits to the size of arthropods which average considerably smaller than the vertebrates.

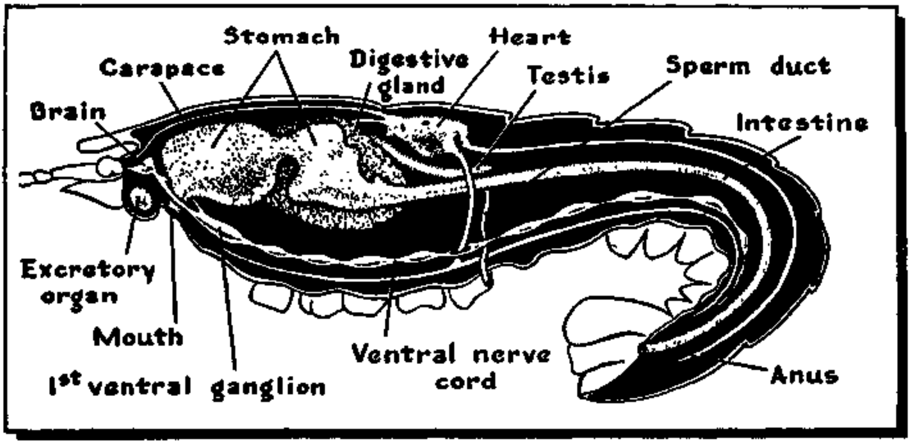

Fig. 17-2. The structure of a typical arthropod, a lobster, diagrammatically indicated.

There seems to be little question that the arthropods evolved from the annelids. Like the annelids, they show segmentation, but it is considerably reduced in extent. In the arthropods, external segmentation is still present, though it is less obvious, and the ventral nerve cord is definitely segmented (Fig. 17-2); but most of the other organs are unsegmented.

The phylum Arthropoda is divided into several classes of which the three most important will be discussed here.

131. The Class Crustacea

The **crustacea** are mostly water-dwelling forms. Most of them have a large number of pairs of legs, typically five pairs. Besides the conspicuous crabs, lobsters, and crayfish, this group also includes small, even microscopic forms, such as various shrimps and "water fleas" (*Daphnia* and *Cyclops*, for example). Barnacles are also crustacea; this seems surprising at first because a barnacle looks like a mollusk (Fig.

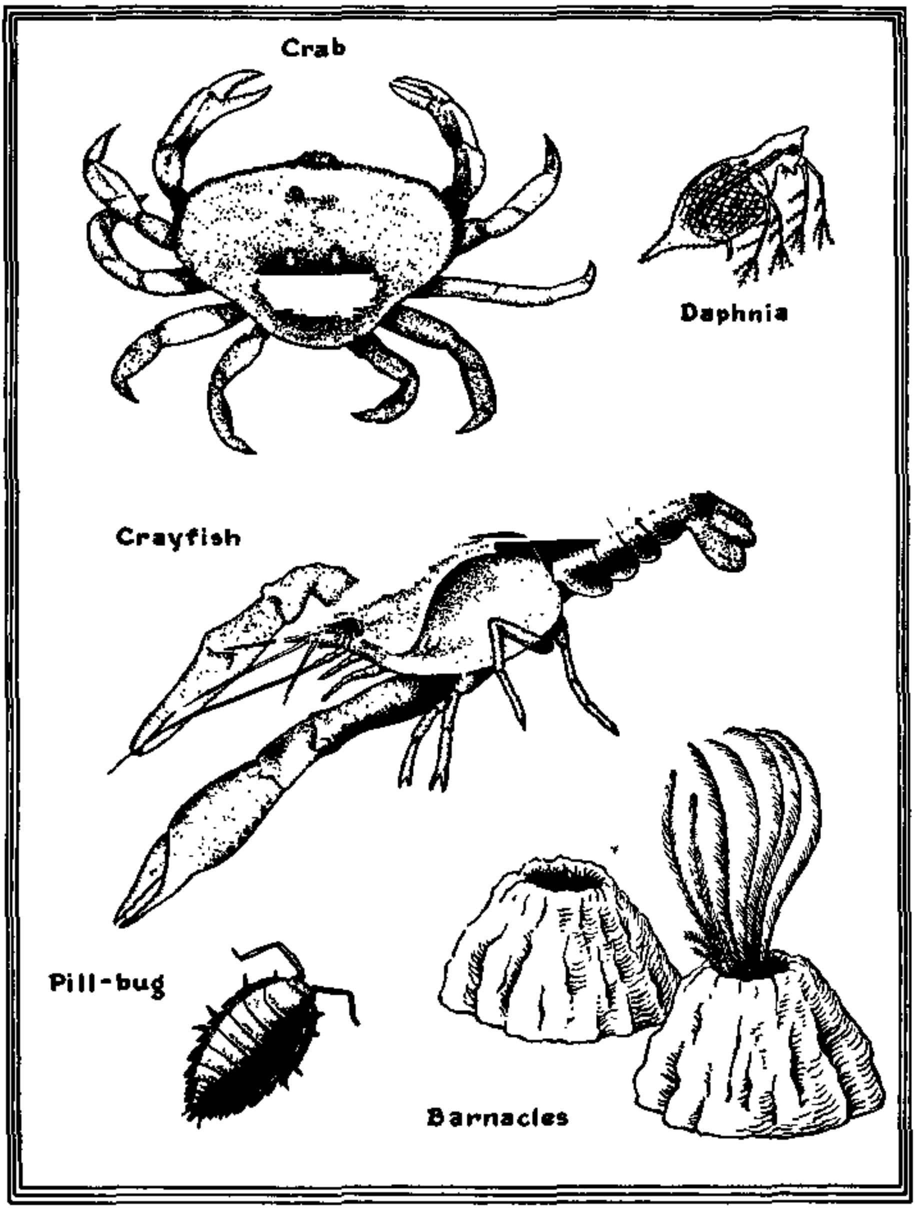

Fig. 17-3. A miscellany of crustacea. (Not drawn to same scale.)

17-3). However, inside the calcareous shell is a jointed-legged crustacean. A few crustaceans occur on dry land (not too dry); e.g., "pill bugs" which can often be found beneath rocks.

As is well known, the larger crustacea, such as the crabs and lobsters, are important items of food for man. Indirectly, the smaller crustacea are even more important. The various shrimps and water fleas are quantitatively the most important items in the diet of the fish that man eats. These small crustacea, in turn, feed on bacteria and other microbes that are too small for the fish to capture.

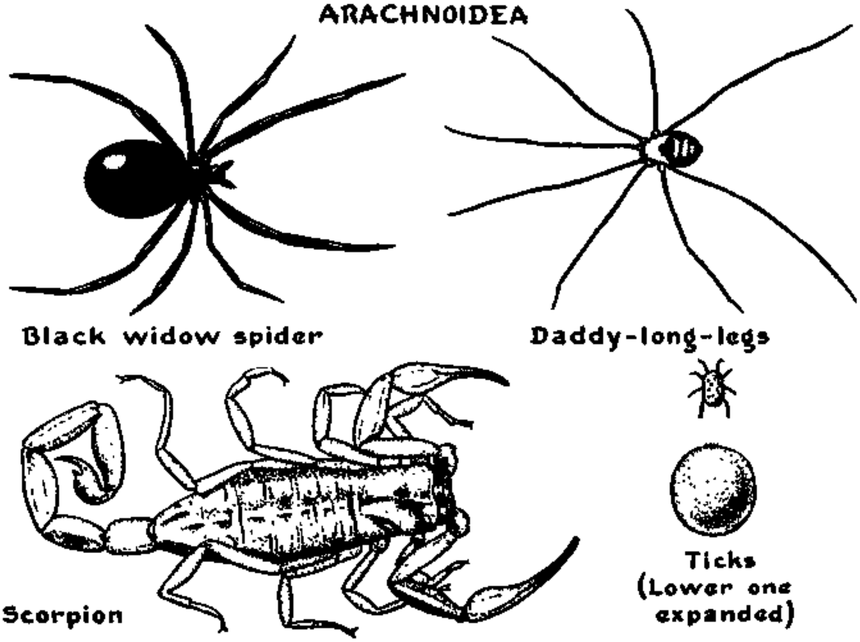

Fig. 17-4. A variety of Arachnoidea.

132. The Class Arachnoidea

To the class **Arachnoidea,** belong the spiders and their relatives: scorpions, "daddy-long-legs," the ticks, and the mites (Fig. 17-4). All of these forms have eight legs which distinguishes them from the insects which have only six. Most of the members of this class are "lone wolves," each individual keeping to himself; an occasional brief flurry of sexual activity is the only form of social intercourse. Many of them, all the spiders, for instance, are wholly carnivorous, being tempted only by living flesh. Spiders mostly live on insects and so are an important agent in keeping down the numbers of insects. This may be good or bad from man's point of view, depending on whether the spider is catching "harmful" or "beneficial" insects.

Ticks are blood-sucking species. As is frequently true of parasites, they serve as agents for the transport of various disease organisms from one host to another, e.g., one kind of cattle fever, typhus, and Rocky Mountain spotted fever.

133. The Class Insecta

Insects, by definition, **are arthropods with three pairs of legs.** The class **Insecta** is a conspicuously successful group. In species, they outnumber all other kinds of living things except, possibly, the microbes.* Their variety and beauty are such that they have long been favorite objects for collectors. The hundreds of thousands of species of insects alive today fall into some twenty well-defined orders. About half of these are described below, and representatives are illustrated in Figure 17-5.

Isoptera—The termites, often mistakenly called "white ants," are important in the economy of nature in that they hasten the rate of decomposition of cellulose, the structural material of plants, including trees. Man, who appropriates this material to make his houses and his books, objects when termites continue to eat the food they have eaten for some two hundred million years.

Orthoptera—Grasshoppers, katydids, roaches, crickets, and the praying mantis belong to this group. Most of the noise-makers of the insect world are orthopterans.

Anoplura—Lice. These, though descended from winged forms, are wingless. Being completely parasitic on vertebrates, including man, they no longer need wings, for the sociality of these species easily enables a louse to transfer from one perambulating "meal-ticket" to another.

Siphonaptera—The fleas also are wingless, but they are more active about transferring from one host to another, having developed remarkable jumping abilities.

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* Someone has stated, as a hypothesis, that every species of macroscopic organism has at least one microscopic parasite that can thrive only on it. (Remember, there are many nonparasitic microbes.) If this is so—and we don't know that it is—then, it logically follows that there are more microbes than macrobes.

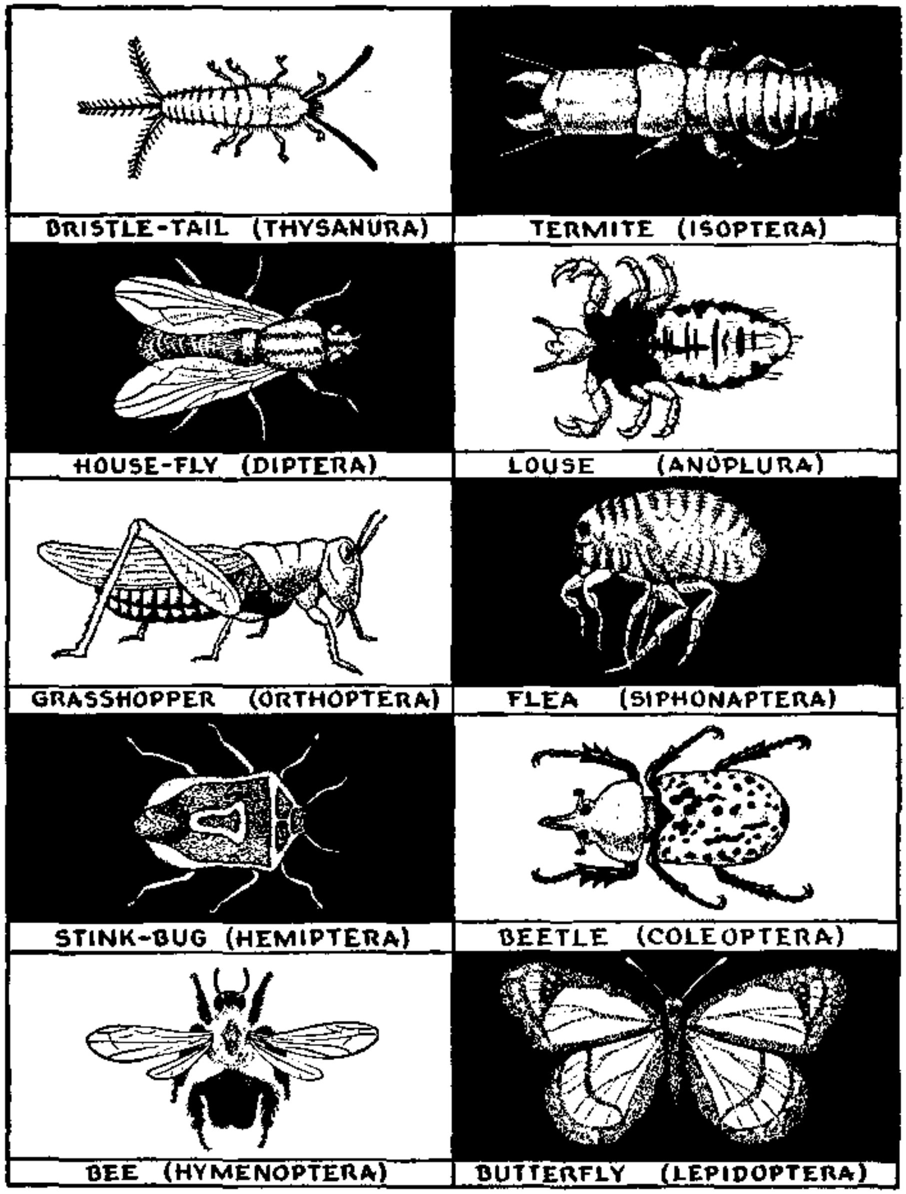

Fig. 17-5. Representatives of some of the *orders* of insects.

Diptera—The word *fly*, as an entomologist uses it, refers only to the two-winged flies, or Diptera. Houseflies, horseflies, cow flies, deer flies, mosquitoes, gnats and midges belong to this order. These insects have evolved from four-winged ancestors. The second pair of wings, in the course of evolution, have "degenerated" into a pair of tiny knobs which are not, however, without function. When the knobs (called **halteres,** or **balancers**) are removed, the fly is no longer able to fly correctly. It appears that, by vibrating while the insect is in flight, the halteres act as gyroscopes and keep the fly on an even keel. Many diseases are caused by flies; in some of them (the ox warble), the insect is the direct cause, while in others (malaria, yellow fever), the mosquito is the carrier or **vector** (Latin *veho,* to carry; *vectus,* carried).

Hemiptera—A precise entomologist restricts the use of the word "bug" to members of this group. Bugs have two pairs of wings, but one pair, half leathery in texture, folds over the other in rest. Bugs have mouth parts designed like a hypodermic needle to pierce and suck. The attention of the great majority is confined to plants, entailing considerable destruction of man's crops. Chinch bugs, squash bugs, stinkbugs, back swimmers, and water striders are members of this order.

Lepidoptera—Scale-winged insects. These are the moths and butterflies, so beloved of collectors. About 80,000 species have been described and named. Probably only a few of the larger and more conspicuous species remain to be discovered. Some of the moths, e.g., clothes moths, and codling moths, cause considerable damage to man's possessions or crops. On the other hand, the larva of the silkworm moth furnishes us with genuine silk which is a good substitute for rayon, nylon, etc.

Hymenoptera—These have thin, membranous wings. There are two pairs, but frequently (e.g., in the honeybee), the hind wing hooks on to the fore wing so that one has to look carefully to see the true structure. Bees, wasps, and ants are the conspicuous members of this order. Though there are many solitary forms, the order is notable for the development of elaborate social organizations in many different species.

Coleoptera—The beetles. In popularity with collectors, these insects have been a close second to the Lepidoptera. About 180,000 species have been described and, unquestionably, many more remain to be discovered. In the beetles, the fore wings do not function in flying, but have been modified into tough covers that fold over the hind wings when the flight is ended. The markings of the body are frequently vivid and interesting. Noteworthy in this group are the "potato bugs," "June bugs," ladybird beetles, scarab beetles, and many destructive weevils, such as the cotton-boll weevil. The "firefly" is also a beetle, though its wing covers are much more delicate than those of most coleoptera.

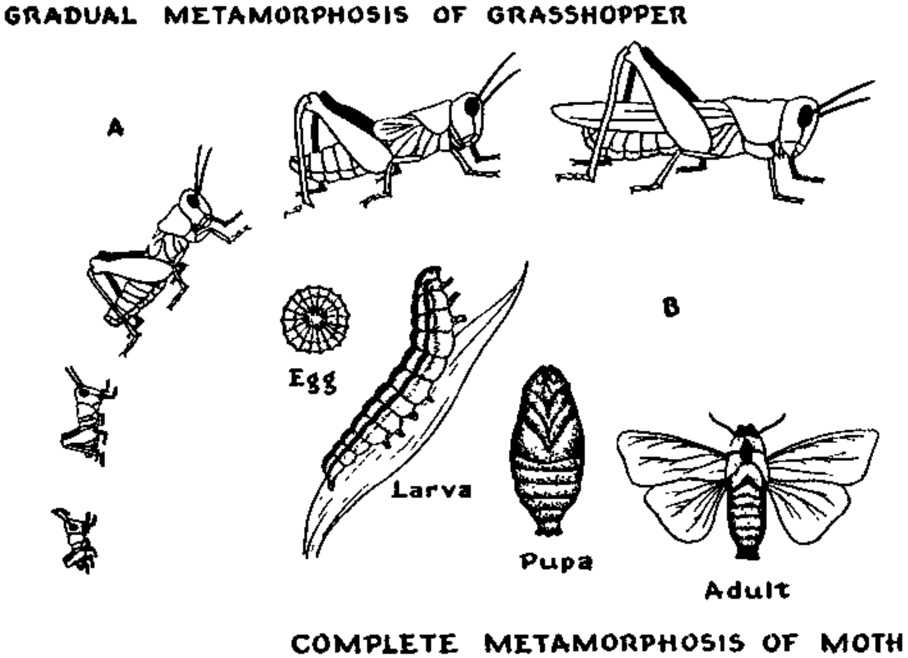

Fig. 17-6. Complete and incomplete metamorphosis of insects.

134. Metamorphosis of Insects

Some insects mature much as do the crustacea—by alternating periods of growth and moulting, each new stage being much like the old. The grasshopper exhibits such a maturation process (Fig. 17-6A). The body proportions change at each moult and usable wings gradually appear, but there is no striking change in appearance. The young stages are recognizably similar to the adult ones.

It is quite otherwise with the development of many other insects. A moth or a butterfly, for example, leads a double life (Fig. 17-6B). The egg first develops into a wormlike being called a **larva.** After a period of growing (without substantial change of form), the larva forms around itself a chitinous case. The whole individual, case and all, is then called a **pupa.** Pupation superficially appears to be a resting stage. Inside the pupa case, however, there is feverish activity. Almost all the structures of the larva are being completely broken down, and from the raw materials, the adult structures are being developed. When this transformation or **metamorphosis** (literally, "change of form") is complete, the new adult ruptures the pupa case and steps forth fully formed.

The double life led by such insects extends to the minutest details. The morphology of the insect larva is very different from that of the adult; the larva resembles an annelid worm and has many pairs of feetlike appendages. Its daily life is different. A moth larva chews up leaves; the adult sips on flower nectar. A midge-fly larva lives continuously under water; the adult drowns if submerged for a short time. The instincts of the two forms are different: they are attracted and repelled by different things.

When one thinks of a species, one habitually has the adult form in mind as being *the* species; immature forms one unconsciously ignores. In keeping with this tendency, the descriptions of the orders above were descriptions only of the adults. But, in insects that show metamorphosis, the emphasis were often better placed on the larval forms. Some species of May flies, belonging to an order not described above, live in the larval state for as long as three years. The adult life lasts but a single day, during which no food is eaten at all. Mating, egg-laying, and death in a few hours—then begins the long larval period for the new generation. The seventeen-year "locust" (cicada) has a similar life history. The larval and pupal stages last for seventeen years, while the sexually mature adults live for only a few weeks. From the insect's point of view (if it has one), the adults would seem to be peculiar, evanescent forms which exist only for the purpose of producing more of the "real" organisms, the larvae. One is reminded forcibly of Samuel Butler's aphorism, "A hen is only an egg's way of making another egg."

135. Behavior: Instinct versus Intelligence

We all have heard of the marvelous things that insects such as ants, bees, and wasps can do; of their complex social organization, and of the complicated structures they can build. The remarkable thing about their actions is that these actions are not the product of learning. A spider knows how to make the kind of web that is proper for its species without ever having seen one. A wasp which paralyzes other insects by stinging certain nervous ganglia knows precisely where to insert her stinger the first time she does it. Actions of this sort we say are due to **instinct.** An instinct may be thought of as a complex chain or network of innate reflexes. When one of the reflexes is set off by a stimulus, the rest follows mechanically.

Instinct is a splendidly efficient way of reacting to the environment. The high development of instinct in the insects no doubt accounts to a considerable extent for their success in life. Like most efficiency, it is purchased at the expense of flexibility, the ability to adapt actions to a completely new situation. The danger involved is evident in the following particular case.

In the tropics, there are species of ants, belonging to the genus *Eciton*, known as "army ants." The name is apt because colonies, 100,000 to 150,000 strong, march for days on end through the jungle, destroying and eating any insect or even small vertebrate that cannot get out of their way. Their marching is all the more remarkable because they are virtually blind. Observation shows that there are no leaders, only followers. The ones at the head of the column are pushed into their position by the force of numbers behind. The instinct of each ant is to follow a chemical trail, the smell on the ground laid down by the ants that precede it. Normally, this instinct is completely adaptive, making possible the forages of the colony over miles of territory. In exceptional circumstances, the instinct may have tragic consequences, as in the following instance observed by T. C. Schneirla at Barro Colorado, in the Panama Canal Zone:

> "The ants, numbering about 1,000, were discovered at 7:30 a.m. on a broad concrete sidewalk on the grounds of the Barro Colorado laboratories. They had apparently been caught by a cloudburst which washed away all traces of their colony trail. When first observed, most of the ants were gathered in a central cluster, with only a company or two plodding, counterclockwise, in a circle around the periphery. By noon, all of the ants had joined the mill which had now attained the diameter of a phonograph record and was rotating somewhat eccentrically at fair speed. At 10:00 p.m., the mill was found divided into two smaller counterclockwise spinning disks. At dawn the next day, the scene of action was strewn with dead

> and dying *Ecitons*. A scant three dozen survivors were still trekking in a ragged circle."*

By 7:30, 24 hours after the mill was first observed, various scavenger ants of other species were busy carting away the corpses.

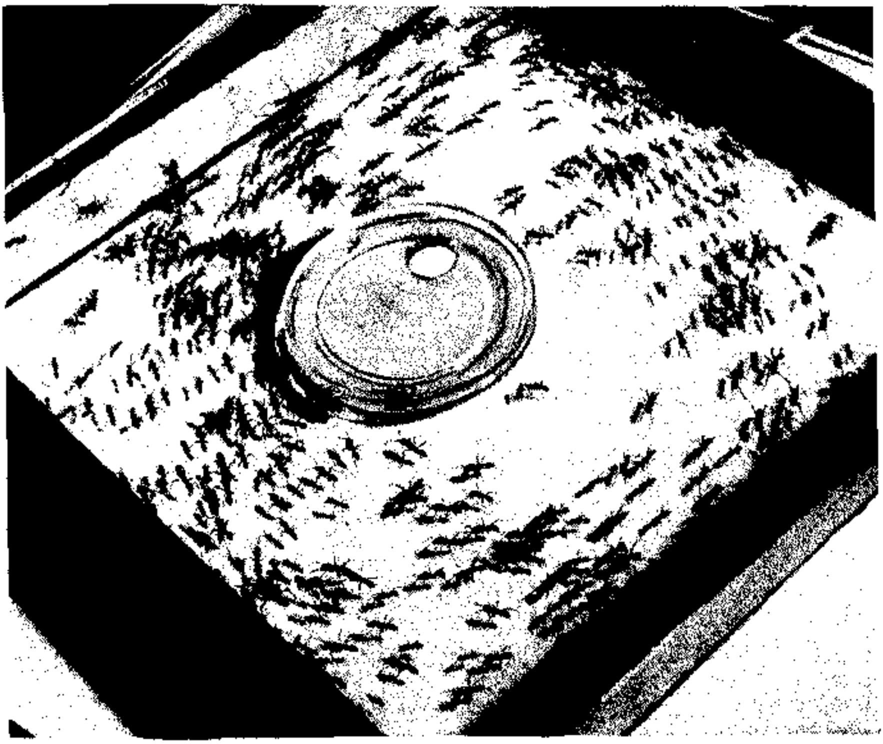

Fig. 17-7. Circular milling of a group of army ants (*Eciton*), induced by the presence of a circular obstacle (water-dish), which turns the blindly marching column back on itself. (Photo by Roman Vischniac, courtesy of *Scientific American*.)

As the authors point out, "This peculiarly *Eciton* calamity may be described as tragic in the classic meaning of the Greek drama. It arises, like Nemesis, out of the very aspects of the ant's nature which most plainly characterize its otherwise successful behavior." The tragedy can be easily reproduced in the laboratory by setting up a situation that tends to turn the ant column back on itself. (See Fig. 17-7.)

It should not be inferred that all instincts are completely unmodifiable. Careful studies have shown that some insects are capable of learning to

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* Schneirla, T. C. and Piel, Gerard, "The Army Ant." *Scientific American*, **178:** 16-23, June 1948.

act slightly counter to their instincts. In general, however, instincts in insects are not very plastic. Also, in general, the life of an insect from birth through growth and reproduction to death is governed by instinct, whereas, in man, only the main directions of his actions are influenced by the innate reflexes; learning by experience determines his particular actions. It is probable that the daily life of the ant today is the same as it was a million years ago, whereas, man's life, outwardly at least, seems to have been revolutionized in the last hundred years. Both the intellectual and the instinctive approach to life's problems have proved adequate in these two different groups of animals. From the rate of change, one might say that ultimately the intellectual approach will prove the more successful. But there are clouds on the horizon that make one hesitate to predict.

If you and I could come back to earth together 100,000 years from now, which would we find—man, or insect?

Or neither?

QUESTIONS AND PROBLEMS

17-1. Find the etymological derivation of each of the following terms, and point out its aptness: Arthropoda, Diptera, Lepidoptera, Hymenoptera, metamorphosis.

17-2. In tabular form, compare and contrast exoskeleton with endoskeleton with respect to the following characteristics: phyla in which it is found; protection furnished muscles; chemical composition; flexibility; ease of growth permitted.

17-3. The arthropods most probably evolved from what phylum?

17-4. Why is it an error to refer to a spider as an insect?

17-5. What is metamorphosis? Give an example.

17-6. The May flies, whose life history is recounted at the end of § 134, are put in the order Ephemeroptera. Explain the aptness of this name.

17-7. What are the relative advantages and disadvantages of instinct and intelligence?

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Chapter XVIII

The Vertebrates and Their Ancestors

136. The Echinodermata

The phylum **Echinodermata,** which is one of the very few phyla that are confined to marine habitats, includes starfish, sea-urchins, sea-cucumbers, brittle stars, sand dollars, and sea lilies. Adult members of this phylum are sedentary or relatively slow-moving. Various species occur at all depths in the ocean, from the water's edge to 3¾ miles down. The rough, spiny skin which is characteristic of members of this phylum is in part composed of the inorganic compound calcium carbonate, the elements of which are removed from the sea water by the animals. Where large numbers of echinoderm skeletons have accumulated in the past, a kind of marble has been produced. Accumulations of this sort act to decrease the amount of calcium in sea water.

Among the most commonly seen echinoderms are the starfish (Fig. 18-1). Dead starfish are frequently found cast up on the ocean beach; the living individuals are found in shallow water. The diet of a starfish consists largely of living shellfish. By grasping the two shells of a bivalve mollusk with its tube feet and exerting a steady pull, a starfish can eventually force an opening between the valves. The stomach of the starfish is then extruded and wrapped around the flesh of the mollusk. Digestion thus takes place outside the body of the starfish; only the digested products are taken into the starfish. The mollusk-eating activities of these animals are seriously regarded by commercial shell-fishermen who spend a considerable amount of time trying to reduce the population of starfish in their beds of oysters and other mollusks. Starfish can be caught by dragging mops along the ocean bottom; the animals grab hold of the mops with their tube feet and, while still entangled, are raised to the surface and destroyed. In the early days of shell-fishing, it was customary to cut the starfish in half and dump the fragments overboard. Biologists later found that these animals possess

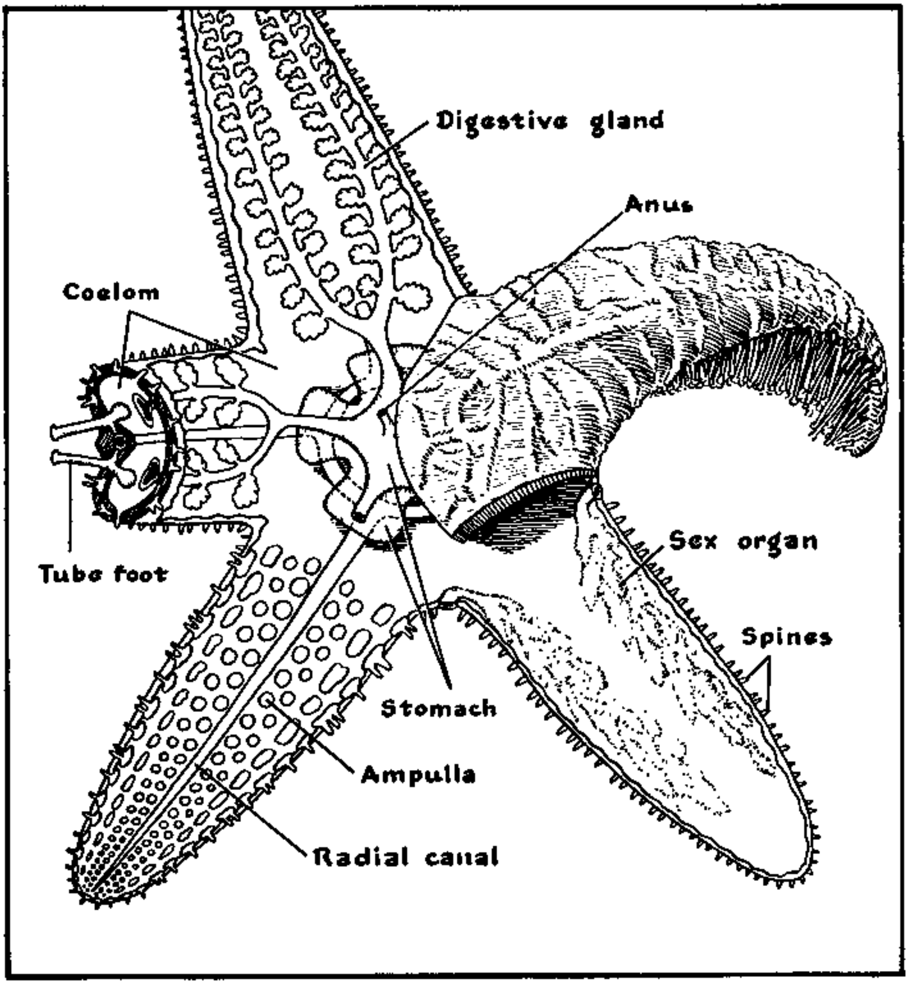

Fig. 18-1. Analytical view of a starfish.

powers of regeneration similar to those of the platyhelminthes (§ 126); the effect of the fishermen's efforts was to make two starfish where there had been only one before. Once this fact had been discovered, the fisheries' practice was suitably modified.

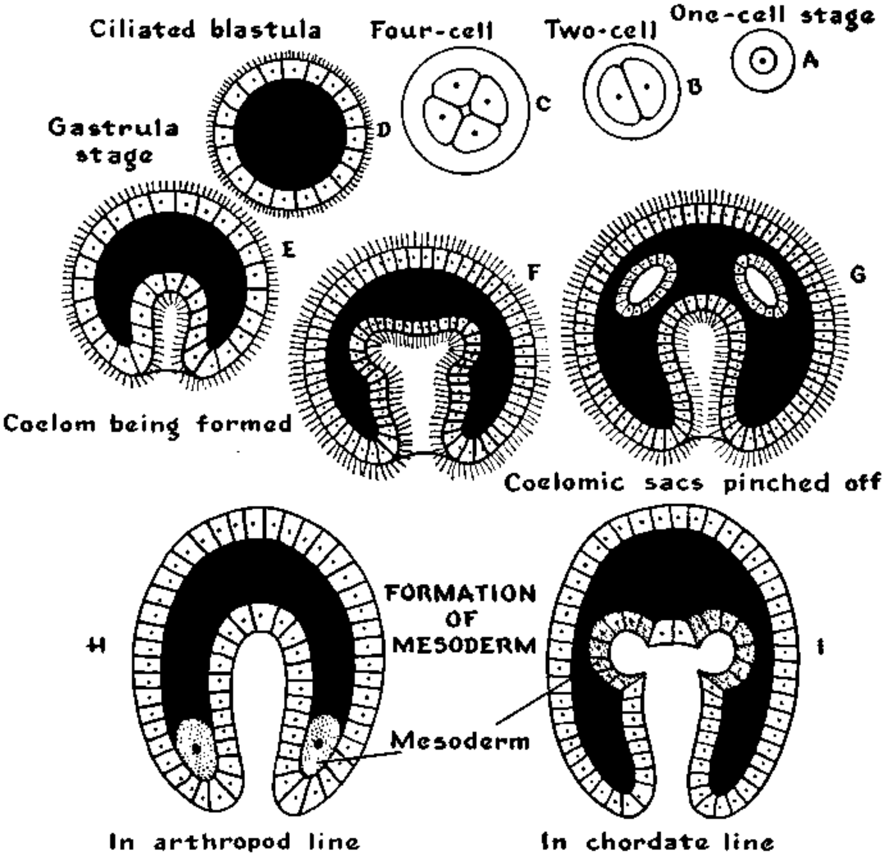

Fig. 18-2. Embryonic stages of a starfish, A-G. Note that the way in which the mesoderm is formed (F, G) resembles the method found (I) in the chordates (including vertebrates), rather than that found in the arthropods (H).

That the phylum to which the starfish belong, the Echinodermata, should be considered to be one that is fairly closely related to the vertebrates—such things as dogs, cattle, and men—seems superficially unreasonable. Neither externally nor internally does the adult starfish in the least resemble a man. The spine-encrusted skin constitutes an exoskeleton; this characteristic reminds us of the arthropods. The radial symmetry reminds us of the coelenterates. The slowly waving, hydraulically actuated suckers that we call **tube feet** are *sui generis*, a feature to be found in no other phylum. Why, then, do biologists think that things like starfish are related to things like guinea pigs?

The principal evidence of relationship is found in the similar early development of echinoderms and vertebrates. Selected stages of the development of a starfish are shown in Figure 18-2A-G. Notice the origin of the **coelom,** or body cavity. (In man, this is the cavity in which the viscera lie.) This cavity is lined by mesoderm. The method of formation of mesoderm is essentially the same in all of the vertebrates. Among the arthropods and their allies, mesoderm is formed in quite a different way as shown in Figure 18-2H. This difference in embryological development appears to be a fundamental difference between the two lines. The development of the echinoderms resembles that of the vertebrates and, for that reason, echinoderms are believed to be related to the stock from which the vertebrates have sprung.

Only the very early stages of the development of an echinoderm are shown. As development proceeds, a bilaterally symmetrical, free-swimming larva is produced (Fig. 18-5). Still later, the larva becomes modified to the adult type of radially symmetrical animal. Radial symmetry in the echinoderms is a secondary development.

The starfish and their allies, the sea urchins, sea cucumbers and brittle stars, are exclusively marine. They are important predators of the seashore. Starfish consume considerable quantities of clams, mussels, and oysters, to man's displeasure. In the biological laboratory, starfish have been useful for embryological studies because of the resemblance of their development to that of the vertebrates.

137. The Phylum Chordata: Definition

In Figure 18-3, are shown, for comparison, a typical insect and a typical vertebrate. It will be noted that the nerve cord is ventral in the former and dorsal in the latter. The presence of a dorsally placed nerve cord constitutes one of the important characteristics of the vertebrates. The presence of a vertebral column is (of course) an important characteristic also. However, modern taxonomists do not believe that the vertebrates constitute a group of the rank of a phylum, but rather assign them to a subphylum. The phylum of which they are part is the phylum **Chordata** and is characterized by these three possessions:

a. A dorsal nerve cord.
b. Gill slits.
c. A notochord.

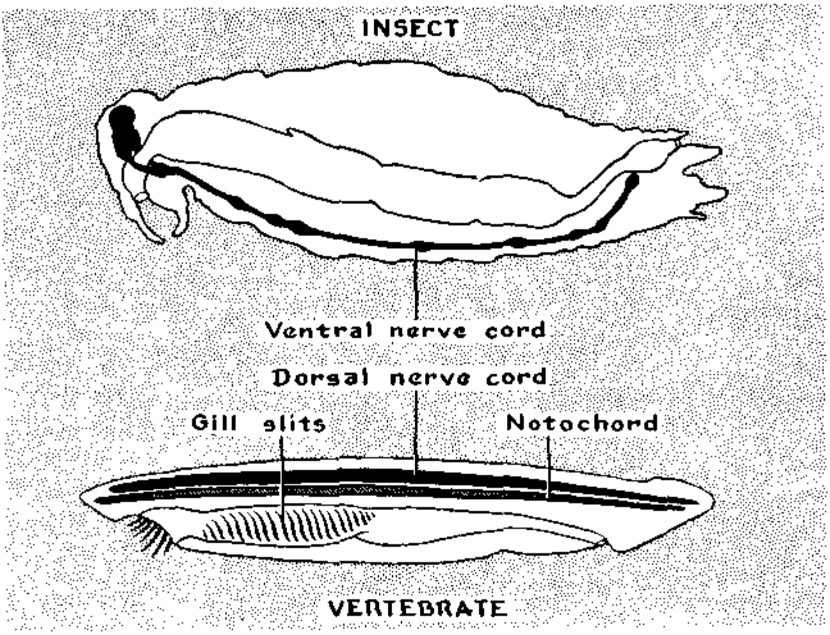

Fig. 18-3. Typical arthropod and typical chordate contrasted. Note position of nerve cord in each.

It is the last of these, the notochord, which serves as the basis for the name of the phylum. The notochord is a flexible, cartilagelike rod present, at some stage or other, in all members of the phylum. In those members in which vertebrae are present, the vertebrae form around the notochord which may later disappear. In the higher vertebrates, the vertebrae also encircle the nerve cord as well.

138. The Acorn Worms

The simplest of the chordates are the acorn worms, assigned to the subphylum **Hemichordata.** These uninspiring creatures (Fig. 18-4) are to be found burrowing in the sandy shores of the ocean. Externally, they look like but another worm. Internally, they exhibit gill slits, a dorsal nerve cord (as well as a ventral one!), and a small notochord confined to the head region. The presence of these three characteristics clearly links these animals with the vertebrates. In the other direction, they are related to the echinoderms as is indicated by the similarity of the larvae of the two groups (Fig. 18-5).

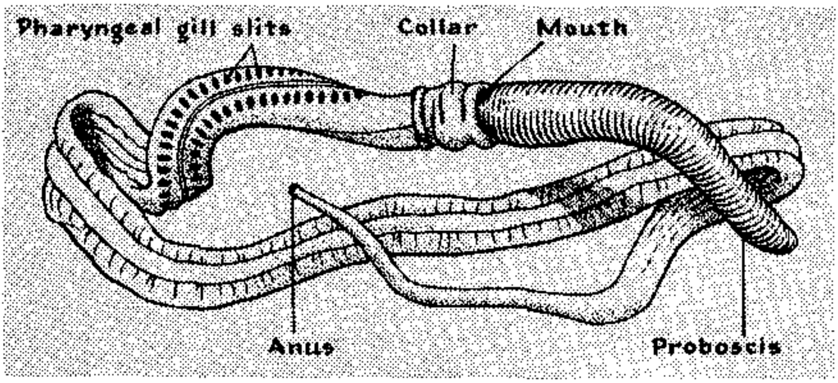

Fig. 18-4. An acorn worm. It took close, analytical study to show that this object resembles man more closely than does an earthworm.

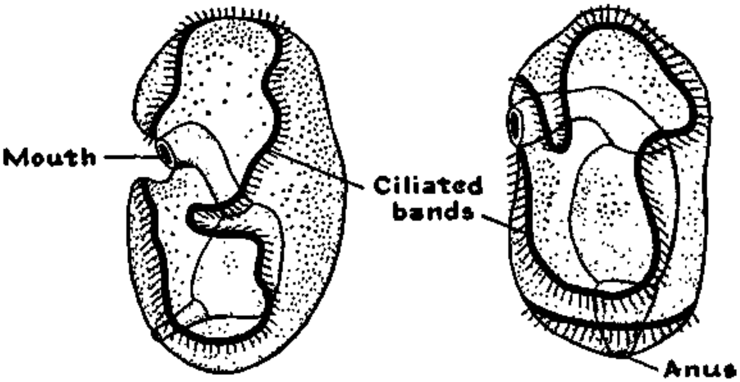

Fig. 18-5. Larval forms. On the left, an echinoderm. On the right, an acorn worm. When the first acorn worm larva was discovered, it was mistakenly identified as an echinoderm by an eminent biologist.

139. The Tunicates

Another exclusively marine group of chordates is the subphylum **Tunicata.** Here again, we are dealing with a group that, after only a superficial examination, would never be suspected of being closely related to the vertebrates. Most tunicates are rather shapeless blobs of tough tissue, often brilliantly and beautifully colored, that are to be found on rocks and pilings below low-tide level. One is often uncertain whether one is dealing with a sponge or a tunicate until one resorts to dissection.

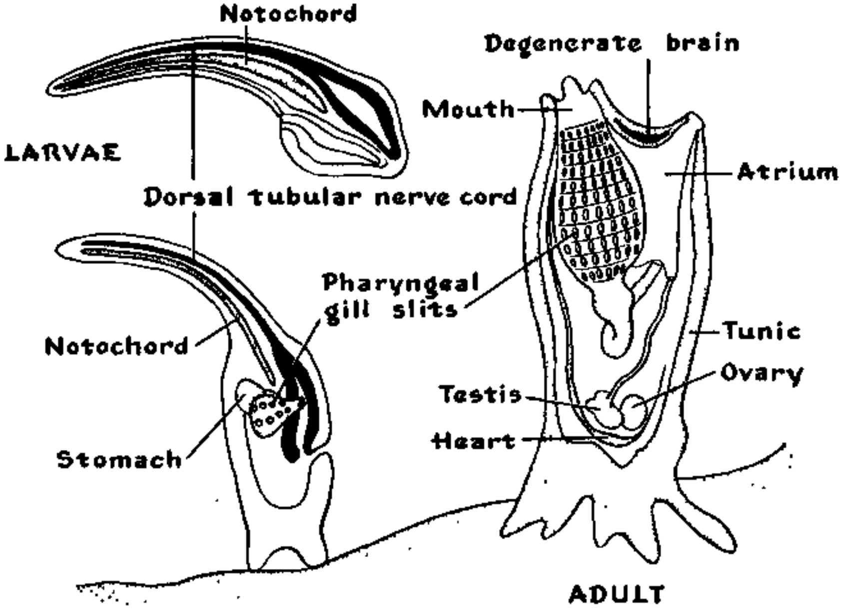

Fig. 18-6. The structure of a tunicate.

The embryology of a tunicate (Fig. 18-6) clearly indicates its kinship. A tunicate begins life as an actively swimming larva possessing a definite notochord. When it settles down on a substrate, its notochord and some other structures degenerate. The adult tunicate lives a spongelike existence, taking in water through one hole, straining microscopic food out of it by means of its gill slits, and discarding the filtered water through another hole.

140. Amphioxus

The subphylum **Cephalochordata** includes *Amphioxus*, a little fishlike worm, long a familiar creature in the biological laboratory. It exhibits, in almost diagrammatic fashion (Fig. 18-7), the three characteristics of the phylum Chordata. The notochord extends the whole length of the body and persists throughout life.

Along some marine coasts, these animals are quite numerous. Although they are good swimmers, they spend much of their lives buried in clean sand up to their necks, straining microscopic food out of the water that they pump past their gill bars. Some species are several inches long, but most are smaller. Along part of the China coast, some species are found in great enough abundance to be collected as food for man.

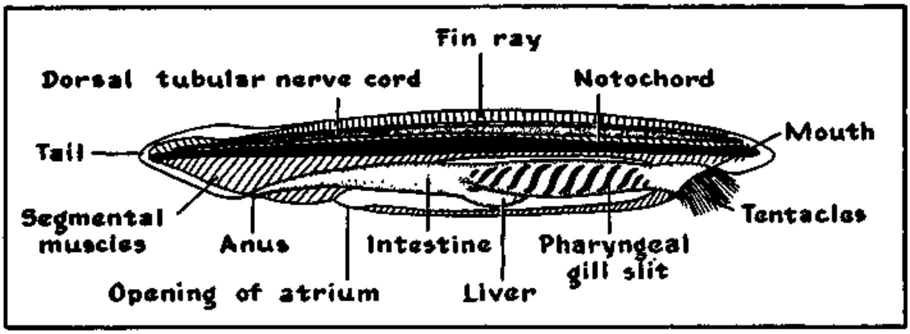

Fig. 18-7. Amphioxus.

141. The Vertebrates

Chordates that have developed vertebrae are put in the subphylum **Vertebrata.** In all of these, a notochord is present in the embryonic stages. It persists into adulthood only in some of the fishes.

The **fishes** are the most primitive of the vertebrates. There are several classes of fishes, of which the cartilaginous fishes (e.g., sharks) and the bony fishes (e.g., trout) are the most important. In size, various species range from less than an inch to more than fifty feet in length. All are water-dwelling, though some can survive limited periods of dryness. Of the latter, some (the "lungfish") possess primitive lungs that enable them to breathe air. Most fishes get their oxygen only through their gills, structures which can function only in water. All fishes are "cold-blooded" or **poikilothermous,** that is, animals-without-thermostats (see § 102). The importance of fish to man scarcely need be mentioned. It has been estimated that the money value of the fish caught thoughout the world each year amounts to about one billion dollars, if money means anything.

Members of the class **Amphibia** were unquestionably the first vertebrates to take to the land. The name of this class implies that they have two lives, which they have, a larval life in the water (e.g., a tadpole) and an adult life more or less confined to dry land (e.g., a frog). During its larval life, an amphibian has fishlike gills (Fig. 18-8C) and cannot survive exposure to air. As an adult, it has lungs and cannot long survive submersion in water. Amphibian species are, therefore, confined to regions near the water's edge, where they can satisfy the necessities of both their lives. Since no species of amphibia passes its larval stage in sea water, it is believed that the class evolved from fishes that lived in fresh water.

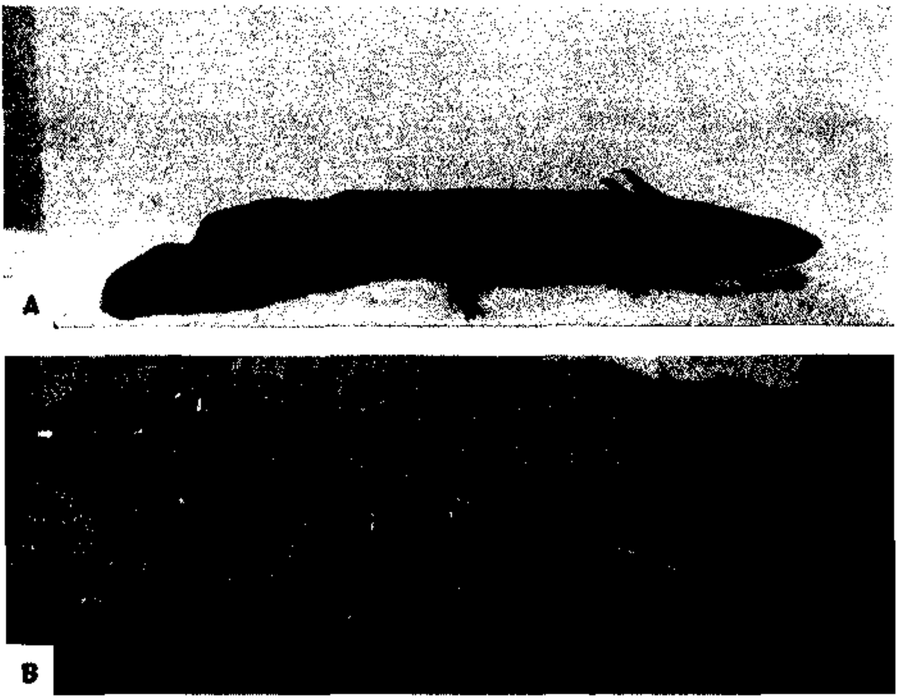

Fig. 18-8A, B. The double life of a salamander. Top: the larval stage, a water-dwelling animal with external gills. Below: the adult stage, a slimy-skinned, land-dwelling animal with internal lungs. (Copyright by General Biological Supply House, Inc. Chicago.)

Economically, amphibia are of no great importance. Frogs' legs are a table delicacy, but the supply of them is limited because the farming of frogs is not possible; only natural populations of large species can be exploited, and these are not very extensive. If different pleasures could be measured and compared, one might find that man derives a greater pleasure from amphibia through his ears than through his taste buds. The peeping and croaking of various kinds of frogs and toads contribute greatly to the beauty of the audible landscape, where the encroachments of civilization have not too severely altered it.

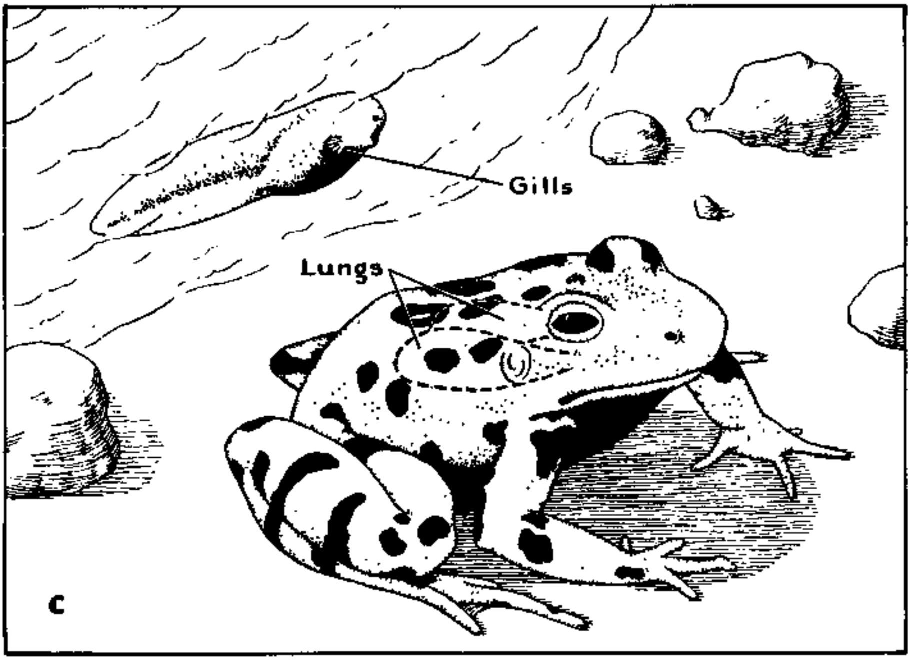

Fig. 18-8C. The double life of an amphibian, a frog in this case. Note the two different mechanisms for gas exchange.

The **reptiles** are a truly land-dwelling class of chordates. Life-long survival in the aerial environment is made possible by the presence of a special structure to protect the embryonic stages against the dangers of desiccation, namely the eggshell, or egg sac. In spite of the fact that its apparent environment is dry air, the embryonic snake or bird or man develops in a watery environment, just as does the amphibian. In the case of snakes and birds, the watery medium is made possible by the somewhat impervious enclosing shell of the egg.

About one hundred million years ago, reptiles were the dominant vertebrates of the earth, various kinds of dinosaurs and their relatives dominating the land, the water, and the air. Today, the big reptiles are all gone, leaving only the quantitatively unimportant snakes, turtles, and lizards. The reasons for their fall from dominance are not known, but probably one of the contributing factors has been the competitive disadvantage of the cold-blooded physiology of the reptiles when matched against the warm-blooded physiology of the two classes the reptiles gave rise to, the birds and the mammals.

Fig. 18-9. Lizards. Lizards are sometimes confused with salamanders. But lizards, like all reptiles (e.g., snakes, turtles, crocodiles), have a dry, scaly skin. (Copyright by General Biological Supply House, Inc. Chicago.)

The **birds** are one of the two classes of homoiothermous vertebrates. Historical and circumstantial evidence points to their having evolved from reptiles, the reptilian scales being modified into avian feathers. In the course of evolution, teeth have been lost, and their grinding function has been taken over by a gravel-filled gizzard.

Most birds fly, and it is for this reason that few of them are very large, since the mechanics of their type of flying sets an upper limit to size. Ostriches, which are exclusively ground-dwelling, may weigh as much as 300 pounds.

With the possible exception of the mammals, no class of animals is as completely known as the birds. The great variety and beauty of their feathers and singing early made them favored subjects of study among biological amateurs who have produced a large literature on the taxonomy and habits of this group. One of the remarkable habits of many species of birds is that of migration. Some birds migrate over thousands of miles of the earth's surface to precisely defined breeding grounds. How they manage to carry out such precise navigation is not known. The inclination of the sun, the visual landscape, and the earth's magnetic field have been proposed as the guiding factors, but experts have reached no agreement.

Of the **mammals,** one may say, as of the after-dinner speaker, that they are "too well known to need an introduction." But, although we tend to think of the classification, **mammal,** as being a "natural" one and one that has long existed, this seems not to be the case. The word *mammal* has no exact equivalent in the vernacular of any language. In English, "beast" and "quadruped" were not applied to precisely the same aggregation of species; they were not applied to whales and bats, for example. Linnaeus, the man who established our modern system of classification (§ 122), by his keen insight recognized the fundamental similarity of all animals that have mammary glands. The name mammal (or rather, its Latin equivalent) was, in fact, invented by Linnaeus and has since been adopted into the common speech of modern languages.

We have considered one mammal, man, in detail (Part II). Though there is considerable variety in the external appearance of various mammals, their physiology is not significantly different from man's. In the hundred million years since the end of the reign of the reptiles, the class **Mammalia** has spread and occupied all regions of the land, part of the air (bats), and waters as well (whales, dolphins). It is the dominant group of the world today, and of its members the species *Homo sapiens* is, temporarily at least, the most powerful.

QUESTIONS AND PROBLEMS

18-1. What is the evidence that starfish are closely related to the chordates?
18-2. Define the phylum Chordata.
18-3. Which is the more inclusive group: Chordata or Vertebrata?
18-4. Why are tunicates put in the same phylum as man?
18-5. What features enable reptiles to prosper better on land than the fishes?
18-6. Explain the etymology of the term Amphibia.

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Chapter XIX

What Is A Plant?

142. A Simple Definition

The distinctions of biology are seldom absolutely clean cut. So it is with the distinction between plants and animals. Trees and ferns we call plants; crows and katydids we call animals. On the *ma*croscopic level, we seldom have trouble deciding in which kingdom to place an organism. Among *mi*croscopic beings, however, there are many that we are puzzled about. It might be thought that movement would be a distinction between the two but it has proved an unsatisfactory criterion. There are some organisms that seldom or never exhibit any gross movement but which every student puts in the Animal Kingdom. There are other organisms that are as active as the most vigorous animals but which are universally put in the Plant Kingdom. How shall we decide whether to call a thing a plant or an animal?

There are no universally satisfactory criteria for deciding. Perhaps the most satisfactory criteria are these:

1. Presence of a green pigment called **chlorophyll.**
2. Presence of a rigid cell wall made of an insoluble carbohydrate called **cellulose.**

If both chlorophyll and cellulose are present, we have no hesitancy in calling the organism a plant If neither is present, we usually call it an animal.* But if one is present and not the other? Well, then it becomes a matter for further thought. Many borderline cases have never been pigeonholed to the satisfaction of all students. We shall point out some of these cases as we come to them.

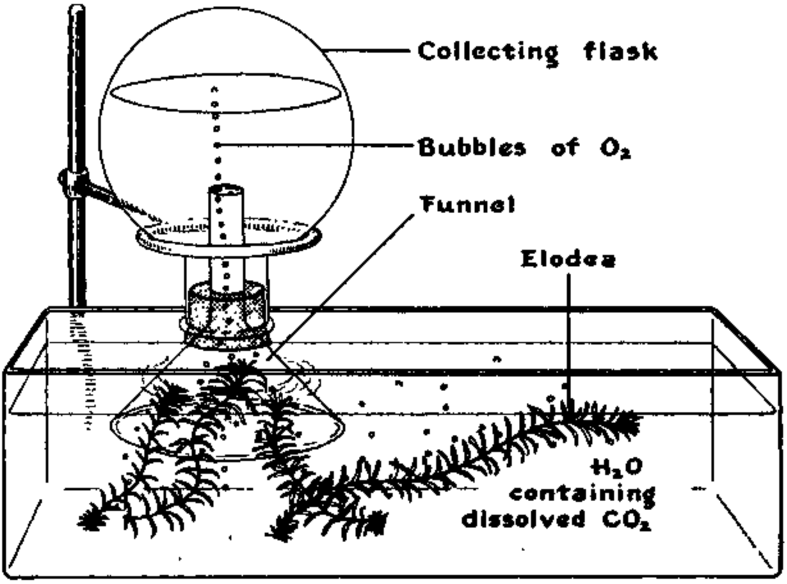

Fig. 19-1. The production of oxygen by an illuminated green plant.

143. Photosynthesis

What is the significance of the characteristic green plant pigment chlorophyll? We can get a clue as to its function from the results of an experiment that can be carried out with any vigorous green plant.

If a handful of *Elodea*, a water plant, is placed in an apparatus designed to collect gas (Fig. 19-1) and the whole placed in bright sunlight, after a period of some minutes, bubbles will be observed rising from the leaves. When enough gas has collected to permit an analysis, it is found to be oxygen. How can we account for the oxygen?

Other observations, not so easy to make, have shown that, concomitant

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* The only conspicuous exception that comes to mind is the bacteria. Only a few bacteria have been proved to possess cellulose walls, and there is doubt that all do, but bacteria as a group are generally considered to be part of the Plant Kingdom.

with the appearance of oxygen, carbon dioxide disappears from the surrounding water in which it is dissolved. We might then write:

$$\textit{Hypothesis:}\quad CO_2 \longrightarrow O_2 + ? \qquad (1)$$

This equation implies that the oxygen comes from the carbon dioxide, that is, that each carbon dioxide molecule breaks down in such a way as to release an oxygen molecule. How can we find out if this is so? We cannot see individual molecules undergoing reactions inside a living cell, so it might be supposed that there is no way to know which molecule arises from which atoms or molecules. Fortunately, although we cannot see individual molecules, we have at our disposal "marked" or "tagged" atoms which we can use in the synthesis of molecules. By tracing the wanderings of tagged atoms, we can determine the chemical reactions involved. Experiments of this sort are called **tracer experiments.**

It was at one time thought that all atoms of a given element were alike. Today we know that this is not so, that each element has several **isotopes;** that, of each element, there are atoms of several different weights. There are, for instance, several different kinds of hydrogen atoms, one with an atomic weight* of 1, another of 2, and another of 3. If these atoms have different weights, why do we call them all by the same name? The answer: because they all have the same chemical properties. The chemical properties of an atom are determined by the number and arrangement of the electrons around its nucleus, a subject which we need not go into here. The weight of an atom is determined by the particles present in the nucleus, but these particles do not affect its chemical properties. That **all isotopes of a given element have the same chemical properties** is fortunate from an experimental point of view, for it means that we do not alter the chemical reactions of a system when we introduce unusual isotopes into it. To see how the use of rare isotopes may permit us to resolve chemical enigmas, let us return to the problem of the origin of the oxygen released by illuminated plants. To solve this, we shall use an uncommon form of oxygen which has an

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* The units of the atomic weight scale are defined in terms of the commonest type of oxygen atom which is arbitrarily said to have a weight of 16. A hydrogen atom of the commonest sort weighs almost exactly one-sixteenth as much as the commonest sort of oxygen atom.

atomic weight of 18 instead of the usual one of 16. The rare O^{18} (as it is written) is thus $12\frac{1}{2}$ per cent heavier than the common O^{16}. One can weigh a sample of a known compound and calculate what fraction of its molecules contain "normal" oxygen atoms and what fraction "heavy" oxygen atoms. In the discussion that follows, for simplicity of visualization, we shall write the heavy isotope of oxygen as O^*, to contrast with normal oxygen, O.

To see where the oxygen comes from, we can furnish an illuminated plant with carbon dioxide made with heavy oxygen, that is, CO^*_2. If the hypothesis of equation (1) is true we should find:

$$\textit{Hypothesis:}\quad CO^*_2 \longrightarrow O^*_2 + ? \tag{2}$$

When, however, this experiment was performed, as it was first by Samuel Ruben and Martin Kamen of the University of California in 1941, it was found that:

$$\textit{Fact:}\quad CO^*_2 \longrightarrow O_2 + ? \tag{3}$$

i.e., that the oyxgen produced is not of the same weight as that furnished in the carbon dioxide. What, then, is the source of the oxygen?

It has been known for a long time that plants use copious amounts of water. It was early suspected that some of this water was used in the same process that resulted in the production of oxygen. Since water is H_2O, perhaps water is the source of the molecular oxygen? With tagged oxygen, this can be proved to be the case:

$$CO_2 + H_2O^+ \longrightarrow O^*_2 + ? \tag{4}$$

By such experiments, we have learned the origin of the oxygen. But we should look again at equation (4). It is not a satisfactory equation because it is not "balanced," i.e., there are some atoms that appear on the left-hand side that do not appear on the right. The equation implies a destruction of matter, a phenomenon that is never observed in a chemical reaction. What happens to the remaining carbon, hydrogen, and oxygen atoms? Observation has shown that, accompanying the evolution of oxygen from the plant, there is an increase in the weight of the plant, and that this increase is due to the appearance of carbon compounds, that is, to organic substances. We can now write:

$$CO_2 + H_2O \longrightarrow \text{organic material} + O_2 \tag{5}$$

We have used the vague term "organic material" because we do not at present know what substance(s) is formed as the immediate result of the process. It should be possible to solve this problem also by tracer experiments. Such experiments are now being carried out, but the organic substances containing the tagged atoms have not yet been identified.

Equation (5) is still not complete. The reaction which it represents does not take place whenever CO_2 and H_2O are brought together in the cell, but only when the plant cell is in the presence of adequate light, such as sunlight. It can be shown that light energy is absorbed during the process. That such a process would require energy we might have been able to predict from the known fact that it takes a great deal of energy to split the H_2O molecule, freeing O_2. In the laboratory, this is done with a powerful electric current. The plant does it with the energy obtainable from light. Since light is used and organic material is synthesized, the process is called **photosynthesis** (Greek *photos*, light) and may be more accurately written:

$$CO_2 + H_2O + \epsilon \longrightarrow \text{organic material} + O_2 \qquad (6)$$

This equation should look at least faintly familiar. In fact, if we turn it around and conceive of the process going the other way, we have the equation of respiration:

$$\text{Organic material} + O_2 \longrightarrow CO_2 + H_2O + \epsilon \qquad (7)$$

The fact that we can make this reversal on paper suggests that one process is the simple reverse of the other. *This is not the case.* The two processes involve quite different steps, and many of the enzymes involved in one process are not involved in the other.

Both plants and animals respire. In the light, the respiration of green plants is not obvious because the opposing reaction, photosynthesis, is usually going on faster, resulting in a net increase of O_2 which is released into the environment. Photosynthesis is carried on only by plants, if we neglect for the present those organisms of questionable classification.

Observation of the tissues of variegated plants, that is, plants that have leaves composed partly of chlorophyll-bearing tissue and partly of non-chlorophyll-bearing tissue*, has shown that only those parts of the

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* Many ornamental plants, such as some varieties of ivy and geranium, have variegated leaves. The white spotting is sometimes regular, sometimes irregular.

leaf that are green can photosynthesize. This is further evidence that chlorophyll is required for the process.

The localization of photosynthesis to chlorophyll-bearing material has been made still more precise. When we look at plant cells under a microscope, we see that the chlorophyll is localized in definite bodies called **chloroplasts.** *If chlorophyll is required for photosynthesis, oxygen should be produced only by those parts of the plant cell that contain chloroplasts.* Can this be demonstrated?

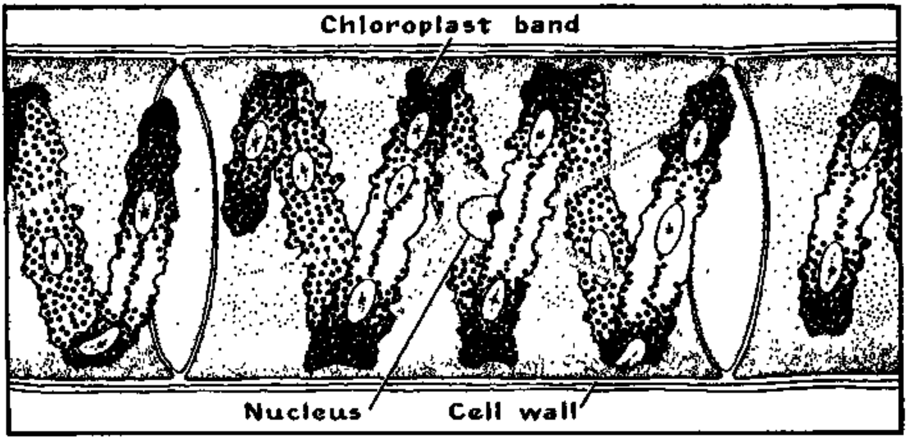

Fig. 19-2. *Spirogyra.* Many such cells make up long green filaments which are slimy to the touch.

A very ingenious testing of this prediction was made by T. W. Engelmann, German botanist, in 1887. For this demonstration, two things were needed: (1) a large plant cell that had well-defined chloroplast regions and nonchloroplast regions; and (2) a very sensitive microchemical test for oxygen. The first, Engelmann found in an alga called *Spirogyra* (Fig. 19-2). Everyone has observed long slender green filaments growing as a scum on the surface of ponds, or as a beard trailing from dead branches immersed in flowing streams. Such filaments are usually *algae* (to be discussed in § 144). If the algae feel decidedly slippery to the touch, microscopic examination will often show cells something like those in the illustration, cells in which the green chloroplast occurs as a spiral band against the inside wall of the cell.

As a test for photosynthesis, Engelmann made use of another plant, this one a colorless plant of the sort called bacteria (§ 145). Some rod-shaped bacteria, members of the genus *Pseudomonas*, move very actively in the presence of oxygen but are immobile when oxygen is absent. They are sensitive to extremely small amounts of oxygen, being far more sensitive than any known chemical reagent.

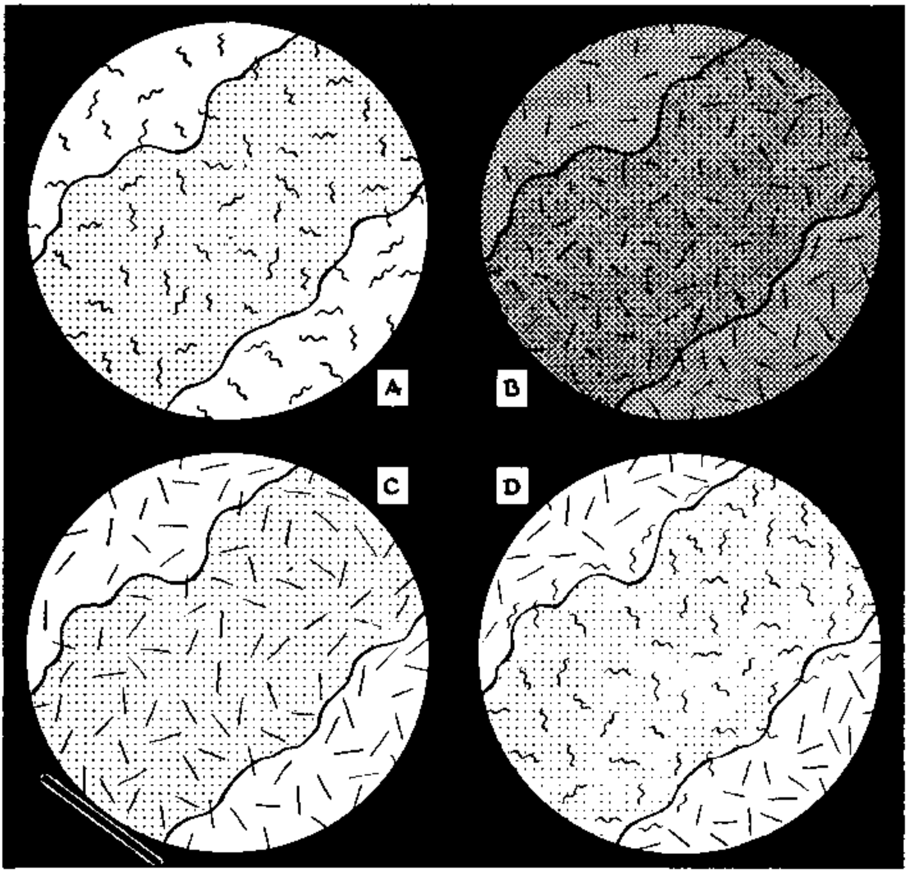

Fig. 19-3. Engelmann's experiment, by which the photosynthetic function of the chloroplast was proved, using oxygen-sensitive bacteria.

Using *Spirogyra* and *Pseudomonas*, the origin of the O_2 produced by photosynthesis was demonstrated as follows: The two were put together on a microscope slide, in water, and then the mount, microscope and all, left in complete darkness (Fig. 19-3B). While in the dark, the living algae and bacteria were respiring and thus using up all the available oxygen in the water. After allowing enough time for all the oxygen to be removed, the set-up was abruptly uncovered to the light and the mount immediately examined. The first sight to be seen was that shown in Figure 19-3C; all the bacteria were motionless, indicating the absence of O_2. In a very few seconds, the bacteria began to move, **but only in the immediate vicinity of the spiral chloroplasts** (Fig. 19-3D).

Thus, was it demonstrated that the chloroplasts are the cell organs in which the process of photosynthesis takes place.

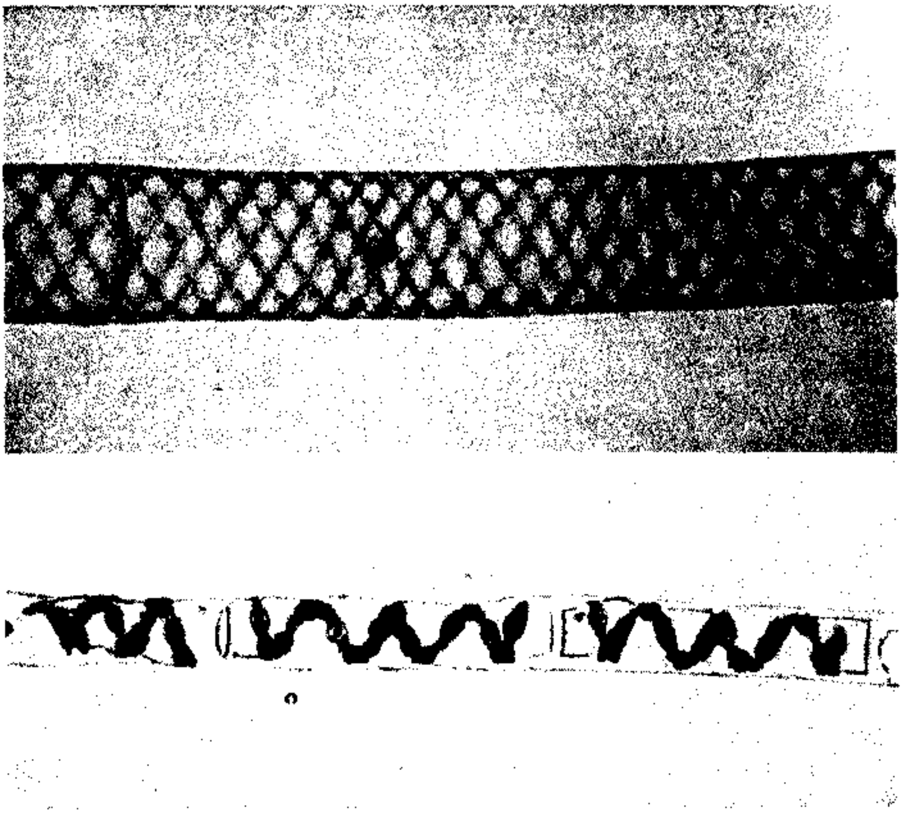

Fig. 19-4. Two different species of *Spirogyra*. Both species possess nuclei, though the nucleus is apparent in only the upper one. (Copyright by General Biological Supply House, Inc.)

QUESTIONS AND PROBLEMS

19-1. Define photosynthesis.

19-2. Define respiration.

19-3. What is the chemical source of the oxygen that illuminated plants give off? Give the evidence for your statement.

19-4. At what physical location in the plant is the oxygen released? Give the evidence.

19-5. It is commonly said that it is nice to have plants in a room because they keep the air "fresh." In terms of chemical substances, what does this statement mean?

19-6. In the same sense (see above), would plants keep the air "fresher" in the daytime or at night?

19-7. If you had your choice of sleeping, at night, in a hermetically sealed room packed full of living plants or in the same room devoid of plants, which would you choose and why?*

19-8. The earth's atmosphere is composed of about 21 per cent oxygen, 79 per cent nitrogen, and 0.03 per cent carbon dioxide, to mention only the more abundant gases. If all the photosynthetic plants were to perish, how would the composition of the atmosphere change? What effect would this have on man?

19-9. The success of an experiment often depends on the proper choice of experimental material. Figure 19-4 shows two different species of the genus *Spirogyra*. Which species would be more favorable for carrying out Engelmann's experiment (§ 143)? Why?

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*No doubt the idea implied here has been used in some mystery story.

Chapter XX

The Thallophyta

144. The Algae

A curious thing about the larger divisions of the plant and animal kingdoms is the difficulty encountered when we try to define them in a succinct and unexceptional manner. We say "curious" because there is seldom any disagreement among specialists as to what should be included in the group (whatever it is called). There is almost no difference of opinion as to what constitutes an alga. But it is hard to frame a definition that will include all the organisms it should include and exclude all others. A recent attempt defines **algae** as those **green plants that have simple sex cells.** Among these plants, either the sex cells are missing altogether; or they are single celled; or, if multicellular, they are never surrounded by sterile sex cells.

The above definition may be precise, but it is not very helpful to the neophyte. What sorts of things are algae, speaking in everyday language? In fresh water, they include various single brightly colored cells, and small packets of cells swimming around in the water, and a number of fine green or yellowish or brownish filaments attached to submerged objects or floating as a scum on the surface of the water. In the ocean, the things men call "seaweeds" are, with few exceptions, algae.

A quick survey of the principal classes of algae will give a better idea of the variety of algae.

Cyanophyceae—(Greek *cyaneos*, dark blue; *phykos*, painted). Blue-green algae. The cells of blue-greens have no well-defined nucleus (*no* nucleus?), and sexual processes are unknown. Chlorophyll is present in these plants but with a difference. There are several very slightly different chemical forms of chlorophyll called *chlorophyll a*, *chlorophyll b*, etc. Most green plants contain both chlorophyll *a* and one other chlorophyll. The blue-green algae are unique in containing only chlorophyll *a*. The blue-greens also possess a blue pigment, whence their name. Many species possess other pigments which may make them look dark green, brown, or red. Representative types of blue-greens are seen in Figure

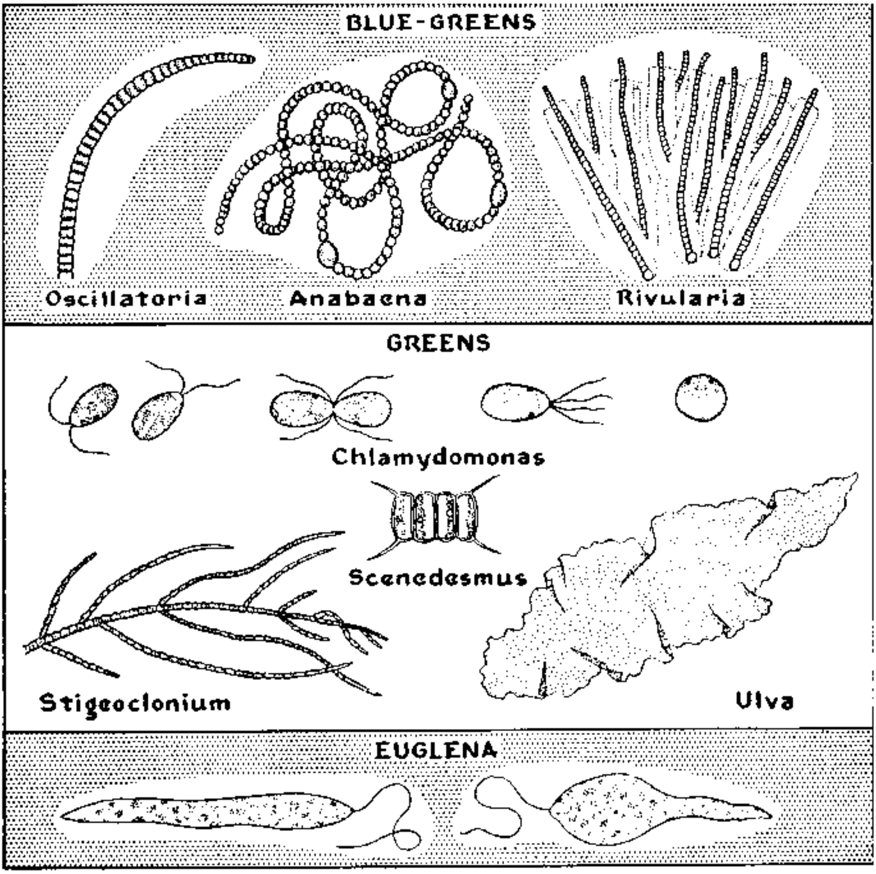

Fig. 20-1. Representative Cyanophyceae (top), Chlorophyceae (center), and a member of the Euglenaphyceae. Sexual fusion is seen in the *Chlamydomonas*. The *Euglena* is shown in two different phases of its squirming method of locomotion. (Not drawn to same scale.)

20-1. The filamentous forms are particularly likely to be found on damp soil and damp rocks as well as in some ponds. Certain species are able to grow and multiply at temperatures as high as 70° C*, and these algae are, in part, responsible for the brilliant coloring in the outflows of the hotsprings in Yellowstone National Park and similar regions.

Chlorophyceae—(Greek *chloros*, green). Green algae. This is a very large and diverse group, the cells of which contain a well-defined nucleus. Sexual phenomena occur in many species. (See Fig. 20-1.) The two forms of chlorophyll present, chlorophyll *a* and chlorophyll *b*, are the same as are found in all the "higher" plants, i.e., mosses, ferns, and all flowering plants. Green algae form a conspicuous part of the flora of fresh-water ponds. A few species are marine, e.g., *Ulva*, the sea lettuce. The algae that grow in extremely salty environments, such as Great Salt Lake, Utah, and Searles Lake, California, belong to this phylum. In such waters, the salt content may be so high that salts are precipitating out of solution, yet algae manage to survive without becoming pickled. Some other species of green algae are occasionally found growing on snow at high elevations. Red snow algae, as they are called, have additional red pigments that mask the green.

Euglenaphyceae—(Greek *eu*, good, true + *glenos*, star; so named because some euglenoids have a star-shaped object in the center). Euglenoids. These closely resemble the green algae, possessing both chlorophyll *a* and chlorophyll *b*, but they are sometimes separated from them because of their animal-like characteristics. *Euglena* (Fig. 20-1) is green but has no rigid cell wall. It propels itself by an anterior whip called a *flagellum* and also by squirming movements. It can photosynthesize. It can also live in the dark when supplied with soluble food. Because it resembles both plants and animals, it is included in treatises on protozoa (one-celled animals) and ones on algae. Euglenoids are found only in fresh water.

Rhodophyceae—(Greek *rhodon*, a rose, hence red). Red algae. The red algae have chlorophyll *a* and chlorophyll *d* as well as a red pigment that gives them their color. Except for a few rare species that live in cold, rapidly flowing, fresh water, the red algae are all marine. They reproduce by sexual processes that are rather complex. One genus,

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* Is this higher or lower than the body temperature of man? How much higher or lower?

Porphyra (Fig. 20-2), is used by the Orientals to make a seaweed soup. Another genus, *Gelidium*, furnishes the greater part of commercial *agar*, a jellylike material that is indispensable in the bacteriological laboratory. Both of these genera of seaweeds are deliberately planted on rocks and in tidal flats along the seashore in the Orient by "marine farmers."

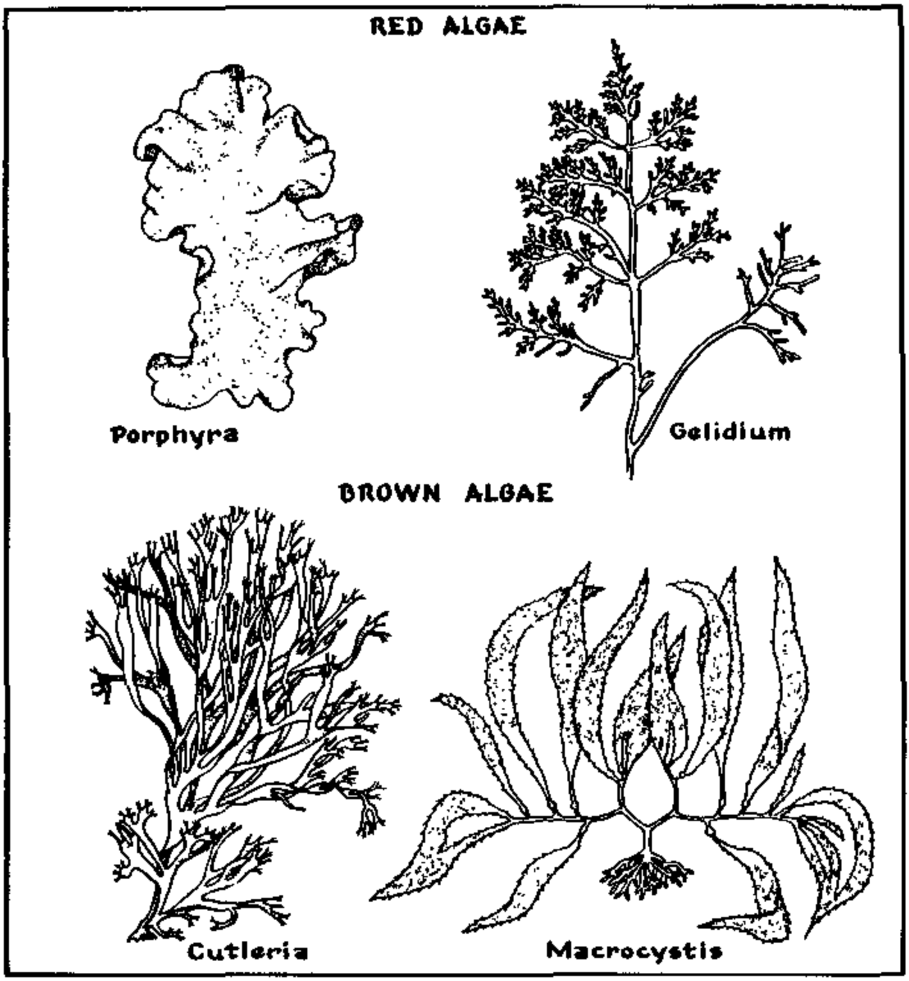


Fig. 20-2. Rhodophyceae, above; and Phaeophyceae, below. (Not drawn to same scale.)

Phaeophyceae – (Greek *phaios*, dark). Brown algae. Present in these algae are chlorophyll *a* and chlorophyll *c* and other pigments which give them their dark colors. Sexual processes of considerable complexity are found among them. The brown algae (see Fig. 20-2) include the giant kelps found along many shores. Certain species of kelp are the source of *alginic acid* which is used to impart a smooth consistency to ice cream. The largest of the kelps may be as long as thirty meters. Fresh-water brown algae are inconspicuous and rare.

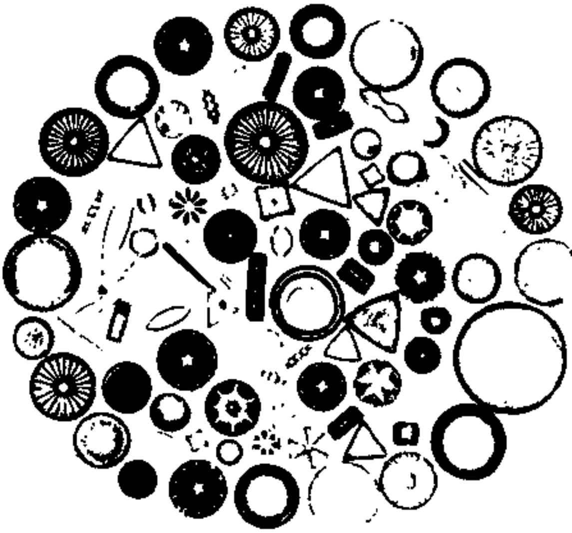
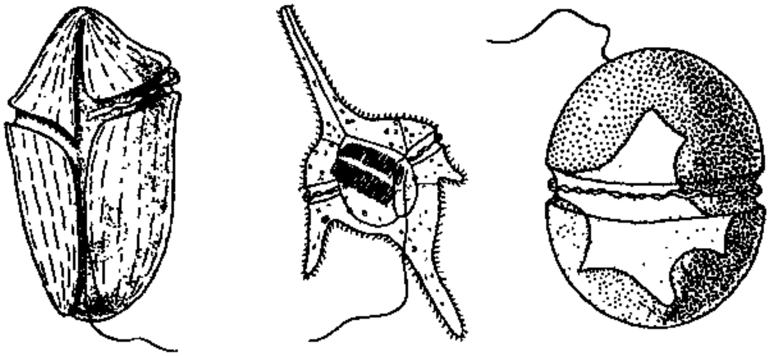


Fig. 20-3. An assortment of diatoms. The organisms have been completely destroyed by strong acid, leaving behind only the sculptured quartz shells, seen above. (Copyright by General Biological Supply House, Inc. Chicago)

Bacillariophyceae—(Latin *bacillus*, a staff or rod). Diatoms. Chlorophyll *a* and chlorophyll *c* are present in diatoms as well as other pigments which make almost all species appear brown. Most species are solitary and of microscopic size (Fig. 20-3). The cell wall of a diatom is remarkable in that it consists of an organic silica compound whose function is not known. Though now little studied, diatoms are of great importance. They are found not only in all streams and all damp soils, but also in tremendous numbers in the oceans. They, together with the Dinoflagellates (see below), unquestionably photosynthesize more organic material than all the rest of the plants combined. One competent authority has estimated that 90 per cent of the world's organic material is synthesized by marine diatoms and dinoflagellates. Because, directly or indirectly, they serve as the principal source of food of all marine animals, they are often referred to as the "grass of the sea." When diatoms die and their organic material is decayed away, the silica shells are left behind. These sift to the bottom of the ocean and accumulate in unbelievable quantities. Near Santa Maria, California, diatom shells are found in beds more than half a mile thick. Expressed in terms of the diatoms, such beds are about one hundred million diatoms thick. When one learns that these beds cover many square miles, one gets a faint conception of the uncounted numbers of diatoms that must have lived and died to produce these great deposits. Where the beds are purest and most easily accessible, the *diatomaceous earth*, as it is called, is mined, to be used in making scouring powders, fire brick, insulating boards, and filtering materials for beer and other liquids.



DINOFLAGELLATES

Gymnodinium **Ceratium** **Glenodinium**

Fig. 20-4. Dinoflagellates, one of the two most abundant groups of plants in the sea.

Pyrrophyceae — (Greek *pyrrhos*, flame-colored, or reddish). Dinoflagellates. These also contain chlorophyll *a* and chlorophyll *c*. They are reddish-brown in color, and most species are very actively motile. They are found in both fresh and salt waters but, like the diatoms, their greatest role is played in the ocean. They are usually outnumbered by the diatoms but, occasionally, for quite unknown reasons, great masses of them are found over many acres of sea water causing a phenomenon known as "red water." In some cases, the red-water organisms give off a potent substance very poisonous to other forms of life, and an epidemic of the Dinoflagellates is followed by the dying of masses of fish whose corpses are thrown up on the beaches in great numbers, there to decay and make the air offensive.

So, briefly, have we sampled from among many thousands of species of algae. We have not discussed all the classes. Many species and groups —for instance, the Cryptomonads and the golden-brown algae—are not well enough known to permit confident classification. The most important groups have been mentioned, however.

145. The Fungi

Many of the **fungi** are called "molds" by the layman. The moldy growth that covers old, damp bread; the mold sometimes found on damp plaster; and that which appears on the top of an open jar of jelly are all examples of fungi. Also included in the fungi are mushrooms which might not be immediately recognized as bearing any similarity to ordinary molds, and bacteria. The fungi are divided into several classes, of which we shall consider four. All of the class names end in *mycetae,* a suffix derived from the Greek *myketos*, fungus.

Phycomycetae—The name of this group is not particularly apt because, although these molds are frequently colored, the molds of other classes exhibit this characteristic even more conspicuously. It is also not possible to give a definition of the group that means much at the outset. Phycomycetes bear spores in a simpler manner than do the Basidiomycetes and Ascomycetes. And the living material enclosed by four walls usually has more than one nucleus floating in it. An example may make these remarks clearer.

The best known example of the phycomycetes is *Rhizopus nigricans* (Greek *rhiz*, root; *opsis,* having the appearance of; *nigricans,* black). *Rhizopus* is usually referred to as "bread mold" because, a generation ago, it was the most commonly found mold on old bread. Today, however, all large bakeries add an anti-mold chemical that particularly discourages this species. It is now more commonly observed growing on overripe, bruised bananas. It has the appearance of dingy cotton, peppered with black spots.

Under low magnification, the structures diagrammed in Figure 20-5 can be seen. Each fine cottony filament is called a **hypha** (Greek, web; plural, **hyphae**). The whole mat of hyphae is often referred to as a **mycelium.** The distinction between these terms, distinctions which often elude the student, may perhaps be made clear by saying that the relations between *hypha*, *hyphae*, and *mycelium*, are the same as those between *person*, *persons*, and *people.*

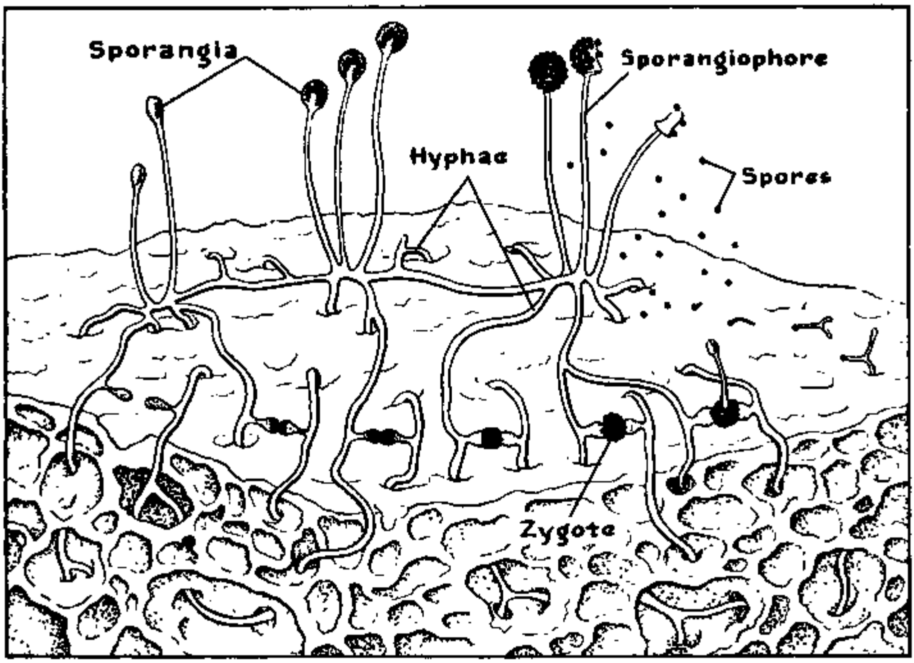


Fig. 20-5. *Rhizopus*, the black bread mold. In background, asexual reproduction. In foreground, sexual reproduction.

The black spots that can be seen with the naked eye prove, upon microscopic examination, to consist of clusters of tiny black balls, each ball being able to germinate and thus produce a new mycelium. Each tiny ball is called a **spore.** The delicate sac in which spores are produced is called a **sporangium** (Greek *angeion*, a vessel; plural, **sporangia**). The modified hypha on which a sporangium is borne is called a **sporangiophore** (Greek *phoros*, bearing, wearing).

In what might be called the everyday life of *Rhizopus*, the mold reproduces by the formation of spores which, landing on a favorable substrate, germinate to produce new mycelia. This sort of reproduction is called **asexual reproduction.** *Rhizopus* also has, however, a less common method of reproduction, **sexual reproduction,** diagrammed in Figure 20-5. There are two different sexes in *Rhizopus* but, since no one knows any grounds on which they could be called male and female, they are referred to as + and −. If two opposite sexes, or two opposite "mating types," are growing near each other, adjacent hyphae of the two types send out projections which meet, fuse, and form a heavy-walled **zygote.** This zygote, when it germinates, forms what looks like an ordinary sporangiophore, but the spores borne thereon are of two different kinds: + and −. They do not look different, but if these spores are germinated, their mycelia can then be shown to differ in sex. They can be identified by testing them against mycelia of the two known mating types.

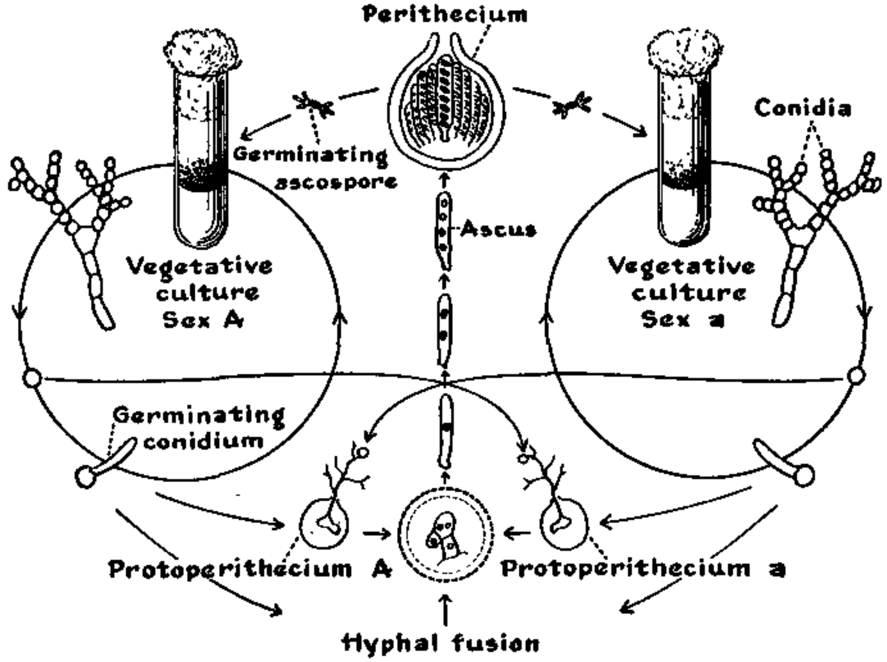


Fig. 20-6. Life cycle of the ascomycete, *Neurospora*. (After Beadle.)

Ascomycetae—These are molds that at some stage produce an **ascus** (Greek, leather bottle or bag) inside which are found spores. Such spores may be called **ascospores.** As an example of this class of fungi, we shall consider *Neurospora*, a mold that has been used for much important research.

Neurospora is an orange-colored mold that is occasionally found growing on bread that has not been chemically treated. The color is due to the **conidia** (Greek *konidion,* dust), spores formed by segmentation of the terminal branches of the hyphae. Each conidium is capable of germinating into a new hypha. Asexual reproduction is accomplished by this means, as well as by the growth of hyphal fragments that break off the parent mycelium.

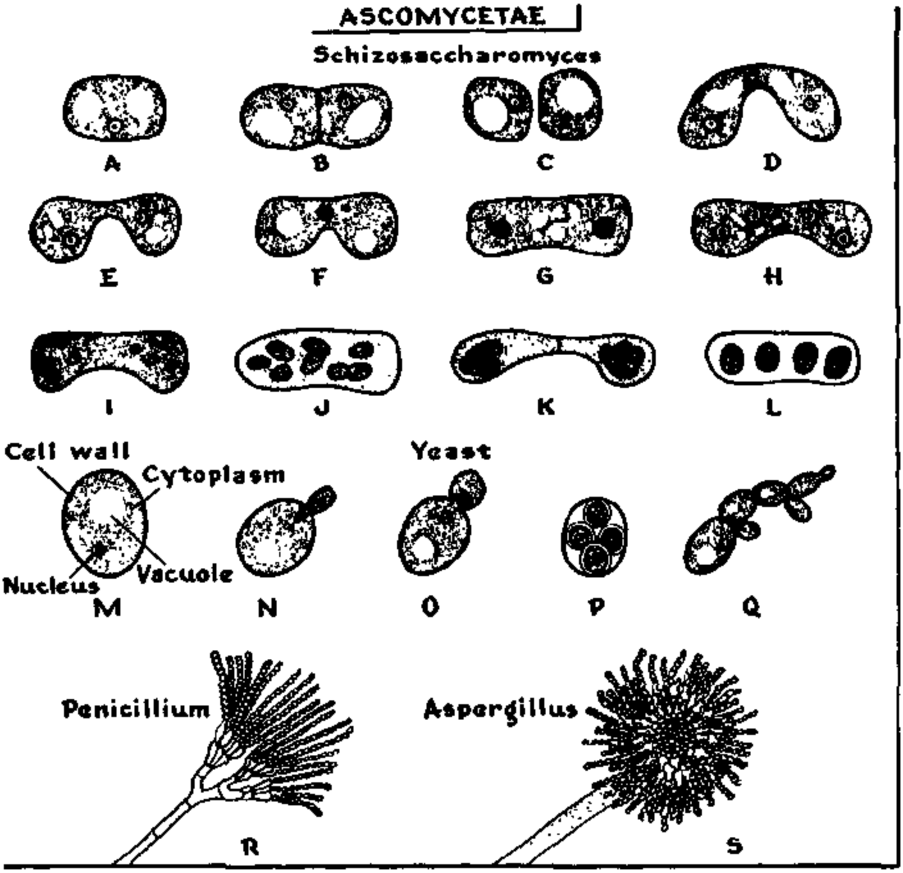


Fig. 20-7. Sexual reproduction in the yeast, *Schizosaccharomyces* (A-L), with the resultant formation of ascospores. Asexual reproduction of bread yeast (N-O) by a method called **budding.** Ascospores of bread yeast are shown in P. In Q, note how budding may lead to a hypha-like chain of cells. In R and S are two common genera of molds which undoubtedly belong to the Ascomycetae but which, since they have never been known to reproduce sexually, are sometimes placed in a catch-all class known as *Fungi Imperfecti.*

Sexual reproduction also occurs. By the union of two different sexual strains, a **perithecium** (Greek *peri*, around; *thekion*, a case) is formed, inside of which are found many sacs or **asci** (singular, *ascus*); in each ascus there are eight *ascospores*. (See Fig. 20-6.) Details of the formation of these will be taken up later. At the moment, we point out only that, of the eight ascospores, four are of one parental mating type and four of the other.

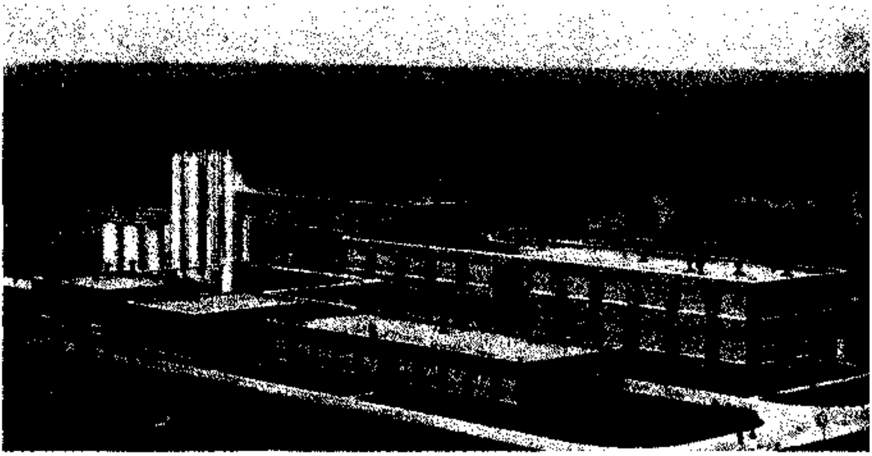


Fig. 20-8. This factory is one of dozens throughout the country devoted to the production of a single species of *Penicillium*, a mold which produces the powerful inhibitor of bacteria, *penicillin*. (Courtesy of Commercial Solvents Corporation.)

The class Ascomycetae includes, besides "mold," the yeasts. Some of the yeasts obviously belong to this group, for instance, *Schizosaccharomyces octosporus* (Fig. 20-7 A-L). In this species, two daughter cells from the same parent conjugate to produce an ascus. This species is said to be **homothallic** (Greek *homo*, common; *thallos*, a branch). (*Neurospora* is *heterothallic*.)

The common species of yeast, *Saccharomyces cerevisiae*, seldom produces spores. When it does, there are usually only four (or less) per ascus (Fig. 20-7 P). This is the species that is used for the production of alcoholic beverages and for leavening bread. In the absence of oxygen, it decomposes sugar as indicated by the over-all reaction of equation (1).

$$C_6H_{12}O_6 \rightarrow 2\,CO_2 + 2\,C_2H_5OH + \epsilon \qquad (1)$$

When we are interested in producing alcohol, the carbon dioxide is a by-product, one which is, however, used in making "dry ice," and carbonated beverages. In bread-making, the alcohol is a by-product which evaporates when the leavened dough is baked.

There are a number of molds included in the Ascomycetae, even though it cannot be proved that they belong there since they never produce ascospores. Among the most important of these, are the genera *Aspergillus* and *Penicillium* (Fig. 20-7 R,S). Certain species of the latter genus produce a substance called **penicillin** which is harmful to many bacteria and, for that reason, is useful as a medicine. The need for great quantities of penicillin has led to the establishment of many factories (see Fig. 20-8) designed for the sole purpose of growing *Penicillium* in quantity. Most species of this genus do not produce penicillin, but many of them are useful for other purposes, e.g., for curing and contributing flavor and color to Roquefort, Camembert and Danish Bleu cheese. *Aspergillus* is also a large genus. One of the species is used for the production of citric acid, useful in making fountain drinks. *Aspergillus* and *Penicillium* are the commonest molds encountered as spoilers of jellies, fruits, moist leather goods, and many other products. They occur in many colors, the commonest being green.

Basidiomycetae—This class includes the largest species of molds, the mushrooms. Most mushrooms belong to this class though a few are ascomycetes.

To the layman, mushrooms and bread mold do not seem to have much in common. However, what we call a "mushroom" is only a small part of the individual organism. Most of the organism consists of an extensive mycelium that is entirely underground. The mycelium grows at the expense of dead and buried vegetation for many months and finally, at the proper season, sends up the aboveground growth we call a mushroom. The aboveground portion grows by transference of material from the underground mycelium. It is because its growth is really a matter of transfer of food, rather than synthesis of it, that the mushroom can grow so fast.

What is the significance of the aboveground part of the mushroom? A clue is furnished us when we cut off the cap of a mushroom and place it over both some black and some white paper (Fig. 20-9). If we leave it undisturbed for some hours, when we remove it, we shall find on the paper radiating lines of a fine powder which will be evident on either the black or the white paper, depending on the color of the powder. If we look at this powder under the microscope, we see that it is composed of small bodies which we recognize as spores. These spores are

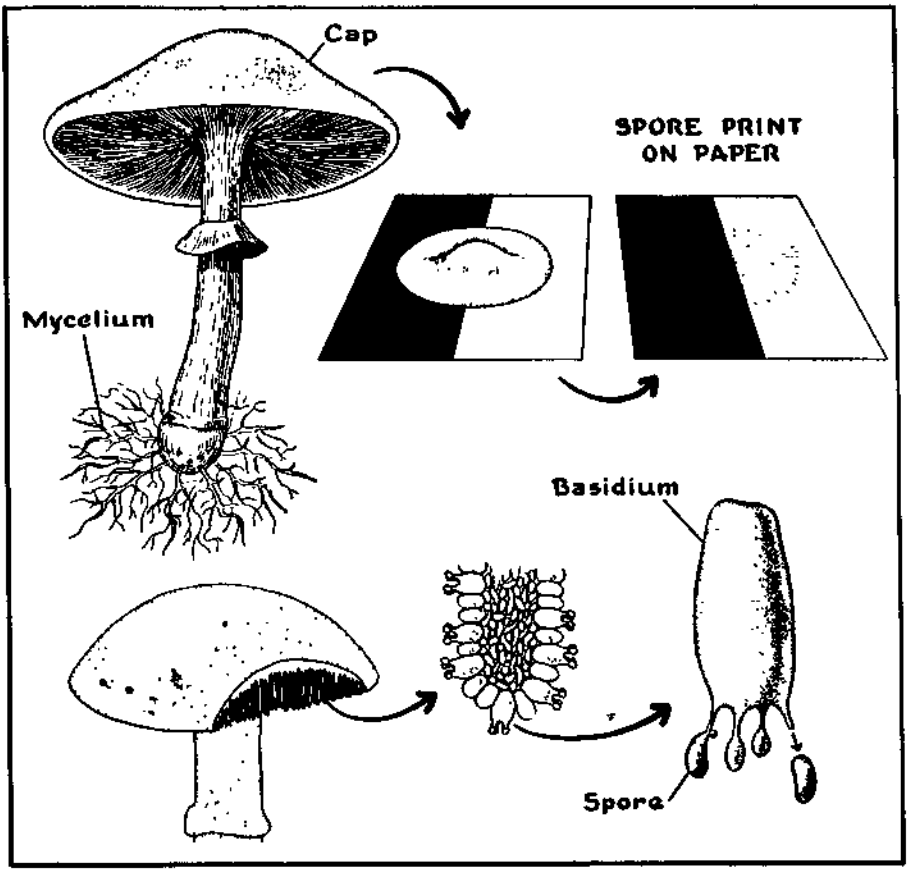


Fig. 20-9. A mushroom, showing a small fraction of the mycelium from which it grows. The spores (upper right) are borne on structures called **basidia** (magnified, lower right) from which they are forcibly snapped off.

continuously shed by the mushroom cap. They are heavier than air but, being tiny, can easily be carried about by air currents. Teleologically speaking, the purpose of the mushroom (aboveground portion) is to get the spores well up off the ground so that they will have a reasonable chance of being wafted by the winds to new locations where they may germinate and thus spread the species over more territory. The number of spores produced by a single mushroom is numbered in the millions. In the case of a giant puffball (a mushroom), it has been estimated that a single large puffball may produce as many as seven billion billion spores. Some conception of the magnitude of this figure may be possible when it is pointed out that this number is *even larger* than the number representing the value of the national debt in dollars.

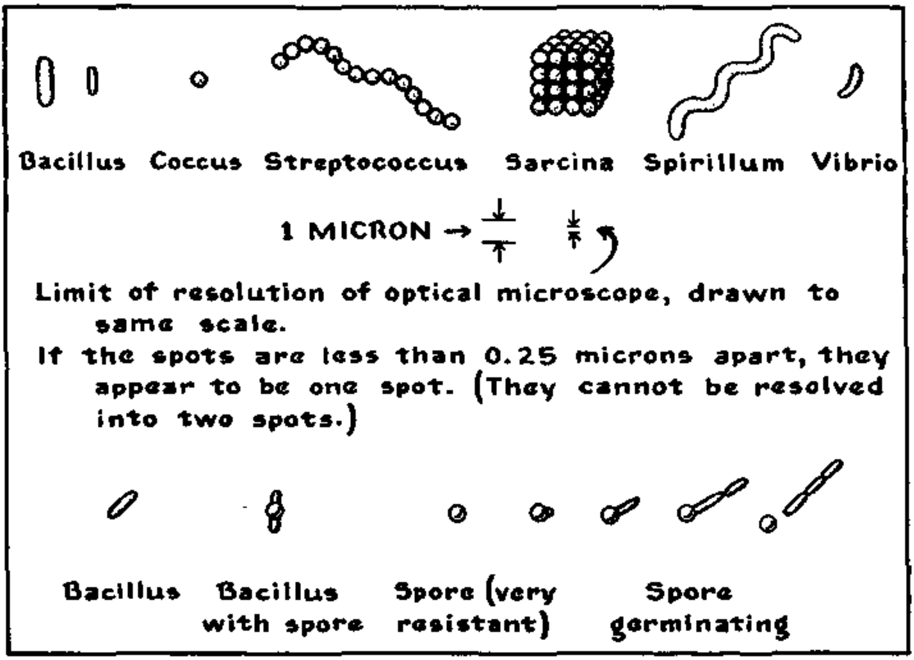
It takes careful dissection to show the exact structure on which are borne the spores of the mushroom. With luck, the structure diagrammed in Fig. 20-9 may be seen. The spores are borne in groups of fours on a **basidium** (Latin, pedestal). It is this structure that gives the name to the class *Basidiomycetae*. The spores are often called **basidiospores.**

Parenthetically, it may be well to say a word about mushrooms from a gastronomic point of view. The layman frequently wants to know how to distinguish a "mushroom" from a "toadstool." The mycologist is unable to answer him because the distinction has no taxonomic meaning. The word "toadstool" comes from the German *Tod-Stuhl* or death stool. Some mushrooms are death stools. Most mushrooms are life stools, so to speak. There is no simple way to tell them apart (such as seeing if the mushroom will tarnish silver). Distinguishing species of mushrooms is a job for an expert taxonomist, as is distinguishing species of grasses, or mice, or of any other organisms. Unless the student wishes to subject himself to the discipline of *learning* the mushrooms, he had best regard all mushrooms as being divided into two groups: mushrooms-found-in-the-stores, and mushrooms-found-on-the-ground; and eat only the former.

Schizomycetae — These are the bacteria. Until very recently, it was thought that there were no sexual processes among the bacteria, that reproduction took place only by cell division or "splitting," hence, the class name (Greek *schizo*, to split, or cleave). They are the smallest of the fungi. They vary considerably in size, but an idea of the magnitude of a typical species may be had by looking once again at Figure 19-3, where the alga *Spirogyra* and the bacterium *Pseudomonas* are drawn to the same scale.

Everyone has heard of bacteria. But most everyone has a distorted view of their significance, thinking of them as being predominantly disease-causers. Quite the contrary is the case; one bacteriologist has estimated that for every one disease-causing bacterial cell there are at least 30,000 bacterial cells that are harmless, or even beneficial, to man.

This is fortunate, from our point of view, because we are surrounded by bacteria. The air we breathe is loaded with them; a not-unusually dirty atmosphere may have one hundred bacteria per liter. Breathing such air, we take in around one hundred thousand bacteria per day, usually without ill effects.



Limit of resolution of optical microscope, drawn to same scale.

If the spots are less than 0.25 microns apart, they appear to be one spot. (They cannot be resolved into two spots.)

Fig. 20-10. A variety of bacteria

There are many thousands of species of bacteria which exhibit, however, not much morphological variation (see Fig. 20-10). Because of their small size and little variety in form, most species of bacteria cannot be identified by sight. There are identified by what they do—what diseases they cause, or what foodstuffs they can turn into what other substances. **Bacterial species are identified by their metabolism.** Various species produce a bewildering variety of organic chemicals, many of them of industrial value. Among these substances, are ethyl alcohol, acetic acid (in vinegar), lactic acid (used in baby food), propionic acid (used in lacquers and perfumes), acetone, butyl alcohol, and glycerine, to mention only a few. These substances are used by the tons. In the past quarter of a century, there has developed a great industry built around the activities of bacteria and molds. This industry, which employs thousands of persons, is called the "fermentations industry." The oldest function of the industry—to produce potable alcohol—is now overshadowed by the production of medicines, solvents, and other chemicals.

146. Research with Microbes

Today a great deal of research into the principles of general biology is carried on with molds, yeasts, or bacteria as the immediate objects of study. These **microbes,** as they are called, are particularly well suited to research for the following reasons:

1. Their rapid metabolism. Vitamin assays that used to take months, using guinea pigs or mice, can now be run in a few hours, using microbes.
2. Their small size. This is an advantage for two reasons:
   a. Laboratory apparatus and vessels can be small, hence, relatively inexpensive.
   b. Large numbers of them can easily be used, thus reducing the sampling error. With large organisms like dogs, conclusions must be based on tests made with only a few individuals. Individuals vary, and so the results obtained with a few organisms may not be generally applicable. With microbes one can easily have experimental and control groups consisting of millions of individuals, thus virtually eliminating the sampling error.
3. The similarity of their metabolism with that of higher organisms. Were this not true, the other considerations would count for little. They cannot, of course, be used for those lines of research that bear specifically on the peculiarities of higher organisms: e.g., the conduction of water in the stem of a higher plant, or the speed of propagation of the nerve impulse in a higher animal. But, for questions related to the *general* problems of living things—the problems connected with metabolism and inheritance—the microbes are most useful.

QUESTIONS AND PROBLEMS

20-1. In tabular form, compare the various classes of algae with respect to their chlorophylls.

20-2. Which classes of algae are almost completely confined to the ocean?

20-3. How are the fungi distinguished from the algae?

20-4. To what classes of fungi do the following organisms belong: yeast, *Rhizopus nigricans*, the commercial mushroom, the organism that produces penicillin?

20-5. Define: Ascomycetae; Basidiomycetae.

20-6. How are bacterial species distinguished?

20-7. What advantage for research do the microbes possess? What kinds of problems can they not be used to solve?

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Chapter XXI

Mosses and Ferns

147. Haploidy and Diploidy

Most organisms are made of one or more clearly delineated bits of living matter called cells. With some exceptions, each cell has in it a well-defined body called a nucleus which is needed for the continued existence of the cell. If the nucleus is examined microscopically, within it will be seen some ill-defined tangles of threads. Under certain conditions, using special techniques of observation, these threads can be seen as well-defined, stainable bodies called **chromosomes.** (See Fig. 21-1.)

Different kinds of chromosomes are distinguishable, and they vary in length and breadth, and in shape. If the nucleus of a cell has only *one* of each distinguishable kind of chromosome, the cell is said to be a **haploid** cell (Greek *haploos,* single). If the cell has *two* of each kind of chromosome, the cell is said to be **diploid** (Greek *diploos,* double). Within any discrete organism, most or all of the cells are of one kind of -ploidy. The mechanism of cell division is such that ordinary daughter cells have the same kind of chromosomes as the parent cell. Change in chromosome number occurs either as a result of fusion of two cells (e.g., an egg and a sperm) or as the consequence of a special sort of division called **meiosis** or reduction division. The details of this latter process will be considered later (Chap. XXVIII).

In animal cells, diploidy is the rule, haploidy being almost entirely confined to the sex cells. In man, for example, all the cells of the body are diploid except the sperm and the egg cells, which are haploid.

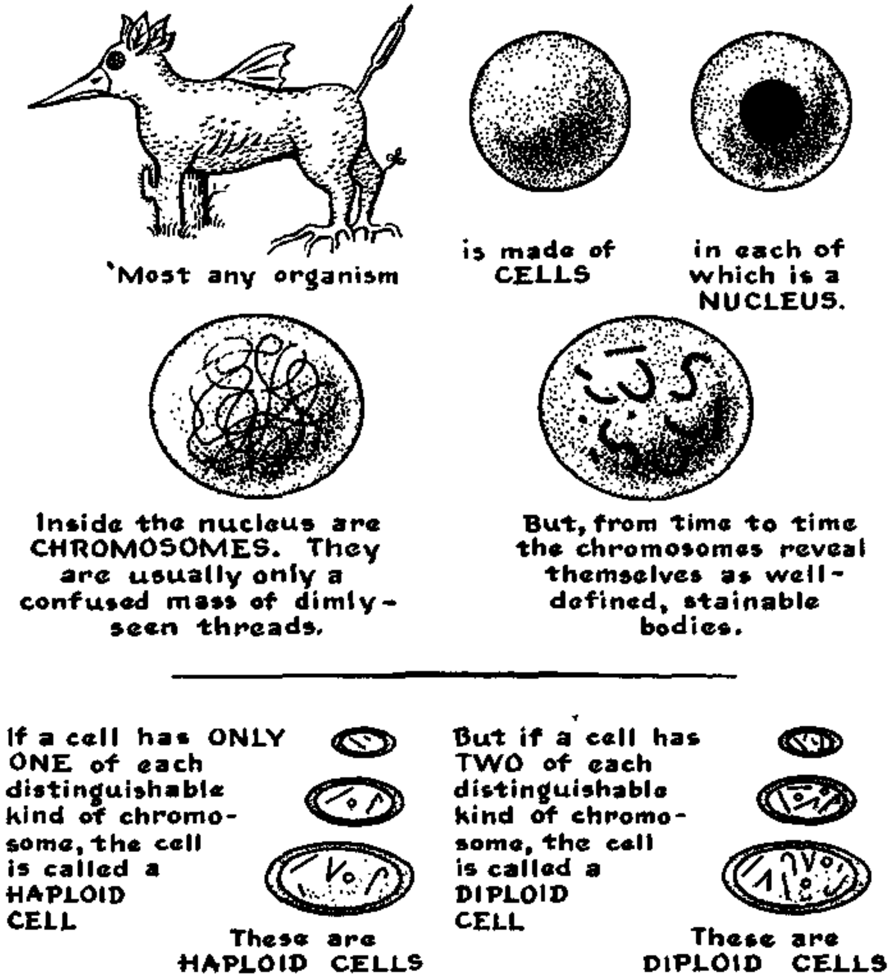

Fig. 21-1. Ploidy.

Among plants, however, no such generalization can be made. Many of the so-called "lower" plants are haploid as a rule. As we ascend what we believe to be the evolutionary tree, diploidy becomes more and more prevalent. It is this change in the haploidy-diploidy ratio that the following account should make evident.

148. Thallophyta: Predominantly Haploid Organisms

The Plant Kingdom is usually divided into four great phyla, namely:

Thallophyta
Bryophyta
Pteridophyta
Spermatophyta

Among the main plant groups, the Thallophyta are unquestionably the most primitive. Bacteria, molds, yeasts, and algae undoubtedly existed long before ferns and trees. Although some species are of considerable size, e.g., the giant kelps of the seashore, nevertheless, as a group, thallophytes are small. Though many live in more or less dry locations (e.g., some molds, some algae), most are aquatic organisms. Though "simplicity" is a hard term to define, they seem to be morphologically simpler than members of other groups. They reproduce rapidly, and their reproduction is mostly asexual.

Sexual reproduction necessarily involves the production of at least one diploid cell, a cell whose nucleus contains two members of each kind of chromosome, two complete sets of chromosomes. This diploid cell may divide in such a way as to give rise to more diploid cells. Or it may fairly soon undergo a reduction division, thus rapidly bringing the cells back to the haploid condition once more. The haploid condition is typical of the thallophytes. Most species of thallophytes either never enter into sexual union, in which case the cells are always haploid; or, if sexual fusion occurs, very promptly return to the haploid condition. There are exceptions—some of the large seaweeds, for instance. But the generalization is safe.

149. Bryophyta, with a Parasitic Diploid Generation

When we examine the next higher group, the Bryophyta, a different situation prevails. The Bryophyta includes two principal groups, the liverworts and the mosses. Since more people are aware of mosses, we shall confine our discussion to them.

Not everything that the layman calls a moss is regarded as such by the botanist; "Spanish moss," for instance, is something quite different. Mosses are usually not-too-conspicuous resilient pads of greenness growing at the base of trees or on a tree-trunk (north side, of course), never on rolling stones. Around waterfalls, they flourish on well-sprayed rocks. One kind of moss, *Sphagnum*, grows on the surface of acid ponds in the more northerly regions, its intermeshed filaments forming a thick, firm mat on which one can walk, though there may be twenty feet of water beneath one's feet. The cushion of moss quakes underfoot but holds firm. A delightful experience.

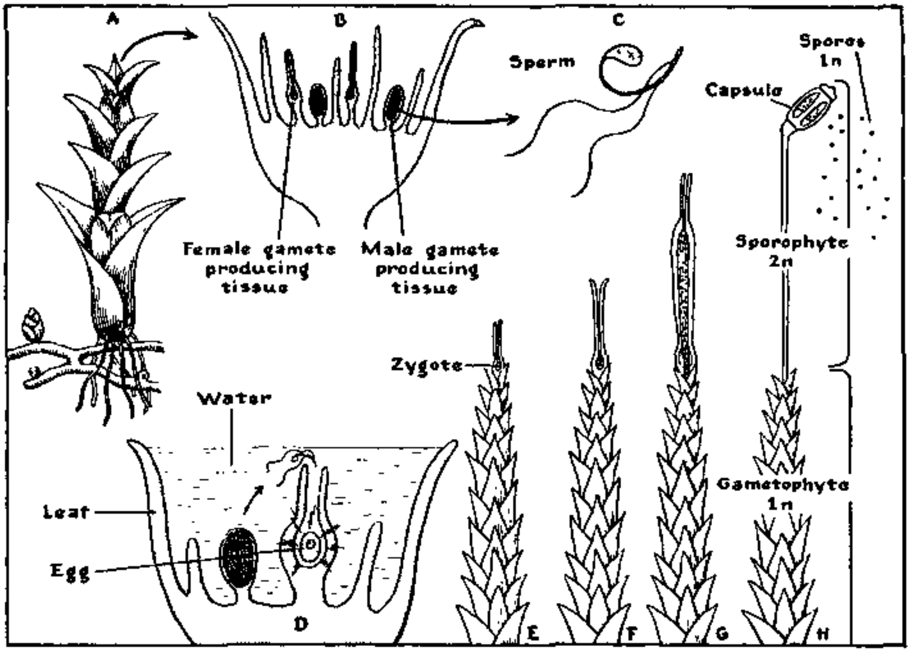

Fig. 21-2. The life cycle of a moss, with haploid ($1n$) and diploid ($2n$) tissue identified.

But to get back to the less spectacular forms, let us examine a small moss closely to see how it is put together. (See Fig. 21-2A.) The bulk of the moss is a tangle of small, but multicellular, filaments of which we are ordinarily unaware. From these filaments, grow the green, leafy shoots which we think of as the moss. *All of this tissue is haploid.*

At certain times of the year, hidden in the leafy tips of the shoots, gamete-producing organs are formed (Fig. 21-2B). Two types of gametes are produced, male and female, sperm and egg. In some species, these are both produced at the tips of the same shoot (as drawn); in others, they are produced on different plants. In either case, before a sperm can get to an egg, there must be a continuous watery pathway between the two for the sperm to swim in. In this regard, mosses, though dry-land plants, never evolved to complete independence of the watery environment in which their ancestors must have lived. For fertilization, the old-fashioned watery environment must prevail. When it does, the sperm soon swims toward an egg, attracted by a chemical substance exuded by the egg (Fig. 21-2D). The product of the union of the two is a zygote *and is diploid.*

Without moving from the place of its formation, the zygote now begins to develop into a multicellular plant (Fig. 21-2 E-H). In this process, each cell division is an *equational division,* i.e., each division involves a doubling of the chromosomes preliminary to cell division, the consequence being that each daughter cell has the same complement of chromosomes that the mother cell had. Such equational division is called *mitosis,* and is described more fully in § 169. The repeated mitotic division of the diploid (*2n*) moss zygote produces a multicellular *2n* plant growing at the top of the old *1n* plant. In many species, this new plant is "colorless," that is, it is not green (though it may be buff-colored). The lack of green color indicates a lack of chlorophyll, hence, lack of ability to photosynthesize. In other species, the new plant is a pale green and can make at least part of its own food. When this diploid plant is completely formed, it bears at its tip a capsule from which are presently shed some minute spores which are *haploid.* Evidently in the process of their formation, the process of meiosis takes place. These spores, landing on a suitable substrate, can grow into new green, haploid plants.

Thus, there are two distinct types of moss plant produced. These are spoken of as belonging to separate "generations." The green, haploid, gamete-producing plant is called a **gametophyte.** The diploid, spore-producing plant is called a **sporophyte.** The regular alternation of the two in time is spoken of as an **alternation of generations.**

Notice that, in the moss (and in Bryophytes generally), the diploid generation is much more conspicuous than it is in the Thallophyta, though, even in mosses, the gametophyte generation is the dominant one. The moss plant that one sees most of the time is the haploid generation. Only occasionally, is one aware of the slender brown spikes—

the diploid sporophytes—protruding from the surface of the spongy green mass.

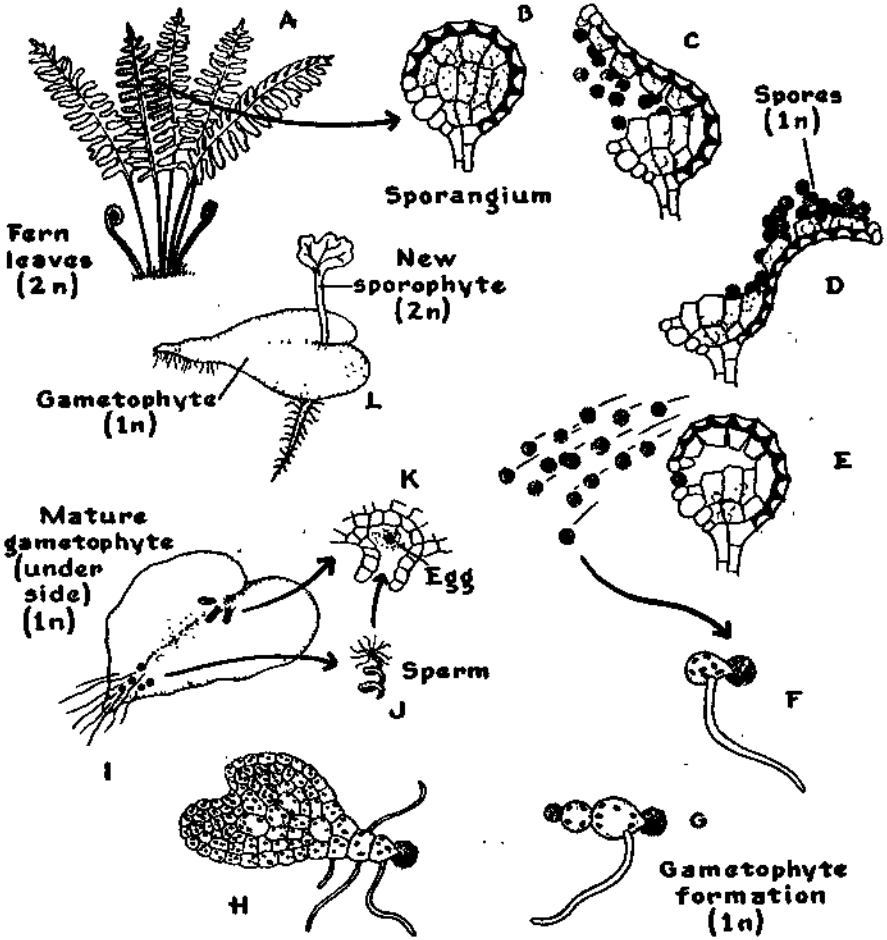

Fig. 21-3. The ferns and their reproduction.

150. Pteridophyta, with an Inconspicuous Haploid Generation

Everyone knows what a fern looks like. Anyone who has handled a fern may well have turned a leaf over and discovered rough brown spots on the underside (Fig. 21-3A). He may have said, "Hmm-m. Disease, no doubt." In which case, he was wrong. Closer inspection of the brown protuberances shows that each one is made up of a number of little cases, each of which has a very elegant way of expelling its contents

(Fig. 21-3 B-E). *The little pellets that are expelled are spores.* They are haploid. They arise by reduction division from specialized cells of the fern leaf which is made of diploid tissue.

Then, is the whole fern plant a sporophyte? Such is, indeed, the case. It is, obviously, a far more conspicuous sporophyte than is the moss sporophyte. Where is the gametophyte?

If we follow the journey of a spore, so rudely expelled from its **sporangium,** we will learn. If the spore lands in a favorable place, it germinates (Fig. 21-3 F-H) and, by cell multiplication, presently produces a thin little pad of tissue, lying prostrate on the ground, quietly photosynthesizing in some moist, shady place in the forest. This object, made entirely of haploid cells, is the gametophyte. If we turn it over, we find, on the underside, sex organs, male and female (Fig. 21-3I). The male produces sperms and the female eggs. As in the Bryophytes, the sperm is chemically attracted to the egg which it fertilizes. For this to take place, there must, of course, be water, which is found as a thin film between the underside of the fern gametophyte and the ground.

The fertilized egg develops *in situ,* very much as did the moss egg, only, in this case, the sporophyte which results (Fig. 21-3L) is green and can make its own food. It soon grows into a conspicuous sporophyte fern plant, overshadowing the diminutive gametophyte which presently withers away.

Thus it is among the **Pteridophyta,** the large group to which the ferns belong. In this group, the haploid generation has become, for the first time, the less conspicuous generation. The sporophyte, the diploid generation, is the conspicuous one.

QUESTIONS AND PROBLEMS

(See also Questions and Problems, Chapter 22)

21-1. Define or describe: haploid, diploid, sporophyte, gametophyte.
21-2. Compare and contrast the Bryophyta and the Pteridophyta.

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Chapter XXII

The Flowering Plants

151. Spermatophyta: The Predominant Diploid

We come now to the fourth and last of the great groups of plants, the **Spermatophyta** or Seed Plants (Greek *spermatos*, seed, semen). These are the organisms the layman has in mind when he mentions the word "plants." These are the plants that, almost by themselves, cover the earth. These are the plants that make the world beautiful.

Before taking up the subject of the life cycle in some of these plants, it is desirable to point out that the Spermatophyta are divided into two subgroups, namely:

Gymnospermae, the cone-bearers
Angiospermae, the flowering plants

The cone-bearers are the more primitive spermatophytes. This group includes the great bulk of the lumber trees of the world: pine, spruce, fir, hemlock, juniper, and sequoia, to mention a few of them. All of these trees have relatively soft wood.

The angiosperms, or flowering plants, include all those plants that bear seeds following the production of flowers. Besides the group which the layman refers to as having "flowers," this group includes many other species whose flowers are so inconspicuous as to escape ordinary notice—oaks, maples, grasses, etc. Most of the hardwood trees are angiosperms

The life histories of gymnosperms and angiosperms differ in a number

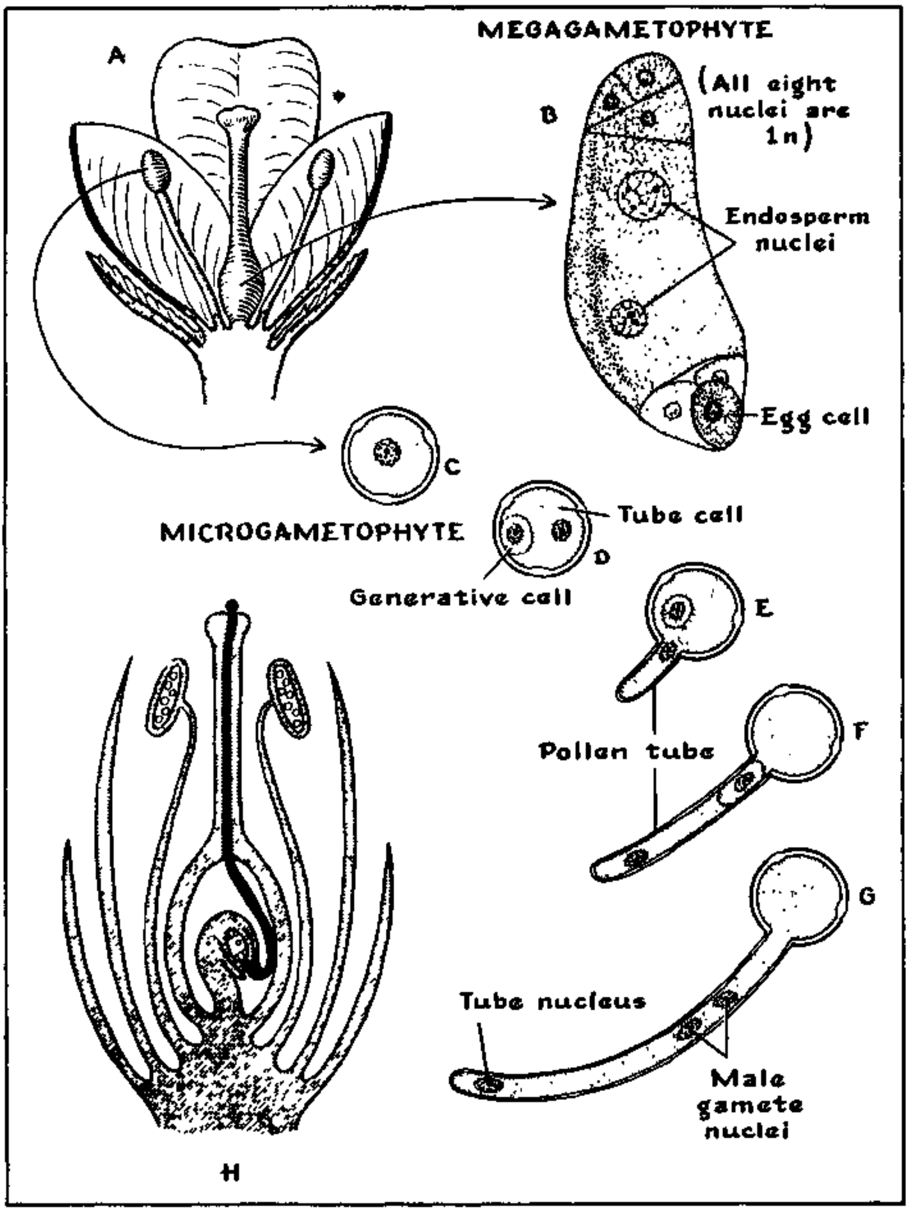

Fig. 22-1. The parts of a flower, and their fates.

of details but, in both, the diploid generation is even more predominant than it is in the ferns. Here we shall describe only the life cycle of a flowering plant. The student interested in comparing it with that of a cone-bearer should consult a standard textbook of botany, some of which are listed at the end of the chapter.

In a flowering plant, all the tissues of which one is ordinarily aware are diploid. These tissues are the sporophyte generation. The spores produced, unlike those of the ferns, are never released but, buried in the flower parts, develop into the gametophytes while still on the parent sporophyte. There are two gametophytes here, one male and one female. The male gametophyte is the pollen grain and is, as every "hay fever" sufferer knows, released from the sporophyte. The female gametophyte is completely buried at the base of the ovary (Fig. 22-1A). If we cut across a mature flower, we can find the **megagametophyte,** as it is called, completely surrounded by other tissues. The megagametophyte has eight nuclei (Fig. 22-1B), all of them haploid, most of them in separate cells. One of these cells is the egg. The others are destined to live various lengths of time, but none of them gives rise to a new generation.

The male gametophyte, the pollen grain, is called the **microgametophyte** (Fig. 22-1C) because of its smaller size. At the time of the release of the pollen grain, there are only two nuclei in this gametophyte, both haploid.

The spermatophytes are the only large group of plants completely adapted to dry land. No longer is a water film required for the male nucleus to get to the female nucleus. Gone is the spermlike gamete, and in its place is a microgametophyte that grows in a funguslike manner, carrying haploid nuclei forward in a hyphalike extension (Fig. 22-1D-G). When this **pollen tube,** as the extension is called, reaches the megagametophyte (Fig. 22-1H), one of the haploid nuclei, called the **male gamete nucleus,** fertilizes the egg nucleus, thus forming a zygote and so starting a new sporophyte generation.

Curiously enough, another male gamete nucleus fertilizes the binucleate endosperm cell, thus making a **triploid endosperm cell.** This triploid cell multiplies considerably, and it may furnish nourishment to the embryo as it develops from the zygote. The development of embryo, endosperm, and surrounding tissues goes on for awhile, then stops. By this time, there is a more or less hard coat enveloping all these tissues. The whole is known as a *seed* and is the means whereby the species is dispersed more widely. Although the end which the seed serves is the same as that of the spores found throughout the plant kingdom, namely dispersal of the species, the two are not otherwise comparable. A seed is a new individual (sporophyte) whose development has been arrested for awhile. It is a multicellular individual.

The evolution of plants from water to land brought with it various problems which have been solved in several ways. Some of these problems and solutions occur among the Bryophyta and Pteridophyta, but they are more strikingly exhibited in the Spermatophyta. These problems revolve around the necessity of dispersal. In a watery medium, dispersal is a relatively simple matter because living substance has a density very nearly the same as water, and consequently, living cells can easily propel themselves about or can be carried passively by the currents of the medium. Once plants are on dry land, the problem of dispersal becomes more difficult. No plant has developed means of active flight through the air; no flowering plant can move over dry land in the active manner that characterizes animals. How, then, do the land- and air-dwelling plants become dispersed over the face of the earth?

It will be worth while to consider, first, the space relations of the individual. The adult size of a spermatophyte is seldom as fixed a thing as that of, say, an insect or a mammal. A pine tree grown in a dense forest grows to a very great height with only as much extension of the limbs around it as its competing neighbors permit. In a clearing, the same species of pine will spread laterally to a much greater extent and, so, will occupy a larger fraction of the available environment. Thus, it may be said that, by individual measures, the species becomes somewhat dispersed over the earth.

Dispersal of the species by individual spreading is more effective in those forms that have a prostrate form of growth, forms such as ivy. Many grasses also can spread by this means. Quack grass and Bermuda grass have underground stems which grow out in all directions, from time to time sending up bunches of grass leaves. But for the competition with other plants, and the boundaries of the favorable environment, a single such grass plant could spread over an indefinite extent of earth.

When a grass plant has spread out and produced several clumps, the destruction of an underground stem between two clumps will result in two plants from one individual. This is a method of asexual reproduction; it is called **vegetative reproduction,** since it is brought about by vegetative (i.e., nonsexual) tissues. Many plants are capable of vegetative reproduction. A small part of a geranium, or ivy, or barberry plant readily produces a complete new plant when it is partially buried in soil. The smaller branches of willow trees have brittle sections at their bases which allow them to break off easily. Branches so shed readily form new root systems if they fall in damp ground.

Another method of vegetative reproduction that is of especial importance is that brought about by man by various methods of **grafting.** In preparation for making a graft, a stem or branch of one plant is cut off and joined to the cut stump or stem of another by placing the cut surfaces in contact and then binding them together. The plant that furnishes the roots in this artificial union is called a **stock;** the plant stem which thereafter draws nourishment from new roots is called the **scion.** One plant can, of course, furnish many scions. When these grafted scions have grown to maturity, they, in turn, can furnish many more scions. By serial grafting, a particular type of plant can be vegetatively increased in numbers indefinitely. Such vegetative reproduction has proven especially valuable in the multiplication of valuable strains of fruit trees. Most of our present strains of fruit trees have arisen as single "sport" or "mutant" (see § 171) branches on trees of slightly different type. Experience has shown that such mutant branches, if allowed to reproduce themselves sexually, do not breed true to type. Mutant branches may, however, be subdivided into many scions, all of which will remain true to the original type until the day when a new mutant appears among the many individuals so vegetatively developed. If the new mutant is valuable, it may be saved; if not, discarded. By vegetative reproduction, a desirable type of sport is readily conserved, an important consideration since the appearance of mutants is a fairly rare phenomenon. The Washington navel orange arose as a single sport in South America early in the Nineteenth Century, and there has been no recorded recurrence since.

But vegetative reproduction, widespread as it is, is probably not as quantitatively important in the propagation of flowering plants in nature as is sexual reproduction. The essence of the mechanism has already been described. It remains now to discuss the means by which sexual reproduction and dispersal of seed are made possible in land-dwelling plants.

In some flowering plants, the act of bringing together the male and female gametophytes is made relatively simple by having each flower fertilize itself. The pollen and the stigma of a single flower are not far apart; a slight swaying of the plant may bring them together. Such **self-fertilization** is the rule among the legumes (peas and beans), violets, and various others. It is possible only because both male and female parts are within the same flower which, for that reason, is called a *perfect flower.*

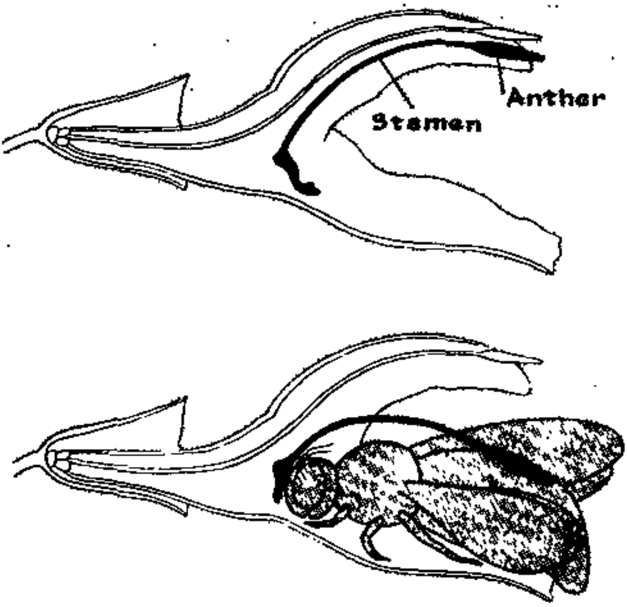

Fig. 22-2. How the flower *Salvia* is adapted to utilize bees as pollen-transporting agents.

Self-fertilization is unlikely or impossible if:

a. The flowers are *imperfect flowers,* i.e., male and female parts are not both found in the same flower.

b. The plant is **dioecious** (Greek *di,* two; *oikos,* house), i.e., if the two sexes are found on separate individual plants. [Where both sexes are found on the same plant, the species is said to be **monoecious,** a term which is the botanical equivalent of the zoologist's *hermaphroditic.*]

c. The flowers are self-sterile, as is true in tobacco and other plants.

d. The flowers are so constructed as to make difficult the access of pollen to the stigma in the same flower.

How is cross-fertilization, or **cross-pollination,** brought about? Various agencies are involved among the many species of plants, but the two most common ones are **wind** and **insects.** Wind pollination occurs among some grasses and many trees. Wind pollination is particularly conspicuous among the cone-bearers (Gymnospermae); at the proper season, a veritable yellow cloud may be seen drifting down wind from a pine tree.

The most spectacular transporting agents are the insects. A great many flowers are dependent on insects for their fertilization, and the modifications that have been developed in both flower and insect have long excited the admiration and astonishment of naturalists. We could easily fill a book with an account of the various adaptations—in fact, Darwin did, in his *Fertilization of Orchids*, a book concerned with only one group of plants. But we shall content ourselves with citing one example, that of the flower *Salvia.* This flower has a **stamen** that is modified into a two-ended lever which swings about a fulcrum. When a bee enters the flower (Fig. 22-2), it pushes on the short end of the lever, bringing the long end down against its fuzzy back which rubs some of the pollen grains off of the **anther.** These pollen grains will then be carried to another flower where they may be deposited on the **stigma.**

The dependence of many flowers on insect pollination has sometimes complicated man's migration. When settlers first took red clover into Australia, it failed to set seed, and consequently, the immigrants were for awhile dependent on other countries for their red clover seed—until they also imported some bumblebees to pollinate the flowers. Similarly, the Smyrna fig depends on certain Hymenoptera (wasps) for its fertilization. When Smyrna fig trees were brought to the United States, the wasp was brought too, to insure fertilization and the setting of fruit.

After fertilization and the formation of seeds, there arises the problem of dispersing them. The solutions to this problem are at least as various as the solutions to the pollination problem. The seeds of many plants have hairy extensions which give the seed buoyancy in the air, enabling it to be carried long distances by comparatively feeble winds. Such adaptations are exhibited by dandelions, salsify and clematis. Another

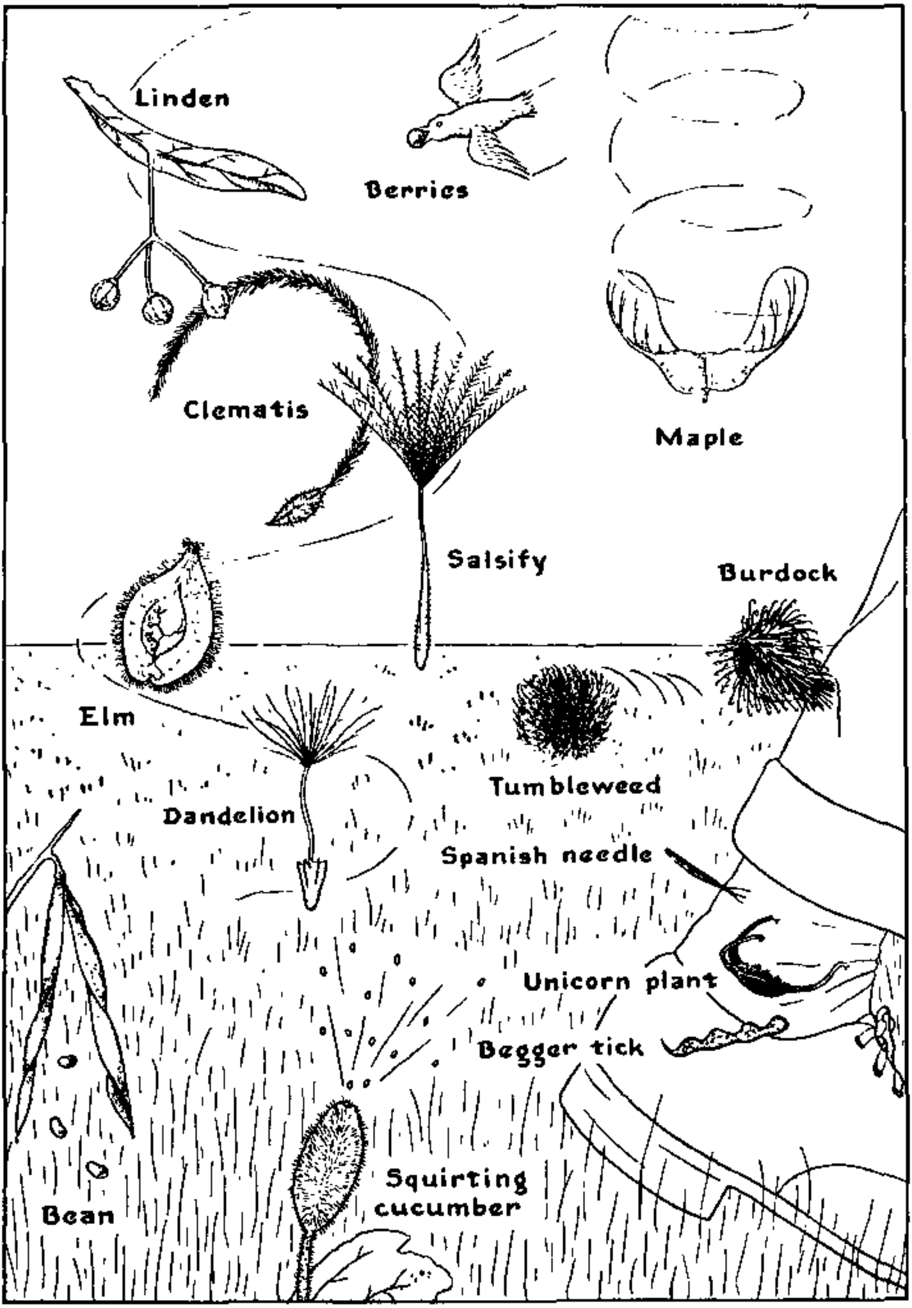

Fig. 22-3. Various methods of seed dispersal.

spectacular form of wind dispersal is shown by tumbleweeds, which inhabit open plains regions where there are strong winds. When the seeds mature, a whole plant breaks off at the base of the stem and is blown end over end across the plains, scattering seeds as it goes. Other plants have adaptations for throwing seeds to some distance. The seed pods of legumes, when they dry, curl, and expel the seeds forcibly. Many plants surround their seeds with tissues that are esteemed as food by various animals; such, for instance, are the berries. When a berry such as the strawberry is eaten by a bird, the seeds may pass through the intestinal tract unharmed and may be deposited in the bird dung many miles from the parent plant, there to germinate. Other ways in which animals are exploited as carriers of seeds are exhibited by the various plants which produce seed cases with hooks on them which can attach to animal fur, e.g., cockelburs, Spanish needle, beggar tick, and unicorn plant. Some of these adaptations are to be seen in Figure 22-3.

All of these adaptations constitute methods of dispersing plants in space. The seed is also a method of dispersing the species in time. The vegetative parts of many seed-forming plants are incapable of surviving a normal winter. Seeds are generally resistant to cold and many other stringent environmental factors. By producing seeds, a plant species manages to disperse itself through the following years.

The ability of seeds to withstand environmental factors is tied up with their *dormancy*. A seed shows very little metabolism; the life processes are virtually at a standstill. Because of this, the relatively small amount of food material contained in a seed will suffice for a long time. There is a wide range of longevities among the various seeds. The seeds of all our food cereals (wheat, oats, rye, etc.) will survive well for two years but, after ten or fifteen years, only a few per cent of the seeds will germinate. At the other extreme, are lotus seeds for which there is an authentic record of viability after 150 years. Most botanists put no credence in the stories of the germination of cereal seeds exhumed from Egyptian tombs. Seeds taken from tombs opened under strict supervision do not germinate. The only seeds which germinate are those purportedly removed from unsupervised tombs by native guides catering to tourists. It is considered not without significance that such seeds show a striking similarity to modern varieties of cereals, rather than to the ancient Egyptian varieties which are known to have been rather different.

QUESTIONS AND PROBLEMS

22-1. To what phyla of plants do the following organisms belong: liverwort, *Euglena*, fern, moss, marine kelp, lily, pine tree?

22-2. Briefly characterize the four phyla of plants in terms of their life cycles.

22-3. For each of the four phyla, draw a circle and then divide it into pie-shaped sectors to show the relative importance of gametophyte and spermatophyte generations in each group.

22-4. What are the two subdivisions of the spermatophytes?

22-5. How does a seed differ from a spore?

22-6. What is endosperm? What is its importance?

22-7. What is vegetative reproduction? What is its importance to plants? To man?

22-8. Do you know the folk story of Johnny Appleseed? What relevant comments might a botanist make on hearing this story?

22-9. Define scion and stock.

22-10. Define monoecious and dioecious. Which one is a synonym for hermaphroditic?

22-11. What are the two most common agents for cross-pollination? Cite an instance in which each is effective.

22-12. If DDT, or other insecticide, were so effective as to enable us to kill *all* the insects in a region, would you recommend its use on a wholesale scale? Explain.

22-13. What function or functions do seeds serve?

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Chapter XXIII

Plant Physiology

152. The Leaf, a Photosynthetic Organ

As we shall see in some detail in Part IV, in its basic physiology, a plant is not very different from an animal. Both respire, and the process of respiration is made possible by enzymes many of which are nearly or quite identical in the two kingdoms. However, although the basic physiology of plants and animals may be the same, the over-all physiology of one group differs somewhat from that of the other. The special physiology of humans, with which we were so greatly concerned in Part II, tells us almost nothing of the special physiology of plants. Plant physiology is a distinct discipline. Because plants are of the greatest importance to man's continued existence, the elements of this science will be presented here.

The single process which is most characteristic of plants is photosynthesis (§ 143), which may be represented by the over-all equation:

$$CO_2 + H_2O + \epsilon \text{ (light)} \longrightarrow \text{organic material} + O_2 \qquad (1)$$

In flowering plants, this process takes place in any green tissue, but the greater part of the synthesis of food is carried out by plant leaves which are admirably designed for this function.

The primary adaptation of a leaf is toward the presentation of a great amount of surface that can intercept the sun's rays and, thus, "collect" the light; hence, the broad flatness of most leaves. The arrangement of leaves on the plant is also such as to insure that almost every beam of light within the compass of the plant is intercepted by at least one leaf. Under many trees in the summertime, the shade is almost unbroken.

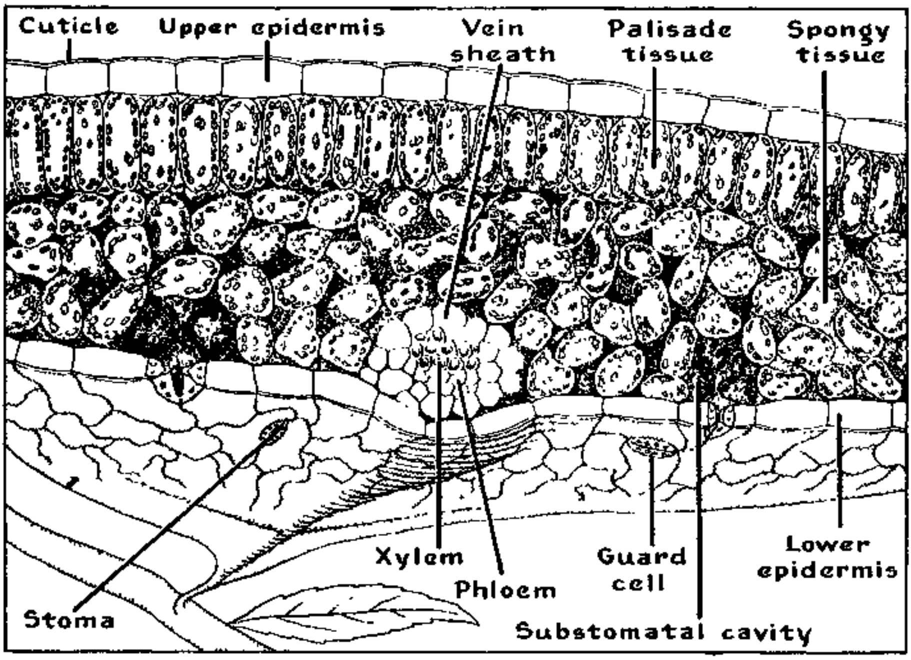

Fig. 23-1. The leaf, the photosynthetic organ of the flowering plants.

Figure 23-1 diagrammatically shows the cross section of a typical leaf. Notice that the **epidermal cells** do not contain chloroplasts. Photosynthesis is carried out by the internal cells, the **palisade layer** being the most important.

Besides light, carbon dioxide must be available. Some of this enters by diffusion through the epidermis; perhaps more comes through the openings called **stomata** (singular, *stoma,* Greek, mouth). Oxygen, the by-product of photosynthesis, leaves by this same route.

Water is also required for the process. Water is brought up from the ground through narrow tubes that are made up of the cellulose walls of plant cells that have died. The tubes in which water travels upward are collectively called the **xylem** (Greek *xylon,* wood; lumber is almost entirely xylem tissue).

As a result of photosynthesis, organic material is produced. Some of this stays in the leaf, but most of it is conducted to other parts of the plant via the **phloem** (Greek *phloios*, bark of a tree; when you strip off the bark of the tree, you are likely to remove the phloem layer). Phloem and xylem are surrounded by various other tissues to form a **vascular bundle.** The vascular bundles we identify in the leaf as the **veins** of the leaf.

Photosynthesis presents many problems to the plant. To intercept the maximum amount of light, it is desirable to have a broad, flat leaf. But this sort of leaf is subject to the loss of considerable water by evaporation. The waxy **cuticle** present on the outer surface of the epidermis helps to keep evaporative losses at a minimum.

For photosynthesis, a good exchange of gas (CO_2 in; O_2 out) with the air is desirable. But water vapor is a gas and can be lost. Here, again, are conflicting needs: to retain the water (vapor) without impeding the exchange of other gases. The plant resorts to a compromise. The size of stomata is adjustable. When they are illuminated, the **guard cells** on either side of each opening spread apart so that the stomata are open. At night, the guard cells bend together again and close the stomata. Also, under conditions of high temperature and low relative humidity, such as would prevail during a summer drouth, the guard cells will close the opening, thus decreasing the loss of water.

153. The Stem: Translocation of Materials

The stem functions for **conduction** and **support.** Green stems carry on photosynthesis, too, but, in most plants, this activity of the stem is quantitatively unimportant.

If a woody stem is cut across, the greater part of it is seen to consist of xylem, or wood (Fig. 23-2). The phloem is peripheral to it, and the two are separated by a layer of **cambium** cells (Latin, exchange). These cells multiply by cell division, adding new cells, now to the phloem layer, now to the xylem layer. The phloem layer, being to the outside, is gradually sloughed off as discarded bark tissue. The xylem, to the inside, necessarily accumulates. Only the most recently formed xylem cells have living cell material in them. Most xylem cells are devoid of living substance. Moreover, the top and bottom ends of their walls have disintegrated, resulting in the formation of continuous tubes in which watery solutions pass from the soil upward. By far the greater part of a tree is xylem.

The size of the cells produced by the division of the cambium cells is determined by the amount of food and water available to the cambium. In the spring, when there is an abundance of both food and water, large cells are formed. The spring xylem cells constitute what is called "spring wood." As the season wears on, water becomes scarcer, and the activity of the leaves diminishes; as a result, the size of the xylem cells decreases. To the naked eye, the smaller, more tightly packed cells of "summer wood" look like a dark ring separated by lighter areas of spring wood. Since most years have only one good growing season, the number of rings visible in a cut tree gives the age of the tree in years. Since no two

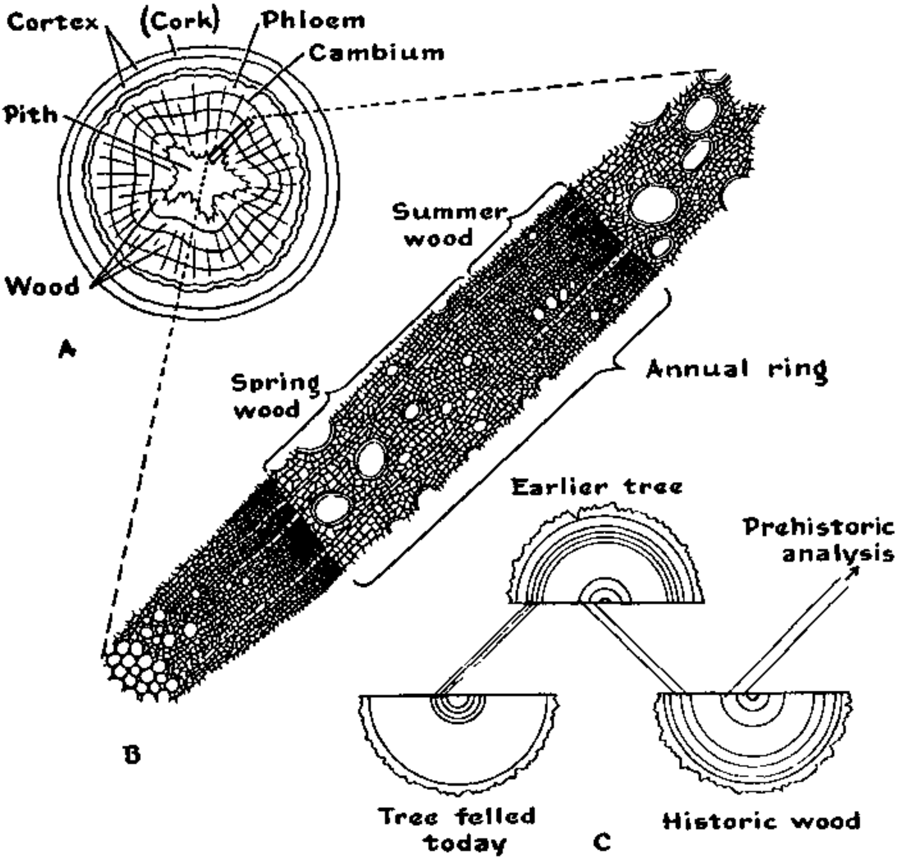

Fig. 23-2. The structure of a stem, and the significance of tree rings.

years are climatically identical, the relative amounts of spring and summer wood vary. From a tree whose felling date is known, one can deduce the wetness or dryness of every year during its lifetime. By matching the rings of a tree felled today against the rings of a long-fallen tree or a piece of lumber the geographic origin of which is known, one can extend this record backward indefinitely. Thus, we have learned about the climate of some parts of North America for every year since long before the birth of Christ. (See Fig. 23-2C.) Study of the tree-ring patterns also makes it possible to determine the date of felling of the tree that yielded a piece of wood used in making a prehistoric house and, hence, the probable date of construction of the house.

154. The Root: Absorption of Solutions

If the root system of a mature plant is carefully worked free from the soil by a gentle washing process, the extent of its branches can hardly fail to surprise one who has never thought about the matter. (See Fig. 23-3A.) However, what one sees with the eye is scarcely half the story. If a single root tip is examined microscopically, it is seen to be covered by hundreds of root hairs (Fig. 23-3B), each of which is an extension of a single epidermal cell. It is these microscopic root hairs which are responsible for the bulk of the absorption of water and nutrients from the soil.

One ambitious investigator made an attempt to estimate the extent of a root system. He grew a rye plant in the soil of a container 12 inches square by 22 inches deep. When the plant was four weeks old and 20 inches tall, he carefully washed the root system free of dirt. Then, by measurement and estimation, he found that there were, in this small volume, 390 *miles* of roots with a surface area of 2,500 square feet. The 14.5 billion root hairs had an estimated total length of 6,600 miles and an area of 4,300 square feet.

The root system is responsible for supplying the plant with its salt needs (nitrates, phosphates, etc.) and its water. This is all a plant needs from the soil. It needs no organic material, that is, no food as humans understand the word. The plant synthesizes all this sort of food from air and water. This truth has led to considerable experimentation with **soilless culture.** Almost any plant can be grown without soil if the water in which its roots are immersed contains the proper inorganic salts. This possibility has led some men to suggest that soilless culture (or *water culture* or *hydroponics*) be substituted for the traditional soil agriculture. Theoretically, it is possible; on economic grounds, it is out of the question except under special circumstances. Plants growing in water have to be furnished artificial supports. Because the water with the nutrient salts in it is a fine medium for algae, one has to build a covering to keep light from the water. And because the water tends to lose its oxygen (which the roots need), one must either install a system for continuously circulating the water, or a system that causes fluctuations in the water level of the solution that bathes an artificial soil of

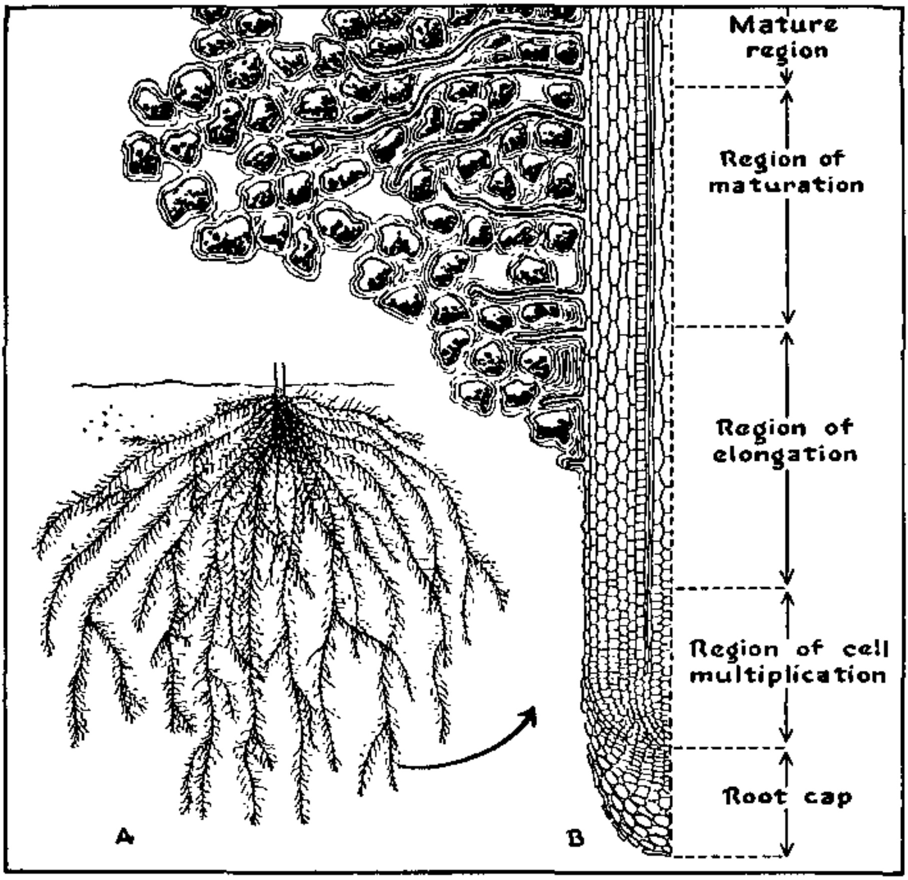

Fig. 23-3. The roots of a plant.

gravel or wood chips. Which practically brings one back to soil agriculture, and at great expense.

For experimental purposes, however, water culture is valuable. Soil is a very complex material, both physically and chemically. If one wants to know the effect of a certain chemical on a plant, one can find out with greater surety under the controlled conditions of soilless culture, than with that variable we call soil.

155. The Movement of Water in Plants

The equation for photosynthesis (equation 1) makes it clear that water is required for the manufacture of food. The utility of the root system is obvious. However, it must not be supposed that all the water absorbed by the roots is used in photosynthesis. On the contrary, only about one water molecule out of twenty absorbed by the roots enters into the photosynthetic reaction carried out by the leaves. The other nineteen water molecules, absorbed by the roots and transported up the xylem in the stem, evaporate from the leaves into the surrounding air without having accomplished any obvious good for the plant. Their movement upward probably helps to bring salts to the leaves. Their evaporation from the leaves helps to cool the leaves somewhat. But there is no proof that the relatively enormous quantities moved upward and *transpired* from the leaves serves a function in the plant. **Transpiration,** as the process of loss of water from plant surfaces is called, accounts for the movement of large quantities of water from the soil back into the air again. A corn plant loses several times its own weight in water per day. A cornfield no larger than an ordinary city lot transpires 250 *tons* of water in one growing season. One begins to appreciate the plant's need for those thousands of miles of absorbent root hairs.

The fact that a plant loses such large quantities of water daily makes clear the need for frequent rains or irrigation. As soon as the roots fail to deliver their customary bounty of water, the leaves wilt. This sometimes happens even in the presence of considerable amounts of water. For chemical and physical reasons, clay soils can hold part of their water so tightly that the root hairs cannot absorb it away from the soil particles. In such a soil, a plant may wilt even when there is still quite a bit of water present. A more striking example of this sort is furnished by acid bogs. Plants that are especially adapted to this environment grow well therein, but most plants cannot grow in a bog. Analysis has shown that the epidermal cells of the ordinary plant root are unable to develop into root hairs under the conditions that exist in a bog. Since most water absorption takes place through root hairs, we may say that the nonbog plant cannot thrive in a bog—surrounded by water—because it cannot get enough water. The situation is reminiscent of "The Rime of the Ancient Mariner."

How is water moved upward in a stem against the force of gravity? A plant has no heart. What is the mechanism that moves the water?

The problem of water transport in plants has long puzzled plant physiologists, and it is not yet solved to the complete satisfaction of all research workers in this field. We will give here a picture that seems to represent the majority opinion.

The three principal factors involved in the upward transport of water in stems are **root pressure, transpiration** and the **tensile strength of water.**

Root pressure can be demonstrated by removing the upper part of a geranium plant and attaching a manometer (§ 33) to the stump of the plant. In a short time, the manometer registers a considerable pressure, sometimes equivalent to one or two atmospheres. This pressure is due to activity of the roots which take in water and force it upward. Root pressure is responsible for the "bleeding" of maple-sugar trees. The fluid that comes out is called sap and is boiled down to yield maple syrup and sugar. The sap that may be collected from a wound made in a single maple tree sometimes amounts to as much as eight quarts per day. Root pressure cannot, however, be the sole agency involved in the ascent of sap because many plants show negligible root pressure. Even a maple tree shows little or no root pressure during the summer when the tree is in full leaf and when upward transport of water is at its maximum.

Transpiration is always a factor in the movement of water in an actively growing plant. As water is evaporated from a leaf surface, the column of water moves upward and replaces the water lost. This action reminds one of a "suction pump." Such a pumplike action can undoubtedly raise water but, in its quantitative aspect, doubts arise as to the adequacy of the mechanism. Recall that a suction pump (see § 33, and problems 5-7, 5-8, and 5-9) does not really operate by "suction" but by pressure—atmospheric pressure. The pressure of the atmosphere is sufficient to raise water in an evacuated tube only about 30 feet. But there are many trees, the redwoods and Douglas firs among them, which are more than two hundred feet high. Plainly, this mechanism is not enough to account for the rise of water to such great heights.

An additional factor believed to aid in the rise of water is the *tensile strength of water.* The tensile strength of a material is its ability to endure stretching without breaking. Many metals have great tensile strength. It may come as a surprise to the student that water has any tensile strength at all. It may not seem reasonable to ascribe tensile strength to a liquid. However, tensile strength is due to the attraction of like molecules for each other; even a liquid may exhibit such attraction under special circumstances. When liquid is confined in very tiny capillary tubes, it can exhibit tensile strength. Such tubes constitute the xylem of a tree. The evaporation of water from the leaf exerts a pull on the column of water; the whole water column can be pulled upward without breaking because of the tensile strength of water. In this movement, root pressure may aid. So, in brief, goes the most widely accepted theory of water transport in plants.

156. Tropisms and Plant Hormones

The city-bred man, planting his first backyard garden, is frequently asked by a more knowing neighbor if he was careful to "turn all the seeds rightside up, so the plants wouldn't grow with their roots in the air and their leaves in the ground?" Surprisingly enough, this bucolic jest frequently has the desired effect of worrying the agronomic neophyte. Fortunately, seeds know better. Regardless of how the seed is planted (Fig. 23-4 A-C), the growing leaf shoot grows upward, and the growing rootlet grows downward. Experiments show that the effective stimulus for these adjustments is gravity, the root responding positively to it and the shoot responding negatively. Responses of this general kind are called **tropisms** (Greek *tropos*, a turn). This particular tropism is called **geotropism** (Greek *ge*, earth). The root is negatively geotropic; the shoot is positively geotropic.

Other tropisms exhibited by plants are **phototropism,** the reaction to light (Fig. 23-4D); **hydrotropism,** the reaction to water (Fig. 23-4E); various **chemotropisms,** and **thigmotropism,** the reaction to contact exhibited by the twining surfaces of climbing plants (Fig. 23-4F).

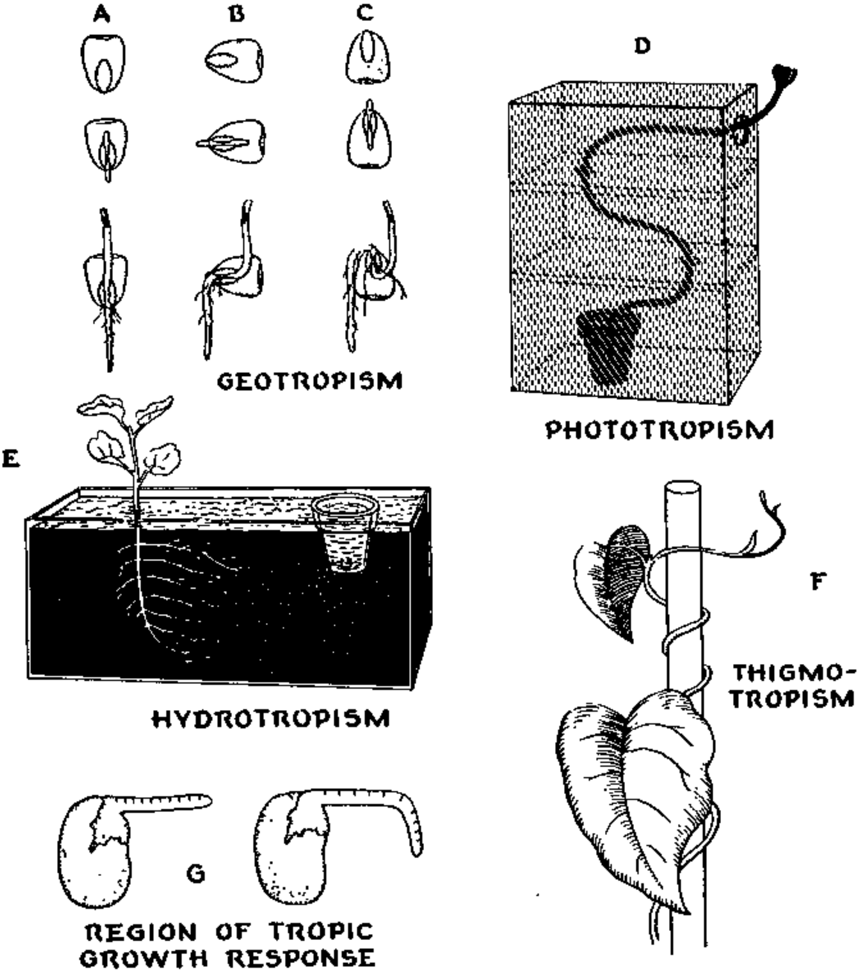

Fig. 23-4. The tropisms of plants.

What is the mechanism of a tropism? If the root of a seedling is marked with equally spaced lines (Fig. 23-4G), it is found that the region in which the adaptive curvature occurs is the most actively growing region. Other studies show that such adaptive curvature results from the *differential growth* of cells on opposite sides of the plant, the cells on one side elongating more than the cells on the other side. This is true in every such tropistic response.

What makes the cells grow longer or faster? This problem can best be attacked by studying the more general problem of the causes of any plant growth. The greatest light has been shed on this problem by studies of the growing tips of oat seedlings, *the coleoptiles*, as they are known (Greek *koleos*, sheath, so named because the primary leaf of the tip is at first completely enclosed in a sheath).

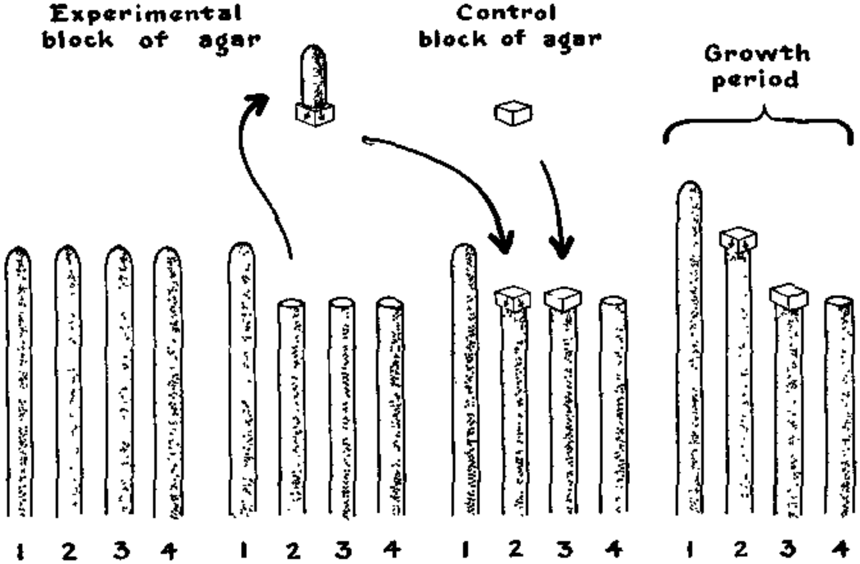

Fig. 23-5. The demonstration of a diffusible growth-promoting substance in the tips of oat coleoptiles.

Figure 23-5 shows, in a simplified way, the essence of the experiment which demonstrates that one part of a plant produces a substance that can stimulate the growth of another. If the tip of an oat coleoptile is removed and placed on a block of agar, there diffuses into the agar a substance which can stimulate growth in a decapitated oat coleoptile. A decapitated coleoptile will not grow otherwise. A control block of agar, which has not been in contact with a coleoptile tip, will not stimulate growth. Since the effective chemical substances diffuse to, and affect, tissues other than the ones that produce them, these substances are called **plant hormones.**

The hormones (for there are several) that can stimulate the *growth* of plants are called **auxins** (Greek *auxe*, a growth or increase). Having established the existence of auxins, the next question is, How can these substances explain the differential growth observed in tropistic responses? The following experiment gives a clue.

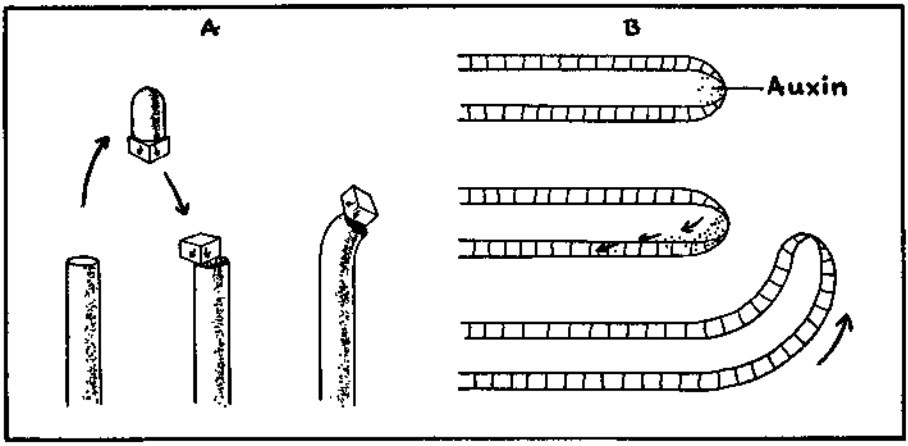

Fig. 23-6. Differential growth of a decapitated oat coleoptile (A) brought about by the asymmetrical application of auxin.

If on the tip of a decapitated coleoptile we place a piece of auxin-containing agar (Fig. 23-6A), *being careful to place it asymmetrically*, the subsequent growth of the coleoptile is also asymmetric, being the greatest on the side overlain by the agar. Evidently, the auxins pass, for the most part, straight downward, giving the greatest stimulation to the cells that are directly beneath the source of the auxin.

Can we now explain tropistic growth? Figure 23-6B shows an attempt to do so. A coleoptile normally grows vertically. If one is placed in a horizontal position, it presently shows the usual differential growth and heads upward again. It is believed that this effect results from the differential translocation of auxin from the producing tip to the cells on the lower side of the shoot below. Thus, could the necessary differential growth be explained. Various other tropisms can be explained in similar fashion, though it is not always clear that the necessary differential translocation of auxins does, in fact, occur; in cases in which the differential translocation can be proved to exist, the mechanism is not known. Plant physiologists have made only a start on the solution of the problems of growth.

Before leaving the subject of auxins, it would be well to point out some of the practical benefits that have resulted from research of the sort described above. In looking for substances that affect growth, a number of chemicals have been found which either inhibit or stimulate plant tissues. Some of these substances are natural plant products, others are only products of the chemist's art. One of the best known of the latter is one that bears the grandiloquent name of *2,4-dichlorophenoxyacetic acid*, which has been conveniently shortened to **2,4-D.** In minute quantities, this substance stimulates respiration and growth. In larger quantities, it stimulates respiration to such an extent that the plant burns itself out, so to speak, and dies. Broad-leaved plants are more sensitive to this effect than are narrow-leaved plants like the grasses. It is, therefore, possible to spray a lawn with the proper concentration of 2,4-D and kill dandelions, plantain and many other weeds without injuring the grass.

Numerous other uses have been found for this and other natural or synthetic auxins. With them, plant cuttings can often be induced to form roots, thus aiding vegetative reproduction (§ 151). Such treatment has proven particularly valuable in the propagation of apple and pine trees, species that can be rooted only with difficulty under natural conditions. The ripening of many fruits can be hastened by 2,4-D, which has been used, on experimental or commercial scales, to ripen bananas, pears, apples, and pineapples. For the last named, the use of growth hormone successively on different parts of a field of pineapples has made it possible to extend the harvest period over a longer period and, thus, to ease the pressure on the harvesting facilities.

Another interesting use of plant growth stimulators is in the production of seedless fruit. The pollen tube, when it grows down the ovary (§ 151), contributes two things to the development of a fruit: (1) male nuclei which unite with nuclei of the megagametophyte, and (2) a stimulus, apparently chemical in nature, to the host plant which causes it to start developing tissue which will surround the seeds, thus making a fruit. It has been found that the second contribution of the male gametophyte can be made just as well by treating flowers with various growth-stimulating chemicals, with the resultant production of **seedless fruit.** On an experimental scale, seedless tomatoes and seedless watermelons have been produced. Further experimentation along this line is awaited with keen interest.

QUESTIONS AND PROBLEMS

23-1. Where, in most plants, is the greater part of the food manufactured?

23-2. What is a stoma? How can it affect the rate of photosynthesis?

23-3. Define the following terms: xylem, phloem, cambium, cuticle.

23-4. What are the two principal functions of a stem?

23-5. "The cliff houses of Mesa Verde National Park were built, and abandoned, by Pueblo Indians before Columbus discovered America." Can you imagine what the evidence is for this statement? What are the assumptions involved? Explain the method used; if necessary, use illustrative diagrams.

23-6. In preparing a plant for transplantation, why is it important to see that some of the roots are surrounded by a considerable quantity of undisturbed soil?

23-7. Following transplantation, it is desirable to remove an appreciable fraction of the leaves of a plant. Why?

23-8. Why is it possible to "sow" seeds with no regard for "right side upness"?

23-9. Define tropism. What is the mechanism of a tropism?

23-10. There is an abnormal form of corn known as "lazy" corn. "Lazy" corn plants, though otherwise normal, grow prostrate on the ground. What is lacking in "lazy" corn?

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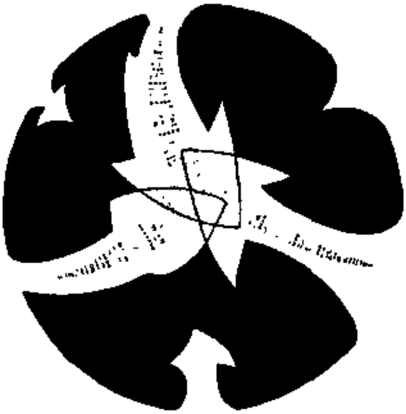
PART IV

The Unity of Living Things



Chapter XXIV

The Cell as a Unit

157. The Necessity of Broad Study

The history of science has shown that broad study is necessary even when interests are narrow. "Had I not studied insects in my youth, from inclination," said Cuvier, a famous French naturalist (1769-1832), "I should have been compelled to study them later, from necessity." Many an investigator, starting out to learn about man, has ended up studying yeast or soil bacteria or the epithelium of a clam. The path of research is unpredictable. One does not know around which corner enlightenment will be found or what training and knowledge will prove most relevant to the investigation of a given problem. The corollary of this is the thesis that the direct attack is frequently not the most fruitful. X-rays, which make flesh transparent, were not discovered by a man who wanted to look through humans, but by a man (Roentgen) who was studying the discharge of electricity in a vacuum. Microbes, which are so important in making our food, treating sewage, and causing disease, were discovered by a man (the Dutch investigator, Leeuwenhoek, 1632-1723) who wanted to know why pepper tasted "hot." It would be possible to cite thousands of similar instances of the unpredictability of research.

To those who would plan research—whether directors of research teams, managers of laboratories, or social planners—the apparent lack of congruence between desires and results is a serious matter. Much thought has been devoted to this problem, and out of the best of it there seem to emerge two generalizations:

First: In the long run, research that is concerned with *general* problems of theory yields greater results, both theoretical and "practical," than research that is directly aimed at the practical solution of a special problem.

Second: Accidents, which have played so large a role in scientific discovery, are fruitful only if they are witnessed by men who have a broad background in theory and who have thought much about the problems in their field. In the words of Louis Pasteur, "Chance favors the prepared mind." The German physicist, Roentgen, discovered X-rays in 1895, when photographic plates placed near his discharge tubes became fogged. This was an accident. But it is interesting to learn that the same accident befell a now-unknown English scientist who made the same observation, but who, conceiving his problem to be the "practical" one of keeping his plates from being spoiled, moved his photographic materials to a safe distance from his discharge tubes—and then went on with his "work."

158. The Need for Culturable Cells

One of the great generalizations of biology is that most organisms consist of cells. This generalization implies that, in somewhat the same sense in which the atom is a unit of physics, so is the cell a unit of biology. It is the smallest unit that shows all the properties of a living organism: growth, irritability, metabolism, movement of some sort, and reproduction. It is reasonable to expect, then, that we can learn of the general characteristics of living things by studying the properties of this small unit.

If a cell of a multicellular organism is really a unit, it should be able to live and multiply when isolated from the organized body. That this prediction is realized was shown in the early 1900's by Ross G. Harrison, an outstanding American zoologist, who succeeded in continuously maintaining living salamander cells outside the body of the salamander. Since that time, cells from many other animals and plants have been so "cultured" in the laboratory. The most spectacular demonstration was made at the Rockefeller Institute where living heart cells from an unborn chick were cultured for some twenty years. During all this time, the cells moved about, metabolized, exhibited irritability, grew, and reproduced themselves. In fact, their continuous reproduction presented one of the serious problems of culturing them. It was necessary to remove some of the cells everyday and throw them away to keep the number of cells within reasonable bounds. At the end of twenty years, the cultured chick heart cells were living as well and multiplying as fast as at first, though the embryo chick from which they had been taken, had it been allowed to live, would long ago have hatched, matured, grown old, and died. No amount of care that we know of could have prevented this natural course of events. The processes of maturing and aging and dying are somehow linked to the organizational complexity of the multicellular organism. A few cells isolated from the whole organism, if properly fed and cared for and kept from overcrowding themselves, are capable of living forever in their descendants. In this sense, **cells are potentially immortal.** An unorganized colony of cells has no inherent reason for dying. The reasons for the death of the organized collection of cells that we call an *individual* are not known.

We can study the general characteristics of living things by studying cells. Theoretically, we might study cells cultured apart from such multicellular organisms as men, salamanders, chickens, and tomato plants. Practically, many difficulties have been encountered in the study of such cells. Accustomed as the cells are to being surrounded by many other living cells, they are difficult to maintain in test tubes and other vessels surrounded only by nonliving "medium," i.e., by some nonliving soup or jelly. Cells of complex organisms are frequently very exacting in their temperature requirements and often require special nutrient media, like blood serum or fluid from the peritoneal cavity. These materials are not easy to obtain in quantity, and they are expensive. It is highly desirable to have cells available that can be grown on distilled water and the common chemicals that can be poured out of bottles. Such unfastidious cells are found in great variety among the "lower" plants, among the yeasts, molds, and bacteria. Because these organisms are so well suited to the study of cellular physiology and because they have been studied so much, we shall consider them at length in the chapters to follow. The student should bear in mind that the principles illustrated by these lowly organisms apply not only to them but to the generality of organisms, including man himself.

QUESTIONS AND PROBLEMS

24-1. Which would you expect to be easier to culture: the cells of a guinea pig or the cells of a lizard? Why?

24-2. Suppose a piece of tissue, cultured *in vitro,* doubles in size every week. If, at the beginning of the experiment, the tissue occupies 0.01 cubic centimeters of space, how much space (if it continues to reproduce at this rate) would it occupy at six months? What preparations should be made to carry the culture through to its first birthday?

24-3. Since cells are potentially immortal, one might suppose that we would one day be able to find the secret of perpetual life for the individual. Would you consider this a desirable discovery? Give your reasons.

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Chapter XXV

Cell Physiology

159. The Precision of Metabolic Breakdown

The over-all course of respiration (§ 36) can be represented by this general equation:

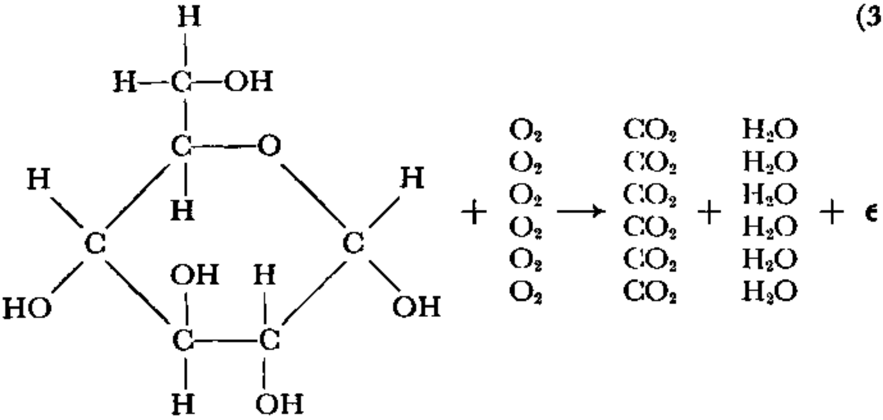
$$\text{Organic material} + O_2 \longrightarrow CO_2 + H_2O + \epsilon \qquad (1)$$

The process of respiration occurs only inside cells. Respiration takes place in all organisms that are large enough to be seen with the naked eye, and in most microscopic organisms. There are some differences in the course of respiration in different species of cells, yet there are underlying samenesses in the process wherever it occurs, whether in the cells of the muscle or brain of a mammal, or in bacterial cells. What we know about respiration we have learned by the study of scores of different species of cells. In the discussion that follows, some of the general principles that have been revealed will be presented. The story necessarily involves some chemistry, for, as Lavoisier put it, "Life is a chemical function." However, only the simplest aspects of the chemical processes will be presented and in such a general fashion that, it is hoped, even one who is almost completely unversed in chemistry can catch the drift of the story.

Equation (1) is not an exact equation, of course; it is too vague. "Organic material" might mean any of millions of compounds or any combination thereof. To see where our problem lies, we shall have to arbitrarily take a particular organic compound and write a new equation (2).

$$C_6H_{12}O_6 + 6O_2 \longrightarrow 6CO_2 + 6H_2O + \epsilon \qquad (2)$$

The above equation represents the respiration of glucose. It is more explicit than (1). It is balanced. But, as written, it oversimplifies the problem. The structure of the organic molecule *glucose* is more complicated than equation (2) would suggest. The glucose molecule is a three-dimensional figure that cannot be easily represented on two-dimensional paper, so we will content ourselves with an approximation to it in our next version of the respiratory process (equation 3).


(3)

Now we begin to get a faint idea of our problem. How can the complex glucose molecule be broken down so as to yield the simple molecules on the right? Can such a complex molecule disintegrate so precisely? Does it decompose in one magnificent explosive reorganization? It seems unlikely. Explosions usually produce many and varied pieces. The fact that such a structured molecule as glucose is taken apart into such uniformly neat pieces as CO_2 and H_2O suggests a process that is more controlled and deliberate, so to speak, then an explosion. Respiration is indeed a controlled, orderly, step-by-step process. We propose now to indicate briefly the kinds of steps involved.

160. Some Fundamental Types of Biochemical Reactions

Respiration is the name that we give to the net result of the cellular burning of foodstuffs, as indicated by equation (1) or (2). But, if we could look inside the cell and see the chemical processes taking place, we would see nothing that we could identify as the respiratory process. This may sound odd, but an analogy should help.

The operation of an automobile factory could be represented by an over-all equation of this sort:

$$\text{X lbs. iron} + \text{Y lbs. glass} + \text{Z lbs. plastics} + \epsilon \longrightarrow \text{1 automobile} \quad (4)$$

But if one looks inside an automobile factory, one sees no process corresponding to equation (4); instead, one sees here a boring machine finishing a block, there a workman tightening a bolt, and there another workman inserting a pin. There is no operation (4). There are hundreds of separate operations which are so organized that the end result of all of them can be represented by equation (4). If we are to understand the operation of making an automobile, we must study the separate operations and the organization of them in the whole manufacturing pattern.

So it is with all metabolism. The over-all process whereby food is built up into cell substance or torn down into CO_2 and H_2O is made up of many individual steps, intricately organized with respect to each other. Of the organization we are just beginning to see dim outlines; of the separate steps we already know quite a bit. Some of the better known steps will be described below. Since the formula of the so-called "simple" sugar glucose is too complex for us to see at a glance what is happening to it, we shall speak of other, simpler substances, or of general types of substances, and the changes they may undergo.

Before the student sets out to read the following sections he is urged to heed this advice:

1. If he feels uncertain of his chemistry, he should reread Chapter VII.
2. In his first reading of the remainder of the chapter, he should try to get the general *picture* of the reactions. He should not try to memorize the particular organic compounds that are used as examples, but should concentrate on the essentials of each reaction. To help focus attention on the significant atoms or chemical groups, **bold face type** is used for the relevant portions of the molecules. The atomic symbols printed in light type should receive only cursory attention.

Aside from the particularities of each reaction, it is important to notice that **all of the reactions that are of biochemical importance**

are relatively simple. In each instance, only a very few atoms change their positions. As we shall see, **the extensive chemical changes brought about by living organisms represent the sum of many simple chemical changes.**

Hydrolysis has been described before (§ 49), using as an example the hydrolysis of sucrose (5).

$$\text{sucrose} + H_2O \longrightarrow 2 \text{ molecules of } C_6 \text{ sugar} \qquad (5)$$

It is more useful to consider the sucrose, a C_{12} sugar, as being made of two partial molecules of C_6 sugar, one called *glucose* and the other called *fructose,* which are linked together in such a way that they lack only a molecule of water to complete the two C_6 molecules. In completing these molecules, the H_2O molecule itself is split into two portions, H and OH (see again Fig. 7-1), one of which goes with one of the C_6 portions, the other with the other, as indicated by equation (6).

$$\text{glucose-fructose} + HOH \longrightarrow \text{glucose(H)} + \text{fructose(OH)} \qquad (6)$$

On the right side of this equation, we have written (H) and (OH) after the names of the sugar products to show what has happened to the water.

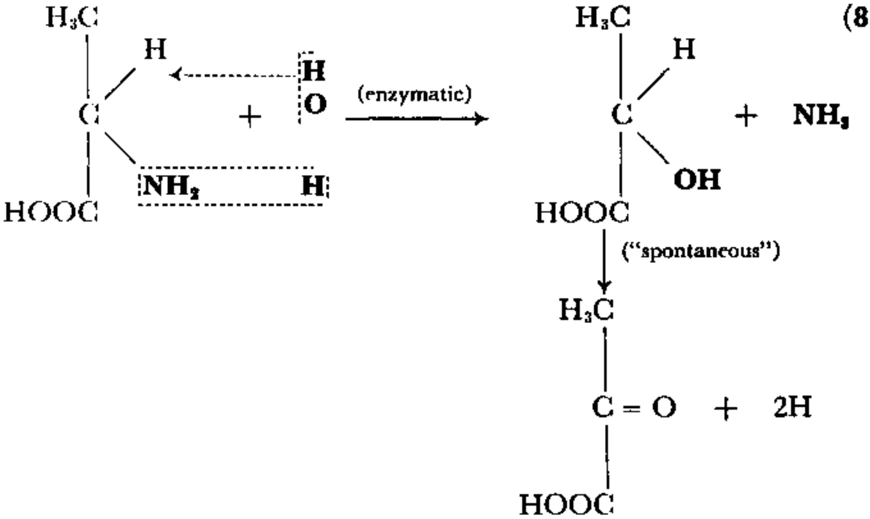
Equation (6) describes a particular example of hydrolysis. We can make it more general by writing equation (7), in which AB stands for any molecule which may be split into two parts, A and B, by the insertion of a molecule of water:

$$AB + HOH \longrightarrow AH + BOH \qquad (7)$$

Thus is starch hydrolyzed to produce sugars (§ 51); proteins hydrolyzed to produce amino acids (§ 53); and fats hydrolyzed to produce glycerol and fatty acids (§ 55). When, considering these particular cases, we perceive the characteristics common to all and express them in abstract or general terms (see equation 7), we are carrying out an intellectual process known as **generalization.** This process, which is a type of classification, is an important one in science. It is important in the development of science in that it focusses attention on fundamental problems. It is important in the learning of science in that it furnishes the student with a single mental *peg,* so to speak, on which he can hang many facts.

Deamination. When an amino group (NH_2) is removed from a compound, the process is called deamination. An example of a deamination is diagrammed in equation (8).

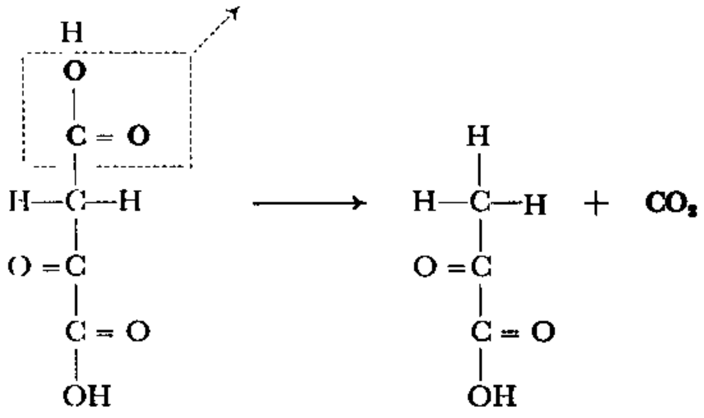
(8)



Two separate steps are indicated in this reaction, the first of which is brought about by an enzyme; the second does not require an enzyme, and we have, therefore, called it a "spontaneous" reaction. For the moment, we are concerned only with the first reaction, the deamination. In the living cell, this reaction is brought about by an enzyme called a *deaminase*. It will be noted that this type of deamination is a hydrolytic one.

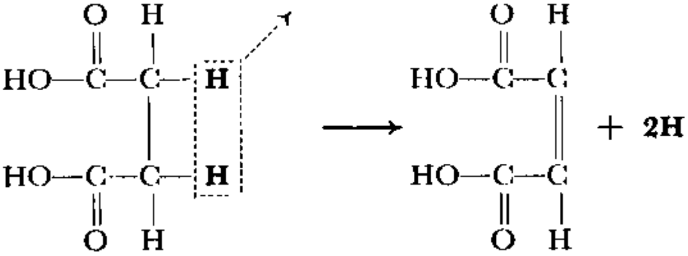
Decarboxylation. In this common type of reaction, the length of the carbon chain is decreased by one carbon atom (Equation 9). It is ap-

(9)



parent that this reaction can be used repeatedly to chop up a large molecule, so to speak; also, that it may account for some of the CO_2 liberated in metabolism.

Dehydrogenation is a term applied to chemical reactions in which one or more hydrogen atoms are stripped from a molecule. An example is shown in equation (10). It will be noted that we have here, as at the end of equation (8), indicated 2H as a product, although there is no such stable substance as H (hydrogen gas is H_2). Although sometimes

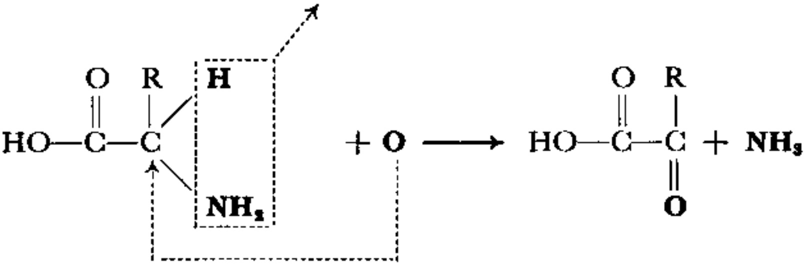


(10)

the gas H_2 may be a product, usually this is not the case, but rather the hydrogen atoms that are produced in the cell are used immediately in other chemical reactions that are taking place in the immediate vicinity of the dehydrogenation reaction.

An **oxygen-addition reaction** occurs when oxygen is added to a molecule as, for example, in the reaction shown in equation (11). It may be wondered why the awkward term "oxygen-addition reaction" is used instead of "oxidation reaction." To justify this usage, we must now present a modern view of the nature of oxidation and of the proper use of the term.

(11)



161. The Nature of Oxidation

The term oxidation was originally applied only to reactions in which oxygen was combined with some other substance. As an example of an "oxidation reaction," see equation (12) in which oxygen combines

$$CH_4 + 2O_2 \longrightarrow CO_2 + 2H_2O \qquad (12)$$

with methane ("marsh-gas") to yield carbon dioxide and water.

However, this was not the only sort of reaction recognized as an oxidation. Other "oxidation reactions" were of the type illustrated by equation (13) in which the oxygen served to strip hydrogen atoms off

$$H_3C \cdot CHNH_2 \cdot COOH + O \longrightarrow H_2C = CNH_2 \cdot COOH + H_2O \quad (13)$$

a larger molecule, yielding a new dehydrogenated molecule and a molecule of water. Such a reaction can be written in a more general form (equation 14). We indicate the molecule that can give two hydrogen atoms by the *general* formula AH_2; such a substance may be spoken of as a **hydrogen donor.**

$$AH_2 + O \longrightarrow A + H_2O \qquad (14)$$

As the knowledge of chemistry developed, it was found that there were other reactions in which a substance *other than oxygen* stripped hydrogen atoms from a molecule. This led to a further generalization of equation (14), namely, equation (15). In such a reaction, the substance

$$AH_2 + B \longrightarrow A + BH_2 \qquad (15)$$

AH_2 is said to undergo oxidation, *regardless of whether "B" stands for oxygen or not.* During the course of the reaction, the original molecule, AH_2, is said to become *oxidized* to A, and the substance B is said to become *reduced* to BH_2. From this usage, we extract these definitions:

Definition:

Oxidation: a substance is said to undergo oxidation when it combines with oxygen or when it releases hydrogen.

Definition:

Reduction: a substance is said to undergo reduction when it combines with hydrogen or when it releases oxygen.

Notice how the process of generalization (§ 160) has led us to a definition of the term "oxidation" that is markedly different from its first definition, and how the etymology of the term gives an insufficient clue to its present-day usage. *We no longer speak of oxidation reactions, but only of substances that undergo oxidation, or become oxidized.* As can be clearly seen by a re-examination of equation (15) in the light of our definitions, in all such reactions some substances become oxidized while others become reduced. There is no such thing as an oxidation-reaction, or a reduction-reaction. But we may speak of an **oxidation-reduction reaction.**

162. The Role of Enzymes in the Chemistry of the Body

The chemical reactions presented in the preceding sections have been selected because of their importance in biology. These reactions take place in living cells. Most of them do not, however, take place outside of living cells *under ordinary conditions*, that is, at room temperature, at atmospheric pressure, and in ordinary glass vessels placed in dim light. How is it, then, that these and many other reactions can take place at the ordinary temperatures and pressures prevailing inside cells?

The answer lies in the multitudinous molecules of enzymes to be found within living cells. In discussing hydrolysis (§ 49), we pointed out that the rate of this reaction is increased many thousand- or millionfold by the presence of organic catalysts called enzymes. Enzymes that speed up hydrolyses are called hydrolyzing enzymes. They are to be found not only in the digestive juices of the gut but, in much greater variety, inside living cells. By their presence, cells are enabled to split a wide variety of large molecules into smaller molecules.

What of the other reactions discussed, decarboxylation and the oxidation-reduction reactions; are these, too, brought about by enzymes? Yes, definitely. Most of the reactions of the living cell are made possible only by the presence of enzymes. We say "most" because, in many reactions, there may be an intermediate product formed by enzyme action that undergoes a further spontaneous nonenzymatic reaction. For an example of this, see again equation (8); the first reaction is brought about by an enzyme; the second occurs automatically because the intermediate product is chemically unstable. The over-all reaction is made possible, however, only by the presence of a deaminating enzyme called a *deaminase*.

Bearing in mind the sort of exception pointed out in the preceding paragraph, we may now safely state the following generalization:

All the chemical activities of living cells are made possible by the presence of specific enzymes.

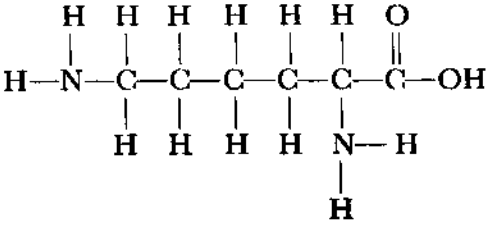
What do we mean by "specific"? In recent years, a considerable number of enzymes have been extracted from cells and purified. An enzyme can be purified by chemical procedures until only one sort of molecule, the enzyme molecule itself, is present in the sample, purity being determined by various chemical criteria of purity, such as that of crystallizability. When the properties of a pure enzyme are investigated, it is found that the enzyme is specific, in that:

a) It can bring about only one kind of chemical **action,** such as deamination or hydrolysis.

b) It can act on only a limited number of kinds of molecules, sometimes on only one class of molecules, in other cases on only one kind of molecule. A substance an enzyme can act upon is called a **substrate.**

With regard to the second sort of specificity, there are considerable differences among the enzymes. The hydrolyzing enzymes of the digestive tract are usually not very specific with respect to substrate since one enzyme is able to act upon members of a large class of chemical compounds. A single kind of *proteinase*, for instance, may be able to act upon many thousands of different kinds of protein. This is probably fortunate for us, since our menu includes many thousands of different kinds of food molecules. It would be rather inefficient, so to speak, if we had to have a different kind of enzyme for each kind of food molecule.

On the other hand, the enzymes to be found inside of cells are usually rather specific with respect to substrate. Some enzymes will act on only a few closely related compounds. The action of other enzymes is completely restricted to a single chemical substance. For example, there is an enzyme called "*l*-lysine decarboxylase," which will not only not decarboxylate any other amino acid, but will act on only one of the two forms of lysine known. These two forms both have the same molecular formula, namely:



$$\begin{array}{ccccccccccccccccc}
 & & \text{H} & & \text{H} & & \text{H} & & \text{H} & & \text{H} & & \text{H} & & \text{O} & & \\
 & & | & & | & & | & & | & & | & & | & & \| & & \\
\text{H} & - & \text{N} & - & \text{C} & - & \text{C} & - & \text{C} & - & \text{C} & - & \text{C} & - & \text{C} & - & \text{OH} \\
 & & & & | & & | & & | & & | & & | & & & & \\
 & & & & \text{H} & & \text{H} & & \text{H} & & \text{H} & & \text{N} & - & \text{H} & & \\
 & & & & & & & & & & & & | & & & & \\
 & & & & & & & & & & & & \text{H} & & & &
\end{array}$$

However, X-ray analysis indicates that molecules of lysine can have two different shapes as indicated in Figure 25-1. These molecules are identical as regards the way in which the atoms are joined one to another, except that one molecule is a mirror image of the other. This might seem to us a trivial difference, but it is not so to the enzyme molecule which can decarboxylate the *l*-lysine molecule but not its mirror image, the *d*-lysine. Such specificity of an enzyme is not uncommon but is rather the rule. There are a great many metabolic processes of living cells that can use only the *l*-type configuration of molecule. Similarly, the molecules synthesized by living cells are, in almost all cases, of the *l*-form.*

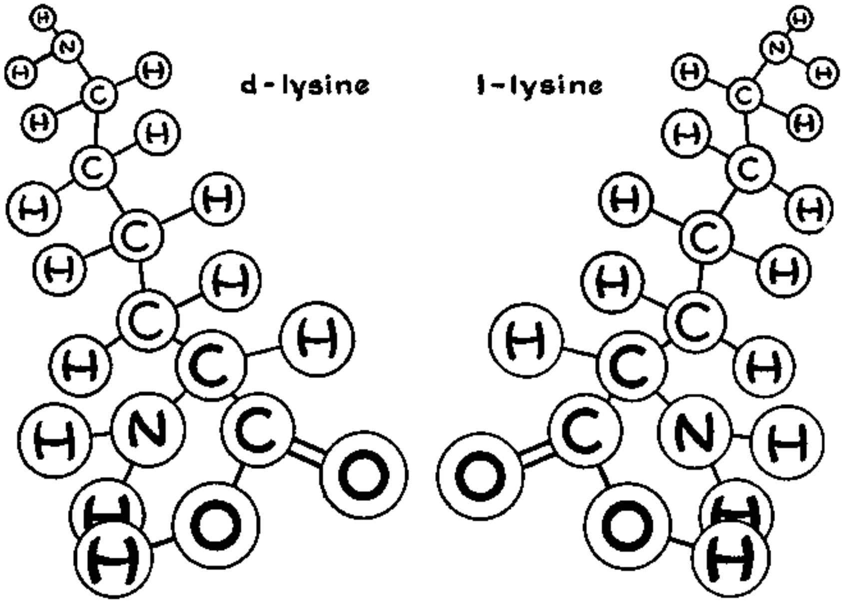


Fig. 25-1. Two varieties of an amino acid. They are called *optical isomers* because only by optical means, e.g., the use of a mirror, can the image of one be made to coincide with the other. Trivial as this difference might seem, for many cells it spells the difference between a food and a waste material.

Where an enzyme is not absolutely specific, its specificity is in terms of certain significant *groups of atoms* of the substrate molecules. For

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* It would take us too far into the field of chemistry to explain exactly how *d*- and *l*- are defined. It should suffice to say that *d* stands for *dextro* (Latin, right) and *l* for *laevo* (Latin, left). If, by definition, one type of molecule is a "right-handed molecule," its mirror image must be called a "left-handed molecule."

instance, there is an enzyme extractable from yeast that catalyzes the decarboxylation of pyruvic acid, $CH_3 \cdot CO \cdot COOH$. It can also catalyze the decarboxylation of $CH_3 \cdot CH_2 \cdot CO \cdot COOH$ and of $CH_3 \cdot CH_2 \cdot CH_2 \cdot CO \cdot COOH$. For this class of compounds, the enzyme is specific. And, in every case, it brings about the same reaction, namely, a decarboxylation which yields an aldehyde ($R \cdot CHO$) and a molecule of carbon dioxide, as shown in the generalized equation (16).

$$R \cdot CO \cdot COOH \xrightarrow{\text{(yeast decarboxylase)}} R \cdot CHO + CO_2 \qquad \textbf{(16)}$$

The evidence presented above, together with a great many other similar facts, has led to the following generalization which guides the researches of modern biochemists:

one enzyme ⟶ one action

163. Synthesis: Reversibility of Enzyme Action

A catalyst, by definition, is a substance which merely speeds up a reaction. A catalyst does not suffer any permanent change; it does not alter the nature of the products; it does not change the equilibrium point of the reaction. It is common practice to write a chemical equation with only one arrow as in equation (15). However, abundant

$$AH_2 + B \longrightarrow A + BH_2 \qquad \textbf{(15)}$$

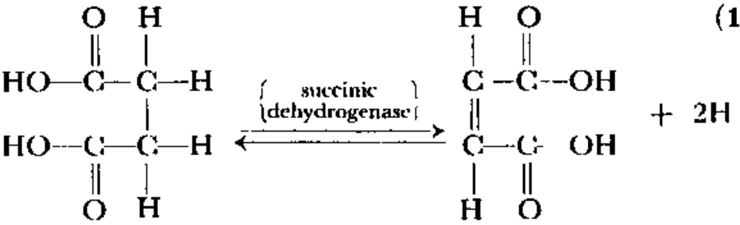
chemical studies show that every equation should always be written with two opposing arrows as in equation (17).

$$AH_2 + B \rightleftharpoons A + BH_2 \qquad \textbf{(17)}$$

Every equation depicts an equilibrium in which there is no *net* change once the equilibrium point is reached. Each reaction has its own equilibrium point. In one case, the equilibrium may be reached when the reaction has proceeded 99 per cent to completion "to the right," i.e., to the formation $A + BH_2$ in equation (14). In another reaction, the equilibrium point may be far to the left. In another, it may be more in the middle. But, wherever it is, the addition of a catalyst to the system does not change the equilibrium point; it merely cuts the time required to reach this equilibrium. So far, as we know at present, enzymes are true catalysts.

The consequences of this we may see by looking further into the reaction indicated in equation (10) which we will rewrite here with verbal additions.

in symbols:



$$\begin{array}{c} \text{O}\ \ \text{H} \\ \text{HO—C—C—H} \\ \text{HO—C—C—H} \\ \text{O}\ \ \text{H} \end{array} \xrightleftharpoons{\left\{\begin{smallmatrix}\text{succinic}\\ \text{dehydrogenase}\end{smallmatrix}\right\}} \begin{array}{c} \text{H}\ \ \text{O} \\ \text{C—C—OH} \\ \text{C—C—OH} \\ \text{H}\ \ \text{O} \end{array} + 2\text{H} \qquad (10)$$

in words: $\text{succinic acid} \xrightleftharpoons{\left\{\begin{smallmatrix}\text{succinic}\\ \text{dehydrogenase}\end{smallmatrix}\right\}} \text{fumaric acid} + 2 \text{ hydrogen atoms}$

This reaction, like all reactions, moves in one direction until the equilibrium point is reached; after that, the rate at which the reaction goes to the left is the same as the rate at which it goes to the right, and there is henceforth no *net* change. The succinic dehydrogenase, since it does not determine the direction of the reaction but only the speed, could as logically be called a fumaric hydrogenase. That it can, in fact, catalyze the hydrogenation of fumaric acid has been shown. If an excess of hydrogen atoms is furnished by a *hydrogen donor*, reaction (10) proceeds to the left until equilibrium is re-established or the hydrogen donor becomes exhausted. On the other hand, if the hydrogen atoms are removed from the scene of action by some "hydrogen acceptor," the reaction will proceed to the right until the equilibrium is re-established or until the succinic acid is exhausted. Notice that one direction, to the right in this case, constitutes a chemical analysis or breakdown, while the other direction, leftward, is a synthesis.

Notice that a single enzyme can catalyze both analysis and synthesis. An enzyme is not, by nature, either a synthesizing enzyme or an analyzing enzyme. Whether the action of an enzyme results in building up the cell or in tearing it down is determined by all the other activities that are going on in the cell and on what the cell is being furnished from the outside. In the presence of ample food molecules (hydrogen donors), many enzymes act in a synthetic fashion [see again equation (10)]. The same enzymes under conditions of starvation (lack of hydrogen donors) may break down the molecules contained in the cell.

164. Protoplasm: Definition

A century ago, when men first realized that the cell was a fundamental unit of living things, scientists turned their attention to the interior of the cell, wondering what it was that accounted for the state of livingness. They saw miscellaneous bodies—nuclei, chloroplasts in plant cells, etc.—floating around in a colorless, fluid matrix. When it was realized that most of the properties of living things were also properties of this fluid material, it was felt desirable to give it a name. The name that was finally agreed upon was **protoplasm** (Green *protos*, primary; *plasma*, something formed). As far as the eye could tell, there was no significant difference between the colorless matrix of a *Spirogyra* cell, a *Paramecium*, or a rabbit-liver cell. So the same term—protoplasm—was applied to this undistinguished material seen in all cells. The application of a single term to the matrix of all cells implied an identity in the living material of all cells, an implication that was surely unjustified at the time it was made. However, though there clearly are differences in the protoplasms of various cells, the surprising picture that has come out of continued research has been the essential oneness of the life processes wherever they occur, whether in trees, bacteria, crayfish or men. So, today, we speak of "the properties of protoplasm" without specifying the plant or animal species whose protoplasm was studied, meaning, thereby, those properties which seem to be common to the living part of the cells of all organisms. There is not as much difference between a tree and a man as a layman might suppose.

165. Colloids, and the Structure of Protoplasm

Investigation of the enzymes that can be extracted from living cells has presented us with a picture of cell metabolism that is bewildering in its complexity. Simultaneously, in a single cell, opposing processes of dehydrogenation and hydrogenation, amination and deamination, hydrolysis and condensation are going on. Different molecules of a single substance may be undergoing a dozen different actions within a single cell. How can we account for the fact that myriad conflicting reactions may proceed simultaneously in so small a volume as that of a cell? We do not really know the answer at present, but what we know of the nature of protoplasm enables us to see dimly how the complexities of metabolism may be made possible.

Protoplasm is a viscous fluid, rather like dilute gelatin. It is over 90 per cent water. Dissolved in it are many different substances, various salts, some carbohydrates, etc. In addition, however, it includes a considerable portion of substances that are not in solution but are in a **colloidal condition.** Protoplasm as a whole is said to be a **colloid.** What do these terms mean?

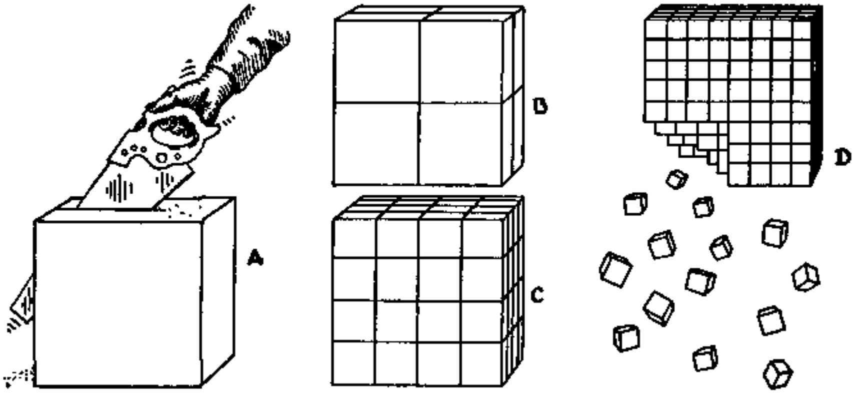


Fig. 25-2. The ratio of surface to volume is greater for small bodies than for large.

To understand the nature of colloids, we need to recall the relation of surface to volume in different sized bodies. Figure 25-2 is intended to help us visualize these relationships. If we subdivide a large body (Fig. 25-2A) into some smaller bodies (Fig. 25-2B), it is quite clear that we do not increase the total volume or total mass of material, but it is equally clear that we *do* increase the total surface. By subdividing greatly (Fig. 25-2C), we can increase the surface to a value many times the original. Even a very small mass of material may, if sufficiently subdivided, come to have a very large surface indeed.

Subdivision of a mass of material brings with it consequences. Gold will not dissolve in or float in water. But, if it is in small enough pieces, the gold will remain suspended indefinitely because the force of the bombardment of water molecules is so much greater than the force of gravity. A permanent suspension of solid particles of this sort in a liquid is called a **colloidal suspension.** Again, oil will not dissolve in or disperse throughout water, but if it is finely divided, it will remain suspended. A dispersion of a liquid in a liquid is called a **colloidal emulsion.**

The particles of most colloids are too small to be seen with an optical microscope. In fact, some authorities would restrict the term colloids to such submicroscopic dispersions, but there is no agreement in this definition. The particles of a colloid, though small, are not as small as molecules. Every colloidal particle consists of a few, or moderately many molecules.* Physically, colloids show properties that are not exactly those of a fluid or of a solid; consider, for instance, the semifluidity of glue and of gelatin dessert.

Protoplasm is a colloidal material. Is this fact of any significance? It is believed that at least two characteristics of colloids may be of importance in determining the properties of living material.

The large amount of surface may facilitate chemical reactions. It is a commonplace of chemistry that many chemical reactions take place more rapidly on surfaces (e.g., the walls of the containing vessel) than they do in the middle of the solution. It is probable that the immense amount of surface presented by particles of colloidal dimensions speeds up some chemical reactions.

The complexity of the structure of protoplasmic colloids may make partial isolation of biochemical processes possible. We know that some cell processes are restricted to visible structures of the cell. For instance, photosynthesis is restricted to the chloroplasts of a plant cell. Such topographical localization may make more readily possible the simultaneous occurrence of photosynthesis and respiration which, it will be recalled, are opposing reactions as far as their net results are concerned. It has been suggested that the submicroscopic structure of colloidal protoplasm may similarly make possible a certain amount of topographical isolation of opposing or competing reactions within the same cell. This is a speculative point, but it is well taken.

166. Complexity of Cellular Functions

The flexibility of cell metabolism is impressive. Every cell is made of thousands of different chemical substances, many of which are unique to that species of cell. A cell can make these many products even when

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* However, some protein molecules are so large that completely dispersed molecules may yield a colloidal suspension.

only a few chemical substances are taken in as food. In many cases, a single organic food substance will suffice for the production of all the thousands of organic chemicals that constitute the protoplasm of the cell. There are, for instance, a great many different soil bacteria that are capable of manufacturing all their organic chemicals from the amino acid glycine. In such cases, we can picture, in a simple way, the transformations the amino acid must be undergoing (Fig. 25-3). Some of the molecules (Path #1) may be deaminated to form simple carbohydrates which may be condensed into larger molecules, such as starch or glycogen, and stored. Other molecules (Path #3) may be oxidized, furnishing the energy that is used to drive other chemical reactions. Still other molecules (Path #2) may be condensed to form proteins, some of which are turned into the enzymes which are used for all the processes including the ones just mentioned! Truly, when conceived in even the simplest fashion, the functions of the cell are impressive. Though we cannot see it, there must be some sort of submicroscopic organization which makes possible the harmonious interplay of all these reactions in such a way as to permit life to go on.

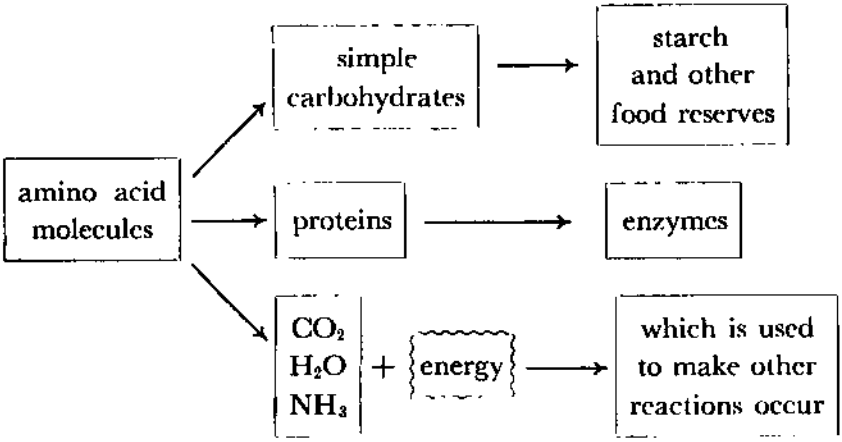


Fig. 25-3. Alternative fates of a food substance.

167. What is Life?

It is time to ask once again a question we asked, and avoided, in § 7, namely, "What is life?" We do not propose, being incompetent, to answer it fully now, but perhaps we can come a bit closer to the central problem.

In almost all living cells, there is a complex of simultaneously proceeding reactions going on continuously so long as the cell is alive. If these reactions are completely stopped, even for a moment, the cell becomes dead, irreversibly so, *in most cases.* There are, however, some organisms, e.g., some bacteria, which can produce certain types of cells (**spores**) which show no signs of life or of any chemical processes, but which can "revive" later and become obviously alive. The existence of these exceptional types of cells makes even more mysterious the fact that, in so many cells, life can never pause without ceasing altogether. In what follows, we shall speak of the generality of cells which have no spore stage.

Inside a cell, chemical substances are in a continuous state of change. Proteins are being changed to amino acids, amino acids to carbohydrates, carbohydrates to fats, fats to amino acids, and these again to proteins or other substances ceaselessly. Not only does this happen to foodstuffs, but the basic substances of the cells themselves, the proteins and the enzymes, are constantly being destroyed and resynthesized. By using radioactive elements as tracers (§ 31, § 143), it has been shown that, in the liver of a rat, for instance, half of the proteins are broken down and resynthesized in the short space of six days! A continuation of this rate would mean that, at the end of four months' time, not more than one protein molecule out of a million in the rat liver would be a molecule that was present at the beginning of that period. Probably the same statement would hold substantially true for all other parts of the body. And yet, if we ignore aging processes for the moment, the rat, as a whole and in its individual cells, remains substantially unaltered. The materials of its protoplasm are being constantly discarded and replaced, and yet, the visible form seems scarcely to change. In fact, continuous, systematic changes are indispensable to constancy.

One tends to think of a constant object—a rat or a liver cell—which carries out operations on ephemeral food materials. Yet, in the light of the above evidence, the rat—the cell—the doer of the operations—must, itself, be regarded as ephemeral. In the long run, we cannot distinguish the framework from the stream that flows through it. The apparent constancy of something recognizable has led some to compare life to a whirlpool at the edge of a river. Because of the underlying topography, such a whirlpool is often quite constant, remaining in the same place for months. Yet, it is easy to appreciate that the material objects of which it is composed, the water molecules, are part of the whirlpool only for a time and then pass on. There is no object that one can point to and say, "This is an essential part of the whirlpool." Yet, there is a sense, certainly, in which the whirlpool exists and continues to exist. So it is with every living thing. One cannot point to any part of its structure and say, "This is an essential, continuing part of this object I call living"; however, something continues. There is something about the organization of a living thing that makes it—the organization, not its particular particles—perpetuating in the face of continuous environmental change. Life is not unlike a whirlpool.

That is scarcely a definitive answer. It is only an analogy. But, perhaps, it will help us see where our problem lies.

QUESTIONS AND PROBLEMS

25-1. In words, tell what is meant by these terms:
  a. hydrolysis
  b. deamination
  c. decarboxylation
  d. dehydrogenation

25-2. In symbols, write a generalized oxidation-reduction reaction and identify the oxidized product and the reduced product.

25-3. Examine equation (2) in this chapter and tell what substance undergoes oxidation and what undergoes reduction.

25-4. What is an enzyme? What does it do?

25-5. What is implied by the dogmatic statement:

one enzyme ⟶ *one action?*

25-6. What is a colloid?

25-7. Distinguish between a suspension and an emulsion.

25-8. What may possibly be the significance of the colloidal nature of protoplasm?

25-9. Life has been compared to a flame. Discuss this analogy critically, pointing out its aptness or ineptness.

Chapter XXVI

The Gene

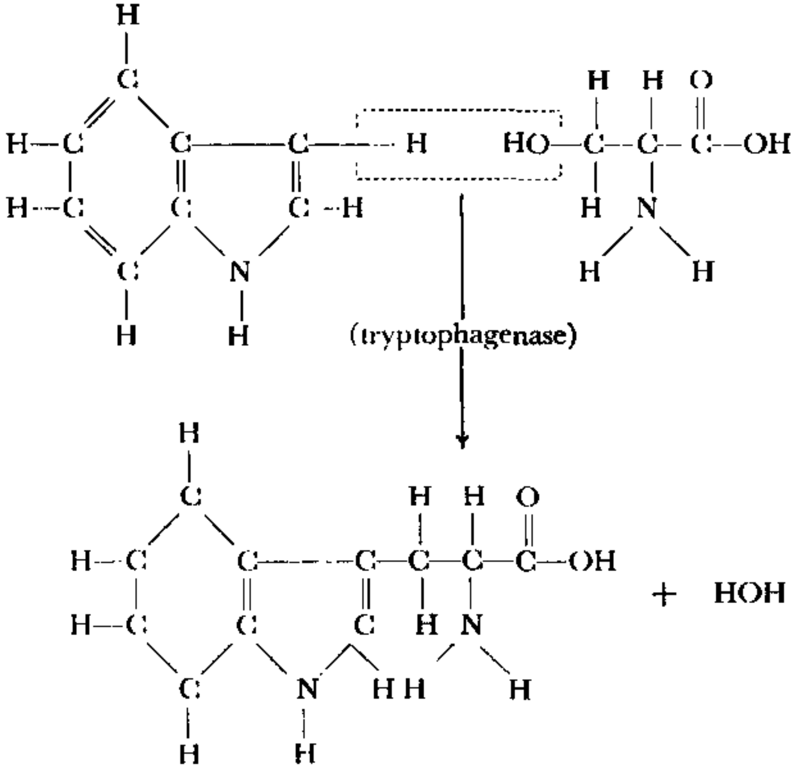
168. Definition of the Gene

Multicellular organisms arise from single cells by repeated cell division. By the same process, unicellular organisms increase their numbers. In both cases, we are dealing with the indefinite multiplication of cells arising, in the last analysis, from a single cell. Let us see what might be the consequences of this unlimited division of cells.

All the chemical activities of cells are made possible by enzymes. For each separate activity, a distinct enzyme is involved. In general, the work of one enzyme cannot be done by any other enzyme. All cells, so far as we know, require the amino acid **tryptophane.** Some organisms have to be fed tryptophane; man, for one, must take it in with his food. Many other organisms can synthesize it from other compounds. When tryptophane is snythesized from very simple molecules, many chemical steps are involved and many enzymes are required, one enzyme for each step.

We may best show the role of an enzyme by considering data that have been gained from the study of the Ascomycete *Neurospora.* Normal, wild-type *Neurospora* possesses the ability to synthesize tryptophane from two other substances, **serine** and **indole,** a synthesis that can be carried out by many other organisms. There is a freak, or "sport," strain of *Neurospora* that cannot carry out this synthesis. The difference between the two strains is traceable to a difference in their enzymes. From the normal strain, may be extracted an enzyme, which we will call **tryptophagenase,** that can carry out the synthesis *in vitro.** No such enzyme can be found in the "sport." The action of tryptophagenase

In symbols:



In words:

$$\text{indole} + \text{serine} \xrightarrow{\text{(tryptophagenase)}} \text{tryptophane} + \text{water}$$

Fig. 26-1. The action of an enzyme in synthesis.

can be understood by reference to Figure 26-1. By removing a molecule of water from the two raw materials, the product is assembled.

The enzyme tryptophagenase is specific for this action, and no other enzyme can take over its function if it is not there. What will happen,

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* Processes that take place in living organisms are said to take place *in vivo* (Latin *vivus*, alive). A process that occurs outside of living organisms, for instance, in a glass vessel in a chemical laboratory, is said to occur **in vitro** (Latin *vitrum*, glass).

then, to a cell that contains tryptophagenase when the cell divides? If the cell contained only one molecule, a problem would immediately arise as to which of the two daughter cells would get this sole molecule.

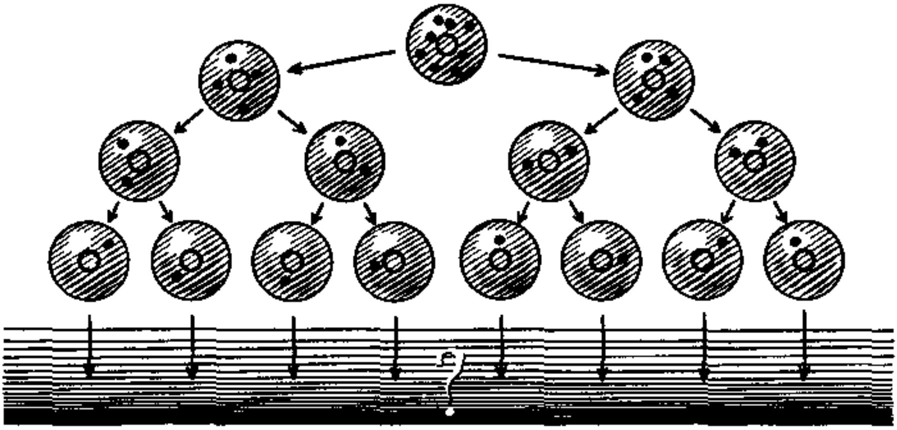

Fig. 26-2. If enzyme molecules (black bodies) were not subject to reproduction, the reproduction of cells would produce enzymeless cells.

However, the rate of the tryptophane-synthesizing reaction in cells clearly indicates the presence of more than one molecule of enzyme per cell. Suppose there are eight. This supposition does not change the essential nature of the problem, as Figure 26-2 should make clear. As the cells continue to divide, the number of enzyme molecules per cell decreases until, after three divisions (if they are all equitable divisions), each cell has only one molecule. The next such division will inevitably produce some cells that lack the enzyme if there is no means by which the enzyme molecules can be synthesized. This will ultimately be true no matter how many enzyme molecules are present in the initial cell, whether one, eight, or eight million. After a sufficient number of divisions, some daughter cells will necessarily be without enzymes if there is no reproduction of enzymes.

But it is an observational fact that the **daughter cells of every cell generation have all the enzymes present in the original parent cell and in as great quantity as in that initial cell.** There is no external source from which a cell can get its enzymes. The conclusion is unavoidable: the enzymes must somehow increase in numbers inside the cell.

How could the enzymes increase in numbers? We can easily conceive of two different ways:

Hypothesis No. 1. The enzyme is self-reproducing. This means that it must have two separate abilities—the ability to cause the reaction which gives it its name and, also, the ability to reproduce more enzymes of its own kind which, in turn, can synthesize tryptophane and reproduce more tryptophagenase which can . . . and so on, without end. We can diagram the sense of this hypothesis by writing:

$$\begin{tikzcd}
\text{Tryptophagenase} \arrow[r] \arrow[d] & \text{Tryptophagenase} \arrow[r] \arrow[d] & \text{Tryptophagenase} \arrow[r] \arrow[d] & \text{Tryp} \arrow[d, dash] \\
\text{tryptophane} & \text{tryptophane} & \text{tryptophane} & \text{tryp}
\end{tikzcd}$$

Hypothesis No. 2. The enzyme is not self-reproducing, but is reproduced by a hypothetical agent called a *gene* which has two actions: production of a particular enzyme and reproduction of itself. This hypothesis can be schematically indicated thus:

$$\begin{tikzcd}
\text{T-gene} \arrow[r] \arrow[d] & \text{T-gene} \arrow[r] \arrow[d] & \text{T-gene} \arrow[r] \arrow[d] & \text{T-gene} \arrow[d] \\
\text{Tryptophagenase} \arrow[d] & \text{Tryptophagenase} \arrow[d] & \text{Tryptophagenase} \arrow[d] & \text{Tryp} \\
\text{tryptophane} & \text{tryptophane} & \text{tryptophane} & \text{tr}
\end{tikzcd}$$

All the evidence available favors the second hypothesis. Many enzymes have been obtained free from cells, but none has been found which can reproduce itself under any conditions we can create. The second hypothesis seems the simpler on all counts. The **hypothetical self-reproducing producer of an enzyme is called a gene.** The word gene is derived from Greek roots that mean, variously, "to produce" or "to be produced." We have spoken of it as a "hypothetical agent," but this is an overcautious attitude. Nobody has ever knowingly seen a gene*, but in cells that have been much studied, we know exactly where each

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* Recently (1949), two scientists at the University of Southern California, D. C. Pease and R. F. Baker, have published photomicrographs taken with the electron microscope that show particles which, the authors say, "it seems reasonable to believe . . . are genes."

gene is and, fairly accurately, what it is doing. The gene of biology is about as hypothetical as the atom of physics—and no one today needs to be told of the striking practical effects of that hypothetical agent.

169. Genes and Chromosomes: Mitosis

To consider a thing "real," we may not demand a sight of it, but we would at least like to have a pretty good idea where it is. Where is the gene?

From the argument presented by Figure 26-2, we would suspect that the gene is to be found in, or on, some part of the cell that multiplies its volume and divides its substance as regularly as the cell as a whole and, thereby, keeps up with cell division. Such a cellular part is the nucleus. Other visible objects inside the cell are rather variable in their behavior. But the nucleus remains a very constant size and shape for countless cell generations. It would seem to fit the requirements for the locus of genes. Furthermore, microdissection experiments with some cells have shown that, when a cell is cut in half, that half which contains the nucleus continues to live and divide, whereas the enucleate half does not divide and ultimately dies. The shock of the operation cannot be the cause of such death, for the nucleated half is equally exposed to this shock. Although an enucleate cell can live for awhile, it evidently cannot keep going indefinitely. In view of what we have learned about the continuous normal destruction of cell chemicals (§ 167), including proteins and enzymes, this is what we would expect if the producers of enzymes, the genes, were no longer present. As the initial supply of enzymes diminishes at the normal breakdown rate (the causes for which we do not understand) and is not replenished by newly formed enzymes, metabolism, perforce, comes to a stop. The protoplasm dies. Since this happens in enucleate protoplasm, we deduce that genes are located in the nucleus.

We can locate genes still more precisely. If we use suitable lighting or staining procedures in studying the process of cell division, we can discover that there are bodies inside the nucleus that divide with great exactness during cell division. These bodies are called **chromosomes,** so called because they are colorable by certain dyes (Greek *chroma*, color; *soma*, body).

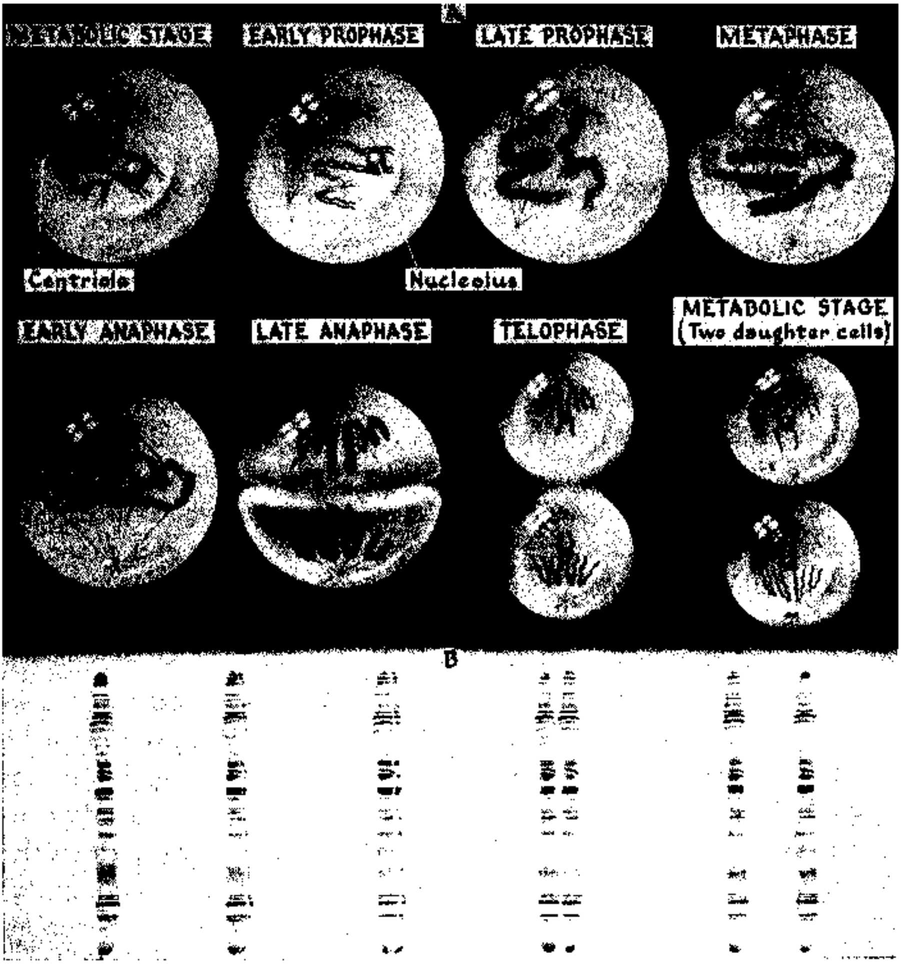

Fig. 26-3. The process of mitosis (A) in the course of which each chromosome splits into two identical daughter chromosomes which separate and become parts of the nuclei of two daughter cells. The daughter cells have the same number of chromosomes as the parent cell. At the left, in B, is diagrammed a chromosome as it appears under the highest magnification of the optical microscope. Each region or *locus*, represented here as a shaded strip, is perhaps a single gene. Before mitosis can take place, the entire chromosome, including all its genes and loci, must somehow produce a replica of itself alongside itself. The daughter chromosomes (lower right) can then be mitotically divorced. It is remarkable that all the chromosomes in a single cell reproduce at the same rate.

In studying the behavior of enzymes and the transmission of genes, we shall frequently have occasion to mention the Ascomycete *Neurospora* (see § 145). The intensive study of this mold by G. W. Beadle, E. L.

Tatum, and their many able associates has resulted in a firm establishment of the relationship of gene to biochemical action. For that reason, we shall select *Neurospora* as a particular example with which to illustrate general biological principles. We shall consider, first, the phenomena involved in ordinary cell division or **mitosis.** (*Mitosis* should be pronounced with a short *i* as in *mitt*. The word is derived from the Greek *mitos*, thread—referring to the chromosomes visible during cell division.) The process of mitosis includes the division of the whole cell, but we will concentrate our attention on the events transpiring in the nucleus during this process.

The nucleus of *Neurospora* has seven chromosomes. Careful study shows that each of these chromosomes is a distinguishable entity, and the same seven occur in all *Neurospora* nuclei that have been examined. Evidently, there must be some precise mechanism which distributes one of each type of chromosome to each daughter cell in each division. But this can happen only if each different chromosome is first multiplied to form two similar chromosomes. This operation of increasing the number of chromosomes *precedes* the division of either cell or nucleus. Each chromosome somehow induces the formation of an exact duplicate of itself at the side of itself (Fig. 26-3B). When this duplicate is complete, the two closely joined members separate (Fig. 26-3A). Each of the seven chromosomes undergoes this process of self duplication, leading to the subsequent separation of daughter chromosomes. It is a remarkable fact that all the chromosomes in a nucleus reproduce themselves at the same time. What keeps them in step is not known.

After the chromosomes have reproduced themselves, the daughter chromosomes separate, one of each pair going one direction and the other in the opposite direction (Fig. 26-3A). As a result, there soon are found two groups, each of which is composed of a complete set of seven different chromosomes such as were found in the mother nucleus. Each group reconstitutes itself into a nucleus; the cell divides, and there are then two new cells, each of which has the same nuclear content as the mother cell. Thus ends the process of mitosis.

Notice the parallelism between the definition of a gene and the behavior of a chromosome. A gene must be self reproducing; the chromosome is observed to be self reproducing. Is, then, the chromosome synonymous with a gene? No; for there are more genes than chromosomes. All evidence indicates that almost every chemical process that occurs within a cell requires a unique enzyme to make it occur. It seems very probable that each enzyme is produced by a particular gene. We know that every cell must contain hundreds of different enzymes and, hence, several hundreds of different genes. In the case of *Neurospora*, there is ample proof that several dozens of processes are due to the existence of genes. But there are only seven chromosomes, so there must be more than one gene to a chromosome. Probably there are several hundred genes per chromosome. Studies of other organisms have indicated conclusively that the genes are arranged in line along the chromosome, or *in* the chromosome, and that each gene is too small to be seen with an optical microscope. The evidence for these statements is too involved to present here; the interested student is referred to a textbook on **genetics.**

From many genetic studies, two generalizations have emerged:

One. **Each chromosome consists of many genes, arranged in single file.**

Two. **Each gene produces one enzyme which, in turn, catalyzes one chemical reaction.**

The second generalization we may summarize by this dogmatic statement:

One gene ⟶ one enzyme ⟶ one action

The hypothesis implied by the above statement is so new that it cannot yet be regarded as irrevocably established. But, it is already proving to be a fruitful working hypothesis.

QUESTIONS AND PROBLEMS

26-1. Define a gene.

26-2. What evidence and argument are presented for the existence of genes?

26-3. In their synthetic abilities, how do genes and enzymes differ?

26-4. Would you say that the gene hypothesis presented *necessarily* demands only a one-step process between the hypothetical gene and the demonstrable enzyme?

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Beadle, G. W. "Genes and the Chemistry of Organism." *American Scientist*, **34**: 31-53. Jan. 1946.

Beadle, G. W. "The Genes of Men and Molds." *Scientific American*, **179**: 30-38. Sept. 1948.

Chapter XXVII

Nutrition and the Gene

170. Is *Neurospora* a Simple Organism?

In discussing small organisms, such as algae, bacteria and molds, biologists frequently speak of them as being "simpler" than such large forms as mulberry trees and armadillos. Is this custom justified? Is a mold, for instance, really simpler than a mammal?

It should be apparent that this question is not one to which a rigorous answer can be given. Simplicity is a concept that is hard to define. Organism A may be simpler than Organism B in some aspects but more complicated in others. Who is to say which aspects are more important? Only an incurable optimist could seriously hope for universal agreement in such a matter. Asking whether one organism is simpler than another would appear a foolish thing to do.

Yet, it is a question of this sort that we propose to ask here, namely, "Which is simpler, *Neurospora* or man?" We cannot, consistent with the above discussion, honestly hope for a simple, unqualified answer to the question. We ask it, however, because the question leads to a discussion that reveals principles of importance in the field of general biology.

As regards its form, or **morphology,** the mold is certainly simpler than the man. Whole books are devoted to the details of man's macroscopic and microscopic anatomy, whereas it would be difficult to devote so much space to the morphology of *Neurospora.* If, however, we decide to discuss the nutrition of the two species, the answer, as we shall see, is not so certain. The facts are these:

Man requires for his sustenance a diet that includes water; various inorganic salts; the amino acids lysine, valine, tryptophane, histidine, phenylalanine, leucine, isoleucine, threonine, arginine, and methionine; and the vitamins vitamin A, thiamine, riboflavin, pyridoxin, niacin, pantothenic acid, inositol, para-aminobenzoic acid, ascorbic acid, vitamin D, vitamin K and biotin. These things, at least, are required by man. *Neurospora*, on the other hand, requires only water, inorganic salts, sugar, ammonia-nitrogen, and the one vitamin biotin. Which is simpler, man or mold?

One's first impulse is to say the mold is simpler because it has simpler requirements. But it is the view of modern biologists that this is quite the wrong answer. There are reasons, as we propose to show in the following sections, for believing that the mold's simpler nutritional requirements actually imply a more complex cellular physiology, in certain aspects, than that present in an organism that has complex nutritional requirements. Before we can develop the evidence for this statement, we shall present some needed experimental background.

171. The Production of Mutants

In the previous chapter, we spoke of two different strains of *Neurospora*, one that could synthesize tryptophane and one that could not. Where did these come from? The tryptophane-synthesizing form can be found in nature. It is called the "wild type," i.e., the natural type. The other form, previously called a "sport," is not found in nature and must be produced in the laboratory. We propose to show how it can be produced, endeavoring to distinguish between experimental data and hypothetical explanations.

Genes are arranged in linear order on chromosomes. Each chromosome is conceived of as consisting of the genes somehow connected, perhaps by a certain amount of inert material. Chemical analysis shows that a chromosome is largely proteinaceous material; therefore, we conceive of each gene as being one, or possibly more, proteins. This conception fits in with the enzymelike character of the gene. About the structure of proteins, only the most general characteristics are known.

Some proteins seem to have a structure like that diagrammed in Figure 27-1B; perhaps the gene does. In any case, the structure of the gene must be at least that complicated, so this model, whether correct or not as to details, will serve as a useful illustration. Each dot in the model represents some chemical group—CH_3, CHO, $C=O$, etc.; the lines between dots represent carbon-to-carbon bonds or carbon-to-nitrogen bonds. We need not know in detail what the symbols mean but merely observe that all proteins, including genes, are very complicated molecules.

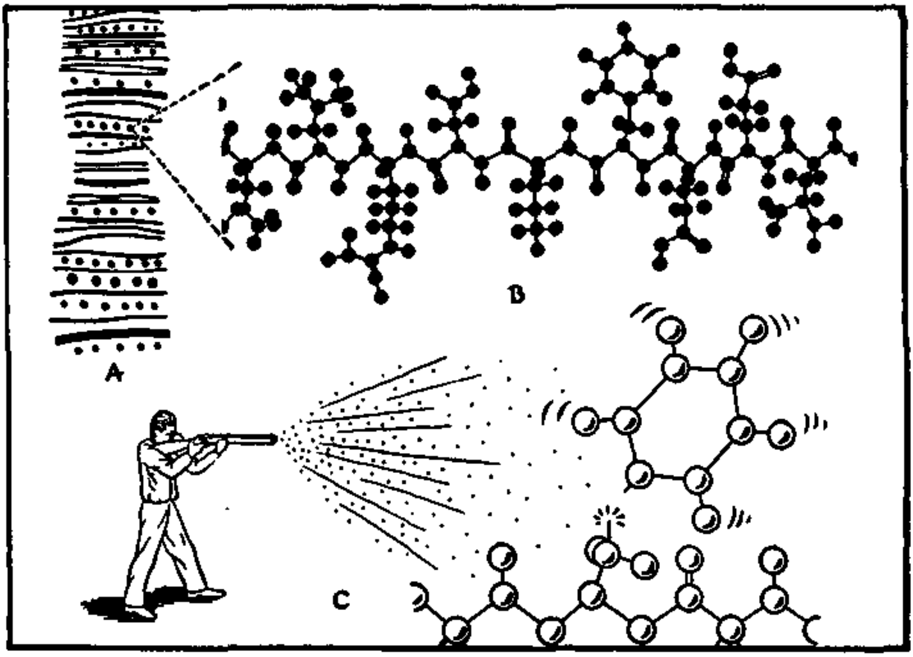

Fig. 27-1. The production of gene mutation by X-radiation. A is a small segment of a long chromosome; each line or row of dots is a gene. A gene is a protein molecule at least as complicated as the example shown in B. Subjecting such molecules to X-radiation or other *mutagenic agents* is like shooting at them with buckshot: there is no predicting what atoms will be hit, that is, what genes will be caused to mutate, or in what way.

X-rays consist of high-energy particles. Subjecting a cell (hence chromosomes, hence genes) to X-rays is like firing at it with a shotgun (Fig. 27-1C). We don't know what we will hit, but if we fire often enough, we are sure of hitting something. When a high-velocity X-ray particle hits a chemical group in a gene, it does something to it. It may knock it out completely, or merely break a few atoms off of it, or turn it around so that it is bonded in a new way to the rest of the protein molecule. *We really do not know what the X-rays do to the molecule,* but we do know that they modify it somehow. The verbal picture presented above helps us summarize and remember the facts about X-ray action on chromosomes. That is our excuse for using it. But we must remember it is only a picture-hypothesis.

When a gene is hit by an X-ray particle, it is not destroyed but merely modified, so that it no longer produces the enzyme it used to produce. We know the gene is not destroyed, for we can permit the changed genes to multiply (via cell multiplication) and then X-ray the new genes, whereupon an occasional gene will change back to the old form again and start producing the old enzyme once more.

The process in which a gene changes from one form to another is called **mutation.** By convention, the common type of gene that occurs in nature is called the "wild-type gene," and any other form of the same gene is called a "mutant-type gene" or simply a "mutant." The *Neurospora* gene which produces the enzyme which synthesizes tryptophane is called a wild-type gene. The gene which does not produce this enzyme is called a mutant. (Whether it synthesizes some other enzymes is not known.) We may indicate the wild-type gene concerned with the synthesis of tryptophane by the symbol *T*. Its mutant we will indicate by *t*. Symbolically we may write:

Gene *T* ⟶ tryptophagenase ⟶ synthesis of tryptophane
Gene *t* ⟶ ? (no tryptophagenase)

But there are other genes involved in the synthesis of tryptophane. One mutant has been found which does not synthesize tryptophane when fed only salts and sugar but which does produce the enzyme tryptophagenase. Evidently this mutant contains the wild-type gene *T* but has another abnormal gene which stops the chain of steps leading to the synthesis of tryptophane at some other point. Feeding experiments showed that this mutant gets along perfectly well if fed salts, sugar, and serine. Evidently this mutant lacks the enzyme for synthesizing serine which we may call *serinase*. This must mean that the normal *Neurospora* contains an *S* gene, and that our mutant has a non-serinase-synthesizing gene we will call *s*. Notice:

(a) We discover the gene only when its normal action is missing as it is in mutant types.

(b) We learn of the normal steps involved in the synthesis of a product only when we have an abnormal strain available for study. This second statement shows us why the production and study of mutants are valuable. It is very difficult to know normal physiology when only normal organisms are available for study. It is the abnormal organism that reveals to us, through comparative study, normal function. We were led to look for tryptophagenase only when we had a strain in which the *T* gene had mutated to *t*.

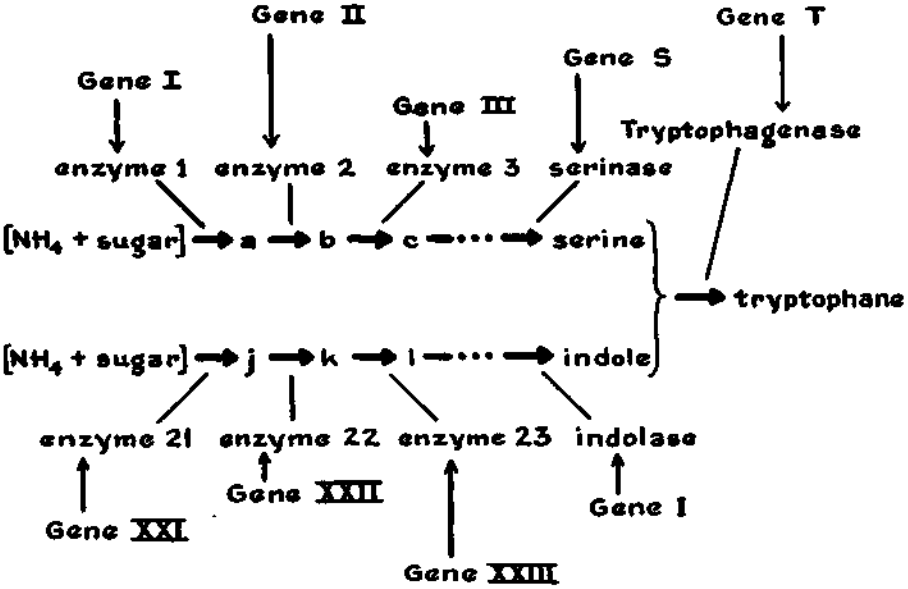

Fig. 27-2. The biological synthesis of tryptophane from ammonia and sugar. Only some of the genes indicated have been identified; the rest are postulated on the basis of general genetic theory. In other words, this scheme is a *working hypothesis*.

The picture we have of the normal synthesis of tryptophane is shown in Figure 27-2. This is a hypothesis. It is based on three premises:

(a) A chemical premise: that chemical syntheses take place one step at a time. There must, for instance, be many steps between the raw materials ammonia and sugar, and the product indole.

(b) A physiological premise: that each step is catalyzed by an enzyme. (The fact that a few steps may occur "spontaneously" is no serious objection.)

(c) A genetic premise: that each enzyme is produced by a gene.

Figure 27-2 is mostly hypothetical; the details cannot be filled in.

Research along these lines was only very recently started and is being vigorously pushed forward at this moment in many laboratories. Undoubtedly before this page comes off the press, more specific details will have been filled in in the scheme presented.

172. The Significance of Nutritional Needs

In the few years during which biologists have been taking potshots at *Neurospora* with X-rays (and other ammunition), many mutants have been produced. There is a mutant which cannot synthesize phenylalanine, another which cannot synthesize leucine, and others which cannot synthesize arginine or methionine or adenine, as the case may be. Each mutant is caused by the alteration of a wild-type gene to an incompetent mutant form.

Besides the mutants that cannot synthesize amino acids, there are also mutants that cannot synthesize particular vitamins, although the normal mold can synthesize all but biotin. One mutant cannot synthesize thiamine, another riboflavin, another niacin, and so on. Although no one has set out to do it*, it would probably be possible to produce a strain of *Neurospora* which would have exactly the *same nutritional needs as man,* requiring all the same vitamins and amino acids. And note: *such a strain of Neurospora would be simpler than the wild-type strain,* nutritionally speaking. It would contain fewer enzymes.

We see now an answer to the question asked at the beginning of the chapter, *Which is simpler, man or mold?* With respect to nutrition, man is simpler. He contains fewer enzymes for the synthesis of foodstuffs. The wild-type mold can synthesize all its foodstuffs except salts, ammonia, sugar, and biotin, because it has so many enzymes—enzymes which man lacks. In this sense, the mold is a more complicated organism than man.

173. The Unitary Nature of Protoplasm

Is *Neurospora* an exceptional organism? Not at all; there are many hundreds, perhaps thousands, of different organisms that have as simple nutritional needs as *Neurospora.* Scores of different bacteria have been found, for instance, which need not a single amino acid or vitamin,

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* And probably no one will, for it would be just a technical *tour de force,* rather than a real advance in science.

requiring only a single simple carbon compound, such as glucose or acetic acid. In every case that has been adequately studied, it has been found that these bacteria do not have to be fed the various amino acids or vitamins *because they manufacture their own.* Protoplasm, wherever it is found, whether in bacteria, yeasts, molds, fruit flies, grasshoppers or men, includes the same fundamental building blocks. The protoplasm of some cells may include a complete set of enzymes with which it can make all its own building blocks, whereas the protoplasm of another species may be lacking some of these enzymes. But whether it makes its own or imports them from the outside, **protoplasm is always made up of the same building blocks.**

Here, at last, we find a justification for the century-old term *protoplasm*. The use of a unitary term when speaking of the living material of all cells implies a unity of substance which, for about eighty years of the life of the word "protoplasm," was quite unjustified. The work of the last decade or so has finally given justification to its use. There *is* a unity of living substance. There are differences, of course, between the protoplasm of a mold and a man, otherwise there would be no differences between the two species, but there is a most important unity as well. It makes one wonder if there is only one fundamental organization of matter which will permit the qualities we imply by the noun *life*.

QUESTIONS AND PROBLEMS

27-1. In what sense is *Neurospora* more complicated than man? In what sense simpler?

27-2. Which is more dependent on other living organisms for its nutrition, man or *Neurospora?* Explain.

27-3. What is a mutation?

27-4. Can we produce whatever mutations we want with X-rays? Explain.

27-5. What is meant by the term "protoplasm"? Justify its use.

27-6. In the last sentence of this chapter, it was suggested that there may be a unique organization of matter that we call "life." This has not been proved. (Cannot be?) But the assumption of its truth has led to speculations as to the rarity with which conditions favorable to the existence of life are to be found in the universe, speculations that have been interestingly presented by L. J. Henderson in his book, *The Fitness of the Environment.* New York: The Macmillan Co., 1913.

Chapter XXVIII

The Significance of Sex

174. The Separation of Alleles in Meiosis

In § 169, we described the multiplication of genes and their division during mitosis, using *Neurospora* as an example. As a result of these processes, each daughter cell receives one of each kind of gene that the mother cell possesses, and, thus, the mycelium can extend itself indefinitely without losing its ability to carry out its many syntheses.

But a mycelium, extending itself by growth along the substrate in a crawling fashion, will not get far in the world. It will snake along to the edge of the suitable substrate and then stop. A species that has a way to disperse itself across unsuitable deserts to new nutritional oases will do better in the world. Therefore, teleologically speaking, we find that most species are modified in some distinct way for dispersal. *Neurospora* is well dispersed by means of the dust-fine conidia (see Fig. 28-1) that are produced in great abundance at the ends of aerial hyphae.

Neurospora has another method of reproduction available to it. There are two mating types in this organism, usually called *A* and *a*. Like the sexes in *Rhizopus*, they are distinguishable only by mating tests. Mating can occur in more than one way, as indicated by the diagram, but, however it occurs, the end result is the same: the two nuclei from the two opposite mating types presently find themselves together in the same cell which is called a binucleate cell. Each nucleus contains a single set of chromosomes; each nucleus is said to be *haploid* (Greek *haploos*, single). In the cell that is to become the ascus, the two nuclei fuse to form a single nucleus which, since it contains two sets of chromosomes, is called *diploid* (Greek *diploos*, double). This diploid nucleus presently undergoes a process, called *meiosis* (pronounced: my-o-sis), which can best be understood by a close inspection of the middle column of Figure 28-2. There are, at the beginning of meiosis, seven pairs of chromosomes. Since each pair behaves like the others, and seven pairs are too many to watch at one time, we have drawn the behavior of just one pair. Notice that each member of a pair first multiplies to form two chromosome strands. That makes four chromosome strands. Then, separation of strands takes place twice without any further multiplication of the strands so that there are produced four nuclei, each of which has only one strand (chromosome) of each kind—in other words, a haploid set again. Notice that the result of the meiotic process is a reduction of one diploid nucleus to four haploid nuclei; hence, the name (Greek *meiosis*, reduction).

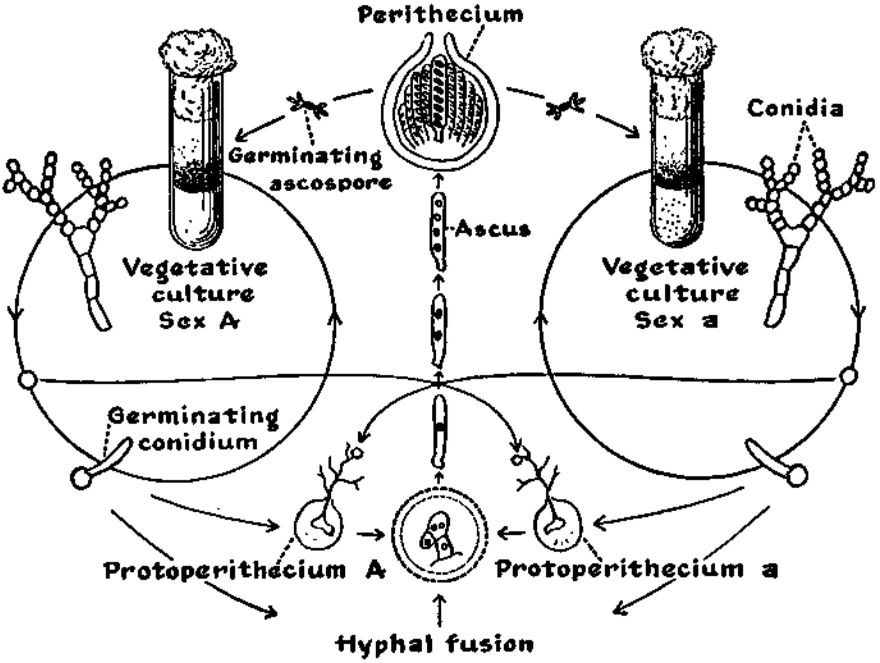

Fig. 28-1. Life cycle of *Neurospora.*

It happens that meiosis in *Neurospora* is followed by a further *mitotic*

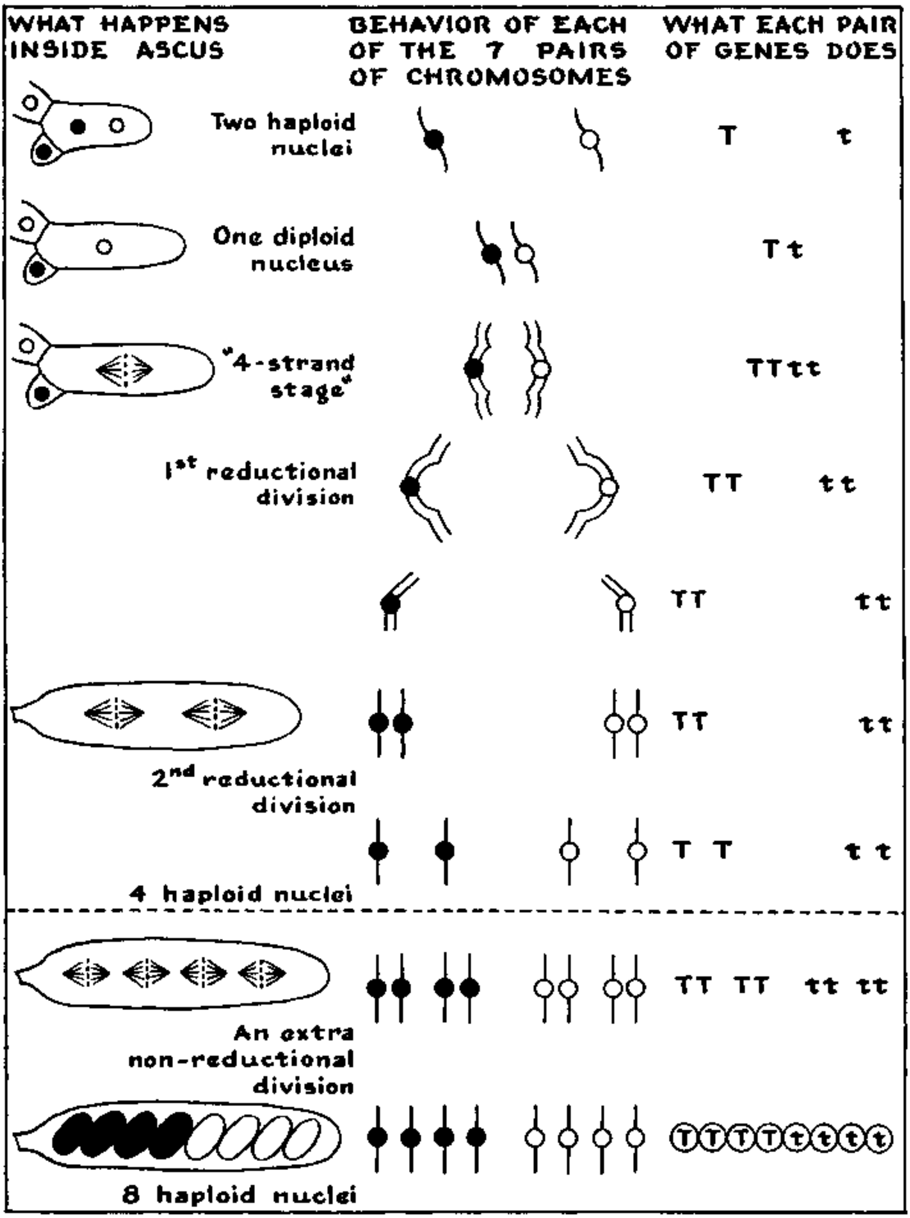

Fig. 28-2. Meiosis, or reduction division, as it occurs in *Neurospora*, to take a particular example.

division resulting in eight instead of four haploid nuclei. Many ascomycetes do not show this extra division, which is without significance, as far as we know. Each haploid nucleus becomes the nucleus of an *ascospore*.

What happens to the genes during this process? Being part of the chromosomes, they are multiplied and distributed in the same way. If, previously, hyphal fusion had occurred between one strain of *Neurospora* that contained the *T* gene and another that had the *t* gene, each ascus would contain exactly four ascospores containing *T* and four containing *t*. The temporary intimacy of the two alleles in the diploid nucleus has no effect on either one. Each gene is a discrete, incorruptible particle.* If we could see the genes, we would see that, during meiosis, they were being multiplied and distributed as shown in the right-hand column of Figure 28-2.

175. The Behavior of Two Pairs of Alleles in Meiosis

Suppose we have two different stocks of *Neurospora* and cross them, what will happen? Will the ascospores be genetically just like the two parents, or different?

This question is a double one. Either: the two mutant genes are on the same type of chromosome (recall, there are seven different types of chromosomes in this organism); or they are on different chromosomes. As it happens, the end results in these two cases are not greatly different, but we must consider both of them because the course of events leading to the same result differs in the two cases.

Genes on Different Chromosomes—There is a gene involved in the synthesis of niacin that is on a different chromosome from the one that bears the tryptophane-synthesizing gene. Suppose we cross a strain that is genetically *Nt* with one that is *nT*. What will happen?

In meiosis, one member of each pair of like chromosomes goes one direction, and the other in the opposite direction; but, which one goes to the left, and which to the right is a matter of chance.

If there are two pairs of chromosomes that we are "watching," each pair is governed by the principle stated above. Consequently, an *N*-

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* The chromosomes are not so incorruptible, however. Similar chromosomes ("homologues") frequently exchange parts ("crossing over"), but when they do so, it is in a precise fashion, part for part, with neither chromosome being shortchanged; at the conclusion of crossing over, each chromosome has one and only one member of each pair of alleles, though it may not have the same assortment it started with. (See § 175, and Fig. 28-3D.)

containing chromosome will sometimes go to the same spore as a *t*-containing chromosome, but, at other times, the *N* and the *T* will be found together. Similarly, some spores will contain *n* and *T*, and others *n* and *t* (see Fig. 28-3 A, B). No spore will contain two *n's* or two *t's* or two *N's* or two *T's*, because meiosis—the reduction division—separates the members of a homologous pair of chromosomes, hence, the members of every pair of gene-alleles.

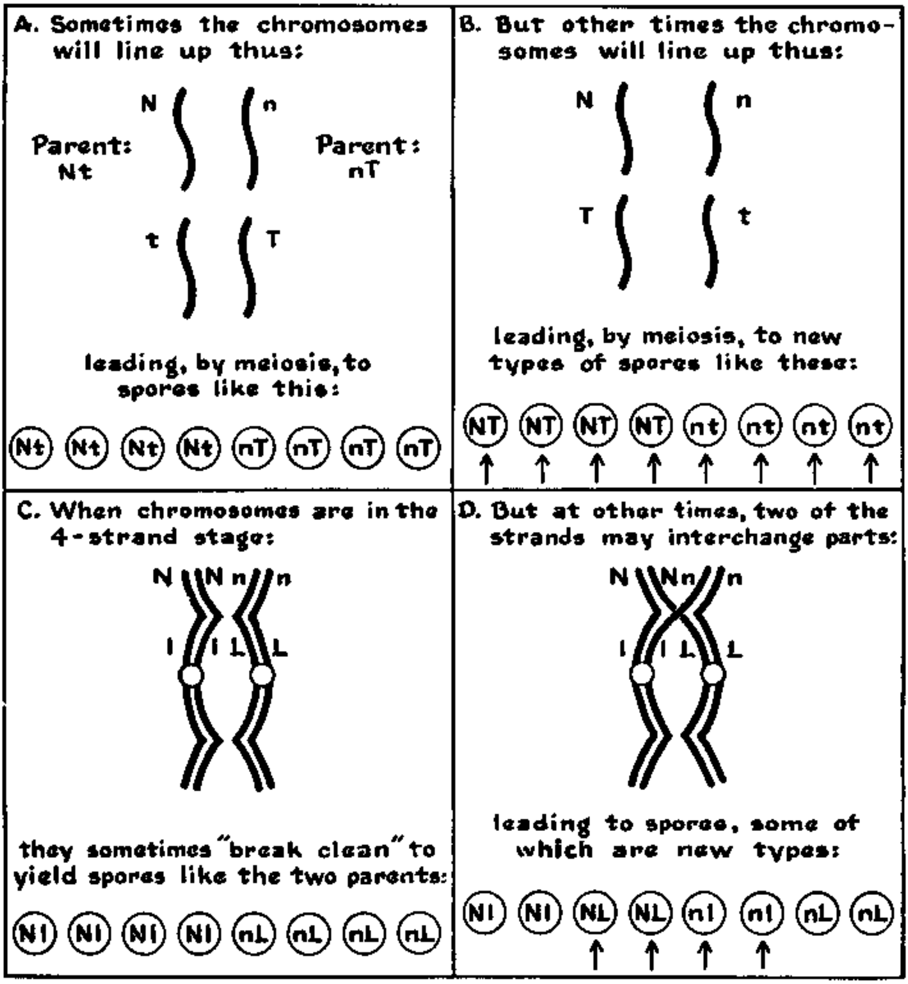

Fig. 28-3. The significance of sex: the possibility of the production of new strains by the meiotic process.

Genes on the Same Chromosome—When two genes are on the same chromosome, they tend to remain together since the chromosome is a unit. But, sometimes during the "four-strand stage" of meiosis, two adjacent chromosomes will break at precisely the same point and exchange parts, a process known as **crossing over.** (See Fig. 28-3 C, D.) When crossing over takes place, some of the spores produced contain a combination of genes not found in either parent strain.

Thus does meiosis produce new genetic combinations, whether one is dealing with genes on the same chromosome or ones that are on different chromosomes.

176. The Significance of Sex

Thinking over the data presented in the preceding section, we see that **the sexual mechanism is an efficient system for producing new strains,** strains which have gene combinations that are not to be found in either parent. The poet, the novelist, or the moralist may have a different view of the matter, but to the biologist, *qua* biologist, this is the significance of sex.

This principle was employed rather ingeniously in 1946 to settle a century-old dispute in bacteriology. Bacteria, recall, are very small; a "typical" bacterium is about one micron long by a half wide. Such a cell is only about four times as long as the smallest object one can examine with the optical microscope. The activities of such cells are not easy to follow. Ever since the discovery of bacteria, people have speculated about their sexual life. Many man-hours have been spent watching bacteria to see if they ever did anything besides swim around and multiply by cell division. Sometimes, an observer sees two bacteria come together for a few minutes and then separate. In such a case, who can say whether anything has passed between the two cells? Some more imaginative, or more romantic, bacteriologists have claimed they have observed sexual fusion, but they have been unable to convince their more skeptical colleagues.

The disputed point was neatly settled by Joshua Lederberg and E. L. Tatum of Yale University, using two different strains of the bacterium *Escherichia coli*. The wild-type *E. coli* can synthesize all its own vitamins and amino acids, including biotin, methionine, threonine and proline.

When a wild-type cell is placed in a medium containing only sugar and inorganic salts, it multiplies, showing that it can synthesize all the building blocks of its protoplasm.

By X-radiation, two mutant strains of *E. coli* were obtained; one of them could synthesize neither biotin nor methionine; another could synthesize neither threonine nor proline. The genetic constitution of the former we may indicate by writing *bmTP*, thus indicating its ability to synthesize threonine and proline, but not biotin or methionine. Similarly, the other strain may be written *BMpt*.

When either strain was placed alone in a sugar-and-salts medium, it could not grow. Out of billions of cells tested, none could grow in such a medium. But if *BMpt* were first mixed with *bmPT* and cells from this mixture were later placed in sugar-and-salts medium, it was found that about one cell out of every ten million tested could grow and multiply. This meant that the two kinds of mutant cells had somehow exchanged genes, thus producing an occasional BMPT cell which, of course, is the wild type that can synthesize all of its own building blocks. Exchange of genes can occur only if some sort of sexual or fusion process takes place. Thus, was the existence of sex in bacteria proved, after nearly a century of dispute. No one has yet seen bacterial fusion taking place. The extreme rarity of fusion as indicated by this experiment, does not, for the moment, give us much hope of observing it, unless a way can be found to encourage bacteria to fuse oftener.

QUESTIONS AND PROBLEMS

28-1. Describe mitosis in an organism that has three pairs of chromosomes.

28-2. Describe meiosis following fusion of nuclei, each of which had three chromosomes.

28-3. Define: haploid; diploid.

28-4. If one parent strain of *Neurospora* is *AbC* and the other is *aBc*, what *new* types could result from the sexual process?

28-5. If one parent is *ABCD* and the other *abcd*, how many types of individuals could one expect following fusion and meiosis? How many of them would be new?

28-6. If one parent is *Abcdef* and the other is *abcdef*, how many new types could be produced by the sexual process?

28-7. How was the existence of a fusion process proven in bacteria?

28-8. If the environment were to change slightly, would you expect a sexual species to be able to adapt itself to the new environment more, or less, rapidly than an asexual species? Why?

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Chapter XXIX

The Consequences of Diploidy

177. The "Hiding" of Genes in Diploids

In the study of *Neurospora*, we learned how genes act in a haploid organism. Practically all the more conspicuous plants and animals that traditionally interest man most are diploid (§ 147). Does diploidy modify the way in which genes act? In principle, no; in detail, yes. The differences caused by the latter, however, are of considerable practical importance, so we must examine the genetics of diploid organisms.

The science of genetics was developed to a considerable extent through the study of *Drosophila melanogaster*, variously called a fruit fly, a vinegar fly, and a garbage fly. It is a harmless creature less than two mm long, and is easily grown in the laboratory. In forty years of study, many billions of flies have been examined. Among these multitudes, have been found perhaps a hundred thousand different mutations.

Among the many mutations in *Drosophila* that have been extensively studied in the laboratory, is one called *claret*, so named because of the color of the eyes. Eye color is determined by a colored chemical or *pigment* present in the eyes. In claret flies, the pigment is light red instead of dark red as it is in wild-type flies. Experimental evidence indicates that the claret pigment is an intermediate product in a biochemical sequence similar to that indicated in Figure 27-2 and discussed in § 171. For the present, we can simplify this sequence to one containing a single step in which the alleles of a single gene determine whether the fly will have claret eyes or wild eyes, as indicated in Figure 29-1. In this figure, the *Cl*-enzyme is enclosed in brackets because it is still hypothetical. It has not been isolated, so its existence has not been proved, as has the existence of tryptophagenase (Chap. XXVII). We hypothesize the *Cl*-enzyme for the sake of uniformity of genetic theory; for the purposes of the present discussion, the truth or falsity of the hypothesis is irrelevant.

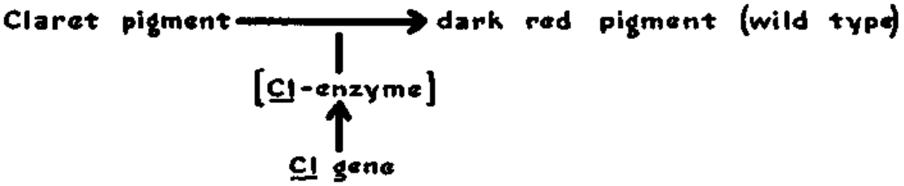

Fig. 29-1. The relation between the wild type *Cl* gene and eye color in *Drosophila*, and the intermediation of a hypothetical enzyme.

A purebred fly of the wild type has dark red eyes and two eye color genes that we will symbolize by *Cl Cl*. A purebred claret fly has light-colored eyes, and two *cl* genes. The genes *Cl* and *cl* are alleles (§ 174), i.e., a given chromosome or a given haploid cell may have one allele or the other, but not both.

Purebred wild-type flies produce only wild-type offspring, i.e., flies with dark red eyes. Purebred claret flies produce only flies with claret eyes. What happens if we mate a purebred fly with a dark red eye to one of the claret strain? As an aid in visualizing the results of such a mating, Figure 29-2 has been prepared. The drawings therein should be closely scrutinized and integrated with the reading of the following paragraphs.

Every *Drosophila melanogaster* has four pairs of chromosomes, i.e., the diploid number is eight. Every ordinary body cell, or **somatic*** cell, has these chromosomes, two of each kind, as we have diagrammatically indicated in the figure.† The *Cl* gene has been found to be on what is

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* The adjective *somatic* (Greek *soma*, body) is applied to all the cells of the body except the reproductive or *germinal* cells. In many diploid organisms, e.g., fruit flies and men, only the germ cells (eggs, sperm) are haploid; all the somatic cells are diploid.

† There is one "odd" pair in which, in the male only, the two members of the pair are not the same. They behave like members of a pair in meiosis, however. The significance of this odd pair will be pointed out in § 180. For the moment, the odd pair need not be given special consideration.

called the third chromosome, so each such chromosome in the wild-type stock has one such gene. There are two *Cl* genes in each somatic cell, as indicated in Figure 29-2 by a black bar drawn across each member of the third pair of chromosomes in the somatic cells of the dark-red-eyed parent. Purebred claret flies have a different allele (*cl*) at the same location on each third chromosome; the *cl* allele we have represented by a colorless bar. Although we can, by indirect means,

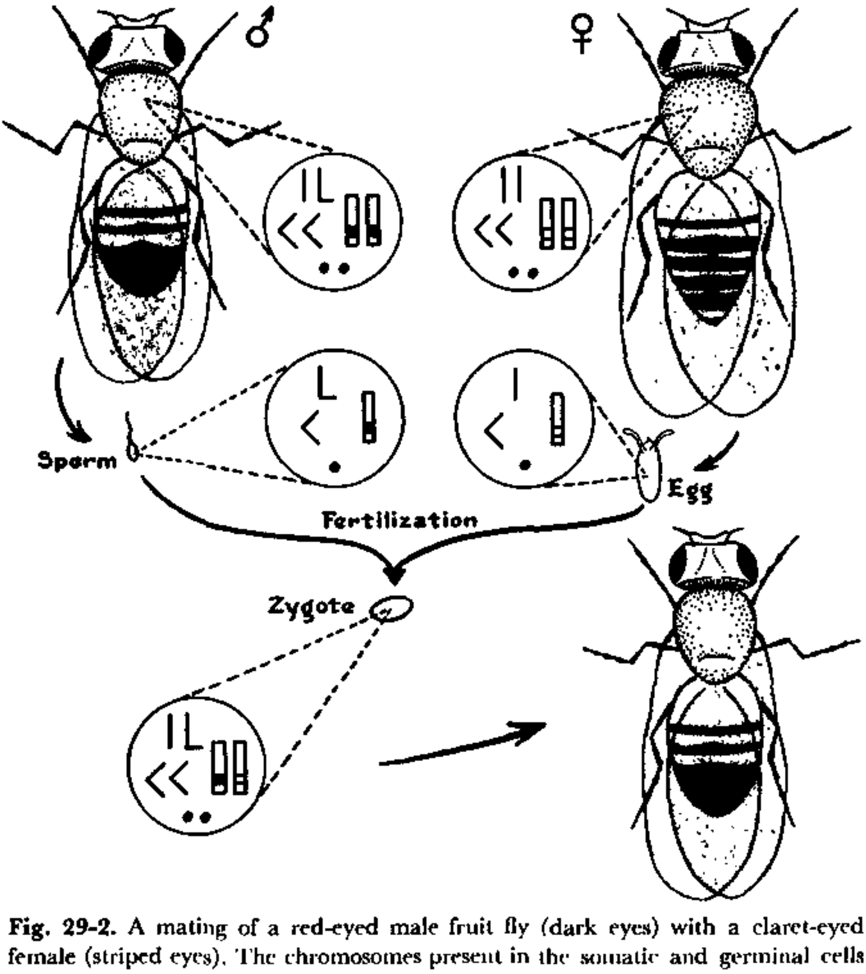

Fig. 29-2. A mating of a red-eyed male fruit fly (dark eyes) with a claret-eyed female (striped eyes). The chromosomes present in the somatic and germinal cells are diagrammatically indicated. The gene for red eyes (*Cl*) is indicated by a dark bar, its allele (*cl*) by a colorless bar. The heterozygous offspring (*Cl cl*) has red eyes, showing that *Cl* is dominant to *cl*. A reciprocal mating, claret ♂ × red ♀, would give the same results.

locate genes precisely, it must be realized that there is no microscopically visible difference between alleles. The bars drawn in the figures are merely symbols.

Sperm produced by a male *Cl Cl* fly are all of one type, as far as this gene is concerned, namely *Cl*. Similarly, only *cl* eggs are produced by a female of type *cl cl*. If a *Cl Cl* male mates with a *cl cl* female, all the zygotes will be *Cl cl*. Since the adult arises from successive mitotic divisions of such a zygote, all of its cells, including the cells of the eyes, will be diploid and genetically *Cl cl*. What will be the color of the eyes in such an adult? On observation, they prove to be red. Evidently, whatever enzyme may be produced by the *Cl* allele, one "dose" of the *Cl* allele produces enough enzyme to exert the full effect on the eye-color pigment. In conventional genetic language, "*Cl* is **dominant** to *cl*," or "The wild-type gene is **dominant** to the claret gene." The same fact can also be expressed thus: "The gene *cl* is **recessive** to *Cl*," or "The claret gene is **recessive** to the wild-type gene." However we state the facts, it must be understood that the *Cl* gene does not alter the *cl* gene. It merely means that when both are present, the effect of the enzyme-producing gene, *Cl*, is apparent, whereas the action of its allele, *cl*, is not.

Because we cannot always deduce the genes present from the appearance of the organism possessing those genes, some new terms will be useful:

Phenotype: which refers to the *appearance* (from the same word root as *phenomenon*) of an individual. The phenotype of the offspring in the example above is dark red eye, the same as the phenotype of the male parent.

Genotype: which refers to the *genetic constitution* of an individual. The offspring in the above case is *Cl cl*. The phenotype can be determined by *looking*, but the genotype is often revealed only by *breeding tests* or by a *knowledge of ancestry*.

Heterozygous: an adjective indicating a diploid individual in which the members of a pair of genes are different alleles. In our case, the offspring is heterozygous (*Cl cl*) whereas both its parents are—

Homozygous: If both genes of a pair are the same (as *Cl Cl* or *cl cl*), the individual is homozygous.

What will happen if we now use the heterozygous fly *Cl cl* as a parent? What will his children be? Obviously, it will depend on the mate selected by, or for, this heterozygous fly. First, we shall assume that he mates with a homozygous claret female, *cl cl* (see Fig. 29-3). Such a female can produce only one type of egg, namely, *cl*. The heterozygous male, however, can produce two types of sperms, namely, *Cl* and *cl*. Recall that in meiosis (§ 174) one member of each pair of chromosomes goes into one gamete while the other chromosome goes into another

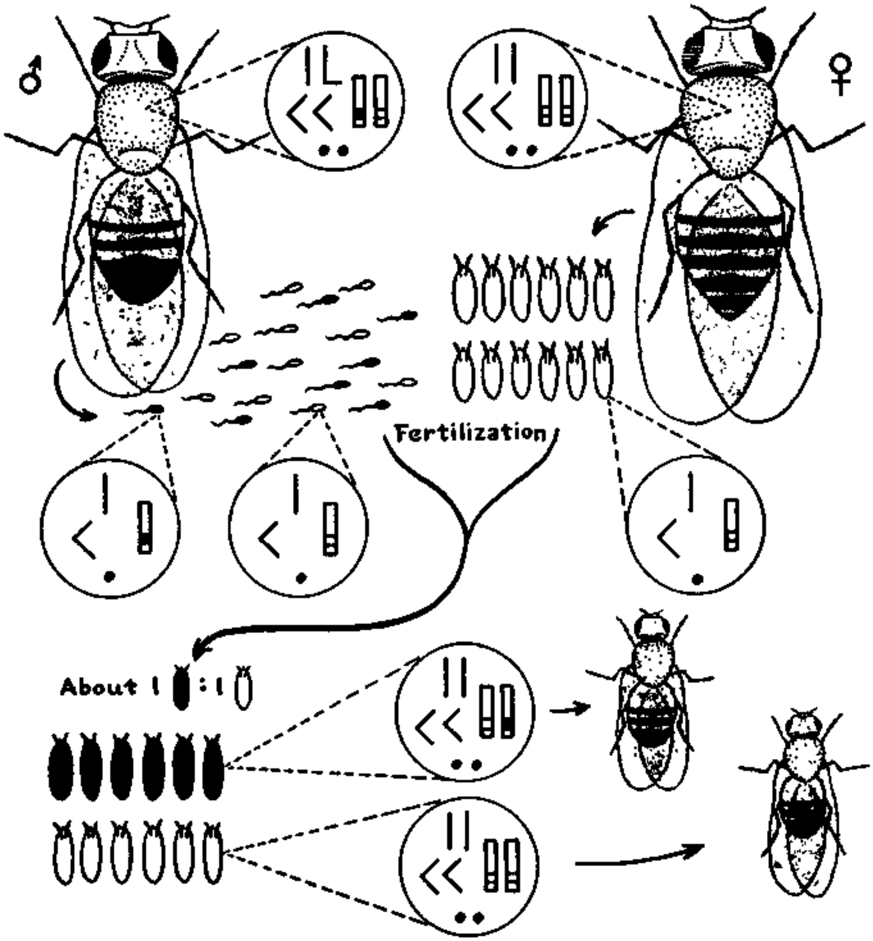

Fig. 29-3. The results of mating a heterozygous fly with a homozygous recessive fly. The homozygous fly produces only one kind of gamete. The heterozygous fly produces two sorts of gametes, as indicated by difference in shade of sperm cells. Two kinds of gametes occur in *approximately* equal numbers. A reciprocal mating, heterozygous ♂ × homozygous recessive ♀, would give the same results. Only the ♀ offspring are indicated; equal numbers of ♂♂ would be produced.

gamete; and, since genes are on chromosomes, one member of a pair of genes goes into one gamete while the other member of the pair goes into another. We would, therefore, expect a *Cl cl* fly to produce about as many *Cl*-containing gametes as *cl*-containing gametes. It is possible that the heterozygous male *Drosophila* produces *exactly* as many *Cl* gametes as *cl* gametes, but we cannot verify this because we cannot recover all of the spermatozoa that he produces and ejects. Although we have indicated a difference in the shade of the sperm in Figure 29-3, no difference of any kind is visible. We can deduce the genotype of a sperm cell only after it has joined with an egg to produce a zygote. In a mating between a *Cl cl* male and a *cl cl* female, *approximately* half of the zygotes develop into claret-eyed flies and half into wild-eyed ones. The eggs produced by a *cl cl* female will all be *cl*, hence the phenotype of the zygote indicates the genotype of the sperm involved in such a mating. Since the ratio of wild zygotes to claret zygotes is approximately 1:1, we deduce that the ratio of *Cl*-sperm to *cl*-sperm must have been approximately 1:1.

Notice that we could learn the genotype of a fly of unknown parentage by mating it to a homozygous recessive individual. From the resultant zygotes, one may deduce the genotype of the gametes of the unknown fly, hence, the genotype of the unknown diploid organism itself. *A mating to a homozygous recessive individual is called a* **test-mating** *or* **test-cross** because such a mating is capable of revealing hidden genes.

In the test-mating of a heterozygote, why is the genotypic ratio among the offspring only *approximately* 1:1? Because not every sperm cell encounters an egg. Which sperms do and which don't is a matter of chance. So even *if* the original ratio of the two types of spermatozoa were precisely 1:1, we would not expect a precise ratio among the resulting zygotes. In genetics, we are dealing with matters of probability. To illustrate the point made above by an analogy, suppose we had a box containing precisely 1,000,000 black balls and 1,000,000 white balls. If, blindfolded, we draw only twelve balls from the box, we would expect approximately six of each kind, but not exactly six and six, except occasionally, and by chance. The same sort of statement applies to the results of the mating we are considering. If the female produces only twelve eggs, as indicated in Figure 29-3, chance encounters with sperm from a *Cl cl* male will produce *approximately* six wild and six claret offspring, but seldom exactly these numbers. It is important that the student understand the approximate nature of the results diagrammed.

If we recall the concepts of probability developed in § 5 and § 30, it should be apparent that:

First. **The larger the number of offspring from a given mating, the greater the probability that the relative deviation from the expected ratio will be small.** In the present instance, if the female fly laid only four eggs, three of them might have been of one kind and only one of another, a ratio of 3:1 instead of 1:1. Calculation shows that the probability of the deviation from the expected being that great or greater is slightly more than $\frac{1}{2}$. If, from the same mating, eight eggs were produced, the probability of a distribution as extreme as 3:1 would be only $\frac{15}{64}$. From the trend of these data, it is apparent that, with a large number of offspring, we can reasonably expect the ratio actually observed to be quite close to expected ratio. This same idea can be expressed in another way:

Second. **The ratio observed in one small family gives almost no clue to the "true" ratio.** This principle is of small importance in fruit flies where families of a couple hundred children are common, and ones of as few as twelve (as diagrammed in Fig. 29-3) are rare. But, in humans, small families are the rule; therefore, a considerable deviation from the expected ratio will often occur. To take an example, wavy hair is dominant to straight hair. If a heterozygous wavy-haired human ($W w$) marries a person who has straight hair ($w w$), we would expect a ratio of 1 wavy:1 straight among their offspring; but we would not be greatly surprised to encounter a family of eight in which seven of the children had straight hair and only one had curly hair.

Third. **With only a small number of offspring, there is a good probability that an expected class will be completely missing.** In the human example just cited, there would be a fair probability that the children in a family of four would all have straight hair or all have wavy hair. The probability would, in fact, be $\frac{1}{8}$; i.e., out of eighty families of four children produced by matings of $Ww \times ww$, in ten families, all the children would have the same kind of hair. When the parents are $W w \times w w$, the probability that all the children in one family will be alike with respect to this hair characteristic is given in Table 29-1 in which families of different sizes are considered.

TABLE 29-1

THE RELATION OF FAMILY SIZE TO THE PROBABILITY THAT AN EXPECTED CLASS WILL BE MISSING. MATING: $Ww \times ww$. (SEE TEXT FOR EXPLANATION.)

NO. OF CHILDREN IN FAMILY	PROBABILITY THAT ALL THE CHILDREN WILL HAVE THE SAME KIND OF HAIR
2	$\frac{1}{2}$
4	$\frac{1}{8}$
6	$\frac{1}{32}$
8	$\frac{1}{128}$
10	$\frac{1}{512}$
12	$\frac{1}{2048}$

To a student with a very exceptional memory, this table may look familiar. It is, in fact, Table 5-1, from § 30, reprinted with new headings over the columns of figures. In § 30, we were concerned with the probability that all the molecules in a two-compartment box would be in the same compartment. Now we are concerned with the probability that all the children will be alike when there are two equally probable types that may show up. As the logician would point out, these two cases are **materially** different, but **formally** identical. The "material" in one case is molecules, in the other, genes. But, once the problem is reduced to formal symbols on paper, the calculations are carried out in the same way, regardless of the material involved.

It is a great virtue of the theory of probability that it furnishes us with powerful intellectual tools that can be applied to a wide variety of problems. In Chapter V, we used the concepts of probability to arrive at an understanding of the behavior of molecules. In the present chapter, we are learning how these same concepts can explain the behavior of genes in heredity. But, before we can continue along this line, we must interrupt the account of genetics to develop the principles of probability more explicitly.

178. Elementary Principles of Probability

Probability is measured on a scale running from 0 (impossibility) to 1 (absolute certainty). The probability of a coin turning heads is $\frac{1}{2}$, that is, we expect about half of a large number of throws to result in heads. The probability of a die (singular of *dice*) turning four is $\frac{1}{6}$ (there are six sides to a die). In the long run, we expect the four on a die to turn up about one-sixth of the time, i.e., in about one out of every six throws of the die.

A further concept is needed, the idea of the **product rule of probability:**

> **If an event is composed of two subevents, both of which must occur, then the probability that the compound event will occur is the product of the separate probabilities of the subevents.**

At this point, the student is likely to exclaim, "*That* is about as clear as mud!" It would be difficult to clarify the meaning of the statement by further definitions. Fortunately, however, the consideration of some simple examples should make it clear.

A coin and a die are both tossed in the air at the same time. What is the probability that the coin will fall *heads* and the die show *four?* Both subevents must occur simultaneously, so the probability of both occurring at the same time is $\frac{1}{2} \times \frac{1}{6} = \frac{1}{12}$. That is, out of every twelve times that we throw coin and die together, heads and four will appear together approximately once.

About half of the people are males. Suppose, in a given population, about one-tenth of the people have red hair. A man walks down the street. What is the probability that the first person he runs into is a red-haired woman? Answer: $\frac{1}{10} \times \frac{1}{2} = \frac{1}{20}$. (Of course, we assume no interference with nature, by either sex.)

In the case of the mating, *Cl cl* (male) × *cl cl* (female), what offspring may result, and with what probability? (See again § 177 and Fig. 29-3.) *cl cl* offspring will result when a *cl* sperm gets together with a *cl* egg. The probability that the egg will be *cl* is 1 (certainty). The probability that the sperm will be *cl* is $\frac{1}{2}$. The probability that both the egg and the sperm involved in a specified fertilization will be *cl* is therefore $1 \times \frac{1}{2} = \frac{1}{2}$.

With these statements in mind, reread the statement in boldface above and see if it is any clearer . . . .The ideas of probability are seldom as difficult as the problem of expressing them in words.

179. The Mating of Heterozygotes

Suppose we mate two heterozygous flies: *Cl cl* × *Cl cl*. What offspring may result, and with what probability? *Cl Cl* offspring will result only when a *Cl* sperm meets a *Cl* egg.

$$\text{Probability: } \tfrac{1}{2} \times \tfrac{1}{2} = \tfrac{1}{4}$$

cl cl offspring will result only when both sperm and egg are *cl*.

$$\text{Probability: } \tfrac{1}{2} \times \tfrac{1}{2} = \tfrac{1}{4}$$

Cl cl offspring may result in *either* of two cases:

(a) *Cl* sperm meets *cl* egg. Probability: $\frac{1}{2} \times \frac{1}{2} = \frac{1}{4}$

(b) *cl* sperm meets *Cl* egg. Probability: $\frac{1}{2} \times \frac{1}{2} = \frac{1}{4}$

Since both cases yield *Cl cl*, we add, getting: $\frac{1}{2}$

Therefore, the offspring of *Cl cl* × *Cl cl* will be composed of about $\frac{1}{4}$ *Cl Cl* + $\frac{1}{2}$ *Cl cl* + $\frac{1}{4}$ *cl cl*. Out of a hundred offspring, we would expect about 25 *Cl Cl*, about 50 *Cl cl*, and about 25 *cl cl*.

Such are the genotypes. However, recall that *Cl Cl* and *Cl cl* are indistinguishable, without resort to a test-mating. What would be the *phenotypes* from a mating of two heterozygotes? Obviously, about $\frac{3}{4}$ dark-red eyed and about $\frac{1}{4}$ claret eyed, or a ratio of about 3 red:1 claret. Out of 100 such offspring, we would expect about 75 to be red eyed.

180. The Heterosomes and Sex Determination

A careful examination of the diagrammatic cells of the flies in Figure 29-2 or Figure 29-3 discloses that, in the male, there is one pair of chromosomes that is not quite a well-matched pair. This is not true of the female. The corresponding chromosomes of the female, the uppermost pair in each figure, are called the **X-chromosomes.** The male has only one *X*-chromosome, and its odd mate is called a **Y-chromosome.** The *X* and the *Y* behave in meiosis as if they were good mates, but microscopic evidence reveals that they are clearly different. The *X* and *Y* chromosomes are called **heterosomes** to distinguish them from all the other chromosome pairs which are called **autosomes.**

Since the male contains two different heterosomes, and since heterosomes behave like members of a pair in meiosis, it is apparent that the male will produce two different kinds of gametes, one an *X*-sperm, and the other a *Y*-sperm, as indicated in Figure 29-4. The male is, therefore, called the **heterogametic sex.** The two kinds of gametes appear in approximately equal numbers, which we have indicated in the diagram by writing *ca.* $\frac{1}{2}$ below each type of gamete. (The abbreviation *ca.* stands for Latin *circa*, meaning about, hence, *approximately.*) The female is the **homogametic sex** and produces only *X*-eggs.

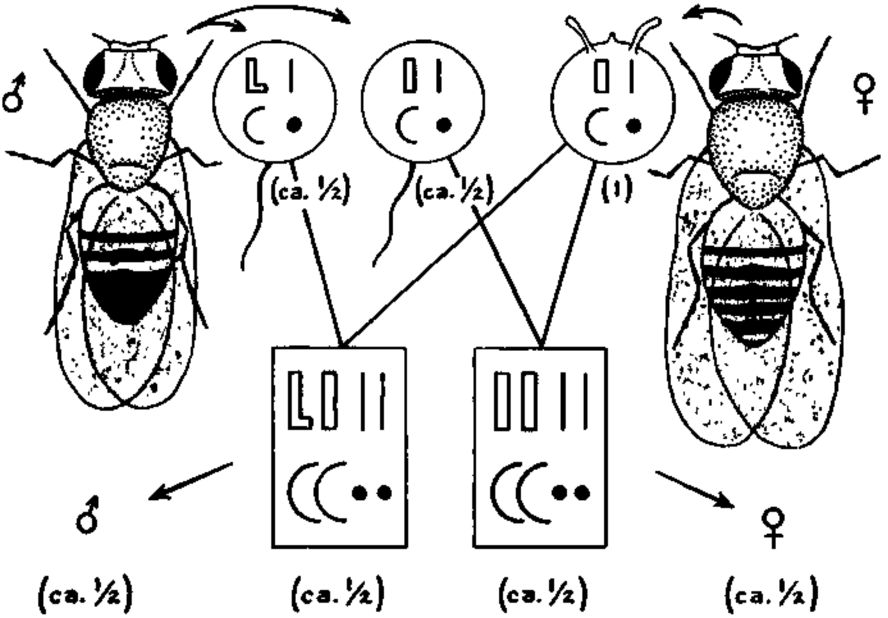

Fig. 29-4. The method of sex determination. The male produces two sorts of gametes in equal numbers, *Y*-gametes (left) and *X*-gametes (middle). The female produces only *X*-gametes. The *XY*-zygotes develop into ♂♂; the *XX*-zygotes develop into ♀♀. This mechanism insures the approximate equality in numbers of the two sexes. The sex-determining mechanism is the same in humans in whose somatic cells, however, there are forty-six autosomes instead of six, as in the fruit fly.

When an *X*-egg mates with an *X*-sperm, the *XX*-zygote develops into a female.

When an *X*-egg unites with a *Y*-sperm, the *XY*-zygote produces a male.

Since males must mate only with females (and vice versa), a little thought will show that this mechanism insures the appearance of males and females in approximately equal numbers, generation after generation. Sex is determined by chromosomal make-up.

Why is an *XY* individual a male and an *XX* individual a female?

The simplest hypothesis would be that there is some dominant male-determining gene on the *Y*-chromosome which is not present on the *X*-chromosome. *This is not the case.* Here, as is so often true, the causes of the normal condition are revealed by abnormal events. Occasionally, meiosis fails to work as it should, resulting in the nonseparation of the *X*-chromosomes at reduction division. Because of this there are produced two* new types of zygotes:

XXY – – – – – – – which is a female
X only – – – – which is a male

Both of these types contain the normal complement of autosomes, namely, two haploid sets.

The sexual outcome of these new types suggests a new hypothesis as to the determination of sex, namely, that **it is the ratio of *X*-chromosomes to autosome sets that determines sex.** If the ratio is 2:2, a female is produced. In fruit flies, an individual with 2 *X*-chromosomes and 2 autosome sets has a ratio of 2:2 and is a female, even if there is a *Y* present—as there is in the *XXY* individual cited above. But, if there is only 1 *X* present and 2 sets of autosomes, the ratio is 1:2, and a male is produced. The *Y* seems not to be required to produce maleness. (Though, incidentally, in the absence of the *Y*, the male is sterile.)

In many other animals, including man, the same situation holds. In humans, a female has two *X*-chromosomes, and two sets of autosomes that consist of 23 chromosomes each, making a total of 48 chromosomes. The male has an *XY* set of heterosomes. No chromosome abnormalities are known in man.

181. "Sex-Linked" Inheritance

In all of the matings considered so far, it makes no difference whether the genotypes of the two sexes are as stated, or whether the sexes and genotypes are interchanged. That is, a mating of *Cl cl* ♂ × *cl cl* ♀ produces the same results as the **reciprocal mating** *cl cl* ♂ × *Cl cl* ♀. The great majority of the genes in all organisms behave in this way. There are, however, some genes which do not behave identically in reciprocal matings. Among these, are the so-called sex-linked genes, that is, the genes carried on the *X*-chromosome. The *X*-chromosome, like the

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* Also produced: *XXX* and *Y*-only, but both of these die, for unknown reasons.

autosomes, is made up of hundreds of genes. The *Y*-chromosome, however, appears to be almost devoid of genes. We shall, therefore, regard it as a genetic blank. The *X*-chromosome has many genes on it, one of which, in fruit flies, is called "miniature" because it causes the wings to be smaller than normal. Miniature (*m*) is recessive to normal (*M*). Females must have two "doses" of *m* to be miniature, but males need to have only one dose of *m* to be miniature, since the *Y*-chromosome has no counter-acting gene.

In Figure 29-5, is diagrammed the result of the cross of a miniature male with a wild-type female. In the first generation, called the F_1 ("first filial"), only the females can have the *m* gene because the males necessarily get *X*-chromosomes from their mother*, who has only normal genes (*M*) to contribute. If we now make a brother-sister mating in the F_1, in the F_2 there will once more appear the miniature character, and it will be in the male sex again, as it was in the grandfather. It was this apparent tendency of a mutant character to stay linked to one sex that led this sort of inheritance to be called "sex-linked inheritance."

The sex-linkage is partly spurious, however. Miniature females can be produced by the following mating:

$$Mm \times m(Y)$$

$$\downarrow$$

$$Mm + mm + M(Y) + m(Y)$$

About one-half of the female offspring will have miniature wings since they have no dominant *M* to produce normal wing.

Red-green color-blindness in humans is a recessive sex-linked gene. A father can transmit it to his daughters who will be only "carriers" if they are heterozygous. He cannot transmit it to his sons, who get an *X*-chromosome only from their mother. In the United States, the frequency of red-green color-blind men is about 1 in 12. This means that, out of all the *X*-chromosomes in the United States, only about $\frac{1}{12}$ bear such a gene.

What will be the frequency of color-blind women? For a woman to be color-blind, she must have *two* "color-blind" *X*-chromosomes.† If

---

* Why necessarily?

† This is a ridiculous expression, but "*You know what I mean,*" as the student says.

the frequency of color-blind X-chromosomes is $\frac{1}{12}$, the chance of "drawing" one such chromosome is $\frac{1}{12}$, and the chance of drawing two of them simultaneously (thus making a female) is—by the *product rule of probability*—$\frac{1}{12} \times \frac{1}{12} = \frac{1}{144}$. Observations show that this is approximately the frequency of color-blind women.

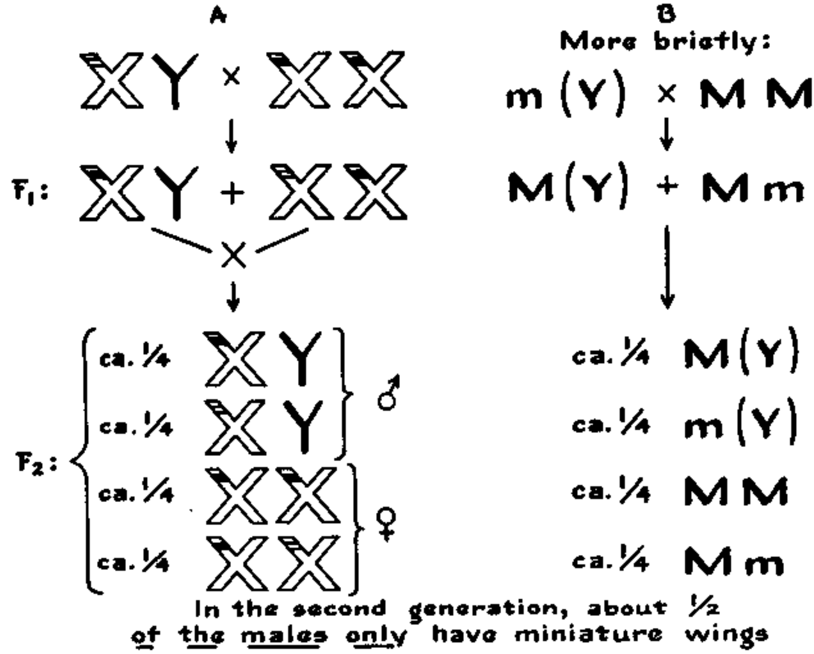

Fig. 29-5. Inheritance of a "sex-linked character" indicated in two ways. In A, the mutant gene is represented as a light band on the X-chromosome, the wild type gene as a dark band. The Y-chromosome may be considered a genetic blank. In B, the symbolization is simplified by the elimination of the X-chromosome. The Y-chromosome is retained in order to avoid errors in thinking of meiosis, but it is written in parentheses so the chromosome will not be mistaken for a gene.

Color-blindness is much rarer in women than in men. This difference has nothing to do with sexuality as such, but is merely a consequence of the fact that the responsible gene is on a heterosome.

182. The Genetic Danger of Atomic Radiation

We have frequently mentioned that mutations may be produced by X-rays, that a gene may thus somehow be altered so that it no longer produces its usual enzyme, perhaps producing none at all. Mutations may also be caused by exposure of genes to various other agents: gamma rays, ultraviolet light, and mustard gas, for example. We can deliberately produce mutations. But mutations also occur "spontaneously," when we do not knowingly expose genes to **mutagenic agents.** The rate of "spontaneous" mutations is low; the probability of a particular gene's mutating in a given generation is only about one in a million, typically. There is great variation in the mutability of genes. Many are much more stable than that, and a few are less stable.

There are certain characteristics of mutations that everyone should know:

1. Mutation is a random affair. There is no way of predicting what gene will mutate next in an organism or what the mutant gene will do.
2. When a "wild-type" gene mutates, the mutant is usually recessive.
3. The mutation is usually "bad" or, at best, neutral. The existing "wild-type" mutations have been naturally selected from countless, repeated mutations, over a period of millenia, as genes that do something useful for the organism. Most "new" mutations are ones that have already occurred countless times before, have been tested in the struggle for existence, found wanting, and have been discarded.
4. Mutagenic agents, e.g., the radiations from atomic bombs, greatly speed up the rate of mutations of all genes without altering any of the characteristics of mutations listed above.

From these facts, follow practical consequences. Wherever mutagenic agents, such as atomic bombs or unshielded atomic reactors, raise the level of mutagenic radiations, we can expect many new mutations to be produced. Most, if not all, of these mutations will be of no value to the organism, or will be deleterious. Most will be recessive mutants. Therefore, in the children of a man exposed to such radiations, we could reasonably expect no deleterious mutations to show up, phenotypically, for it would be improbable that a man bearing a particular mutant gene (say *a*) would mate with a woman who had the same gene. That is, the mating might be, say *AaBBCCDD* . . . × *AABbCCDD* . . . which would yield no children homozygous for any of the recessive mutant genes. Genetically, however, these children might harbor many deleterious recessive genes which they could pass on to their offspring. Such genes would remain hidden for several generations until two individuals heterozygous for the same recessive gene mated ($Aa \times Aa$) when it would be possible for some of the children to receive two "doses" of the recessive gene and, hence, to be phenotypically of the recessive type. Because of diploidy and the recessive character of deleterious genes, the immediate genetic effects of atomic radiation might *appear* to be of no consequence.

It is this consideration that has led biologists to take such a dim view of the use of atomic disintegrations. Whether used for destructive purposes (in bombs) or for socially constructive purposes (in atomic power plants), atomic disintegration produces a great amount of dangerous radiation that is difficult to control and dangerous by-products that are difficult to dispose of. No one knows, in quantitative terms, what a "safe" amount of radiation is, *genetically speaking*. A half-century's experience with various radiations, such as X-rays and radium emanations, has taught us what the dangerous level is *for the individual*. But we do not know the probability of his gametes' being altered, nor is it likely, in a species in which we cannot control matings so as to reveal hidden recessives, that we will soon find out. There is a grave danger that man may, with his atomic engines, build up a store of deleterious recessive genes that will plague his species with unwanted phenotypes for centuries to come.

Other organisms are as susceptible to mutations as man, of course. But, with them, the problem is not so serious, for two reasons:

First. All but a handful of organisms overproduce immensely. A single pair of salmon, for instance, produces several million eggs. The loss of ninety-nine per cent of these, due to the cropping up of double recessives, would be no serious matter. The one per cent remaining would be more than enough to continue the species.

Second. When poor phenotypes do appear in other organisms, there are no social traditions or moral standards tending to save them for breeding another generation. Through the perishing of the recessive phenotypes, deleterious genes are soon reduced to a very low frequency in all organisms but man. Our traditions, in this part of the world, compel us to save the offspring, however they may turn out.

QUESTIONS AND PROBLEMS

Preliminary Note: Problems of inheritance in diploid organisms will seldom cause trouble if the student proceeds slowly and systematically. In solving problems, the following course of action is suggested:

1. Find out if dominance is involved.
2. Translate the phenotypes into genotypes before proceeding. It is a gene that is inherited, not an appearance.
3. Predict the gametes; and their probabilities, if necessary.
4. Predict the zygotes; and their probabilities.
5. Convert the genotypes of the zygotes to phenotypes.

In the following problems, you are to assume that the genes involved are on the autosomes, unless you are informed otherwise. Ignore possible mutation.

29-1. In dogs, wire hair is due to a dominant gene, smooth hair to its recessive allele. What kinds of gametes will a heterozygous female produce? In what proportions?

29-2. If a heterozygous wire-hair mates with a homozygous smooth-hair dog, what kinds of offspring may show up? In what proportions would you expect them?

29-3. If two heterozygous wire-hair dogs mate, what genotypes might show up among the offspring? What phenotypes?

29-4. What two genotypes appearing in the offspring of the preceding problem would be indistinguishable phenotypically? By what breeding test could you distinguish them? Explain.

29-5. Albino humans have almost no pigment in their hair and eyes and, hence, have white hair and pink eyes, the color of the eyes being due to the blood. When albinos marry, all their children are albinos. When an albino marries a normal person, usually all the children are normal but, in some such matings, approximately half the children are normal and half are albino. Explain the inheritance of albinism.

29-6. Would it be possible for two normal persons to have an albino child? Explain.

29-7. John Doe is a normal person whose mother was an albino and whose father was normal. He marries an albino, and half their children are albinos. What is John Doe's genotype?

29-8. If marriage of albinos were forbidden, would this, of a certainty, eliminate albinism from the population? Explain.

29-9. In the four o'clock flower, the genotype *RR* produces red flowers, *Rr* produces pink flowers, and *rr* produces white flowers. Which would be easier to eliminate from a population: whiteness in four o'clocks, or albinism in man? Why?

29-10. Would it be possible to develop a pure-breeding strain of four o'clocks that was red? One that was pink? One that was white? If not, explain why not.

29-11. There is, among dogs, a recessive gene for deafness. Suppose you had a large kennel of dogs, including some deaf ones. You wished to eliminate completely all the genes for deafness from your breeding stock. Tell, in detail, how you could secure reliable breeding stock.

29-12. In man, there is a hereditary anomaly called "haemophilia," in which the blood coagulates very slowly, thereby rendering the sufferer liable to death from bleeding. Haemophilia is due to a "sex-linked" recessive gene. To which parent does a haemophilic man owe his haemophilic gene? To which grandparent?

29-13. If a normal woman marries a normal man and 2 out of 3 of her sons are haemophilic, what is her genotype? Had her husband been haemophilic, would different results have been expected? Explain.

29-14. If a normal woman marries a normal man and 1 out of 11 of her sons is haemophilic, what is her genotype?

29-15. Fig. 29-3 is incomplete, in that only the female offspring are indicated. Sketch a new figure, showing the complete, and correct, story.

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Chapter XXX

Antibodies: Their Nature and Significance

183. The Antigen-Antibody Reaction

Proteins are very complex molecules composed of hundreds of atoms. They are so complex that we do not, at the present time, know the structural formula for a single protein. Of many proteins, we know the approximate molecular formulas (§ 45). When we chemically tear a protein into smaller pieces, we find that amino acids are the most common break-down products. Amino acids appear to be the principal type of building block of the proteins. But we do not have a complete picture of how the building blocks are put together.

An organic molecule made of hundreds of atoms could, theoretically, have any of millions upon millions of different structures. There should be an almost uncountable number of different kinds of protein molecules. The evidence is in keeping with this prediction. If the chemist is unable to tell us the structure of a single protein, how do we know that there are many different types of proteins? Surprisingly enough, the evidence comes not from the chemist's laboratory but from the biologist's. Instead of a test tube or retort, a living body is the piece of apparatus used to distinguish different proteins.

It was previously pointed out (§ 50) that if undigested food were to be injected into the blood stream of a human body, it would cause a serious reaction, perhaps even death. The principal cause of such reactions would be the undigested proteins. Any protein that is different

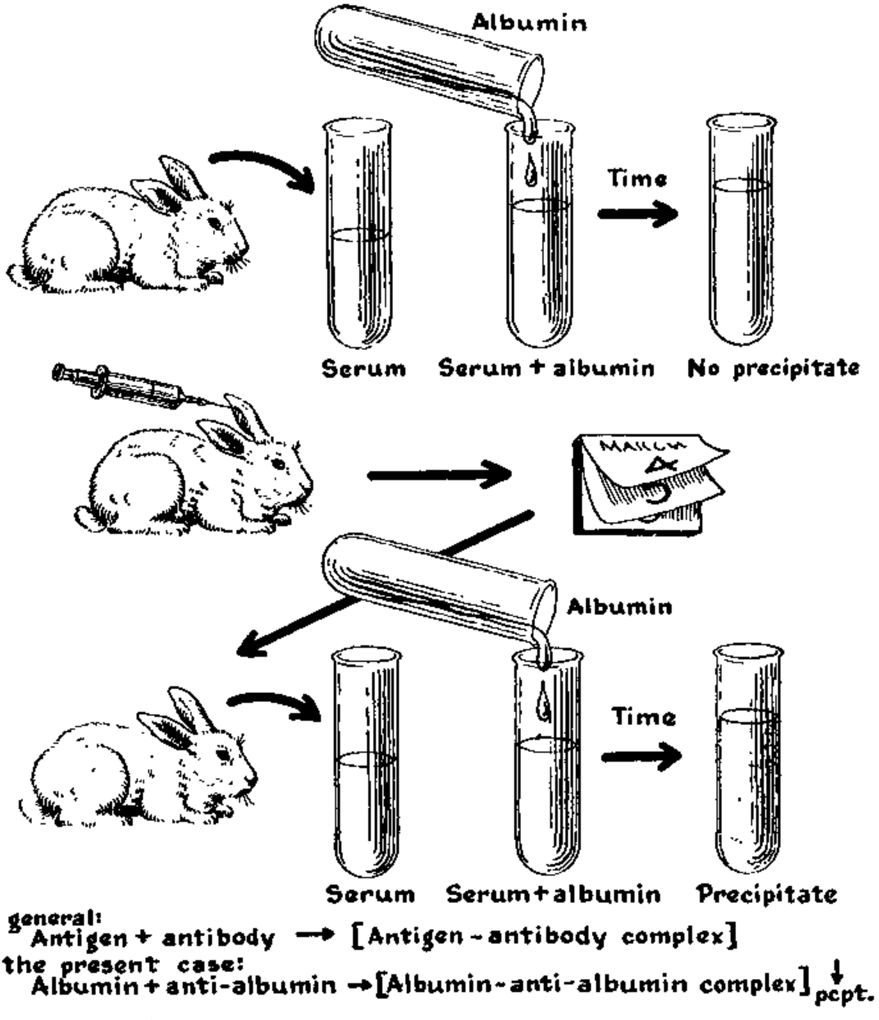

Fig. 30-1. The manufacture and detection of antibodies.

from those present in the body may cause a dangerous reaction to take place when it is injected into the body. Sometimes, the injection of a **foreign protein** (as it is called) is not followed by any untoward effects on the first administration, but does cause a violent reaction when injected a second time. What is the explanation of this phenomenon?

What change takes place in the body between the first and second injections of the foreign protein?

We shall describe the events that take place when a specific protein, egg albumin, is used as the foreign protein which is injected into a test animal, say a rabbit. The first injection of egg albumin may cause only slight untoward reaction. Upon a second injection two weeks later, the rabbit shows evident signs of distress and may become seriously ill. It can be shown that, in the period between the two injections, the blood serum of the rabbit has become subtly modified. The serum of a rabbit that has never been injected with egg albumin, when mixed with albumin, remains clear. But serum taken from a rabbit sometime after an injection of albumin, when mixed with albumin, produces a precipitate, observable as a cloudiness in the test tube (Fig. 30-1). *After exposure to a foreign protein, there is developed in an animal a substance which can combine with the foreign protein. This substance is called an* **antibody.** *The substance which causes its formation is called an* **antigen.***

Only proteins can provoke the formation of antibodies, i.e., can act as antigens, as defined above. The antibody which results from this stimulation is also a protein. It is highly specific in its reactions, precipitating only with the causative antigen, or one very nearly like it. Because of this **specificity,** an antibody can be used for identifying proteins. Suppose one extracts from some material a protein that one suspects is identical with egg albumin. By chemistry alone, one cannot prove the identity. The antigen-antibody reaction permits us to test it, in the following manner:

> *First:* Inject a rabbit with albumin. As a result, the rabbit develops an antibody "against" albumin which we may call "anti-albumin."
>
> *Second:* Take blood from such an injected rabbit, centrifuge out the red blood cells, thus obtaining a clear serum that contains any antibodies the rabbit possesses.
>
> *Third:* Add this serum to the protein to be tested. If a precipitate forms, we know that the unknown is albumin. If no precipitate forms, then the unknown protein is not albumin.

---

* The concepts of antibody and antigen are clear cut and not too difficult to comprehend. Unfortunately, the *words* are much too nearly identical. It is essential that the student never misread these words, at the risk of great confusion.

The above account has been simplified somewhat, in that we described precipitation as an all-or-none phenomenon. Actually, when many similar proteins are tested with an antibody, it is found that many different grades of precipitation may be obtained, ranging from heavy, through intermediate and light, to none. The fact that the **precipitin reaction** (as it is called) is a graded one does not make the antigen-antibody reaction less useful, but more. By this reaction, we can not only identify identical proteins, but near-identical ones, and can estimate the closeness of chemical relationship of two proteins.

184. How Is Antibody Formed?

It is several days after the initial injection of an antigen before any antibody can be found in the blood stream. How is the antibody manufactured? And where? At present we do not know. When antigen plus unaltered serum or whole blood are brought together in a test tube, no antibody is formed. Only an antigen in a living body can provoke the formation of a specific antibody against it. The antibody is probably not formed in the blood stream but somewhere else in the body. Wherever it is formed, it appears in most of the tissues of the body. The major part of our knowledge of antibodies has been gained from studies of antibodies taken from blood serum simply because this convenient source can be exploited most easily without harming the animal.

It is possible to measure the concentration of antibody in the blood serum. When an antigen is injected into the body for the first time, the concentration of antibody in the serum rises slowly (Fig. 30-2A). Ultimately, the concentration reaches a limit and gradually declines. If, after it has declined nearly to the initial level again, one makes a second injection of the same antigen, the amount of antibody in the blood stream increases very rapidly and may reach a higher level than before (Fig. 30-2B). The rate of increase of antibody is almost independent of the amount of antigen injected. To indulge in a figure of speech, it looks *as if* the first injection of antigen had a slow effect because it took time for the antibody-producing cells (wherever they are) to "learn" how to produce this new antibody. Once they have "learned how," a subsequent injection merely "reminds" these cells to get busy.

All this is, of course, only a figure of speech. The mechanism of antibody formation remains a mystery. The fact that antibodies are unable to reproduce themselves, but appear to be produced by something else, reminds one of the enzymes of the body, which cannot reproduce themselves but are produced by genes. Many scientists think there is a fundamental similarity between antibody production and gene action.

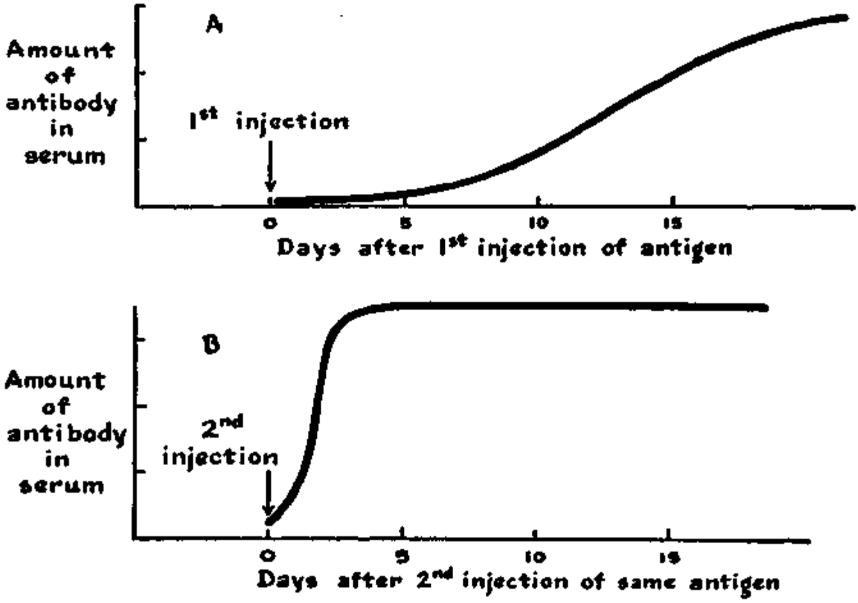

Fig. 30-2. The slow production of antibodies after first injection of antigen (A) is followed by a prolonged decline in quantity of antibody (not shown). If, after this decline, one gives a second injection of antigen ("booster shot"), the rise in antibody level is rapid (B).

185. The M and N Blood Types

A biological species may be defined as a population of organisms, the majority of whose proteins are identical throughout the group.

Even within a species, however, there are differences, as the antigen-antibody test can readily show. If the red blood cells from one human being are injected into a rabbit, the rabbit presently develops an antibody which, when mixed with the red blood cells from the same human, causes them to stick together, or **agglutinate.** The reaction involved here is the antigen-antibody reaction, in which the antigenic protein is a part of these particular human red blood cells. The particular effect of the reaction is to *agglutinate* the red blood cells. We can use such **agglutination** as a test for specific proteins.

If the rabbit-produced antibody evoked by one sample of human red blood cells is tested against the red blood cells of many different humans, it is found that the agglutination reaction sometimes fails to develop. Detailed analysis of many human bloods has revealed that there is one protein which has been called "M" and another one which is called "N," and that every human produces either "M," or "N," or both. All the blood cells of a given individual human are alike. Figure 30-3 shows the essence of the method by which bloods are typed for the M and N antigens. For this typing, antibodies are produced in rabbits, because the M and N proteins are not *antigenic* for humans; i.e., a human of type M is unable to develop anti-N antibody even after repeated ininjections of N type red blood cells. To put the matter in general terms, not all the proteins that are foreign to a given individual are antigenic to him. Because the M-N proteins are not antigenic to humans, these proteins need not be determined preparatory to blood tranfusion (§ 187).

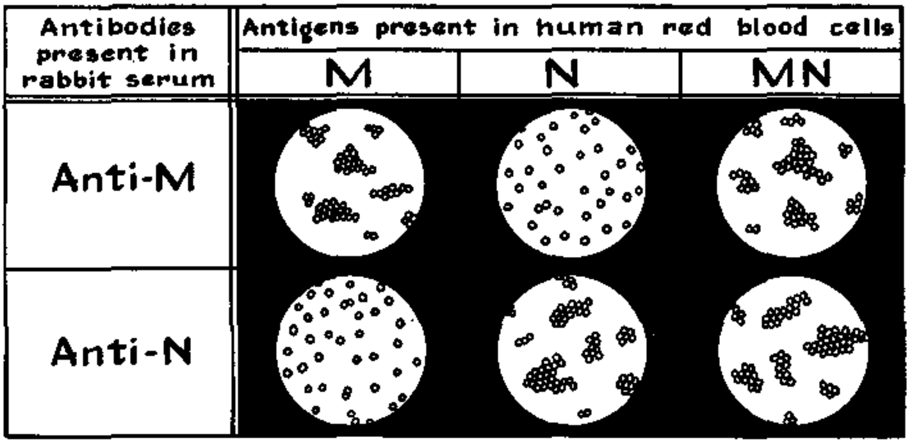

Fig. 30-3. Typing blood for M and N proteins by the agglutination method.

It has been found further that which type of blood cell one produces is determined by heredity. Proteins M and N are due to genes that are alleles of each other. Neither is dominant to the other. If we use the same letters, in italics, to represent the causative genes, every human is of the following genotypes: *MM*, *MN*, or *NN*. So far as is known, the production of the specific proteins is the only effect of the causative genes.

The inheritance of the genes *M* and *N* is in accord with the Mendelian laws developed in the preceding chapter. A man of M blood type mated with a woman of MN type can produce either MN or M children, but no N children. The production of an N child by his MN wife is sufficient cause for a raising of the eyebrows, since only a mutation (which is a very rare phenomenon) could account for the legitimate procreation of such a child from such parents.

186. The Rhesus Blood Factor

Human red blood cells sometimes include another protein which is not constantly present throughout the species. This protein is called the **Rhesus protein** because it was first found in the Rhesus monkey. Subsequently, it was found to be present in about eighty-five per cent of the humans tested. Such humans are said to be **Rhesus-positive.** The other fifteen per cent of the population do not have this protein and are called **Rhesus-negative.** The gene which causes the production of the protein is symbolized by *Rh*. The allelic gene is symbolized by *rh*. An individual whose genotype is *rh rh* produces no Rhesus protein. The genotypes *Rh rh* and *Rh Rh* both produce Rhesus protein and they are indistinguishable.

The particular interest of the Rhesus gene lies in its responsibility for some of the natural abortions and miscarriages of human embryos. If a woman of genotype *rh rh* mates with a man of *Rh rh* or *Rh Rh* constitution, her child may be *Rh rh*. In *some* of the cases in which the mother is Rhesus-negative and the child is Rhesus-positive, trouble is encountered. *If* any of the child's red blood cells—which contain the Rhesus antigen—get through the placenta and into the mother's system, the foreign protein will stimulate the production of antibody (anti-Rhesus). This antibody is a soluble material which can go through an intact placenta. When it gets into the blood stream of the infant, it combines with the child's red blood cells causing their destruction. The sequence of events is diagrammed in Figure 30-4. The damage may be so extensive as to cause the death and abortion of the child. In less severe cases, the child is born with a serious case of jaundice.

One of the interesting points about the Rhesus story is that it is indirect evidence that our first picture of the completeness of the placental barrier (§ 118) may not be entirely true. So far as we know, the Rhesus protein is found only in red blood cells. If there are no exceptions to this, the production of antibodies by the mother means that red blood cells from the child must have gotten into the mother's blood stream. This suggests an accidental break in the placenta. Quantitative studies show that only a drop or two of the child's blood would be enough to produce the effect observed.

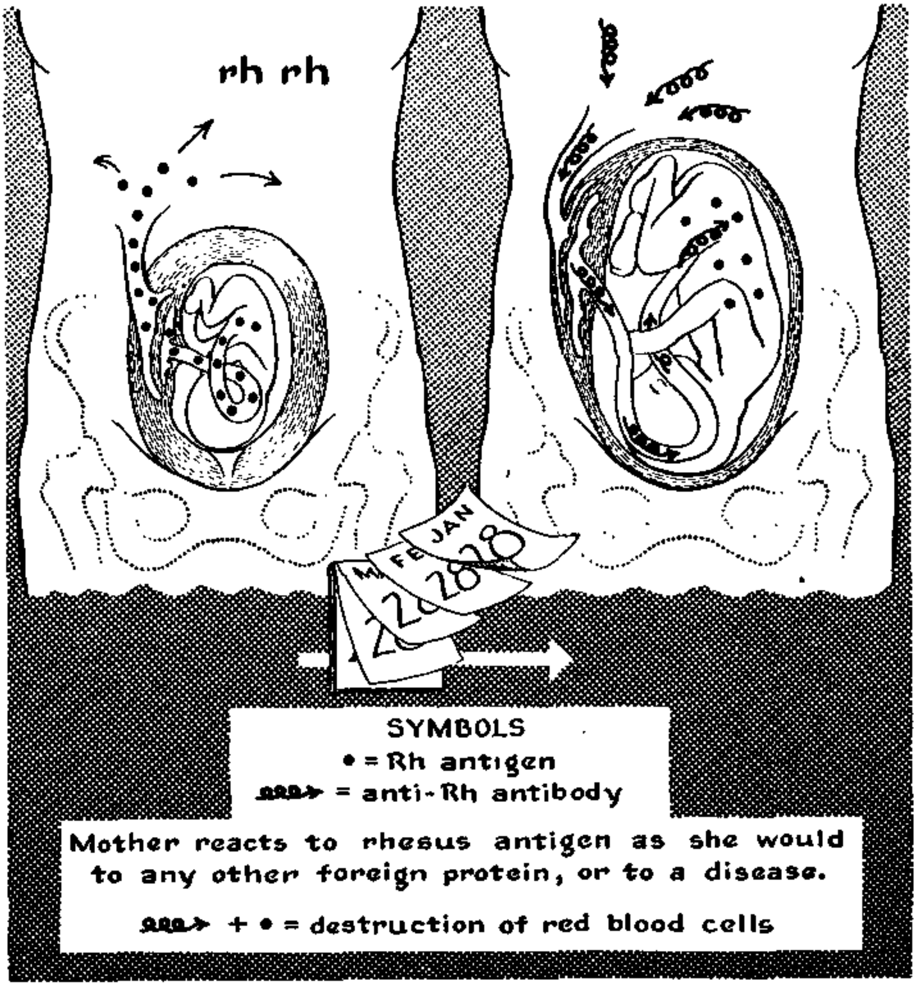

Fig. 30-4. The Rhesus factor and its possible effects.

The instances in which the mother is Rhesus-negative and the child is Rhesus-positive do not all result in complications. The first child is seldom affected. Whether subsequent children are affected probably depends on whether or not there occurs an accidental break in the placenta. *If* the mother is exposed to Rhesus antigen and if she develops antibodies, she may still be able to have several children if their births are spaced sufficiently widely to allow the concentration of antibody in her blood to fall to a low level before a new conception ensues. Even if a jaundiced child is born, it may be saved by prompt and frequent blood transfusions during the first few months of its life. A Rhesus-negative mother married to a man heterozygous for the Rhesus gene would, of course, produce children half of whom would be expected to be Rhesus-negative and, hence, not liable to infantile jaundice, regardless of the integrity of the maternal placentas.

The discovery of the possible effects of incompatible Rhesus types in mother and child has shown the importance of an early typing of the blood of female children. If a Rhesus-negative girl receives a transfusion of Rhesus-positive blood, she may develop so great a concentration of anti-Rhesus antibody that it will be impossible for her ever to bear a Rhesus-positive child, thus restricting her in her choice of a husband. In addition, if she herself receives a second transfusion of Rh+ blood, she may suffer a dangerous reaction. The same danger, of course, besets a Rhesus-negative male who receives repeated blood transfusions. For this reason, it is now becoming routine for hospitals to type blood donors and blood recipients for the Rhesus protein as well as for the A and B proteins to be described in § 187.

187. The A, B, and O Blood Types

The earliest discovered proteins of the red blood cells were the proteins known as "A" and "B." A red blood cell may have the former, in which case the individual is said to belong to blood group A; the latter, and the individual is identified as being in group B; both, in which case his group is AB; or neither, in which case he belongs to group O.

With respect to the problem of antigen-antibody reactions, the A-B blood types differ from the M-N and the Rhesus factors previously considered. The antibodies against A and B may be present without previous exposure to the antigen. The situation is this:

A person with A red blood cells always has anti-B in his serum.

A person with B red blood cells always has anti-A in his serum.

A person with AB red blood cells always has no antibodies.

A person with O red blood cells always has both anti-A and anti-B in his serum.

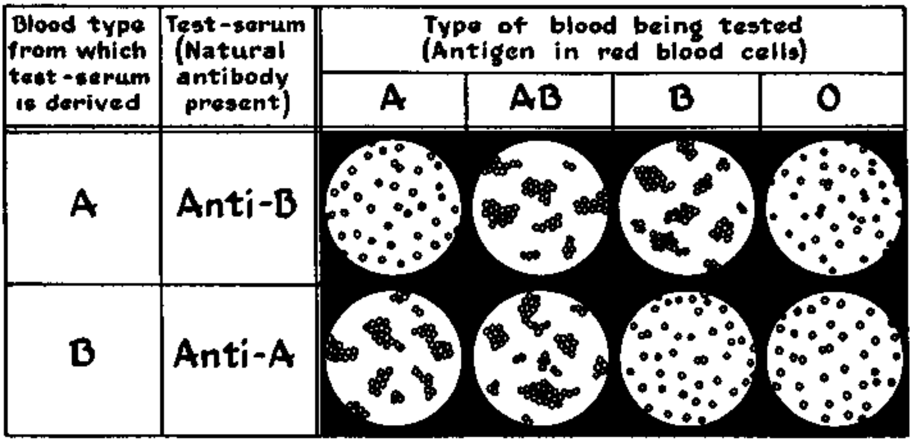

Fig. 30-5. Typing blood for the A and B proteins by the agglutination method.

One might briefly say that each man naturally has as many antibodies in his serum as he can "afford" to have. Since these antibodies are naturally present, without any previous exposure to antigenic red blood cells, it is important, even in the first blood transfusion, to transfuse blood that is of the same type as that of the recipient. It was not until the American-Austrian Nobel prize-winner, Karl Landsteiner, in 1900 discovered the existence of these blood types that blood tranfusion became a feasible medical procedure. Before that time, the unexplained and often fatal effects of a blood transfusion made it a measure of last resort. The agglutination caused by incompatible bloods produced large clumps of erythrocytes, or *thrombuses* (§ 68), which plugged up blood capillaries. Death in such cases typically resulted from kidney failure due to plugging of the renal capillaries (§ 110). It is now very easy to determine the presence of A and B proteins in the blood cells, as shown diagrammatically in Figure 30-5.

In blood transfusion, the ideal is to have the **donor** and the **recipient** of exactly the same blood groups. However, experience has shown that some deviations from this ideal are possible. It is feasible, for instance, to transfuse O type blood into an A type person, but not the reverse.

How can we explain such observations? They can be explained easily if we know two facts:

1. The concentration of anti-A and anti-B present in the plasma is seldom more than barely enough to cause agglutination; therefore, **dilution of blood plasma soon reduces the concentration of erythrocyte-antibodies below the level at which the antibodies can have their effect.**
2. **Red blood cells can be agglutinated even when greatly diluted.**

With these facts, we can now understand why O blood can be safely transfused into an A person. The erythrocytes of the O blood have no antigenic proteins in them, so we need not worry about the effect of the recipient's blood plasma on them. On the other hand, although O blood has anti-A (as well as anti-B) in it, when we transfuse, say, a pint of O blood into a recipient whose body has eight quarts of blood in it, the antibody concentration of the donor's plasma is speedily diluted below the effective level, as explained in Statement 1 above. It is for this reason that a person with type O blood is sometimes called a **universal donor.** This designation must not be taken too literally. If too much O blood were transfused into a recipient of another type, or if the donor's blood be injected too rapidly, agglutination of the recipient's red blood cells may occur. The principle of universal donorship should not be pushed too far.

Statement 1 makes possible another measure of great practical importance. About forty-five per cent of our people are of group O and fifty-five per cent are of other groups. By removing the red blood cells from blood taken from a random sample of the population and mixing the blood plasmas, it is possible to prepare a **pooled plasma** in which the antibody level is below the level dangerous for blood transfusion. Experience has shown that plasma is almost as beneficial as whole blood in counteracting the effects of hemorrhage. Plasma keeps better in storage than whole blood. Pooled plasma makes blood typing unnecessary; consequently, it is extremely useful under battle or disaster conditions.

The inheritance of the A-B blood types presents a somewhat new problem, since there are involved in this case *three* allelic genes which we may call gene *A*, gene *B*, and gene *O*. For the student who wishes to work out the answer for himself, the necessary facts are, briefly, these:

a. Gene *A* and gene *B* are both dominant to gene *O*.

b. There is no dominance exhibited between gene *A* and gene *B*.

c. As always, the adult organism is diploid. A genotype of *ABO* is not possible.

d. As always, the gamete is haploid. The gamete is *A;* or *B;* or *O*.

e. Remember that: by blood test, one cannot distinguish a *BB* from a *BO;* or an *AA* from an *AO*.

With this information, and some hard work, the student should be able to verify the correctness of Table 30-1.

TABLE 30-1

THE USE OF BLOOD TYPES IN DETERMINING POSSIBLE PARENTAGE OF A CHILD, MAKING USE OF THE A AND B PROTEINS ONLY

BLOOD GROUP OF KNOWN MOTHER	BLOOD GROUP OF CHILD	BLOOD GROUPS OF POSSIBLE FATHERS
A	A	A, B, AB, O
B	A	A, AB
AB	A	A, B, AB, O
O	A	A, AB
A	B	B, AB
B	B	A, B, AB, O
AB	B	A, B, AB, O
O	B	B, AB
A	AB	B, AB
B	AB	A, AB
AB	AB	A, B, AB
A	O	A, B, O
B	O	A, B, O
O	O	A, B, O

Whether or not one understands completely the derivation of Table 30-1, it is important that one understand the significance of its use in questions of disputed paternity. Two specific cases should make this clear.

Case I. The child is of group A and the mother is of group B.

> The man accused of being the father is of group O. What should the verdict be? Answer: By referring to Table 30-1, we see that such a man cannot be the father of the child, barring the unlikely event of a gene mutation for which the probability is only about one in a million.
>
> Case II. The child is of group A and the mother of group B. The putative father is of group AB. What should the verdict be? Answer: such a man **could be** the father of the child. *But so could some hundred million other men*. Therefore, the case must be decided on other evidence.

Other blood tests (M-N, Rhesus) may be carried out, too, but it is important to notice that no matter what blood tests are carried out, the only definite answer that may materialize is a negative one, "This man cannot be the father of this child." If the blood tests put him in the other group, then one can say only that: "This man—or any of millions of other men—may be the father of this child." Even if the reader forgets the genetic details, it is well for him to remember the logic of the situation.

188. The Importance of Antibodies in Disease

The antigen-antibody reaction is important in protecting the body against disease organisms, such as parasitic bacteria. Bacteria, like all organisms, are made up of proteins, many of which are foreign to our bodies. Moreover, they often excrete poisonous proteins called **toxins.** The combination of a specific antibody, called an **anti-toxin,** with a toxin, removes the poisonous material from circulation. As for the proteins that do not get free from the bacterial cells, there are antibodies that can combine with them, thus, in some manner, rendering the bacteria more susceptible to destruction by other agencies of the body. White blood cells (§ 74) can ingest and destroy bacteria much more easily when the invading bacteria have been combined with specific antibodies. The antigen-antibody reaction is part of the machinery that helps us combat disease.

Once an individual has been exposed to, and has recovered from, an infectious disease, he has protective antibodies in his body which, for a time, will keep him from getting the disease again. He is said to be immune to the disease, or to possess **immunity** to it. Such immunity lasts from a few weeks to many years, or even for a lifetime, depending on the disease. This type of immunity can be brought about only by the actual presence of the antigen (which may be a toxin or part of bacterial cells themselves) in the person's body. This kind of immunity exists because the person has actively produced his own antibodies. It is called **active immunity.** This is the type of immunity that results from a smallpox vaccination, to mention an example.

It is also possible to furnish the human body with ready-made antibodies. For example, if a horse is injected with tetanus toxin—the poisonous protein excreted by the blood-poisoning bacterium, *Clostridium tetani*—the horse develops antitoxin against the tetanus toxin. The antitoxin from the horse can then be injected into a man, thus protecting him against the tetanus toxin—but only for awhile. Since an antibody (antitoxin in this case) is not self-reproducing, the antibodies injected into man do not increase, and soon "wear out" or pass out of the body, leaving the man as unprotected as before. When the recipient is thus given only pre-formed antibodies, he does not make his own; hence, his immunity is called **passive immunity.** Passive immunity does not last long, frequently less than a year. Its strong selling-point is the speed with which it can be conferred. (Compare with the slow induction of *active* immunity, Fig. 30-2A.)

When active immunity has been induced in an organism, the level of antibody falls off after awhile. There is still present, however, a reserve battalion of antibody-producers that can bring the antibody level rapidly up again whenever there is a new exposure to the antigen (see once more Fig. 30-2). If a human who has been immunized to a given disease expects to be freshly exposed to it in the near future, he is well advised to expose himself deliberately to a controlled dose of the antigen in order to boost his antibodies to a higher level. This, the so-called **booster shot,** is a sound preventive measure.

It is possible to develop active immunity to any antigenic disease organism by exposure to it. Unfortunately, the first exposure may be the last. Fortunately, in the case of many a disease-producer, ways have been found to decrease the disease-producing effect without altering its antigenicity seriously. Frequently, dead bacteria, though no longer able to cause disease, can confer immunity, evidently because their significant antigenic proteins are not too much altered by the killing. This method is used in immunizing people against typhoid fever, whooping cough, and some other disease organisms. It is active immunity. In other instances, it is possible to weaken or *attenuate* the organism in some way so that it cannot cause serious disease. The smallpox virus, after a period of residence in a cow, is so modified that it no longer is a serious disease-producer, though it still confers a good active immunity when one is *vaccinated* with this "cowpox," as it is sometimes called.

QUESTIONS AND PROBLEMS

30-1. Define *antigen* and *antibody*. Can one be defined without defining the other?

30-2. Chemically, what sorts of substances are antigens? Antibodies?

30-3. Why are some proteins called "*foreign* proteins"?

30-4. You are given two test tubes, one labeled "Protein X," the other labeled "Protein Y." How could you tell if these tubes really contain different proteins? Outline the procedure, being sure to mention any time intervals involved.

30-5. What do we know about the formation of antibodies?

30-6. What is meant by the term *agglutination?* Distinguish agglutination from blood clotting (§ 68).

30-7. List the sequence of events leading to the abortion of a Rhesus-positive child from a Rhesus-negative mother.

30-8. Is an Rh+ child in an Rh− mother always aborted? If not, why not?

30-9. Among the Chinese, Rhesus-negative people are almost nonexistent. Would you predict that jaundice of the newborn would be more or less common among the Chinese than among Americans?

30-10. Why is it important to have girl babies blood-typed early?

30-11. The following case occurred in Chicago in 1930:

Two women, Mrs. W. and Mrs. B., bore babies while in the same hospital. When Mrs. W. returned home, she found that the baby she had carried home had a "B" label on it. Mrs. B. discovered she had a baby with a "W" label. The women felt that they had received the wrong babies and demanded that an exchange be made. Blood tests revealed the following situation:

Person	*Blood Group*
Mr. B.	AB
Mrs. B.	O
Mr. W.	O
Mrs. W.	O
Baby "B"	A
Baby "W"	O

Should the babies be exchanged or not?

30-12. Distinguish between *active* and *passive* immunity to a disease.

30-13. What is a "booster shot"? Explain its action.

30-14. What is meant by the term *attenuation*, used in speaking of a disease organism?

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Chapter XXXI

Morphogenesis: An Unresolved Riddle

189. The Gene as a Fundamental Unit

"That the cell is a fundamental unit of higher plants and animals was clearly recognized more than a hundred years ago by Schleiden and Schwann. Their cell theory which holds that cells arise only from pre-existing cells is a landmark in the development of biological sciences that is stressed by all elementary textbooks in biology. In fact, the cell theory has been so strongly emphasized and widely accepted that it has become customary to take for granted that the cell is *the* fundamental living unit. Let us examine this biological dogma by asking the question: is there a *sub*-cellular unit capable of self-duplication? The answer is clearly yes, but the proof of its existence is far less simple than for the cell. It is the gene, the unit of inheritance. It is true that it has not yet been possible to demonstrate the multiplication of genes outside the living cell, but there are reasons to believe that in the remote past they did exist and reproduce in the free state. It is possible that, if a suitable environment could be devised, such reproduction might be possible for the present-day genes of higher plants and animals." — *G. W. Beadle.**

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* Beadle, G. W., "The Gene." *Proc. Amer. Philos. Soc.*, **90**:422-431, 1946.

The viewpoint expressed in the above quotation is coming to be the dominant viewpoint of modern biology. The gene, originally conceived only as a sort of counter to rationalize the facts of heredity, is coming to be thought of as a physiological unit. Some feel that, ultimately, a large part of the data of physiology can be expressed in terms of this unit. This is at present only a hope. There are many fields in which we are very far from reducing the observations to genetic terms. It would be dishonest if we glossed over this fact. But science, as was brought out in Chapter I, is not only a body of knowledge but also a continuing search for knowledge. It is not inappropriate to close Part IV with a consideration of one of the frontiers in which the dynamic aspect of science is so obvious, the frontier called **embryology,** a science concerned with the problems of **morphogenesis** or the mechanistic chain of events leading to the assumption of a particular form or morphology.

190. The Circuitousness of Development

When we study the detailed physiology and anatomy of an adult man or fruit fly or crayfish, we cannot but be impressed with the multitude of nicely constructed devices and behavior patterns that permit the organism to survive and reproduce its kind in a world of many and changing problems. But, when we consider that this intricately organized machine did not spring, fully formed, from the head of Zeus – that it was not formed as it now is, in the beginning, but that it developed from something quite different – then, we begin to have a faint conception of the wonder of the adult form.

The development of an organism is not a straight-line process. What it is to become is by no means obvious from its beginning. Indeed, an organism may develop first into a self-sufficient being of a quite different sort from its final form. Everyone knows the story of the tadpole and the frog (Fig. 31-1A). For an organism that "intends" (!) to become a frog, becoming first a tadpole seems a circuitous route to follow. Or at least so it would seem to a man, though a frog may not share this viewpoint.

Development, in whatever organism we study, seems to take a circuitous route. To get a quick view of a not unusual example of development, notice (Fig. 31-1B) what a strange beginning an organism may have. We select a frog because its development takes place in the water of a pond (or a laboratory dish) where we can watch it easily. We cannot readily watch the development of a young dog or human, sheltered as it is inside its mother's body.

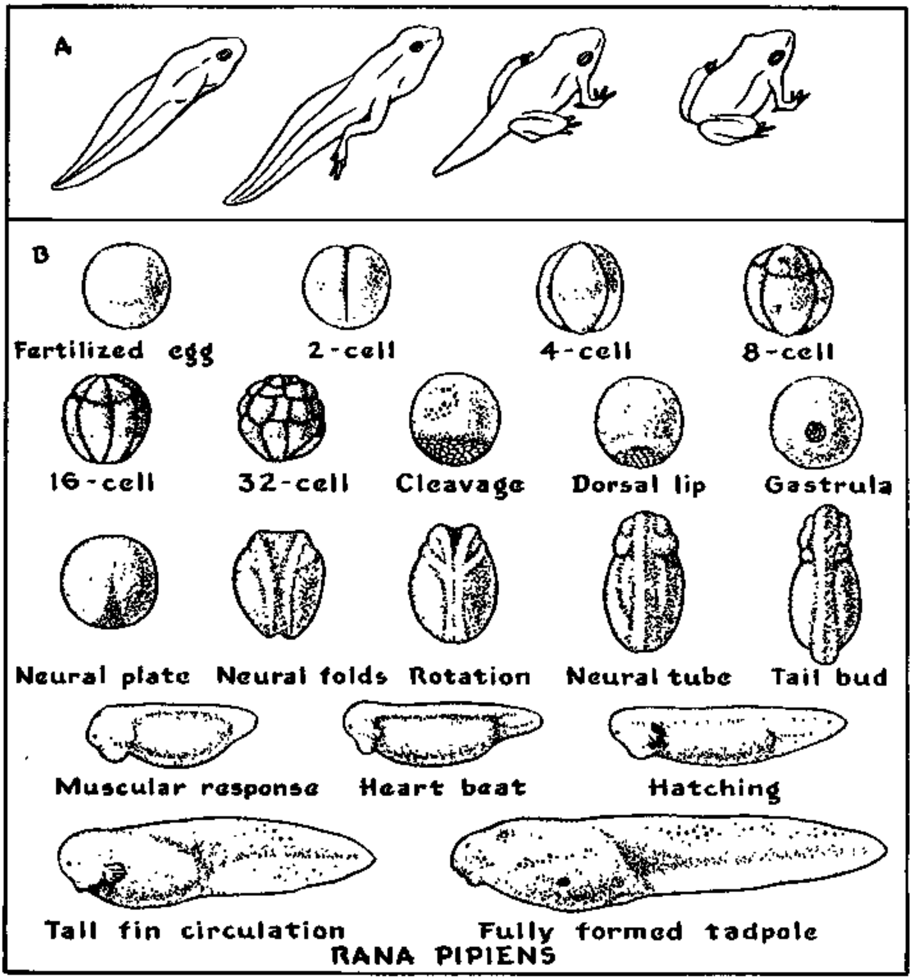

Fig. 31-1. The circuitous way a multicellular organism has of developing from an egg to an adult. Amphibia are taken as particular examples.

We begin with the fertilized egg or zygote. Within four hours after fertilization, the zygote has taken the first step toward adulthood: it has divided into two cells by a plane passing vertically through its middle. In another hour, another vertical plane, at right angles to the first, has divided the two into four cells. An hour later, a third plane, at right angles to both the first two, produces eight cells. After a few more divisions, there are too many cells to see and keep track of individually, so we speak of the egg as being in the **cleavage** stage. By the end of a full day, an opening appears in the ball, through which a sheet of cells moves into the inside to form a **gastrula** stage.

The exterior of the frog's egg presently begins to depart from its spherical shape. Some tissue wrinkles up into **neural folds** which fold over toward each other, meet, and join to form a hollow **neural tube** which later becomes the spinal cord. Other changes take place at the same time, producing a being that definitely resembles a tadpole. All of these stages occur inside the transparent jellylike egg case (not shown in the figures). Presently, the tadpole hatches from the egg case and starts to swim around, though even at the time of hatching, it is not a completely formed tadpole. It is blind because its cornea is not yet transparent, and the circulation in its tail is still to be established. These and other deficiencies are remedied within a few days after hatching.

So goes a brief and hasty story of the development of one kind of organism.

191. Growth and Differentiation

". . . and the zygote grows into an adult." So may we thoughtlessly end the story of fertilization and the appearance of a new individual. From an inspection of Figure 31-1B, it is all too apparent that the fertilized egg does not just *grow* into a tadpole. As a matter of fact, during the time intervening between the fertilization and the hatching stage, the total amount of organic matter *decreases*, because the amphibian embryo is inside a membrane and has no way of replacing the food it is metabolizing. This is scarcely what is usually meant by the term "growth." The significant change that takes place during this time is not growth in the sense of *increase* but change in the organization of the protoplasm or, as embryologists put it, **differentiation.** Starting with a comparatively structureless zygote, the protoplasm differentiates into a manifestly structured tadpole, without *growing* in the least. Later, both growth and differentiation take place at the same time, but it is important that we realize that there is no necessary connection between the two. The central problem of embryology is this: *What are the forces that cause differentiation?*

192. Mechanical Forces in Embryology

We do not propose to give a detailed answer to the question just posed, for no one can at present. Instead, we propose to discuss a few enlightening problems in embryology, showing how they have been attacked and with what results.

By following the developing embryo very carefully, it has been learned that the ultimate fate of various regions of the early stages can be predicted very exactly. Does this mean that the parts of the embryo are subject to a sort of predetermination? Each of the cells of the two-cell stage, for instance, gives rise to one-half of the embryo shown in cross section in Figure 31-2B. Does this mean that each of the two cells is capable of producing only one-half of an embryo?

The first experiment designed to answer this question seemed to give an affirmative answer. The experimenter killed the left of the two cells with a hot needle (Fig. 31-2C). The right cell then developed into an embryonic right half only. (Ultimately, this half also died, probably because of toxic substances coming from the dead protoplasm on the left, but this a matter of secondary importance.)

The correct interpretation of these observations was given by the great embryologist, Hans Spemann, who first carried out another experiment. With a fine hair, he constricted the egg, membrane and all, in the plane of the division between the two cells (Fig. 31-2E). Within a short time subsequent to this treatment, the two cells separated. Then, each developed into a completely normal, though half-sized, tadpole.

How can we reconcile the difference in results of the two experiments? From Spemann's experiment, we can only conclude that each of the first two cells is capable of forming a complete embryo. We must, then, account for the earlier results. The simplest explanation would seem to be this: the unkilled cell is perfectly capable of developing into a complete embryo, but the dead protoplasm (Fig. 31-2D) is in its way. It is prevented by the dead protoplasm from developing into the left half of an embryo, just as it is normally prevented from doing so by the living left half-embryo abutting it.

From experiments like these comes the general principle: *What any cell or tissue does at any moment in embryological development is determined by two factors: its own capabilities, and the influence of the tissues around it.* The influence of the surrounding tissues in the present example seems to be merely a mechanical one.

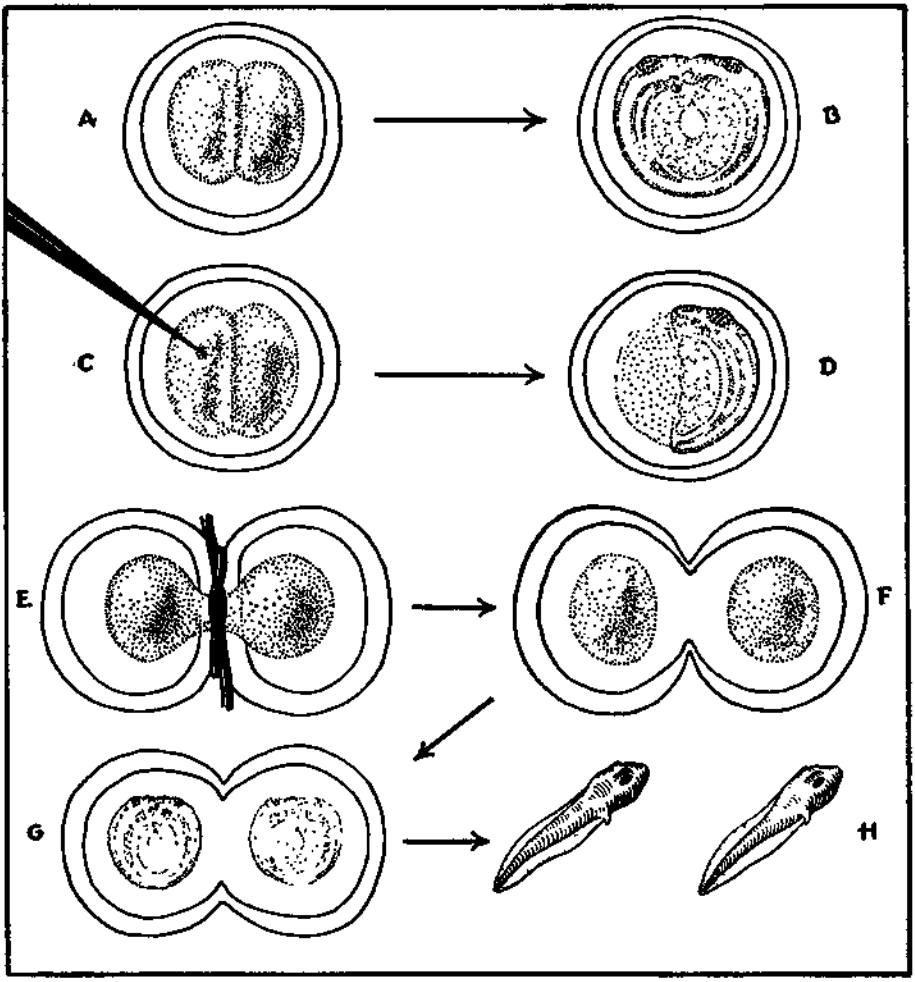

Fig. 31-2. A, two-cell stage of an amphibian. B, cross section of later stage; each cell has developed into a half embryo. If one cell at the two-cell stage is killed with a needle (C), the other cell develops into only half an embryo (D). But, if two living cells are completely separated (E, F) so that neither interferes with the development of the other, two normal, though diminutive, tadpoles result (G, H). These tadpoles necessarily have the same genes; they are identical twins.

Before going on, some sidelights may be pointed out. Since both of the tadpoles produced by the constriction experiment (Fig. 31-2 E-H) come from the same zygote, they must have the same genes, hence—if their environment is the same—they should develop into indistinguishable adults. They do. This experiment gives a clue to the origin of **identical twins** in humans. In some twin births, the siblings are so nearly alike that we cannot but believe that they have the same genes. Such sibs we refer to as identical twins. Because of the inaccessibility of human embryos and the rarity of twin births—about one birth in ninety—we will probably never *know* what happens to make identical twins. But, it is very reasonable to assume that, in the early stages of embryonic development, perhaps in the two-cell stage, the embryo, for unknown reasons, separates into two cells, or two halves, each of which then develops into a normal child, both with the same genes.*

When twins seem not to be very much alike, we call them **fraternal twins.** These are probably caused by multiple ovulations. They may or may not be of the same sex. They resemble each other no more than ordinary brothers and sisters. They are siblings who just happen to have the same birthday.

193. Chemical Forces in Embryology

Differentiation of a tissue depends on its intrinsic ability and its environment. We have seen an example in which the environment exerts an effect that is probably only mechanical. Now we shall give an example of a chemical action of the environment.

The eye, marvelous organ that it is, has a lowly beginning (Fig. 31-3). The first sign of it in the embryo is a thickened tissue lying under the epidermis in the head region of the developing animal (Fig. 31-3B). This thickened tissue bends inward in the middle as it grows to form an eyecup (Fig. 31-3G) which, in the adult, will include the retina and underlying structures. As this process is going on, the epidermis just outside the developing eyecup thickens and pinches off a ball of cells which moves inward and forms the lens of the eye. What makes the epidermis behave so? There appears to be no mechanical force in the

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* Assuming normal mitosis, will identical twins necessarily be of the same sex? (See § 180.)

mbryo that causes this effect. In the early stages, there is no contact etween the eyecup and the epidermis. The simplest hypothesis is a hemical one: the eyecup may produce a stimulating substance that passes to the overlying epidermis. Though no such substance has yet been solated, all the evidence fits this hypothesis.

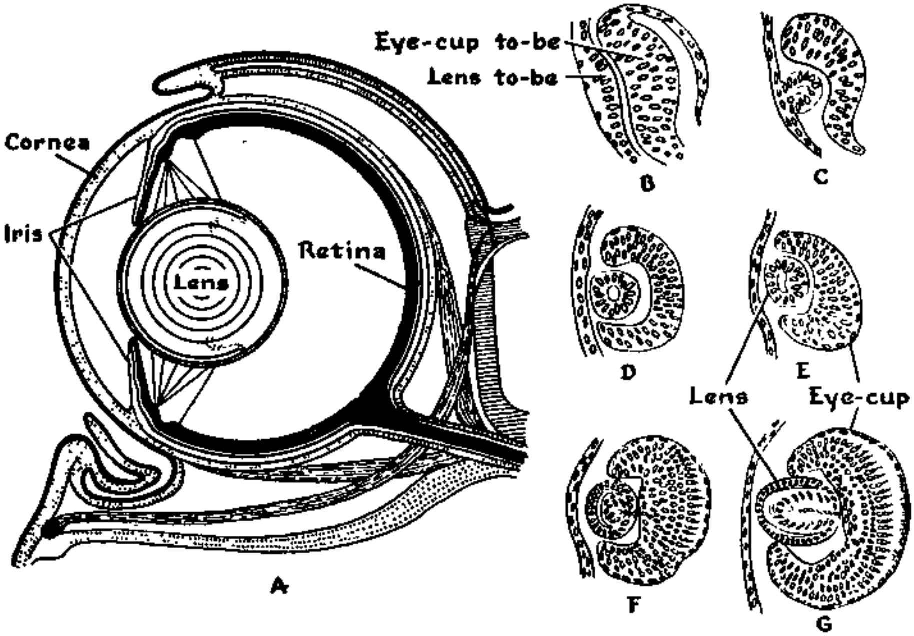

Fig. 31-3. A, adult eye of an amphibian. B–G, induction of lens formation by the developing eyecup.

If the eyecup produces a chemical that can cause epidermis to form a lens, it should be possible to use a detached eyecup to induce lens formation from epidermis that ordinarily would not form a lens. A simple, though delicate, operation proves this to be so. If the eyecup-to-be is detached from its moorings in the head region of the developing tadpole and moved back to the trunk region, as the eyecup develops in its new location, the overlying epidermis thickens and forms a typical lens. This lens will never serve a useful function because the eye, being in the wrong part of the body, will never be innervated. Nevertheless, in response to some subtle message from the eyecup, the epidermis is induced to form a lens. Such **induction,** as the process is called, of one structure by a nearby structure or tissue strengthens the hypothesis that a chemical substance is involved.

194. Competence

The detached eyecup need not be transplanted to another part of the same animal; it can be transplanted to a different animal. Thus one can cause the formation of several eyes, though only the original two will be functional. However, it has been found that a transplanted developing eyecup will not always cause the development of a lens. Induction is successful only if the **host** animal (the one receiving the transplant) is of the right age. If it is too old, the **donor** tissue is unable to induce lens-formation. We say that the old host tissue is *incompetent* to form a lens; that it has lost its **competence.** What competence consists of we do not know, but, as defined by this sort of experiment, it can be shown to be a characteristic which may be initially absent in a tissue, then present for a period, and then lost for good.

The idea of competence has helped explain, in an embryological way, many abnormalities or *anomalies,* as well as structural differences between closely related species. We give an example. In every large cave, there may be found blind animals of several different species. These blind cave-forms include crayfish, insects, fishes, lizards, and salamanders. Their blindness is hereditary. What is the reason for it? One can give a glib teleological answer: they don't need to be able to see in the dark. But what is the embryological course of events that leads to their blindness?

Study has shown that different species are blind for different embryological reasons. In some of the fishes and salamanders, it has been shown that blindness results because the epidermis overlying the eyecup is not competent to form a lens at the time the eyecup is formed. Since no lens is formed, no cornea is formed, and the epidermis in this region becomes opaque as it does in other regions, thus causing blindness. Whether the epidermis is competent earlier, and loses its competence, or whether it is never competent, is not known. But contemplating this sort of situation, one can see that normal embryology involves a nicely integrated complex of *timings* of the developmental course of different tissues, and that merely a slight change in the rate of development of one tissue may throw it out of phase with all the rest, with striking consequences to the adult morphology. One sees, vaguely, at least, why almost any new mutation is harmful to the species (§ 182).

We too often think of development as being a process that takes place only before birth or hatching. Actually, of course, development continues after birth, though at a slower rate and with less spectacular results. The same principles could be expected to apply to development on both sides of the arbitrary date line we call the birth date. As an example of how the idea of competence may be used to include post-embryonic events, consider the effect of the pituitary gland on growth. The anterior lobe of the pituitary secretes many hormones, at least one of which stimulates the growth of bones and cartilage. If this growth hormone is produced in unusually large amount during the period of

Fig. 31-4. Overactivity of the anterior lobe of the pituitary gland during childhood leads to giants like this teen-age boy seen standing with his father, a man of normal size. (From *Textbook of General Surgery*, 5th ed., W. H. Cole, M.D., and R. Elman, M.D., Appleton-Century-Crofts, Inc., 1948.)

growth, a human of gigantic stature is produced (Fig. 31-4), some of these **pituitary giants** being as much as nine feet tall.

At the end of the normal period of growth, the epiphyses of the long bones lose their ability to grow (recall § 20). Normally at this time, the rate of production of pituitary growth hormone also ceases. We may say that the tissue (bone) loses its competence, at the same time as the inductor (pituitary) stops producing this inductive agent. But a few islands of tissue retain their competence after puberty, e.g., the bone-forming tissues of the jaw, hands, and feet, and the cartilage-forming tissue of the nose. If there is a postpubertal flare-up of activity of the inductor, these competent tissues react in a normal way, causing the development of abnormally large jaw, hands, and nose (Fig. 31-5).

Fig. 31-5. *Acromegaly*, a condition due to the production of growth hormone by the pituitary after most of the bones of the body have lost their competence to respond to it. Note the overlarge hands, jaw, nose, and ears that characterize this condition. (From "*Physical Diagnosis*," by Ralph H. Major, W. B. Saunders Co., Philadelphia.)

195. Induction, Competence, and Aging

Our first reaction, when we learn about the loss of competence or of inductive capacity, may be to say, "Too bad; old age is setting in. Something has been lost." But, from the above example, we see how necessary such losses are to normal morphogenesis. If tissues did not lose their competences and their inductive capacities, growth would be one continuous runaway process leading to the early death of the whole disorganized mass of repetitive and hypertrophied organs and tissues. Only if competences and capacities are lost in a fixed, orderly fashion is a final, definite form possible. Specific morphogenesis is made possible by the continuous loss of capacities and competences—by aging, if you will. Since most of these abilities are lost long before birth, it may be said that the process of growing old is nearly completed by the time the law takes cognizance of our existence. The continuous loss of capacities and competences in the years after birth is but a continuation of a process begun long before the natal day. The evidence is not incontrovertible as yet, but it seems not unlikely that old age and death are the inevitable consequences of the development of a complicated morphology.

Before leaving this subject, we want to point out that we have not explained, in physical and chemical terms, what is involved in the possession and loss of "competence." We have merely given a unifying name to a group of phenomena, and the name will be wholly useful only if it focuses our attention on the underlying problems. What, for instance, is the genetic explanation of the loss of competence? Are genes lost during cell division? It seems unlikely, since all the somatic cells of a given individual have the same chromosomes. It is hard to imagine the chromosomes regularly multiplying and dividing without their constituent genes doing so, also. Yet, many cells of the body produce particular enzymes not produced elsewhere. (Consider, for instance, the digestive enzymes.) It is theoretically true that all the somatic cells contain the same genes; it is demonstrably true that not all their enzymes, or abilities, are the same. How can we harmonize these statements? This is the major problem of embryological genetics.

196. Sidelight: Cancer

In the nine months before birth, the human body increases two billionfold in mass. In the years after birth, it increases only about twentyfold. By the time we are old enough to vote, most of our tissues have ceased growing, only the adipose connective tissue retaining its growing capacity to a sometimes embarrassing degree. Occasionally, however, some other tissue will suddenly reassume its youthful character and start growing at the embryonic rate again. Such a rejuvenated tissue we call a **neoplasm** (Greek *neos*, new or recent; *plasma*, image). If it is relatively harmless, it is popularly called a **tumor;** if it is harmful or *malignant*, it is generally called a **cancer.**

The potential seriousness of a neoplasm lies in the fact that it has regained the ability to grow at a juvenile rate. It is precisely because some cells are not "acting their age" that they become potentially dangerous. The more sedate cells around them, which have settled down to an almost nonreproductive old age, are at a competitive disadvantage with these indecently rejuvenated cells. The growth of the neoplasm may completely disrupt the activity of the organ it is in. If the organ is a vital one, death may result. This is the first threat of a neoplasm. Its second threat lies in the danger of **metastasis** (Greek *meta*, signifying change; *stasis*, placing). After a period of several years' growth in one place, the neoplasm may abruptly release some of its abnormal cells into the blood stream, to be carried to all parts of the body, lodging in various places and starting new cancerous growths in a dozen or a hundred places. Once a malignant growth has started to metastasize, the prognosis is unfavorable. At least one of the many new loci of growth is almost certain to be in a vital spot.

With respect to growth rate, neoplastic cells show a reversion to the youthful condition. In other respects, they are something new. They can be recognized microscopically as abnormal cells. Their chromosomes are usually in a state of disrupted confusion, a suggestive point when we consider that the chromosomes are the site of the enzyme-synthesizing genes.

What causes cancer? We do not know. Experimentally, we can induce cancers by the application of certain chemical compounds. It is interesting to note that some of the most effective **carcinogenic* agents** are chemically not very different from substances that are known to be normal growth hormones, normal sex hormones, or embryonic induction agents. It is tempting to speculate that naturally occurring cancers may be the indirect result of metabolic derangements that cause the production of sex or growth hormones that are slightly abnormal in their molecular structure. This is, however, only a speculation.

What can the individual do about cancer? *Have it diagnosed early.* A cancer that is not diagnosed until several years have elapsed may already have started metastasizing. Then it is too late. It is important for all people, particularly those past their youth, to have the cause of every persistent pain traced. A *few* persistent pains may prove to be due to cancer. It is important to catch these few. An early diagnosis makes possible treatment that has a good probability of eliminating the cancer before metastasis sets in.

QUESTIONS AND PROBLEMS

31-1. Distinguish between *growth* and *differentiation.* What would be the result if a zygote underwent one process and not the other? (Consider both cases.)

31-2. How is the existence of identical twins in humans explained? Would you consider this a proved explanation or merely a probable one?

31-3. In armadillos, four young are produced at a birth. In every case, the young are of the same sex, whichever it may be. Give a reasonable explanation of the facts

31-4. Explain, by means of an example, what embryologists mean by the words *competence* and *induction.*

31-5. Explain why the *fact* of competence presents geneticists with a puzzle.

31-6. What is the relation between competences and the aging process?

31-7. Why is a cancer dangerous? Why is an early diagnosis desirable?

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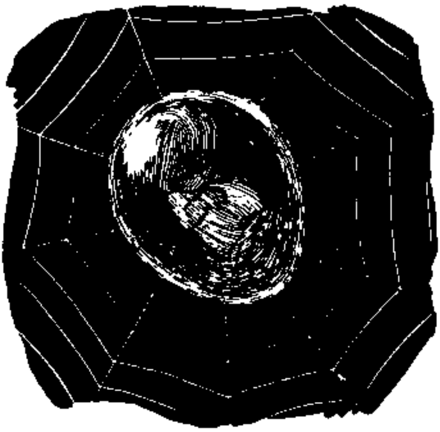
[*] *Carcinoma* is the technical name for one type of cancer.

PART V

The Web of Life



Chapter XXXII

Energy and the Carbon Cycle

197. The Carbon Cycle

Respiration can be represented by the following equation:

$$\text{Organic carbon} + O_2 \longrightarrow CO_2 + H_2O + \epsilon \qquad (1)$$

Photosynthesis is represented thus:

$$CO_2 + H_2O + \epsilon \longrightarrow \text{Organic carbon} + O_2 \qquad (2)$$

It is apparent that the processes are, as far as concerns their net effects, exactly antagonistic. One process uses energy and produces organic carbon compounds. The other uses organic carbon and produces energy. The results can be analyzed in terms of changes suffered by two of the entities, carbon and energy. We shall first discuss the cyclical changes that carbon undergoes, changes that are briefly summarized in the **carbon cycle.**

The carbon cycle can be represented in its simplest form by the following abstraction:

$$\begin{tikzcd} CO_2 \arrow[r, bend left, "\text{(plants)}"] & \text{organic-C} \arrow[l, bend left, "\text{(animals and plants)}"] \end{tikzcd} \qquad (3)$$

The upper process—conversion of CO_2 to organic-C—is brought about by green plants exposed to light. Both decarboxylation and carboxylation (removal and addition of CO_2 to an organic molecule —see § 160) can be carried out by all living organisms. In nongreen organisms, however, if we consider the activities of the individual over a considerable period of time, we find it releases more CO_2 than it "fixes," so the cycle (equation 3 above) need not be qualified.

The conversion of organic carbon to CO_2 is carried out by all living plants and animals in both respiration and fermentation. In plants, there is a *net* production of CO_2 only in the dark.

The scheme we have just presented is oversimplified, of course. To develop it to the point where its complexity is closer to reality, we may consider the ways in which carbon is passed from one individual to another. The passage of carbon from plants to animals is accomplished directly; animals eat plants. **Herbivores** (Latin *herba*, herb; *vorare*, to devour), such as cattle and rabbits, feed on plants (herbs). **Carnivores** (Latin, *carnis*, flesh) are indirectly fed entirely by plants also, since they feed on herbivores. The predacious dog that eats a rabbit is eating grass processed by the rabbit. The chain of organisms *grass* ⟶ *rabbit* ⟶ *dog* is called a **predator chain.** There may be many links in such a chain. A bass may eat a minnow which has fed on water fleas which ate protozoa which were nourished by algae. Short or long, the predator chain is eventually anchored to green plants.

The passage of carbon *from animal to plant* is not so direct. Cartoons to the contrary, there are no man-eating plants, and the insectivorous ones are quantitatively unimportant. Carbon gets back to plants via the carbon dioxide released into the air by the respiration of both plants and animals. This part of the cycle (equation 3) would be more accurate if we amended it to read: *animals* ⟶ *atmosphere* ⟶ *plants*. We will so amend it (Fig. 32-1).

From the figure, it is apparent that the atmosphere acts as a reservoir of carbon. It is almost impossible to estimate how much carbon is bound up in living things as compared with that free in the atmosphere, but it seems probable that there is at least as much free in the air as there is bound in organisms. The percentage of carbon dioxide in the air is very low—only 0.03 per cent. But there is so much air that the amount of atmospheric CO_2 is very great, about two million million tons. The low concentration means that a great deal of air must be "processed" by a plant to furnish its carbon needs. It has been estimated that a single corn plant, during a season's growth, completely removes the carbon dioxide from about one-half million gallons of air. Yet, such are the relative rates of photosynthesis and respiration

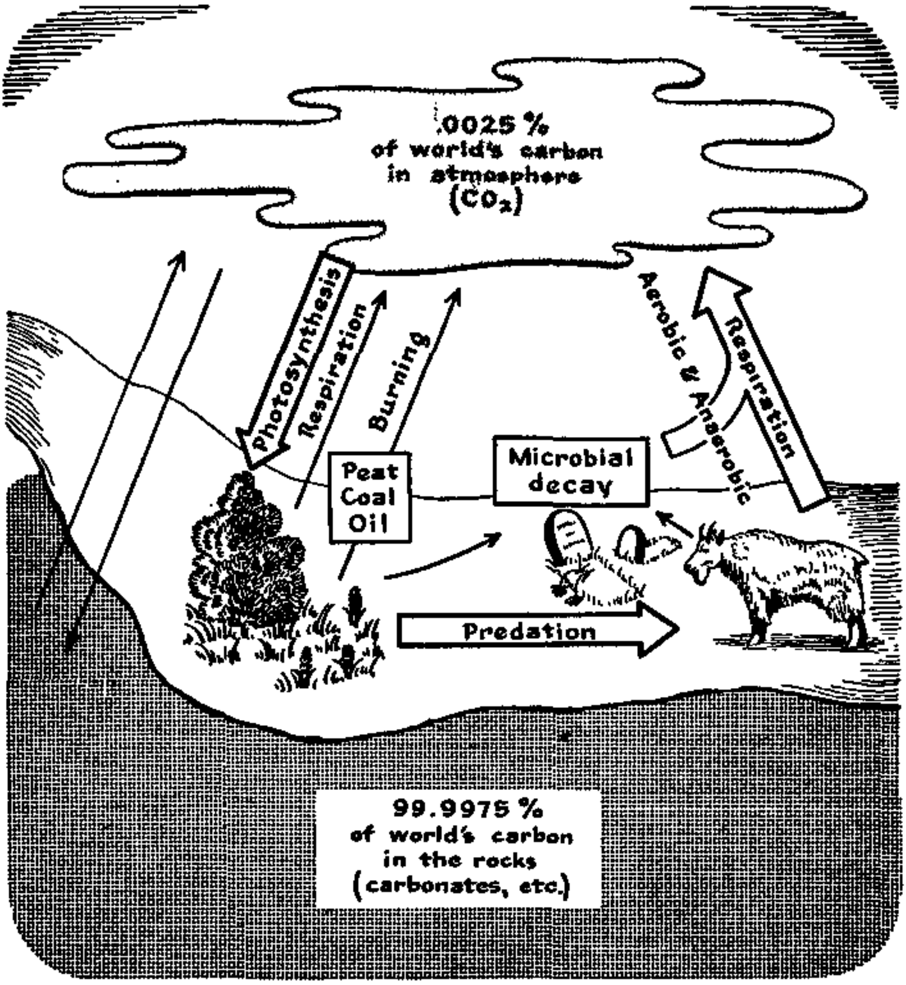


Fig. 32-1. The carbon cycle, briefly stated. The world's supply of carbon atoms is distributed as indicated by the percentage figures above, with most of the carbon in the form of inorganic carbonates in the rocks. The atmosphere is composed of 0.03% CO_2, and this accounts for 0.0025% of the world's carbon.

throughout the world that the concentration of atmospheric CO_2 remains very constant.

Not all plants are eaten by animals. A great proportion of the plants die and decay. What does "decay" mean? We tend to think of it as a spontaneous process, but it is not. **Decay is the digestion of organic material by microbes**—by bacteria and molds, for the most part. In the absence of living microbial scavengers, decay does not occur. In their presence, organic compounds are broken down, step by step, until ultimately all the organic carbon is converted to CO_2.

A small proportion of the plants (and to a lesser extent, the animals) that die escape microbial decomposition. Under certain conditions, these may turn into peat which, when buried and compressed under tons of earth, turns into coal. Various aquatic plants and animals, principally marine diatoms, can be similarly processed to form oil. The result of the formation of any of these fuels is to remove, temporarily—that is, for a few hundred million years—some of the carbon from the cycle. Ultimately, however, when the coal strata are exposed at the surface of the ground or the oil oozes up, this locked-up carbon is released to the atmosphere as microorganisms slowly respire it. In addition, during the latter part of man's stay on earth, these carbonaceous materials are being turned into CO_2 much faster by the process of burning.

The quantities of carbon involved in this carbon cycle—perhaps four million million tons—seem large by human standards; yet, geologic evidence indicates that they are minuscule compared to the carbon available in the earth's crust. Neglecting entirely the carbon dioxide dissolved in the ocean (about twenty times the atmospheric CO_2), it must be pointed out that about 99.9975 per cent of terrestrial carbon is tied up in the form of various inorganic rocks, such as limestone ($CaCO_3$). There is some exchange between this reservoir and the rest of the world, through the processes of weathering and the laying down of more limestone, but, as measured in terms of human time, there is *no net change.* The carbon cycle on which we are dependent involves only 0.0025 per cent of the earth's supply of carbon. The living world is just a sort of scum on the surface of a vast reservoir of inorganic carbon, the carbon cycle only a minute, superficial eddy.

198. The Laws of Thermodynamics

Before taking up energy changes, it is necessary to discuss the principles known as the First and Second Laws of Thermodynamics.

The sense of the **First Law of Thermodynamics** is nowadays common knowledge:

Energy can neither be created nor destroyed.

Energy can only be converted from one form to another. When gasoline is burned in an automobile engine, the energy latent in the hydrocarbon molecules is converted to the kinetic energy of the moving car. In this process, some of the energy is immediately released as heat in the cylinders, and more appears as heat coming from the bearings and all other moving parts. Ultimately, all of the energy appears as heat, some of it being produced by the friction of the tires against the road, some by the heating of the air as the car pushes through it, and some by the heating of the brake bands as the car is brought to a stop by friction. If one were to accurately determine and add up all these quantities of heat, it would turn out that this sum exactly equaled the latent heat in the original fuel.

There is—as many a schoolboy now knows—a slight correction to be made in the wording of the First Law. In an atomic disintegration, some matter is converted to energy. There is an exact equivalence of matter and energy, so that our law could be corrected by saying that the total amount of matter and energy remains constant. In most of our everyday life, we encounter no interconversion of the two; for this reason, we shall leave our statement of the law in the less precise form given above.

The **Second Law of Thermodynamics** is not so readily put into simple words. Consideration of some practical examples may help. If we have a box (Fig. 32-2A) which has fast-moving molecules in one side and slow-moving molecules in the other, with an aperture between, very soon the average velocity of molecules will be the same on both sides (Fig. 32-2B) because the molecules are moving continuously and at random, and are, hence, subject to the "Laws of Probability." The same amount of kinetic energy (energy of movement) in both sides represents the most probable state of this system.

Of course, like anything that is merely most probable, this state would not *have* to be reached. The physicist, Clerk-Maxwell (1831-1879), pointed out that if we could only find a little demon small enough to sit in the doorway and hold back the slow molecules while letting through the fast molecules, then, it would be possible to maintain permanently a difference in energy levels (i.e., average molecular velocity, i.e., the temperature) of the two sides. But no one has ever run across Maxwell's little demon.

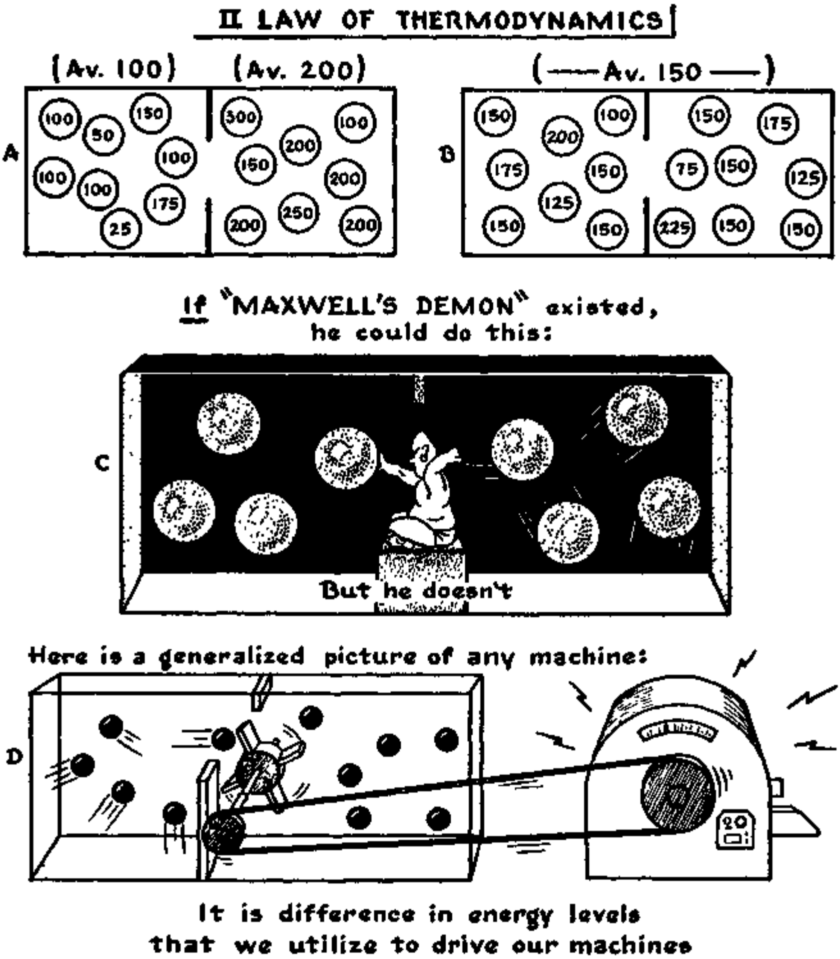


Fig. 32-2. Why there are no perpetual-motion machines.

How do machines work? There are many different kinds, but they all boil down to the sense of Figure 32-2D. If we have a set-up with different energy levels on the two sides, then, the molecules moving one direction will move faster than those moving the other. If there is an opportunity for exchange of energy or molecules between the two sides, then—since so many molecules are involved that we can reasonably expect the most probable event to occur—the net exchange of energy in the system will be in one direction, and we can use it to drive a machine, to do work for us. In essence, all machines are like the one in the picture.

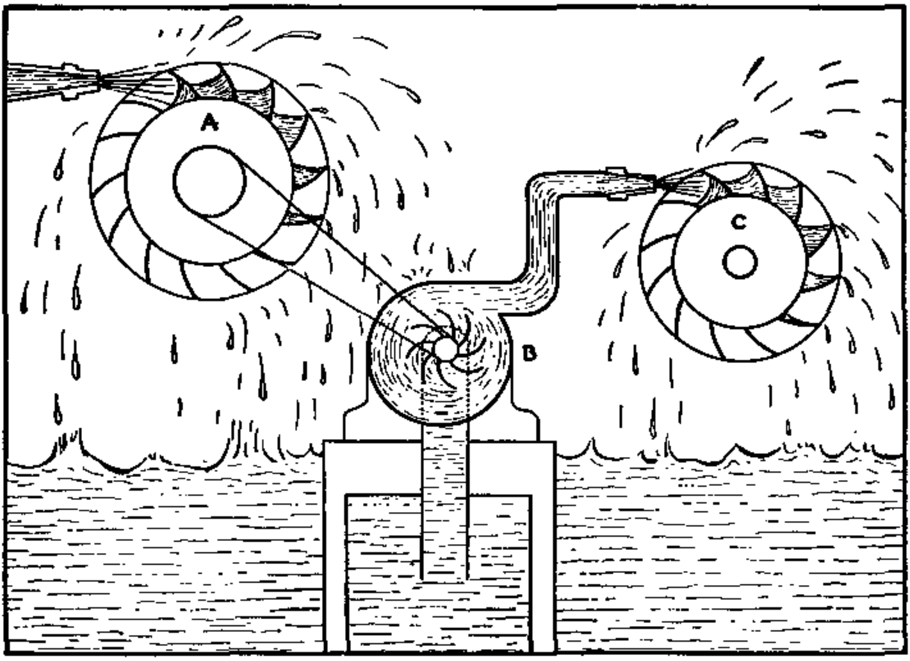


Fig. 32-3. The degradation of energy.

The Second Law of Thermodynamics has a close bearing on the question of the efficiency of machines. To see this, we shall consider a water wheel which can serve as an analogy for all machines. Like all machines, it capitalizes on an existing difference in energy levels, in this case, the difference in (potential) energy of water at two different levels. In our example (Fig. 32-3), water coming from a nozzle, in falling to a lower level, drives the water wheel (A).

We can use the motion of the water wheel to do work. We can, if we wish, use it to drive a pump (B) which lifts water from the reservoir and drives a second water wheel (C). Practical experience tells us that either: (1) the second wheel must be at a lower level than the first, if the quantity of water driving it is the same; or (2) if the second wheel is at the same height as the first, the quantity of water must be less. Since there are obvious power losses in our first machine, due to the sloshful waste of water and friction in the bearings, the above conclusions follow from the First Law of Thermodynamics. Could we, by better design, eliminate these inefficiencies, thus making possible a second wheel (C) which can do as much work as the first (A)? According to the Second Law of Thermodynamics, the answer is No. It is not even theoretically possible to construct a machine of 100 per cent efficiency. Thermodynamic theory tells us that it is not possible to design a machine that will extract for us the full energy potential that exists in a two-energy level system. Putting the matter in a different way, we may say that a perpetual-motion machine is impossible.

It is not easy to express the **Second Law of Thermodynamics** in simple words, but perhaps the following statement will serve the purpose:

> **In any closed system, there is a continuous degradation of useful energy, since the existing differences in energy levels of its parts are steadily diminished until, ultimately, all parts of the system are at the same energy level.**

By a "closed system," we mean one which is not receiving any gifts of energy from the outside, nor suffering any losses. The Second Law of Thermodynamics is to be understood as a probability principle. Maxwell's demon is not impossible, merely highly improbable.

199. The Degradation of Energy

We are now in a position to look at the carbon cycle again with an eye to the energy involved in the compounds. We can simplify the cycle, as shown in Figure 32-4. Plants synthesize organic compounds, thus trapping some of the energy that comes from the sun. These compounds have a great deal of energy in them. When an animal eats a plant, he converts the plant compounds into animal compounds, which have just as high a concentration of energy in them but are much less in quantity. Most of the energy available in plant materials is wasted due to the inefficiency of the animal machine.

If we follow the adventures of a particular bit of plant-synthesized organic carbon, we find that, as a consequence of metabolism, all the organic carbon is sooner or later oxidized to carbon dioxide, which we may regard as being the zero energy level. Carbon dioxide can be changed back to organic material only by a plant that is receiving radiant energy of a certain sort (usually sunlight). Although, in simplifying the cycle, we have left out other units that function in it—carnivores, oil, coal, and cemeteries—we have not falsified the picture in any essential way. Every time the organic carbon compounds are passed from one agent to another, they are decreased in amount, and some of their energy is degraded to heat which dissipates into the environment.

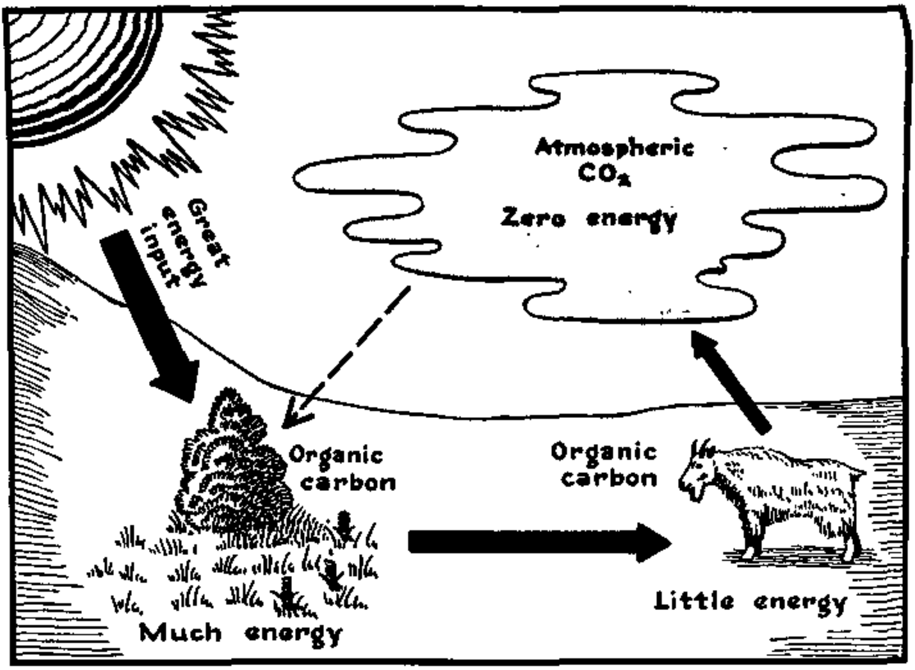


Fig. 32-4. The degradation of solar energy.

There is a carbon cycle. But there is no energy cycle. The changes of energy are a one-way path, ending up with zero utilizable energy. Life on the earth is kept going only by the continuous input of energy by an agent outside the terrestrial "system," namely, by the sun. Extinguish the sun and the carbon cycle would very soon grind to a stop, with no plants and no animals left. Only CO_2.

The struggle for food is a struggle for organic carbon compounds, compounds that are rich in available energy. Plants, by their growth upward and outward, "try" to crowd out other plants. Teleologically speaking, a plant's goal in life is to intercept the sun's energy-rich rays with its leaves before another plant does so. Competition among animals may appear to be different in nature, but this appearance is deceptive. Animals also are striving, however indirectly, for a place in the sun. "*The struggle for existence*," as the physicist, Boltzmann, said, "*is the struggle for the available energy of the world.*"

200. The Pyramid of Protoplasm

The consequences of the Second Law have been neatly summed up in another way by the Chinese, millenia before Westerners put the Law into words. *One hill, one tiger.* The Chinese have another saying, too: *Big fish eat little fish; little fish eat bugs; bugs eat mud.* The ideas behind these two proverbs, when combined, yield a concept we may symbolize by the phrase, the **Pyramid of Protoplasm.**

Suppose a man has a ten-acre pond whose "crop" of fish is just enough to support the man. He eats no food other than that from his lake; for him, everyday is Friday. How much does he eat? We don't know—the example is hypothetical—but it would probably take about five pounds, live weight, of fish per day to support him. If all the fish weighed five pounds each, it would take, in the course of a year, 365 fish weighing a total of nearly a ton to sustain 150 pounds of human protoplasm. The amount needed to achieve this weight (from birth to, say, sixteen years of age) would be a much larger figure. In other words, it takes many pounds of fish (the prey) to make one pound of man (the predator) possible.

And what of the fish? Assuming that the man eats bass and that the bass feed only on minnows, common sense and the Second Law tell us that the number of minnows and the weight of their protoplasm far exceed the number of bass and their weight. The minnows feed on water fleas which are still more numerous and weigh still more. And the water fleas are nourished by a yet larger mass of protoplasm present in the algae, the microscopic, photosynthetic plants at the base of the whole system. Each time prey-protoplasm is converted to predator-protoplasm, there is a loss of organic carbon. The facts may be summarized in the figure of speech, the Pyramid of Protoplasm (Fig. 32-5).

The organisms at the base of the pyramid, plants, occur in the greatest numbers and produce the organic carbon on which all other organisms are dependent. As we pass up the pyramid, each new predator occurs in smaller numbers, and—more important—amounts to a smaller mass of organic carbon.* One medium-sized pond can support hundreds of bass, thousands of minnows, or millions of water fleas, but only one man. *One hill, one tiger.*

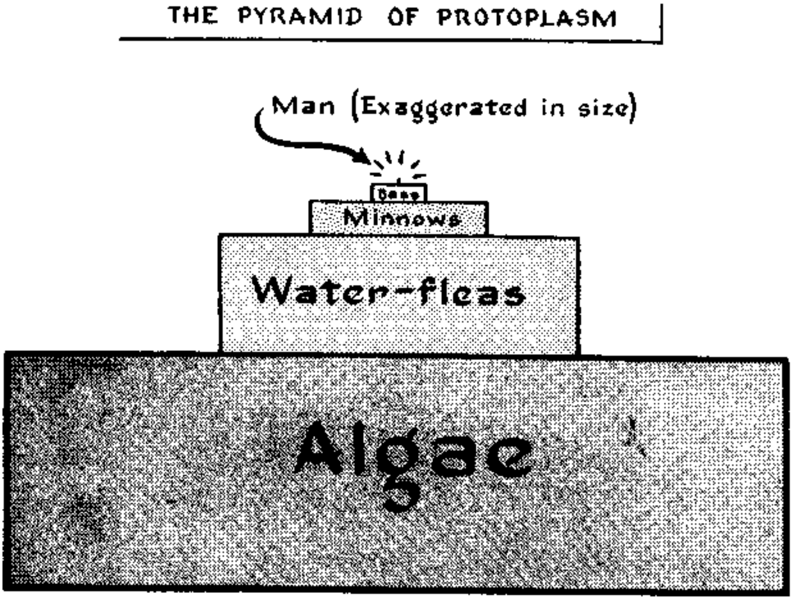


Fig. 32-5. The human significance of the Second Law of Thermodynamics.

The Pyramid of Protoplasm will bear more scrutiny. It implies other truths that man does not like to face. Consider the terrestrial pyramid: *plants* ⟶ *cows* ⟶ *man*. There is necessarily much loss of energy at each of the two transfers of energy. If the number of men living becomes great relative to the amount of organic carbon synthesized, what can be done to make the organic carbon go farther? Obviously, eliminate one of the links of the chain, one of the blocks of the pyramid. The only one we can consider eliminating is *cows*. By feeding directly on plants, a far larger population of men can be supported. Or, to put it another way, only a relatively sparse population can afford to eat meat. *In a*

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* The *number* at each level is influenced by size of individuals. The fleas supported by one man may amount to many dozens, but they cannot amount to a larger weight.

densely populated region, vegetarianism is a necessity. Our great-grandfathers, coming across the sparsely settled Great Plains, could afford to shoot a buffalo, eat only the tongue and leave the rest of the animal to rot. Today, we can hardly afford to buy the tongue of a cow. Tomorrow . . . ?

201. Are We Dependent on the Sun?

According to the simplified diagram of Figure 32-4, we are absolutely dependent on the sun for our daily supply of energy. Is this entirely true? What about coal? Oil? Gas? Water power?

Coal, oil, and gas are all products made (by Nature) from plant (or animal) material buried millions of years ago. The production of the raw material was made possible only by the light of the sun shining ages ago. No escape there. Water power is made possible by the fact that water falls on high places. This water gets there only because the sun's heat evaporates the water of the ocean, which later condenses to form clouds. The sun lifts the water to the mountain tops, one might say. No escape there.

And atomic power? Here there is a real possibility of escape. The energy we can extract from uranium or plutonium is not connected with the shining of the sun. The energy available per pound of material is impressively big. ("A pound of coal, completely converted to energy, would . . . etc.") But against the possibility of its large-scale, long-continued use by man, there are two* practical points that have been strongly urged by experts in the field.

1. Present theory indicates little possibility of generating atomic power on earth with any but the very heavy elements, such as thorium, uranium, and their derivatives. The available supply of these elements in the earth's crust is far from limitless. In North America, for instance, it is estimated that the available supply of heavy elements would meet our total energy needs for only two hundred years,

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* There is a third point, of less basic significance, that is often overlooked, namely, how large a share of the cost of power is due to what one might call social organization. Most of the cost of domestic electricity is accounted for by distribution costs. If the power company paid nothing for its power, the cost to the consumer would be cut not quite in half. "Overhead," interest charges, depreciation and repair of distribution equipment make up the major part of the cost of domestic electricity. Industrial electricity, bought in bulk, does not cost so much, per kilowatt-hour, to distribute.

whereas the purely chemical energy available in our coal supplies will last for several millenia at the present rate of consumption.

2. No one has figured out a way of disposing of the dangerously radioactive by-products of atomic fissions. They can be stored in concrete vaults deep in the ground, but this is only a temporary solution. In a few thousands, or millions, of years, ground waters will work their way into any man-made structure and carry the still radioactive material into man's world outside. The most fruitful suggestion for their disposal is the use of space-rockets. The radioactive wastes could be loaded into rockets and shot off the surface of the earth to circle forever in space.

Of course, tomorrow we may discover a loophole in our atomic theory, and we may learn a safe way to extract the energy from, say, sodium chloride. In the meantime, it would seem intelligent to try to make the best of what we have. At the present time, we are almost wholly dependent on photosynthesis for our supplies of energy. The photosynthetic apparatus, even under the most favorable circumstances, does not achieve better than two per cent efficiency. Ninety-eight per cent of the light that falls on a field of corn is wasted, as far as man is concerned. It does not seem too wild to hope that man may someday achieve an artificial photosynthetic process with a higher efficiency than that of the plant and, perhaps, one that can be used in the dry and sunny deserts where plants can scarcely grow. A hundredfold increase in the amount of sunlight trapped for man's use does not seem too great to dream of.

Must we, then, forego the use of atomic power? Not at all. We are using atomic power now. **The sun is an atomic engine.** Its light and heat are produced by a complex of reactions involving carbon and nitrogen, in which hydrogen is changed into helium. These reactions will proceed only at extremely high temperatures, such as prevail in the interior of the sun, about 20 million degrees Centigrade. It seems unreasonable to hope to set up an atomic engine of this sort on the earth—where all of our materials (including the walls of a hypothetical engine) would vaporize at 6,000 degrees. On the sun, this vaporization does not matter; the whole sun is a vaporized engine held together by gravity.

So, it appears, we are getting our energy from atomic disintegrations after all, disintegrations taking place some 93 million miles away. At the risk of appearing hopelessly old-fashioned, the author would like to suggest that 93 million miles is a nice, comfortable distance to put between us and our atomic power plant.

QUESTIONS AND PROBLEMS

32-1. Write the equations for respiration and photosynthesis.

32-2. In the simplest possible manner, diagram the carbon cycle.

32-3. Diagram the carbon cycle in the most complete detail known to you.

32-4. Define: *herbivore, carnivore, predator, prey.*

32-5. If all living things on earth were to die simultaneously, would the amount of inorganic carbon change? Explain.

32-6. What is the ratio of organic carbon to inorganic carbon on our earth? (Express the amount of the smaller as 1.)

32-7. During the Second World War, populations that were suffering from inadequate food supplies often sacrificed their poultry. (Poultry, in crowded countries, must be fed grain daily.) Was killing the poultry a sound food-conservation measure or not?

32-8. State the First and Second Laws of Thermodynamics in your own words.

32-9. List the foods you ate in your most recent dinner. Each food had in it some available chemical energy. Trace this energy back to the sun, by a probable, fairly direct path.

32-10. There was once a man who proposed to make money by setting up a rat and cat farm. He would grow rats to feed the cats. When the cats were big enough, he planned to kill them and sell the furs to furriers who would make genuine mink coats of them. The cat carcasses he would feed to the rats. Since the cats fed on the rats and the rats fed on the cats, he figured he would not need to buy any feed at all. Criticize this proposed business venture in the light of the Laws of Thermodynamics.

32-11. Trace the energy available in the electric wires of your house back to its ultimate source.

32-12. Is it theoretically possible that man might devise a photosynthetic machine that could displace the green plant?

32-13. (Not discussed in text.) Given a source of energy, can chemists make organic carbon compounds out of carbon dioxide and water?

32-14. (Not discussed in text.) The possibility of deriving energy from the tides was not mentioned in the text. What is the ultimate source of this energy? Has there yet been found a feasible means of harnessing it on a large scale?

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Chapter XXXIII

The Significance of Decay

202. The Nitrogen Cycle

In the previous chapter, we considered the changes and the exchange of carbon as it is handed back and forth between plants and animals. We are now ready to consider the similar alterations of nitrogen as it is bandied about the living world. Nitrogen has its cycle, too, but it is more complex and is best developed piecemeal.

The nitrogen metabolism of higher plants and animals does not involve any gaseous nitrogen (N_2), either as a food or as a waste product. For all the plants above the Thallophyta (and for most of them, too) and for all animals, molecular nitrogen is a strictly inert material. Yet all organisms require the element nitrogen, since it is a constituent of the all-essential amino acids and proteins. What is the source of this organic nitrogen?

Animals are dependent on plants. All but the simplest animals must be furnished with organic-N (either amino acids or proteins) which they get, ultimately, from plants. When either the plant or the animal dies, putrefactive bacteria and fungi decompose the organic nitrogen compounds, releasing ammonia, NH_3, into the soil. This ammonia can be used by plants to build up new proteins. Few animals can carry out such a synthesis; they are dependent on the greater synthetic abilities of plants.

These facts are summarized in Figure 33-1. It will be noted that animals contribute ammonia to the world by two different routes. Some nitrogen they excrete as ammonia; some they excrete in the form of organic nitrogen [e.g., urea, $CO(NH_2)_2$; and uric acid] which is decomposed by soil bacteria to yield ammonia. The nitrogen that stays locked up in the body of animals (and plants) is released only by death and putrefaction. From an examination of the figure, it is clear that, although animals are dependent on the rest of the living world for their nitrogen, the rest of the world could get along well enough without animals. The only indispensable characters in this play are the bacteria and fungi. Without them, all the world's available nitrogen would eventually be locked up in dead and undecomposed plant and animal cadavers. In his burial customs, man tries, unthinkingly, to stop the cycle by protecting human remains from the actions of bacteria. Fortunately, his successes in this direction are only ephemeral.

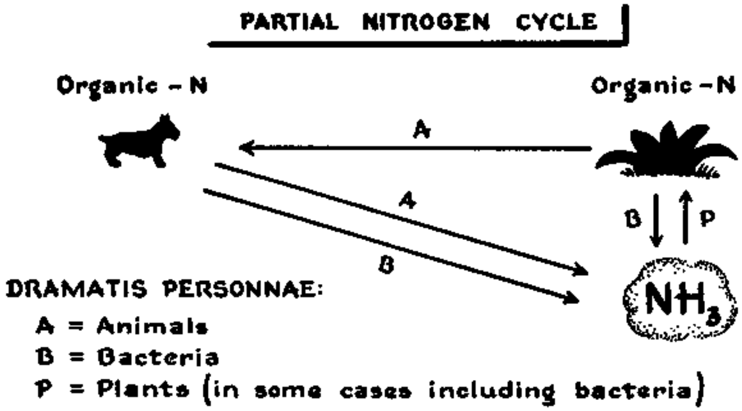

Fig. 33-1. Who is essential?

Bacteria, on the other hand, are quite capable of keeping the nitrogen cycle going by themselves, synthesizing organic-N from NH_3, and decomposing the remains of other bacteria (or other plants or animals) into NH_3 again.

This is not the whole story of the nitrogen cycle. Although plants are quite capable of satisfying their nitrogen needs from ammonia, they seldom get a chance to. Most ammonia, as soon as it is released into the soil, is converted by specialized bacteria into nitrite ions (NO_2^-), and nitrate ions (NO_3^-). Nitrate-N is relatively stable; it is this form of nitrogen that supplies most of the plant's needs. (See Fig. 33-2.) It will be noticed that the conversion of NH_3 to NO_3 takes place in two steps. Not only are these steps distinct, but they are carried out by different bacterial species, each of which is a specialist for its "job."

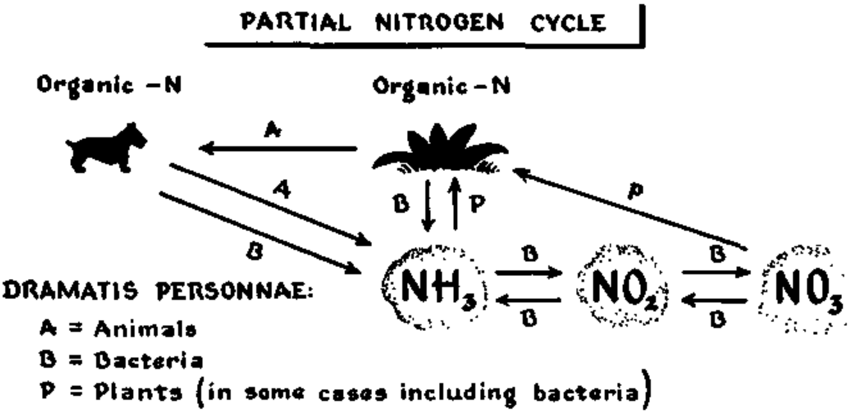

Fig. 33-2. The importance of bacteria becomes increasingly apparent.

Even this, however, is not quite the whole story. As diagrammed, the N-cycle is a nice, tight system. Unfortunately (from man's point of view), there is a rather serious potential leak in the system. There are many species of putrefactive bacteria, including species of *Pseudomonas* (recall § 143) that have a habit of supplying their oxygen needs from NO_3 when O_2 is unavailable. In so doing, they release N_2, which neither they, nor leafy plants, nor animals, can utilize. Obviously, such bacteria constitute a threat to the continued existence of the nitrogen *cycle* and, hence, of all living things. Fortunately, there are a *few* microorganisms that are capable of turning N_2 into organic-N, a process that is called **nitrogen-fixation.** These bacteria not only act as plugs for the "leak" created by *Pseudomonas*, but they also are potential sources of an actual increase in usuable nitrogen circulating in the cycle, since they can fix N_2, a gas that makes up 80 per cent of our atmosphere. (See Fig. 33-3.)

Because of their obvious importance to the living world, it is worth while discussing the nitrogen-fixing microbes. Although there is one *an*aerobic species of nitrogen-fixing bacteria, it seems to be quantitatively unimportant, so we shall ignore it. The important nitrogen-fixing bacteria are *aerobic*. One of them, *Azotobacter*, is free-living and is to be found in all well-treated soils. The other one, *Rhizobium*, may also live in the soil, but when it does, it never fixes nitrogen. Only when it manages to invade the roots of one of the *legumes* (peas, beans, etc.) can it fix nitrogen. In the legume root, it causes what might be called a mild infection, stimulating the plant to form *root nodules* around the colony of bacteria (Fig. 33-4). Far from harming the plant, these invasive microbes aid it, since they furnish it with a richer supply of usable nitrogen than it would otherwise have. In turn, the plant furnishes the bacteria with an environment more favorable to their growth than is the soil. Such an association of living organisms from which both species benefit is called a **symbiosis**—literally, a living-together.

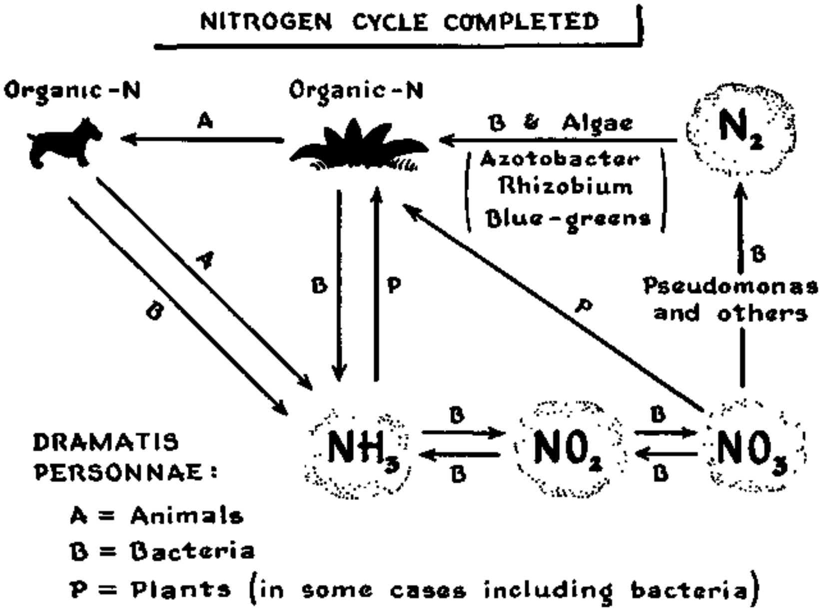

Fig. 33-3. Who is independent?

Besides the bacteria, members of one group of algae, namely the blue-greens, are also able to fix nitrogen. Being able to supply their own organic carbon needs from atmospheric CO_2 and water and their nitrogen from atmospheric N_2, these may be said to be the most independent organisms in the world.

The agricultural importance of the nitrogen-fixing microbes can be readily appreciated. Land that is steadily planted to crops such as corn and wheat continuously loses nitrogen as the proteinaceous grains are harvested and shipped away from the soil that furnished the nitrogen. By periodically letting a field lie fallow, part of its nitrogen is restored through the activity of *Azotobacter*. By planting it to legumes, even more nitrogen is restored to the soil, especially if the mature legume plants are plowed under. In most agricultural regions, bacteria seem to be most important in the process of nitrogen-fixation. In rice-growing countries, however, the blue-green algae are of considerable importance. They grow as a scum on the surface of flooded rice fields. Many rice fields have been continuously cultivated for hundreds of years without any additions of artificial fertilizers.

Fig. 33-4. Legume root nodules (*Lespedeza*). (Photo courtesy Iowa State College.)

203. The Versatility of Microbes

Some of the reactions involved in the nitrogen cycle can be carried out by many species. Others can be carried out by only one or a few species. In Figure 33-3, we have not given much specific information, using the vague "B" to stand for unnamed bacteria and molds. This vagueness springs not from lack of information, but from a belief that the detailed examination is properly relegated to a course in microbiology or bacteriology. However, it will be worth while to describe in greater detail a small part of the nitrogen cycle.

The oxidation of ammonia to nitrate takes place in two steps brought about by bacteria belonging to two different genera, as indicated in equation (1). These bacteria are specialists in carrying out the reactions indicated. The energy that they obtain from these oxidations they use to *synthesize organic material from carbon dioxide and water*, as indicated by equations (2) and (3). In other words, the activities of these organisms bear a close resemblance to those of photosynthetic organisms but, in the present instances, the energy for the synthesis of organic matter is derived from inorganic chemical reactions instead of from light. A reaction of this sort is called a **chemosynthesis,** and an organism that can use the energy obtainable from an inorganic reaction to synthesize organic material is called a **chemosynthetic organism.**

$$NH_3 \xrightarrow{(\textit{Nitrosomonas})} NO_2 \xrightarrow{(\textit{Nitrobacter})} NO_3 \qquad (1)$$

Nitrosomonas: (2)

$$\begin{array}{ll} \text{(a)} & NH_3+O_2 \longrightarrow NO_2+H_2O+\epsilon \\ & \qquad\qquad\qquad\qquad\qquad\quad \downarrow \\ \text{(b)} & \qquad\qquad\qquad\qquad\qquad\quad \epsilon+CO_2+H_2O \longrightarrow \text{organic material}+O_2 \end{array}$$

Nitrobacter: (3)

$$\begin{array}{l} \text{(a) } NH_2+O_2 \longrightarrow NO_3+\epsilon \\ \qquad\qquad\qquad\qquad\qquad\quad \downarrow \\ \qquad\qquad\qquad\qquad\qquad\quad \epsilon+CO_2+H_2O \longrightarrow \text{organic material}+O_2 \end{array}$$

If we are in the habit of thinking of food as being synonymous with organic material, reactions of the sort just described are rather surprising for, in them, the "food"—the energy-providing material—is inorganic. In the microbial world, there are many instances of organisms that can derive useful energy from the most surprising substances. There are bacteria, for instance, that can oxidize hydrogen gas (H_2) to water, deriving energy therefrom. There are others that can grow fat living on methane (CH_4), which is the principal constituent of the gas we burn in our stoves. There are others that can feed on pure carbon monoxide, a deadly poison for most animals.

There is probably no organic chemical that we ordinarily regard as poisonous or noxious that is not used as food by some microbes. The materials that we excrete and discard are welcome food to many ubiquitous bacteria. Urea, uric acid, and all the chemical substances present in feces are used as food by various soil bacteria and fungi. Truly, the saying, "One man's meat is another man's poison," applies to the entire living world. This is fortunate for us, for, otherwise, what we regard as obnoxious materials would steadily accumulate in the world. Microbes, however, feed on them, converting them ultimately to carbon dioxide and inorganic nitrogen compounds which keep the carbon and nitrogen cycles going. The problem of sewage disposal is one of encouraging the proper bacteria to multiply rapidly in the sewage, thus converting it rapidly into carbon dioxide and the various nitrogenous compounds that are safe and suitable for returning to the soil as fertilizer.

Microbes can use not only compounds that we would regard as obnoxious, but also ones which they (the microbes) would regard as harmful. Every organic disinfectant and germicide can be used as food by some species of microbe, if the concentration of the substance is not too great. Carbolic acid, hexylresorcinol and other organic germicides can be metabolized to carbon dioxide and water. As a consequence, the antiseptics we pour on an unenthusiastic microbial world do not accumulate, but are broken down to simpler materials that are returned to the carbon and nitrogen cycles. A further consequence of this observation is this: antiseptics are effective only in the proper concentration. If diluted too much, they not only do not stop the growth of bacteria but may actually encourage it.

Many compounds that we ordinarily regard as being very resistant to decay can be metabolized *slowly* by bacteria. Among these are rubber, petroleum, and coal. These substances, when surrounded by soil or water, are slowly converted to carbon dioxide and water. They, too, decay. Or, more exactly, *they are decayed.*

From nearly a century's intensive experience with microbes, several generalizations have been evolved:

1. With a few unimportant exceptions, **decay is caused only by living organisms.** Without living organisms (principally bacteria and fungi), neither foodstuffs nor "wastes" would decompose. Perhaps one should use only a passive verb: organic material does not decay; it *is decayed.*

2. As a permanent *working hypothesis,* we may say that any **chemical substance that is theoretically capable of being oxidized will be oxidized by some kind of organism.** We call this a "permanent" working hypothesis because it is so stated that proof, or disproof, is impossible, since we have not specified the kinds of organisms. The hypothesis has proved to be a useful one in the search for organisms that can decompose specific compounds. It has made sense out of the remarkable oxidations that go on in nature: the oxidation of recalcitrant materials like peat, coal, gasoline, chitin; of poisonous materials like carbon monoxide and carbolic acid; and of inorganic substances like hydrogen, ammonia, ferrous iron, and sulfur.

3. It follows that **no organic substance accumulates on the earth,** since all organic substances are capable of being oxidized. All such substances are sooner or later broken down to carbon dioxide and inorganic nitrogen which can then re-enter the carbon and nitrogen cycles.

QUESTIONS AND PROBLEMS

33-1. In an effort to prevent confusion of the student, it is necessary to oversimplify too-complex Nature in presenting the nitrogen and carbon cycles. For example, one factor left out of the N-cycle as presented above was the effect of burning. When wood or coal is burned, most of its nitrogen is released as N_2. Make a new nitrogen cycle diagram that includes fire and its effect.

33-2. Insectivorous plants, such as the sundew, Venus's fly-trap, and bladderwort, can get their organic nitrogen from animals, which they digest. Modify the N-cycle to take account of the actions of these quantitatively unimportant plants.

33-3. Discussions of morality are generally considered outside the scope of a textbook in science, but it will not hurt to point out a moral overtone of the carbon and nitrogen cycles. The manufacturers of caskets frequently boast that their products will give "eternal protection to your loved ones." Considering the significance of the carbon and nitrogen cycles, would you say that the implied aim is a thoroughly moral one, assuming that we should be concerned with posterity?

33-4. Why is it more exact to say an organic substance *is decayed,* than to say *it decays?*

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Chapter XXXIV

The Conservation of Natural Resources

204. The Water Cycle

There is no immediate prospect of our becoming independent of the sun (§ 201). At the present time, we have no practical way of garnering the sun's energy on a large scale save through the intermediation of plants. Therefore, the problems of conserving our natural resources revolve around the problem of preserving the conditions in which plants will grow. These problems, in turn, are closely linked with the supply and movement of water, of which plants need large quantities (§ 155).

The movement of the world's supply of water follows a cycle. The principal paths, as indicated in Figure 34-1, are more or less consciously known to everyone. Water evaporates from the ocean into the air where it forms clouds. Moist air masses are moved by the winds. When they reach a region that is cold enough, the water vapor in them condenses to form **precipitation** (rain or snow) which falls to the ground. There it may run directly down the surface, or it may soak into the soil. Subsoil water may later come to the surface as spring water, ooze into river beds, be pumped up by man, or enter the ocean while still below the surface of the ground. Some of the water accumulates in lakes or ponds but only temporarily. Ultimately, all the water either evaporates from the surface of the land or reaches that great water reservoir, the ocean, from which it will someday once more evaporate. The cycle is a complete one, with no leaks. As long as the sun's rays continue to furnish the heat that motivates evaporation, the cycle will continue.

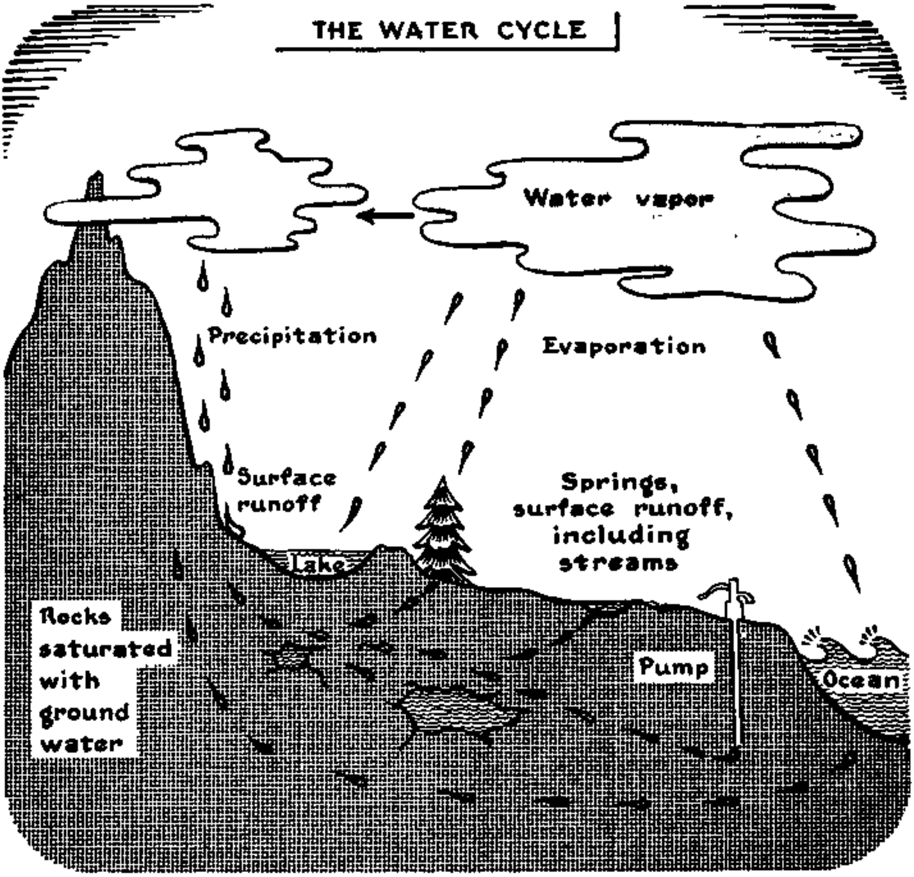

Fig. 34-1. The major pathways in the water cycle.

The general nature of the cycle is fairly well understood by most people. The principal part that is not widely appreciated is the finite nature of ground water. Because extensive pumping from a single well does not seem to have any immediate effect on the supply of ground water, there is a tendency to think of it as inexhaustible. It does not seem to be dependent on precipitation, because the rainfall that is largely responsible for it may have occurred several hundred miles away, and many years in the past, so slow is the movement of water through rock. However, continuous pumping from hundreds of wells soon lowers the "water table" in any district. Man, poor planner that he is, responds to the threat of a falling water table by digging wells instead of by adjusting his withdrawals to match the rate of replacement. It is so hard to live within one's income!

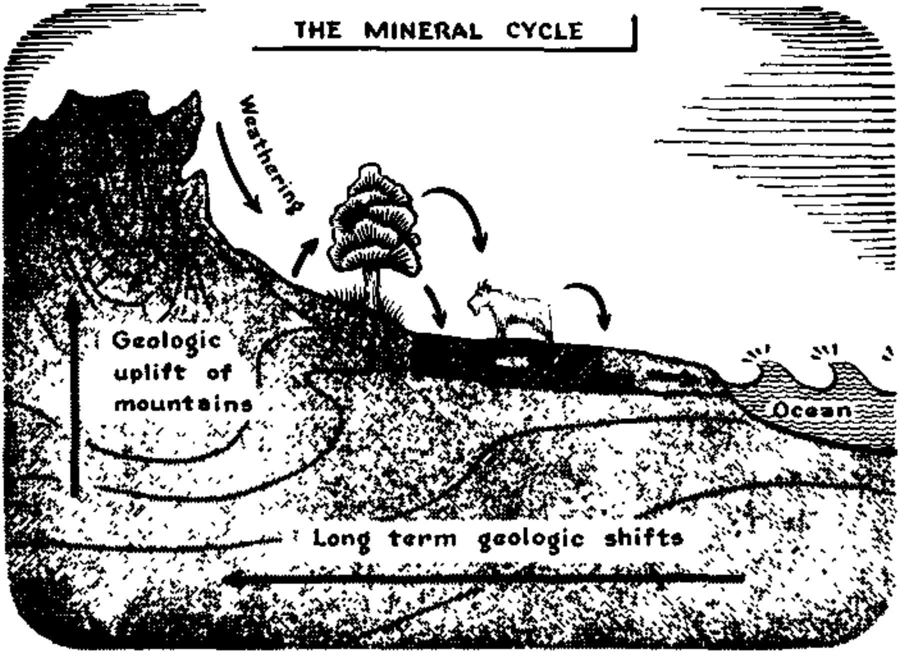

Fig. 34-2. For the purposes of practical, short-term planning, we may say that minerals move in only one direction, from the mountains to the sea.

205. The Mineral Cycle

As the water runs off the surface, it carries with it various minerals in solution and in suspension. These minerals are derived from exposed rock by a **weathering** process that breaks the rocks physically and alters them chemically. This process is brought about by physical forces, e.g., the abrasion of water and rock particles and the freezing of water in crevices of the rocks. Biological forces also contribute: the roots of plants secrete dilute carbonic acid which dissolves some rocks; and roots enter cracks of rocks, grow in diameter, and split the rocks. In the end, rock is disintegrated into soluble salts and unidentifiable particles that constitute part of the complex mixture that we call *soil*.

Soil eventually ends up in the ocean, though under natural conditions it may take hundreds of thousands of years in getting there. During this time, the minerals of the soil will many times be taken up by plants (Fig. 34-2) and, as often, returned to the soil when the plants are decomposed by microbes. On the way to the sea, the minerals may take many a side trip through animal protoplasm, but their ultimate fate remains the same.

The path of the minerals from mountainside to ocean is much the same as that of their motive force, flowing water. But here the similarity between the water cycle and the mineral cycle ends. Minerals are not volatile; hence, they cannot be returned to the land by evaporation and subsequent condensation as water is. Once in the ocean, the minerals are there to stay. The relatively insoluble ones precipitate to the bottom, while the more soluble ones (principally NaCl) remain in solution, thus making the ocean salty. The ocean is a dead end—almost. Geologically speaking, the ocean basins are not entirely permanent. Over periods of millions of years, the mountains and parts of the ocean basins slowly change places, the mountains weathering away to plains which sometimes become submerged under the ocean, as what was once ocean bottom is pushed up to become mountains. One sees the evidence of these changes in the abundance of marine shells found imbedded in the strata of present-day mountains which, under the influence of weathering forces, are giving up their materials to the seas from which they came.

Geologically speaking, minerals move in this cycle. But it seems to be not quite perfect; the return is not complete. As a result, minerals are gradually accumulating in the ocean and in its beds. There is good evidence that the ocean was a body of fresh water many millions of years ago and that its present saltiness is the result of the continuous and gradual accumulation of minerals from the land.

206. The Vicissitudes of the Soil

Soil is an undefinable material, though "we all know what we mean" by the term. It is composed of a variable mixture of minerals, rock particles, clay, and animal and plant tissues in various stages of decomposition. One of its most important characteristics is its texture.

Good soil is more or less loose and spongy, not compacted like clay which is not soil. What is properly called soil is only a thin layer in most parts of the world, underlain by *subsoil* (usually clay) and rocks. In the United States, the average thickness of the soil layer is about seven inches.

Fig. 34-3. An approaching dust storm. High winds have lifted tons of soil from the bare earth. Photo taken near Lamar, Colorado, May, 1937. (Courtesy of U. S. Soil Conservation Service.)

The texture of soil is the result of the accumulated effects of many hundreds of generations of plant growth. Every growing season, the hundreds of miles of tiny roots and root hairs of each plant (recall § 154) divide and subdivide the soil particles. Traces of their activities remain in following seasons. In addition, many small animals, such as earthworms, are constantly "plowing" and turning over the soil.

Soil is necessary for plant growth; reciprocally, plants are necessary for the stabilization of soil. In the absence of adequate ground cover, winds may sweep up the soil (Fig. 34-3) and blow it for hundreds of miles. Extensive damage by wind erosion was unknown in the United States until May 12, 1934, when the first of a series of great wind storms swept across the plains region immediately east of the Rocky Mountains. The first storm carried an estimated 300 million tons of soil into the eastern states. Since that time, repeated dust storms have carried more soil from the "Dust Bowl" to points as far east as New York City. It would be shallow thinking that would place the blame for these dust storms on high winds alone. Winds of equal velocity have swept the Great Plains for centuries, at least. The damage wrought by the winds since 1934 have been the result of the paucity of ground cover. The Dust Bowl has paid the price of the "clean farming" practices that were used in growing seasonal grains in a region that once had a year-round cover of prairie grass. Competent soil experts maintain that thousands of acres in western Kansas, Texas, and neighboring states should not be farmed at all but should be used only for carefully protected pasturage.

Fig. 34-4. A field from which water has eroded the topsoil, leaving a stony subsoil which will not support the growth of plants and, hence, is subject to further erosion. (Courtesy of U. S. Soil Conservation Service.)

Less spectacular than wind erosion, but quantitatively more important, is erosion by water. Figure 34-4 shows a field whose dark topsoil has been completely removed in spots, leaving only a stony subsoil at the surface. Vegetation has little chance of getting started on such ground. In the absence of the soil-binding activities of roots, the subsoil will be eroded even further by future rains. Thus is a vicious circle established, a circle which often has no ending until large areas of agricultural land have been ruined beyond the possibility of reclamation (Fig. 34-5). The steeper the gradient, the heavier the rainfall, and the cleaner the farming, the greater is the damage wrought by water gullies. Large areas in the southeastern part of the United States have been completely removed from the cultivable category as a result of man's improper farming activities. In Stewart County, Georgia, there is one (in)famous gully that now covers 3000 acres and is 200 feet deep in places. This gully had its beginning about 1900 at the side of a barn where the water dripping from a barn roof started a rivulet which, unattended by man, grew steadily in length and breadth until it reached its present Gargantuan proportions. Whole farms have disappeared into this eroding chasm. One observer, viewing the scene of devastation, remarked that it could only be compared with the Yellowstone Canyon.

Fig. 34-5. Twenty-six years before the photograph was taken, this gulch did not exist. Such rapid erosion is likely to occur wherever clean farming or overpasturing is permitted to extend to the very edge of any creek or rivulet. Once erosion has proceeded this far, not even heroic measures can reclaim the land. The most one can strive for is a stalemate. (Courtesy of U. S. Soil Conservation Service.)

What happens to the soil that is removed by eroding waters? Its immediate effect is to make muddy the streams into which it enters. As these streams flow along, they deposit their detritus on river bottoms downstream. A certain amount of such deposition is, of course, normal, and moderate deposits increase the fertility of the bottom lands where they are laid down. Under preagricultural conditions, great floods are rare in regions of moderate rainfall, and the rate of deposition of soil on bottomlands is slow. With the coming of agriculture in the upper reaches of a river system, the water-holding capacity of the land is decreased and, as a consequence, floods become more frequent and more devastating to the areas downstream. Figure 34-6 shows clearly the effects of the inundation of land following the initiation of agriculture. The rocky soil visible in the top half of the illustration is a dep-

Fig. 34-6. The bottom eight-foot-thick section is a fine-grained soil whose deposition required an estimated 10,000 years. With the beginning of agriculture in the drainage shed above, there began the deposition of silty soil from flood waters that periodically overflowed the land. The top eight feet of soil (above the dark line) were deposited in only seventy years. This soil is coarsely and irregularly granular and is of much poorer quality than the slowly deposited soil below it. (Courtesy of U. S. Soil Conservation Service.)

osition of a sort which the downstream farmer would just as soon not have. What the farmer upstream has lost is in no sense a gain to the farmer below him.

Fig. 34-7. One flood was enough to half bury this farmhouse under silt washed down from improperly farmed lands upstream. The deposit in this case was almost pure sand, valueless for farming. There was no recourse but to abandon the farm. (Courtesy of U. S. Soil Conservation Service.)

Under flood conditions, not only are farmlands damaged, but homes are also ruined (Fig. 34-7). In many cases, it is uneconomical to try to reclaim flood-damaged buildings. When the effort of salvaging buildings is deemed worth while, it entails an amount of labor that can scarcely be appreciated by one who has not lived through a flood. Months of moving of dirt, cleaning of surfaces, and replacing of damaged structures are required before buildings are habitable again.

An incidental, but by no means inconsequential, effect of increased erosion is the increase in the rate of obsolescence of dams. Figure 34-8 shows two views of a dammed pond taken only a few years apart. The total useful life of this body of water was only fourteen years. In this short space of time, the silt deposited behind the dam rendered it virtually useless either for water storage or for water power. It should be realized, of course, that such a fate is in store for all dammed areas. A lake is only a temporary affair, geologically speaking. Ultimately, it

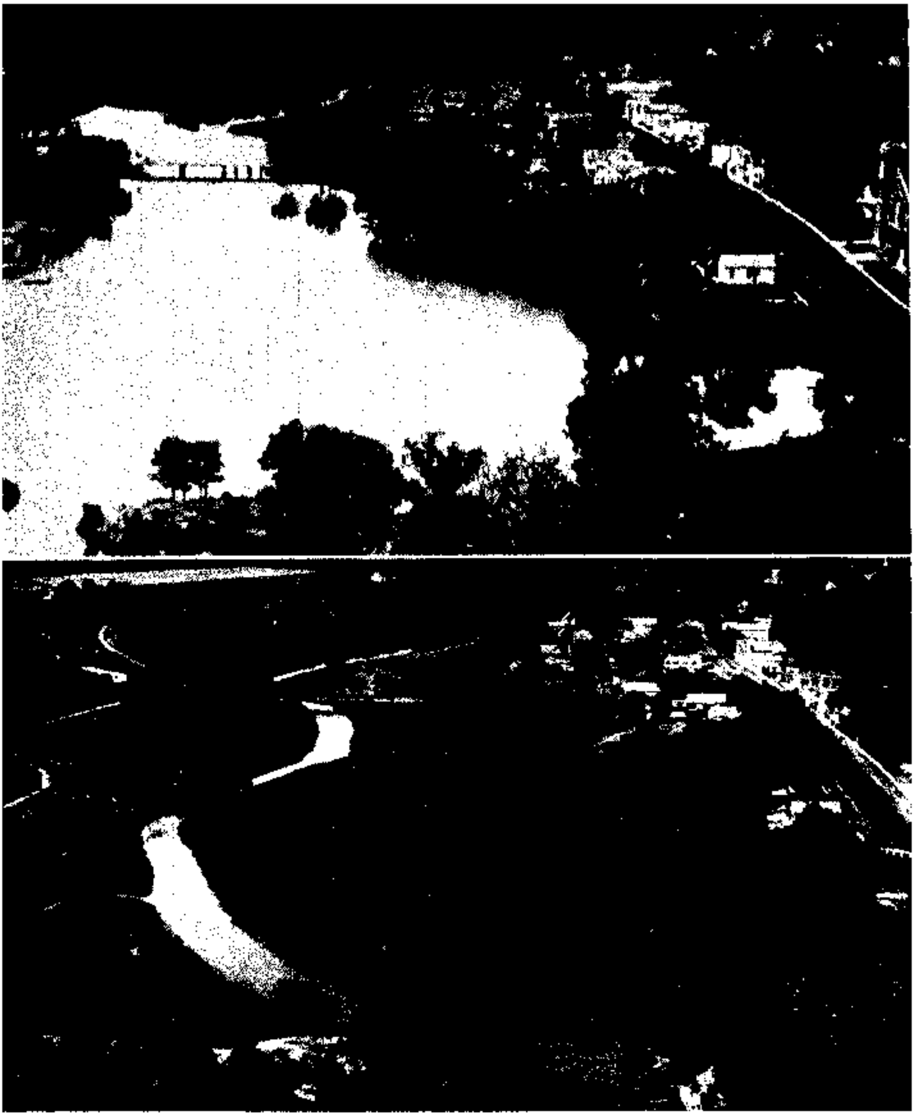

Fig. 34-8. In ten years' time, the attractive man-made lake shown in the top photo was changed to the man-made marsh shown below, as silt was deposited from a stream which drained improperly-farmed and overlumbered lands upstream. (Courtesy of U. S. Soil Conservation Service.)

either loses its barrier of earth at the lower end, or fills up with silt from the upper. A lake made by a dam is no different from any other lake. However, it makes a great difference to man how soon the dam's fate overtakes it. When the lands on the banks of the headwaters are properly managed, "temporary" may mean a hundred or a thousand years for the artificial lake. With eroding drainage basins, "temporary" may mean fourteen years, as in the instance pictured. The economic advantages of extending the duration of *temporary* are obvious.

Fig. 34-9. Lumbering and fire have reduced the ground cover to such an extent that erosion, visible in the foreground, can continue almost without natural impediment. (Courtesy of U. S. Forest Service.)

When soil is lost, floods become more frequent and of greater severity. Seven inches of good soil is seven inches of sponge that can absorb a great deal of precipitation. Remove the soil and one is left with clayey subsoil ("hardpan") or rock, either of which sheds rain readily. Even under ideal conditions, floods occur. But with the absorbent soil stripped off the hardpan, floods occur oftener and are greater in volume.

The removal of forests, whether by the hand of man or by fire, greatly increases the danger of floods downstream. The roots of trees and all the other plants associated with them hold the soil in place. Once the tops of the plants are gone, the root systems become decayed, and no longer can they play their soil-binding role. In Figure 34-9, is a picture of what was once a forest. The ground was first laid bare by lumbering, then by a fire. The signs of beginning erosion in the foreground should be noted. One forest fire may result not only in the loss of millions of dollars' worth of timber, but, by permitting subsequent erosion, may cause increased flood damage in the lands below. So great a quantity of soil may be lost from the denuded forest land that hundreds of years will be required to reproduce the mature forest. During all of this time, the costly consequences of the erosion of bare areas, as described above, must be endured.

207. Further Consequences of Erosion

It is customary to express loss in terms of money. Following that custom, we may report that a reliable estimate places the annual losses due to erosion in the United States at around one billion dollars. However, since money-figures have come to be almost meaningless in our present world, let us see what the human consequences of erosion are.

There are not only soil-erosion processes; there are also soil-making processes. We must know what the comparative rates of these two are before we concern ourselves about losses.

TABLE 34-1

THE CALCULATED TIME REQUIRED TO REMOVE 7 INCHES OF TOPSOIL FROM AN ERODIBLE SOIL IN THE SOUTHERN APPALACHIAN REGION. SLOPE: TEN PER CENT. (FROM BENNETT, 1947.)

TYPE GROUND COVER	YEARS TO COMPLETE REMOVAL OF SEVEN INCHES OF SOIL
Virgin forest	575,000
Grass	82,150
Rotation cropping	110
Cotton	46
Bare ground	18

The rate of soil erosion is greatly influenced by the type of ground cover, as Table 34-1 indicates. On one particular piece of land, the time required for the removal of seven inches of topsoil ranges from about one-half million years with a forest cover, to only eighteen years for bare soil. These estimates are fairly accurate. They are made by collecting all the run-off water from a measured area of soil for a given period of time, determining the weight of solid material in the run-off, and from this, calculating the time necessary to remove any given quantity of soil. These measurements are capable of considerable precision.

What is the rate of soil formation? It can be readily appreciated that here we are up against operational difficulties in determining the facts. The formation of soil is slow—that we know. It is difficult to determine small increments—deposits of the order of thousandths of inches—added to some seven inches of loose, difficult-to-measure, soil. Such measurements as have been made indicate that the rate of soil formation is probably distinctly below one-half inch per century. In other words, if a given piece of ground had been completely denuded of topsoil at the time of the birth of Christ, it would only by now have finally accumulated its normal seven inches of soil. . . . The error of this estimate is not determinable, but it is much more likely that the stated period of time is an underestimate rather than an overestimate.

In many parts of the country, our "expenditure" of soil is greater than our "income." The consequences of this situation, when long continued, ramify in all directions, far beyond the bounds of biology as conventionally defined. Loss of soil fertility means diminished crops, which means less income for the farmer, and higher prices for food for the city-dweller. Lower income in the farming group means social disorganization leading to emigration of the younger generation to the cities or migration of whole families to new areas. Old land may have to be abandoned completely, and the pressure of population may result in making farms of "marginal land" that were better left in grass or forest, with a resultant further increase in erosion and its attendant problems.

The increased load of soil dumped into streams from eroding lands makes the water more opaque, thus cutting down on photosynthesis by water plants. One needs only to look at the Pyramid of Protoplasm (Fig. 32-5) to appreciate the consequences of an increase in the opacity of the water. The piling up of mud deposits behind dams cuts down on their water storage capacity and, ultimately, on electric power production. These are but a few of the consequences of uncontrolled erosion. They all add up to diminished prosperity, not only for the farmer, but for all of us.

208. What Can Be Done About Soil?

The problems of controlling erosion are many and complex, depending on such factors as type of soil, type of crops, design of cultivation machinery, slope of land, other uses the land must serve, etc. For an integrated discussion of these factors, we can best refer the interested reader to Bennett's little book on soil conservation, cited at the end of the chapter.

Fig. 34-10. Contour farming. By such means, is the soil conserved and, in the long run, farm income increased. Frequently, successful contour farming can be carried on only by combined operations on more than one farm. (Courtesy of U. S. Soil Conservation Service.)

Since the passage of the National Soil Conservation Act of 1935, the most influential force in the field has been the Soil Conservation Service. This agency has proceeded slowly, using persuasion more than force. In about ten years' time, roughly ten per cent of the agricultural land in the United States has been brought under sound management. This rate of progress is dangerously slow, were the rate not to increase, but momentum has been gained, and, given public support, the rate of progress can be increased. A few examples of the sort of measures being taken will be given.

Fig. 34-11. Instead of a dangerously eroding gully, this farmer has a half-acre pond, thanks to the earth-fill dam. The pond has been stocked with fish and is now a source of food and recreation. (Courtesy of U. S. Soil Conservation Service.)

Marginal lands are being purchased and removed from farming, thus helping to protect neighboring lands from erosion and lands downstream from unwanted deposition. The planting of farms is, with the cooperation of the owners, being replanned so as to make use of sound erosion-control principles. Figure 34-10 shows land that is farmed "on the contour," thus minimizing both soil losses and water losses. How contouring and interspersing dense-standing crops, such as vetch, between "clean-row" crops, such as cotton, can decrease the soil and water losses are shown by Table 34-2.

The rational planning of a farm frequently involves retiring some more erodible areas from crop production. Such areas can usually be either turned into ponds (Fig. 34-11) or into wooded or shrubby areas

TABLE 34-2

WATER AND SOIL LOSSES FROM THE SAME LOCALITY UNDER DIFFERENT SYSTEMS OF FARMING. (MODIFIED FROM BENNETT, 1947.)

PLANTINGS	SOIL LOSS, TONS PER ACRE	WATER LOSS, PER CENT
Cotton, in straight rows	28	18
Cotton, in contoured rows	17	9
Cotton, and vetch, interspersed in contoured rows.	1	3

(Fig. 34-12). In either case, a local region suited to wild life is thus created which can be not only a source of pleasure but also of a small income derived from fish or from game birds. It might be thought that the removal of areas from conventional farming would decrease the farmer's income. A survey of some nine thousand farmers who had, for several years, cooperated with the Soil Conservation Service in carrying out such plans revealed that their income had actually increased by thirty-four per cent, in spite of the fact that they were farming fewer acres than they were before the Service stepped into the picture.

The rational exploitation of our forests is further from achievement. At the present time, most foresting is done on a one hundred per cent cutting basis, and the rate of removal far exceeds the rate of replacement through growth. Other nations have forestry policies that make mandatory harvesting on a sustained yield basis. With respect to our forests, we are still proceeding under the spell of the "Myth of Inexhaustibility." It is not easy, at the moment, to see how we are to succeed in basing our forestry practices on a saner philosophy, because so much more than biology is involved in our problem. In the short run, it is more expensive to cut only a scattered fraction of the trees in a stand, instead of razing the whole forest to the ground. In the long run, a partial harvest is the only kind that will pay. Unfortunately, each lumbering firm, under the pressure of competition, must carry out operations that make short-term economic sense. Long-term policies will be adopted only when the public is aroused to see its own interest and becomes willing to pay the cost (in one way or another) of the adoption of long-term policies. Only so, will our forests be made perma-

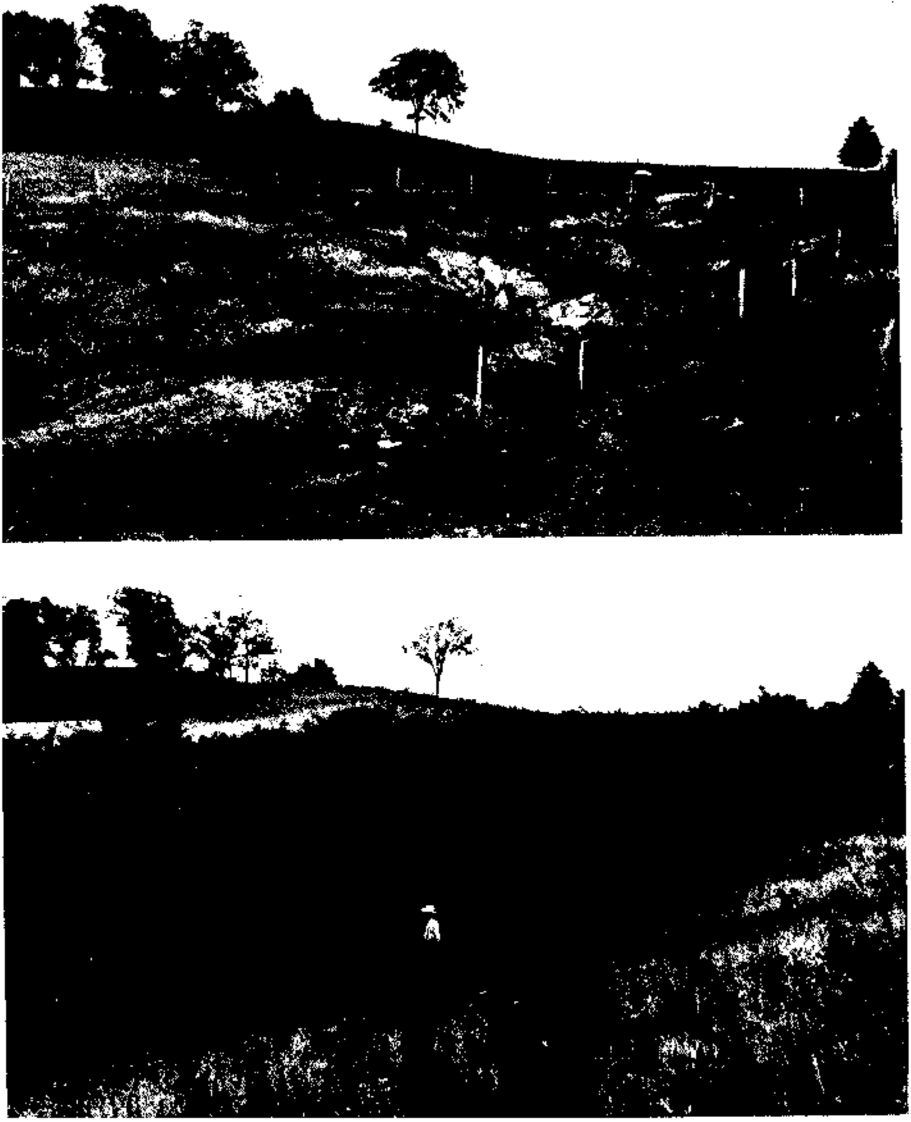

Fig. 34-12. A barren, eroding hillside converted into an attractive refuge for wildlife. Only two and a half years elapsed between the taking of these two photographs. (Courtesy of U. S. Soil Conservation Service.)

nent sources of wealth and beauty; only so, will wild life be maintained and the useful life of our dams extended.

One of the great difficulties standing in the path of sound conservation programs is a psychological one. To the city-dweller—and most of us are town- and city-dwellers now—the farm and the forest seem remote places inhabited by strange people who are unaware of the superiorities of urban life. Most city-dwellers act as if what occurs on a farm or in a forest a thousand miles away does not concern them. Yet all of us are genuinely dependent on the biological productivity of the soil for our continued existence. It is doubtful if any nation can long survive that is not keenly aware of its rural problems. No nation dies of a single wound. But it seems likely that erosion, and all its attendant ills, has contributed significantly to the downfall of many nations in the past. *It can happen here, too.*

How do we stand at present? A balance sheet struck in 1947 gave this picture of the United States:

Farm and grazing land essentially ruined . . . 282 million acres.

Land imminently threatened with ruin by erosion . . . 775 million acres.

Good land, at present not seriously threatened . . . 460 million acres.

We are not down to our last shirt yet, but neither is there excuse for complacence. The destructive activities of man are of hurricane swiftness. The constructive actions of nature are as gentle zephyrs. To continue to exist at a high level of prosperity, we must equilibrate one force with the other. Only one is capable of significant modification.

209. The Logic of Conservation

A population of organisms, multiplying in a finite environment, increases rapidly at first, and then more gradually, ultimately arriving at a relatively constant number (Fig. 34-14). We say *relatively* because there usually are fluctuations, due perhaps to seasonal fluctuations in the environment. Over a long period of time, however, there is a limit which the population does not pass. This sort of population curve has been verified in hundreds of species of plants and animals that have been grown in the laboratory in known, finite, environments. The verification of this curve in less definitely confined nature is more difficult because of the problem of taking accurate censuses; but, in so far as the data permit us to judge, the same general sort of curve holds for natural populations. Granted that a population exists in a finite, relatively constant environment, it is not easy to conceive of any other type of curve of population increase.

This curve may be called an S-curve, because it resembles a somewhat distorted S. What is the reason for its shape? We can answer this if we first remind ourselves of the potentiality for reproduction possessed by all kinds of organisms. To take a specific example, consider the reproduction of a bacterial species, the members of which divide once every hour. Beginning with one bacterium at one o'clock, there would be two bacterial cells at two o'clock; four at three o'clock; eight at four o'clock; then 16, 32, 64, etc. There is, inherent in the organism itself, no limit to reproduction; the organism is potentially capable of increasing indefinitely (Fig. 34-13). Though the *rate* of increase (doubling every hour, in this case) is constant, the *absolute amount* of increase increases steadily. This sort of a potential multiplication curve is characteristic of all organisms, be they bacteria or elephants. A bacterial population can easily double in size every hour; a population of elephants may take twenty years to double. The only essential difference between the two curves is in values written along the time axis.

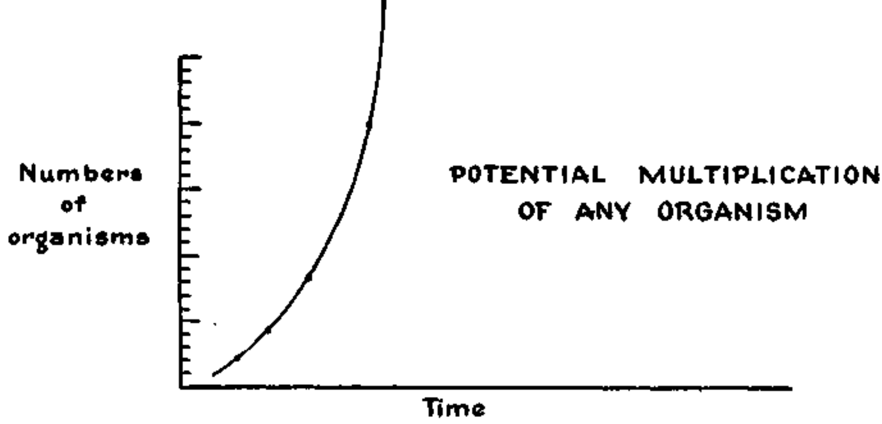

Fig. 34-13. Or, as the matter was put by the English clergyman, Thomas Malthus, in 1798: "Population, when unchecked, increases in a geometrical ratio."

But *no* population increases in this fashion for long. Why? The answers are different for different populations. One population may be held in check by a scarcity of food, another by the accumulation of poisonous waste products, others by cannibalism. Whatever the particular cause, the general cause is **the finiteness of the environment.** The potential rate of increase, leading to a population of infinite size, cannot be realized in an environment of finite extent. The environment may be a test tube, a flask, a lake, an ocean, or the entire world, but no organism that we know of has an infinite universe available to it.

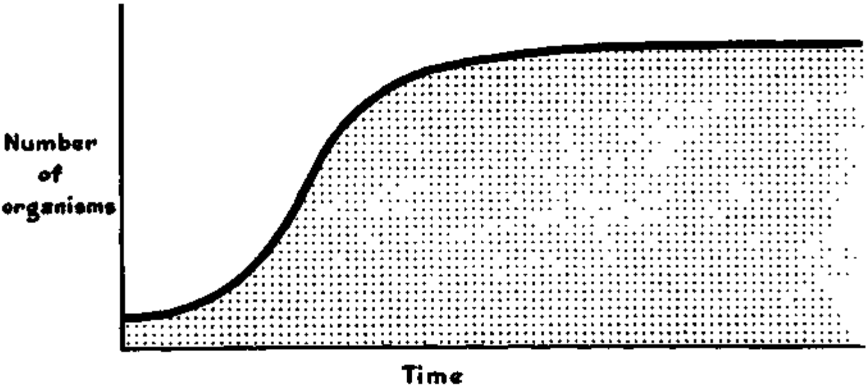

Fig. 34-14. The growth of any population of organisms in an essentially constant, finite environment.

The potential rate of increase cannot, in a finite universe, be maintained for long. The growing lack of food, the accumulation of waste products, or the increase in cannibalism (or other forms of self-destruction) gradually causes the *rate* of population-increase to *decrease.* Ultimately, the population ceases to increase at all. Result: the S-shaped curve (see now Fig. 34-15).

Mathematicians tell us that the rate of increase of a curve at any particular point is given by the slope of the tangent to the curve at that point (Fig. 34-15). This makes intuitive sense. When we examine the S-shaped population curve, we see that the rate of increase *increases* up to a certain point, which we call the Turning Point, after which it decreases until it is nearly, or quite, zero. The first part of the population curve, which we might call the **Region of Unhindered Multiplication,** corresponds to the time during which the potential rate of increase is nearly, or quite, realized. The second half of the curve, the **Region of Decreasing Multiplication,** corresponds to the time during which a complex of factors which we might collectively refer to as **environmental resistance** (increase of wastes; decrease of food; increase of self-destruction) gains the upper hand and ultimately puts an end to the increase in population.

With no important exceptions, all populations of organisms, in the laboratory or "in nature," increase as indicated by the population curve in Figure 34-14. Consider those organisms that man wishes to exploit: the fishes of the sea, lumber trees, and wild game (to some extent). How can man best exploit them? That is, how can he harvest the largest numbers of them year after year? Obviously, the harvesting rate must not exceed the maximum rate of increase of the population. The maximum rate of increase of the population exists in the neighborhood of the turning point of the population. If man tries to harvest at a greater rate, his activities will drive the population to lower and lower levels until (unless he mends his ways) the population will be extinguished. If he harvests at much less than this rate, he is needlessly sentimental about the importance of conservation.

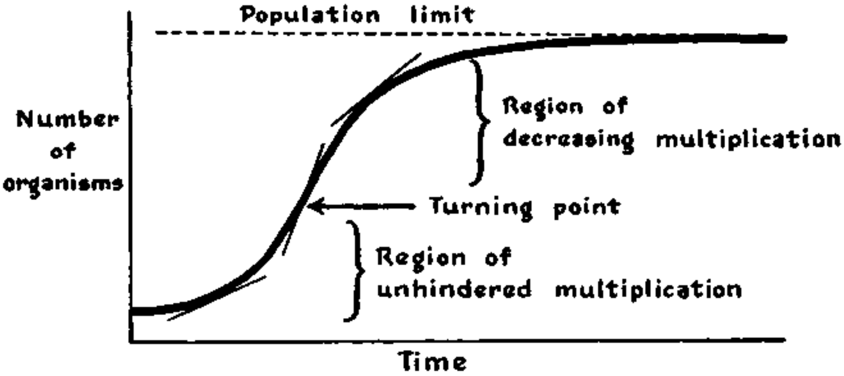

Fig. 34-15. Analysis of the population-growth curve.

In the early days of the so-called "conservation movement," there were many enthusiasts who spoke as if conservation were an end in itself, as if the maximum population (of fish, wild fowl, or whatever) were *ipso facto* the most desirable. There has now come about a change of attitude, a realization that man's own interests are paramount. The aim of conservation is to serve man. The preservation of large, but not maximum, populations of the exploited species is the best way to do this. *How* large a particular population should be, it is difficult to say. It is hard to determine the size of a population that exists outside the laboratory, particularly if it is a population of motile and elusive animals. It is even harder to determine its rate of increase and its population curve. Nevertheless, we now have a clear idea of where the problems lie. By way of generalization, we may say that the problems of conservation can be divided into two categories:

a. **The determination of the facts,** i.e., the population curve for each species, and the extent of the uncontrollable fluctuations for which our exploitation policy should allow.

b. **The control of human exploitation** of the natural populations, either by appeals to conscience, by the encouragement of self-regulation among the exploiters, or by the imposition of restrictive laws by society as a whole.

QUESTIONS AND PROBLEMS

34-1. Diagram the water cycle, including the following factors: evaporation from water surfaces, from soil, from plant leaves; precipitation; streams, ground water, springs, wells.

34-2. How does the mineral cycle differ from the water cycle?

34-3. What evil effects follow too great erosion?

34-4. What factors may cause great erosion?

34-5. What measures may be used to control erosion? List as many as you can.

34-6. What is the eventual fate of all dam ponds?

34-7. What is the average thickness of the soil in the United States?

34-8. Which can be more easily determined: the rate of soil erosion, or the rate of soil formation? Explain.

34-9. About how fast is soil formed, according to the estimate given in the text?

34-10. Why should a sport fisherman concern himself with the occurrence of forest fires?

34-11. "Flood control" is frequently concerned with making the levees of rivers higher. What more fundamental measures should be taken?

34-12. What percentage of the farm and grazing land in the United States is considered essentially ruined?

34-13. What is the shape of the population curve for a population growing in an unlimited environment?

34-14. What is the shape of the population curve for a population growing in a finite environment?

34-15. Do you think that the population curve for humans will conform, in shape, to the general curve? Justify your answer.

34-16. What factors constitute *environmental resistance* for the human population?

34-17. Characterize the modern theory of conservation.

34-18. What are the principal difficulties in the way of instituting a sound program of conservation of a population of plants or animals in the wild?

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Chapter XXXV

Evolution: The Stability Factor

210. The Utility of Abstractions in Science

We have seen something of the dependence of organisms on environmental conditions and of the dependence of all organisms upon the finite supply of energy furnished the world by the sun. The world is not infinite or inexhaustible. The struggle for existence, as the physicist, Boltzmann, put it, is the struggle for free energy. This struggle has taken place not only between individuals, but between species. In the course of geologic time, in response to the challenge of that struggle, species have changed. The appearance of new forms, descended from ancestors that were different, is called **evolution** (Latin *evolvo*, to unroll; *evolutionis*, an unrolling of a scroll).

In taking up the subject of evolution, we shall make certain *abstractions.* Abstractions are always, by definition, false to nature, but their use makes for clarity of thought and the ultimate solution of natural problems. In mechanics, we make the abstraction of a body subject to no forces and, then, ask what will happen if a single force of a certain directed magnitude acts upon this body for a specified time. There is, in nature, no body that is acted upon by no force, not even any that is acted upon by a single force. By the basic law of gravity, which one must assume in physics, every body affects every other body at all times. But the human mind is incapable of dealing with the world in its full complexity. We abstract certain forces or *variables* from the world and consider them alone, that is, we ignore for the moment all the others. By introducing objects or variables one-by-one into our abstract system, we end up with a system that is sufficiently like the real world so that we can, from it, predict what will happen in a natural problem. In the end, abstraction, properly conceived, "pays off." This is our excuse for making abstractions.

In considering the mechanism of evolution, we shall make analogous abstractions. The unit of discourse will no longer be the individual organism. Instead, when discussing problems of evolution, the **unit is a population of organisms of the same species,** organisms that are capable of breeding with each other. We shall first assume a population subject to no forces and see how it behaves. Then, we shall ask ourselves what will happen if certain forces, taken singly, act upon the population?

211. The Stability of the Gene Frequency

Let us take a hypothetical, but highly possible, case. Some fruit flies have shorter than normal wings due to a gene called "miniature," the symbol for which is *m*. The wild-type fly, with long wings, is of the genotype *MM*. *M* is dominant to *m*.

Suppose we cross one wild-type fly to a miniature fly and keep all the offspring, while keeping the generations separate. We would expect results like these:

Parents 1 *MM* 1 *mm*
F_1 100 *Mm* (mated among themselves)
F_2 1,250 *MM* 2,500 *Mm* 1,250 *mm*
F_3 ?

What will the F_3 be like? Plainly, we are up against a more difficult problem, because there are three different genotypes in the F_2, and we don't know which will mate with which. However, we do not need to know. By the condition of our preliminary assumption of no forces operating on the population, we must assume that there is no preference of one kind of fly for another. Preference would amount to a force. (We defer consideration of forces to the next chapter.) If there is no preference, **mating is at random.**

Our initial abstraction of no forces operating on the population implies a further assumption: all flies produce the same number of gametes, that is, all genotypes are equally fertile. If all flies produce the same number of gametes, and all matings are at random, then, we may say that the coming together of gametes is also at random, with the restriction that a sperm can unite only with an egg and vice versa. Therefore, to know the probability of two specified types of gametes coming together, we need only know their relative frequency. That is now to be determined.

Since, by hypothesis, all flies produce the same number of gametes, we shall assume, for simplicity, that each fly produces exactly two gametes. Every gamete is either *M* or *m*. What is the relative frequency of the two types? We count them up:

1,250 *MM* flies produce 2,500 *M* gametes and 0 *m* gametes
2,500 *Mm* flies produce 2,500 *M* gametes and 2,500 *m* gametes
1,250 *mm* flies produce 0 *M* gametes and 2,500 *m* gametes
TOTALS 5,000 *M* gametes and 5,000 *m* gametes

In other words, one-half of the gametes are *M* and one-half are *m*.

What will happen if these gametes, in these relative frequencies, mate at random? We may, for convenience in visualizing the situation, imagine that we have two gene pools, one of male gametes, half of which are *M*, the other half being *m;* and the other are female gametes, half *M*, half *m*. A zygote is formed when we draw one gamete from each pool.

What is the probability of drawing gametes that will produce an *MM* zygote? This is the probability of drawing an *M* gamete from one pool ($=\frac{1}{2}$); *multiplied by* (recall the Product Rule, § 178) the probability of drawing an *M* from the other pool ($=\frac{1}{2}$); that is, $\frac{1}{2} \times \frac{1}{2} = \frac{1}{4}$. Therefore, $\frac{1}{4}$ of the offspring in the next generation will be *MM*.

By similar reasoning, $\frac{1}{4}$ will be *mm*.

What of the heterozygotes, *Mm*? Here we must consider two different cases:

> probability of *M* sperm ($\frac{1}{2}$) multiplied by probability of *m* egg ($\frac{1}{2}$); or $\frac{1}{2} \times \frac{1}{2} = \frac{1}{4}$
>
> probability of *m* sperm ($\frac{1}{2}$) multiplied by probability of *M* egg ($\frac{1}{2}$); or $\frac{1}{2} \times \frac{1}{2} = \frac{1}{4}$
>
> Since either event will result in *Mm* zygote, we *add* their probabilities, getting $\frac{1}{4} + \frac{1}{4} = \frac{1}{2}$

The constitution of the F_3 generation will, therefore, be:

$$\tfrac{1}{4}\,MM + \tfrac{1}{2}\,Mm + \tfrac{1}{4}\,mm$$

Notice that *the constitution of the F_3 generation is the same as that of the F_2*. Obviously, the F_4 will again be the same, and so on indefinitely. In each generation, one-half of the genes will be M and one-half will be m. In other words, **in the absence of selective forces, the gene frequency will remain the same indefinitely**. This principle, which one might call *the principle of inertia in evolution*, is generally referred to as the **Hardy-Weinberg Law.***

212. The Calculation of Gene Frequencies*

The method used above for calculating the frequency of genotypes was rather extended. The calculations can be put in more compact form.

$$\overbrace{(\tfrac{1}{2}\,M + \tfrac{1}{2}\,m)}^{\text{♂ gametes}} \times \overbrace{(\tfrac{1}{2}\,M + \tfrac{1}{2}\,m)}^{\text{♀ gametes}} = \overbrace{\tfrac{1}{4}\,MM + \tfrac{1}{2}\,Mm + \tfrac{1}{4}\,mm}^{\text{zygotes}} \qquad (1)$$

Or, since both "gene pools" are the same:

$$\begin{aligned}(\tfrac{1}{2}\,M + \tfrac{1}{2}\,m)^2 &= (\tfrac{1}{2})(\tfrac{1}{2})\,MM + (2)(\tfrac{1}{2})(\tfrac{1}{2})\,Mm + (\tfrac{1}{2})(\tfrac{1}{2})\,mm \qquad (2)\\ &= \tfrac{1}{4}\,MM + \tfrac{1}{2}\,Mm + \tfrac{1}{4}\,mm\end{aligned}$$

With this simpler way of setting up the problem, we are on the road to finding an attack that will solve more general problems. Suppose we have a large population of equally fertile flies that show no mating preferences, etc., etc., a population in which the relative frequency of A genes is .1 and of a genes is .9. What will be the relative frequencies of the various genotypes in the next generation? Reasoning as before, we write:

$$\begin{aligned}(.1\,A + .9\,a)^2 &= (.1)\,(.1)\,AA + (2)\,(.1)\,(.9)\,Aa + (.9)\,(.9)\,aa \qquad (3)\\ &= .01\,AA + .18\,Aa + .81\,aa\end{aligned}$$

This is straightforward enough. Now let us *generalize*† the method of

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* For the student whose algebra is rusty—as is true of many elementary students—the material that follows may prove rather "stiff." If the student has neither the time nor the motivation to master the mathematical details, no great harm will be done if he ignores the mathematics, providing he is willing to accept as true the Hardy-Weinberg Law. The *sense* of this law must be appreciated in order to understand the succeeding chapters.

† Recall the previous discussion of the process of generalization (§ 160).

attack by asking: What will be the frequency of the various genotypes if the relative frequency of *A* is p and of *a* is q, where $p + q = 1$? (The digit 1 represents totality.) By the same method, we get:

$$(pA + qa)^2 = p^2AA + 2pqAa + q^2aa \tag{4}$$

This is the Hardy-Weinberg Law stated in general mathematical terms. It may seem a colorless and uninteresting generalization, but with it we can do some useful things. Recall that genes, whatever they are, are invisible. We cannot see them. We cannot directly count them or learn the relative frequency of two different alleles. Suppose *A* is dominant to *a*. We cannot tell *AA* individuals from *Aa* individuals phenotypically. Phenotypically, the population is divided into two different groups: the group of *aa* organisms and another group that we may symbolize by writing *A*—, where the dash stands for an unknown gene.

Suppose, in a particular case, that the frequency of *A*— is .19 and of *aa* is .81. What are the frequencies of the two genes? We cannot readily calculate them from the frequency (.19) of A—, because this is a mixed group, being composed of both *AA* and *Aa* individuals. But we can easily calculate the frequency of *a* from the frequency (.81) of *aa*. By equation (4), the frequency of *aa* is q^2. The frequency of *a* is q $(= \sqrt{q^2})$. In our particular case, $q = \sqrt{q^2} = \sqrt{.81} = .9$. By way of a check, we know this is right because this is what we started with in equation (3).

Let us take a concrete example. There is a dominant gene present among humans which permits its owner to taste a particular chemical substance named phenyl-thio-carbamide, or PTC for short. This gene we may symbolize by *T* and its allele by *t*. A *tt* individual cannot taste PTC and is called a "nontaster." In a particular sample of some 3600 American whites, seventy per cent could taste PTC and thirty per cent could not. That is, the observed frequency of *T*— was .70, of *tt* was .30. What is the frequency of the two genes in that population? It should be clear that we must make our calculation from the second of the two figures, thus:

$$\text{Frequency of } t = \sqrt{\text{Freq. of } tt} = \sqrt{.30} \cong .55 \tag{5}$$

$$p + q = 1 \text{ (definition)} \tag{6}$$

$$\text{Hence, by difference, frequency of } T = 1 - .55 = .45 \tag{7}$$

With this result, we are now in a position to calculate the relative frequencies of the three genotypes in our population, using the Hardy-Weinberg Law, equation (4).

$$(.45T + .55t)^2 \cong .2TT + .5Tt + .3tt \tag{8}$$

With this result, we could answer a question such as the following: A woman is a nontaster. Assuming that the ability to taste does not influence her choice of a mate, what is the probability that at least some of her children will be like their mother?

The children will be like their mother only if her husband is either: Tt or tt. The probability of her mate being the former is .5; of being the latter is .3. Since *either* will result in some children like their mother, the probability that some of the children will be like their mother is $.5 + .3 = .8$.

Notice that, in solving this problem, we have assumed a large number of children. If the woman has only a small number of children, in a mating with a Tt man, *by chance* it might happen that none of the children would be like their mother. This chance can be calculated, but doing so would take us too far into the realm of mathematics for our present purposes. The important thing, at this point, is to understand the sort of problem that the Hardy-Weinberg Law permits us to attack.

QUESTIONS AND PROBLEMS

35-1. Brachydactyly (abnormally short fingers) is a dominant trait. In the early days of genetics, a distinguished statistician remarked that, because brachydactyly was dominant, "in the course of time one would expect, in the absence of counteracting factors, to get three brachydactylous persons to one normal." Criticize this statement.

35-2. Suppose that, in a given population, 64 per cent of the people are "tasters" and 36 per cent are nontasters. Which gene is the more common, the gene for tasting or its allele?

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Chapter XXXVI

Evolution: The Effective Forces

213. Mutation

In the absence of forces, the relative frequency of each gene allele in a population will remain constant. What are the forces that may change a gene frequency? One thinks first of mutation. If one *A* gene mutates to the *a* allele, the supply of *A* diminishes and that of *a* increases. If this mutation occurs continually, this process might, by itself, be a deciding factor in determining the direction of evolution. That it is not will appear from the following considerations.

1. Mutation is always opposed by reverse mutation. If $A \longrightarrow a$, then $A \longleftarrow a$, also occurs. The rates of the two are seldom, if ever, equal, however.
2. There are many alleles of each gene. In introducing the subject of genetics, usually only two-allele cases are studied at first. However, every gene that has been closely studied has been shown to have many different alleles. In *Drosophila*, one particular locus on the *X*-chromosome can have any of various alleles that will make for the following eye colors: blood, coral, eosin, cherry, tinged, buff, ecru, ivory, or wild type. In man, the blood types A, B, AB, and O are also due to such **multiple alleles.**
3. The mutation rates operating among the various multiple alleles bear no relation to the adaptive value of the alleles. The relative

magnitudes of the different rates, which seem to be constant, probably bear some relationship to the internal chemistry of the gene and the chromosome, of which we know next to nothing. **Mutation is a random process.** It does not tend to push the characteristics in one direction. Since, by the definition of *best*, only one of a set of alleles can be the best form of the gene, it is almost certain that mutation, by itself, will drive the gene type in the direction of poor adaptation. In summary, **mutation is a nondirectional force** that merely furnishes a large amount of raw material for other forces to act upon.

214. Migration

Migration of members of one population into a region populated by another group (of the same species) that has a slightly different genetic constitution will cause changes in the genetic make-up of both the immigrant and the native populations. Considered as a force, migration between populations of the same species acts in a conservative way, that is, it tends to eliminate differences that have already developed in partially separated but interfertile populations, or to prevent the appearance of differences that might develop were the populations isolated from each other. The significance of migration as an evolutionary force can be better understood in conjunction with a consideration of the *isolation factor*, to be discussed in § 218.

215. Selection

Starting with a population in which several different alleles are present, it is possible to produce a population which is almost completely homozygous for any desired gene by **selecting** individuals possessing the desired gene as breeding stock and discarding the others. Man has produced new kinds of plants and animals time after time by such a process of selection. From a wild cabbagelike thing, he produced the domestic cabbage, rutabaga, cauliflower and Brussels sprouts. From wild dogs, he produced strains as diverse as the Mexican chihuahua and the St. Bernard. These instances are truly instances of evolution in which selection by man has been the driving force. They show that evolution is possible. Does evolution also occur without man's intervention?

We may consider once again the case of the flies with the miniature wings (§ 211). At the time, we said that, in the absence of forces, the gene frequency will remain the same. This is true, but it is not easy to prevent selective forces from operating on a population of flies. If there is a surplus of food, the two phenotypes may multiply almost equally well. But if there is an oversupply of flies and, hence, an undersupply of food, the wild type will flourish more than the miniature mutant. Actual experiments have shown that, after one generation of competition between the two, the frequency of the miniature gene will be only about 69 per cent of its expected frequency (i.e., the frequency predicted from the Hardy-Weinberg Law). After two generations, it will be about $(69\%)^2$ or 48 per cent. After three generations, it will be $(69\%)^3$ or 33 per cent, and so on. As long as the food supply is limited, the survival rate of the flies will be low, and the severe competition that results will insure that the miniature gene will soon be nearly, or quite, eliminated. In other words, under the conditions of our experiment, even though the experimenter does not himself select the long-winged flies for breeding purposes, these wild-type flies have some sort of advantage over the short-winged flies. We may say that they are "selected by Nature," or that **natural selection** favors them in the struggle for existence.

It should be noted, in passing, that natural selection is not an All-or-None proposition. If man were selecting, he would probably select all of one type and discard all of the others. In natural selection, however, there is merely a *difference in the probability of survival* of the competing phenotypes. In any one generation, the miniature flies breed 69 per cent as well as the wild type, which means that a great many of the relatively "unfit" type are reproducing. As a matter of fact, the difference in survival value between miniature and long-winged flies is a rather extreme one. Most mutant alleles are almost as good as the wild type. Most mutant alleles produce only very slight effects and are only slightly selected against. Nevertheless, modern evolutionary theory, which is too mathematical to present here, shows that even very slight differences in the selective value of different alleles is enough to permit evolutionary processes to go on.

216. The Theory of Evolution Briefly Stated

The first scientifically acceptable theory of evolution was published in 1859 by Charles Darwin (1809-1882) in his book, *The Origin of Species by Means of Natural Selection, or The Preservation of Favored Races in the Struggle for Life.* Darwin's work is, quite properly, weighted down with a mass of evidence favoring the theory of evolution. However, this theory, as Julian Huxley has pointed out*, has a strong deductive element in it and can be reduced to a logical system of three facts and two deductions, as follows:

First Fact. **Every species tends to increase indefinitely in numbers** in a geometric manner. If, in the absence of outside pressures, it doubles in fifteen years, it will quadruple in thirty years, and so on. (See § 209.)

Second Fact. The actual size of the population in any species remains approximately the same over long periods of time. There may be considerable fluctuations about a mean value, but **there is no net increase in numbers** of individuals.

Deduction I: Therefore, **there must be a struggle for existence,** since not all the individuals that are produced can survive.

Third Fact. **There is variation within every species.**

Deduction II: In the struggle for existence, **those variants that are the better adapted to their environment will reproduce in greater numbers** than their less-favored contemporaries.

217. Random Fluctuations in Gene Frequency

In the absence of effective forces, gene frequencies remain the same, *but only in a large population.* This amounts to a partial contradiction of the previously stated doctrine (§ 211). Following the lead of the eminent American geneticist, Sewall Wright, we shall show why this modification is necessary and what its consequences are.

Suppose we had a population of *Drosophila* permanently held at the level of *only 4 flies.* Suppose that initially the population consisted of 1 *MM*, 2 *Mm*, and 1 *mm* flies. What would the next generation of four flies be?

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* Huxley, Julian, *Evolution, The Modern Synthesis.* New York: Harper & Brothers, 1943.

According to the Hardy-Weinberg Law, it should be the same as the parental generation. But, since so few offspring are produced and the coming-together of gametes is a chance affair, there is a good probability that the next generation would not be what we have predicted. It might be 3 *MM* and 1 *mm;* or even 4 *MM;* or 4 *mm.* (Just as, when flipping coins, there is a good probability of getting 4 heads in a row, even though one expects, in a group of 4, to get 2 heads and 2 tails.)

Notice two facts:

(1) In a small population, there is a very good probability that an initially heterozygous population will become homozygous. The Hardy-Weinberg Law implies permanent heterozygosity and applies only to large populations. Small populations are very likely to become homozygous. Once a small population becomes homozygous for a given allele, it is very likely to remain so for a long time to come, because random fluctuations are no longer possible, unless mutation produces another allele.

(2) In a small population, the fluctuations may even cause the gene frequency to move counter to the selection pressure. In § 215, it was pointed out that, under competitive conditions, the reproductive rate of the flies carrying the miniature gene is only 69 per cent that of the wild-type flies. Nevertheless, an elementary knowledge of probability tells us that if we had a population that at all times consisted of only four flies, there would be a reasonably large chance that the less fit, the *mm* type, might actually become the predominant type.

We have been vague about one word: "small." How *small* must a population be to be seriously subject to the dangers of random fluctuations of gene frequency? No cut-and-dried answer can be given to the question, but, roughly, one may say that a population that consists of as many as one hundred breeding pairs is not *small* in the present sense. If the number falls much below one hundred pairs, the population becomes significantly subject to changes in gene frequency due to random fluctuations.

In Nature, most species, most of the time, consist of breeding populations that are far from small. The conclusion of the preceding paragraphs might be of only academic interest. However, there are a number of instances in which there is evidence that the effect of a small breeding population is felt. We shall mention only two, one here and one in the following section.

At one time there was a species of fowl, known as the "heath hen," that roamed over New England. With the increase in the human population, the population of heath hens became steadily smaller until, in the early 1900's, only a few dozen were left. Then, efforts were made to preserve the species, the remaining individuals being given the best of protection. In spite of this, the last of the heath hens—a rooster—died in Martha's Vineyard about 1930. We do not know why a few dozen animals were unable to maintain the species. But it is possible, in such a small group, that deleterious alleles, through fluctuations, reached a high frequency, thus making the race incapable of coping adequately with its environment. Since heath hens are no longer with us, this hypothesis is not capable of proof, but it serves to make sense of this and similar instances in which a once-numerous species, when reduced to a few score individuals, becomes extinct even though given adequate protection at the last. Whatever the explanation, the moral is obvious: don't wait until the eleventh hour to start conservation measures.

218. The Role of Isolation

Among the experiences which led Darwin to conceive his theory of evolution, some of the most influential were his repeated encounters with island species of plants and animals that differed slightly, but definitely, from similar species on nearby continents. The resemblances between island and mainland species indicated that they were genetically related. The differences between the two suggested that evolution had taken place after the two populations became separated.

Why is an island population frequently different from its probable mainland progenitor? The two environments frequently seem virtually identical, and the differences are so frequently trivial—slight variations in the feathers in birds, for instance—that it seems unlikely that natural selection is the guiding force. In the light of present-day genetics, however, the situation is understandable. In every case where the problem arises, the island is at such a distance from the mainland that migration of the species from the mainland to the island must have been a comparatively improbable event. Being improbable, when it did occur, the migration was probably one of a few individuals only. Since only a few individuals were involved, the relative frequencies of the alleles of some of their sets of genes were almost certain to have differed significantly from the stabilized frequencies of the mainland population. Consequently, the island population began with different gene frequencies which became stabilized as the island population grew larger. We would expect such a process to affect, for the most part, only relatively unimportant characters, ones of little selective importance, which seems to be exactly the case with these island populations.

Isolation is important in another respect in that it permits a new type to breed true, whatever the cause of its origin. Initially, a new type of organism may be so like its parental strain that it can freely interbreed with it. If it interbreeds with it, the two types will become one variable species. If it is isolated from it, however, it remains a distinguishable type and may, from various causes, evolve further until an obviously new species is produced.

219. The Role of the Environment

Before Darwin proposed his theory of evolution, there was in existence a different theory called the Lamarckian theory of evolution, named after its originator, Jean Baptiste Lamarck (1744-1829). According to this theory, the environment has a more or less direct effect on the evolution of a species through the inheritance of acquired characteristics. The essentials of the theory can be summarized not unfairly by the following well-known example. Over the course of thousands of years, the present-day long-necked giraffes have evolved from shorter-necked ancestors. Giraffes are browsers; their long necks enable them to eat leaves from high branches. According to the Lamarckian concept, the great length of the neck is the accumulative effect of many generations' neck-stretching by giraffes. This implies that what the neck does is somehow communicated to the sperm and egg cells that give rise to the next generation.

The Lamarckian theory is in complete disrepute today, for two reasons:

(1) Extremely numerous experiments, designed to test it, have not led to any repeatable results that support the Lamarckian concept.

(2) The Darwinian scheme (§ 216), which is based on a multitude of observable facts, makes any Lamarckian proposal superfluous. Heritable variations are due to random changes in the genes. These variations are exposed to the selective action of the environment, and the more "fit" genes survive in greater numbers than the less fit. It is important to realize that **fitness is defined in terms of the environment.** There is no such thing as *fitness, per se*. In the regions of Africa where it lives, a giraffe with long legs and a long neck is more fit than a stubbier giraffe. If the giraffe were transported to the arctic tundra where all the food grows within a few inches of the ground, its great height would no longer make it more fit, but rather less. The fact that "fitness" cannot be defined, save in terms of the environment, is all too often lost sight of in discussions of the social problems connected with the inheritance of human abilities, problems which will be discussed in the last chapter.

220. Evolution as Mutual Adjustment

Before leaving the subject of evolution, it would be wise to point out some dangers in the way in which we customarily speak of it. It is common to use such phrases as "the evolution of man," "the evolution of the horse," etc., the implication being that each organism evolves in a vacuum, or possibly in a world in which it is the only living thing. That this is distinctly not true will appear from the following examples.

There is, in the southwestern part of the United States, a flowering plant named *Yucca filamentosa* which can be fertilized only by a single species of moth, *Pronuba yuccasella*. The moth gathers pollen from the flower by means of its highly specialized mouth parts, shapes the pollen into a ball, and then flies to another flower. She thrusts her sawlike ovipositor into the ovary of the new flower, lays an egg or two therein, and then "deliberately" pushes the pollen pellet down the style of the flower. The larvae which develop eat some, but not all, of the seeds that develop. The adult moth, by fertilizing the flower with pollen, makes seeds possible. The larval moth, by not eating all of the seeds, makes the continuation of the *Yucca* species possible. The *Yucca* is completely dependent on the *Pronuba* for its continued existence. And the moth is completely dependent on the *Yucca* for its continued existence.

Were one to die, the other, perforce, would perish. This extreme instance of the interdependence of two species emphasizes the truth of a saying of Pope Sixtus V: "He that has partners has masters."

How did such a **symbiosis** (Greek *sym*, together; *bios*, life) evolve? There must have been a time when the ancestral plant either did not require the services of any insect or could be fertilized by several; and when the ancestral insect was not absolutely dependent on this one species of plant. However the **obligate symbiosis** may have evolved, once it did develop, each species of the pair was no longer free to evolve independently of the other. Whatever evolution the moth and the plant have undergone since that time has necessarily been a mutual evolution.

This is an extreme instance and a rare one. Less extreme instances are common. Although some pollination is brought about by wind and other agents, the flowering plants, as a group, are dependent on the insects, as a group, for pollination. In turn, many of the insects (e.g., the bees) are dependent on nectar-producing flowers for their existence.* Evolution of the two groups has undoubtedly occurred together. To look at it another way, such examples emphasize the fact that living organisms themselves are an important part of the environment to which each species, in its evolution, is sensitive. The evolution of one species, altering the biological environment of other species, may cause them to evolve, too. If an apposite example is wanted, think how the evolution of man has affected the survival and evolution of other organisms.

QUESTIONS AND PROBLEMS

36-1. Consider a trait like the ability to taste PTC, which, so far as we know, is of no selective value. (That is, natural selection does not "prefer" one gene to its allele.) If the mutation rate of T ⟶ t were seven per million gametes and of t ⟶ T were one per million gametes, which gene would you expect eventually to be the predominant one?

36-2. In the example considered above, would one gene ever completely replace the other?

36-3. Consider all the various types of chickens: White Leghorns, Plymouth Rocks, bantams, fighting fowl, etc. How did such animals evolve, do you suppose? What was the principal selective agent?

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* Because of this flower-insect tie-up, biologists look askance at the indiscriminate spraying of an area with DDT in an effort to get rid of malarial mosquitoes or other noxious insects. If the spraying is so thorough that it kills nearly all insects, many flowering plants fail to set seed that year. As a consequence, the landscape in succeeding years may be appreciably modified. This is a potential danger.

36-4. What is meant by the term *natural selection?*

36-5. State the theory of evolution as a series of propositions. Give evidence for the propositions, where evidence is needed.

36-6. The squirrels on the south side of the Colorado River differ slightly in markings from those on the north side. The Colorado River is a torrential stream that flows all year long and has been in existence for thousands of years. The environments on the two sides of the river seem to be the same. The differences between the two kinds of squirrels seem to be in no way related to the environment. How do you explain the differences in these populations?

36-7. Why should conservation measures be instituted before a species is down to less than a hundred breeding pairs?

36-8. What is the Lamarckian theory of evolution?

36-9. Why is the Lamarckian theory now in disfavor?

36-10. Define "fitness," as the term is used by biologists.

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Chapter XXXVII

Evolution: Historical and Circumstantial Evidence

221. The Nature of the Historical Record

It is a matter of common knowledge that there existed, in the past, plants and animals that were different from those now alive. In the case of vertebrates, numerous collections of bones have been found which, when assembled into the arrangement they once must have had, present us with skeletons of animals the like of which no living man has ever seen (Fig. 37-1). Such creatures are not now living; when did they live? This is the historical problem of evolution.

The remains or evidences of dead plants and animals are called **fossils** (Latin *fossilis*, dug up). The problem of dating these fossils is, in principle, simple. Fossils are always found in **sedimentary rock,** i.e., rock that has been formed by the laying down of sediments, as by a stream that is depositing its silt in a flood plain, or at its mouth in the ocean. Under the proper conditions, a few plants or animals may be buried in such sediments and may decompose in such a way as to leave traces of their existence, for instance, bones or casts of the external form. From these traces, or fossils, we can reconstruct a more or less complete picture of the appearance of the original organism. The sequence of the formation and the uncovering of fossils are shown in Figure 37-2.

Thus are fossils formed. How is the date of their formation estimated? This involves two separate problems that we must keep distinct, the problem of **relative dating,** and that of **absolute dating.**

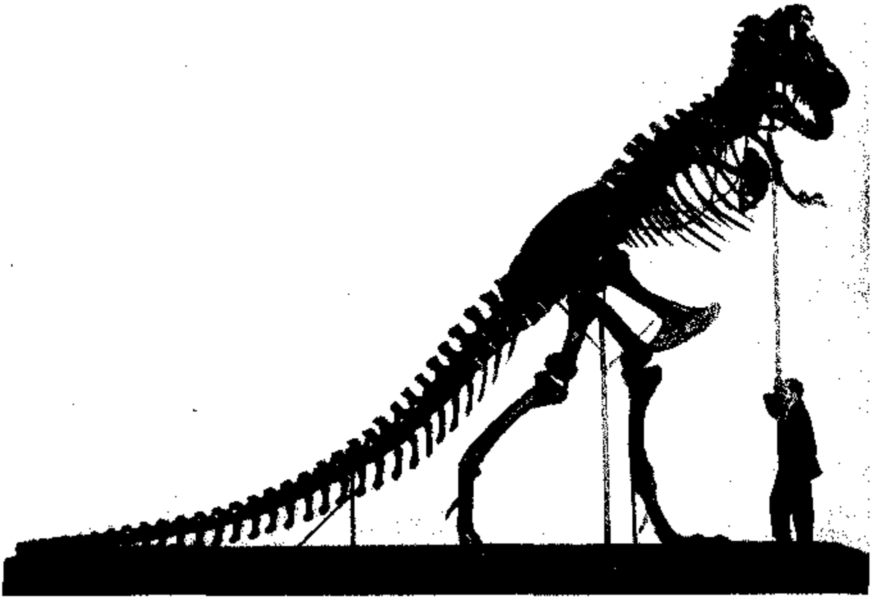


Fig. 37-1. Skeleton of *Tyranosaurus rex*, a flesh-eating dinosaur, with a man, for comparison. Comic strips to the contrary notwithstanding, dinosaurs died out about one hundred million years before man arrived on the earthly scene. (*Courtesy of American Museum of Natural History.*)

From inspection of Figure 37-2, it is apparent that each later layer of sediment is laid on top of the earlier layers. The deeper a layer of sedimentary rock lies, the older it is. This principle permits us to establish the relative dates of different layers of rocks and, hence, of the fossils found in them.

The problem of absolute dating is not so exactly soluble. From the known rates of deposition of silt today and from the thicknesses of beds of sedimentary rocks, the approximate time required to deposit these sedimentary layers can be estimated. The rates of formation of sedimentary layers are measured in fractions of an inch per year; therefore, one can appreciate the difficulty of achieving complete accuracy in the estimation of the ages of old rocks. When a geologist says that a given layer of rock was formed 50,000,000 years ago, it is to be understood that its true age might be as little as 25,000,000 years, or as great as 100,000,000 years. It is, however, unlikely that the error is greater than this.

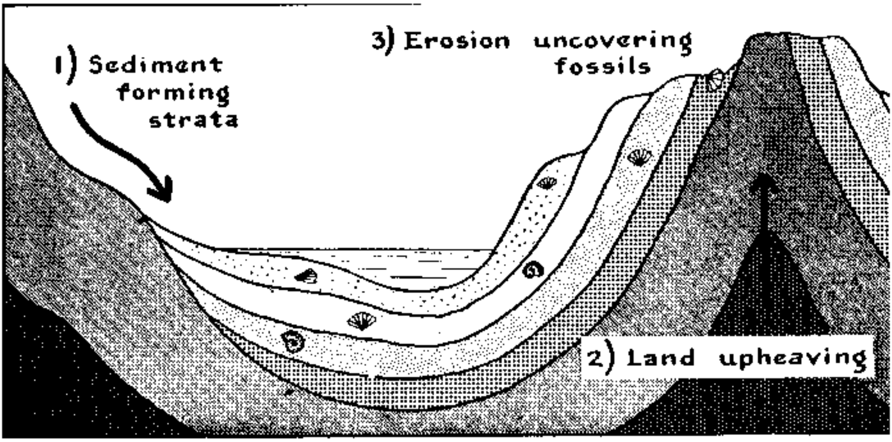


Fig. 37-2. How fossils are preserved. In general, a lower bed of sedimentary rock is older than one above it. There are exceptions, due to the upthrust and overthrow of thick sections incident upon natural mountain-building activities, but there are logically sound ways of deducing the relative dates of different layers even in these cases. This illustration shows the basic principles involved in dating fossils.

The problem of dating rocks has here been simplified, but not dangerously so. The technical details of such work constitute the subject matter of historical geology. As concerns the problems of evolution, the most important aspect is the *relative* dates of different layers, and this is known with almost absolute certainty. The absolute dating of the rocks, which is less accurate, is relatively less important.

222. The Temporal Sequence of Forms

As the various layers of rocks have been explored and their fossil contents noted, it has been observed that each group of organisms has had its period of maximum abundance, and that for each group there is a layer of rocks below which it has never been found. For many groups, such as the dinosaurs, there is a layer of rocks above which such fossils are never found. The apparent abundance of various groups of vertebrates in different geological eras is shown in Figure 37-3, in which the width of the band indicates the frequency with which fossils are encountered in each era. It will be noted that there is a general sequence of groups. Groups which are considered, on morphological grounds, to be the more primitive flourished early; note that the jawless vertebrates were very abundant about 400 million years ago, though

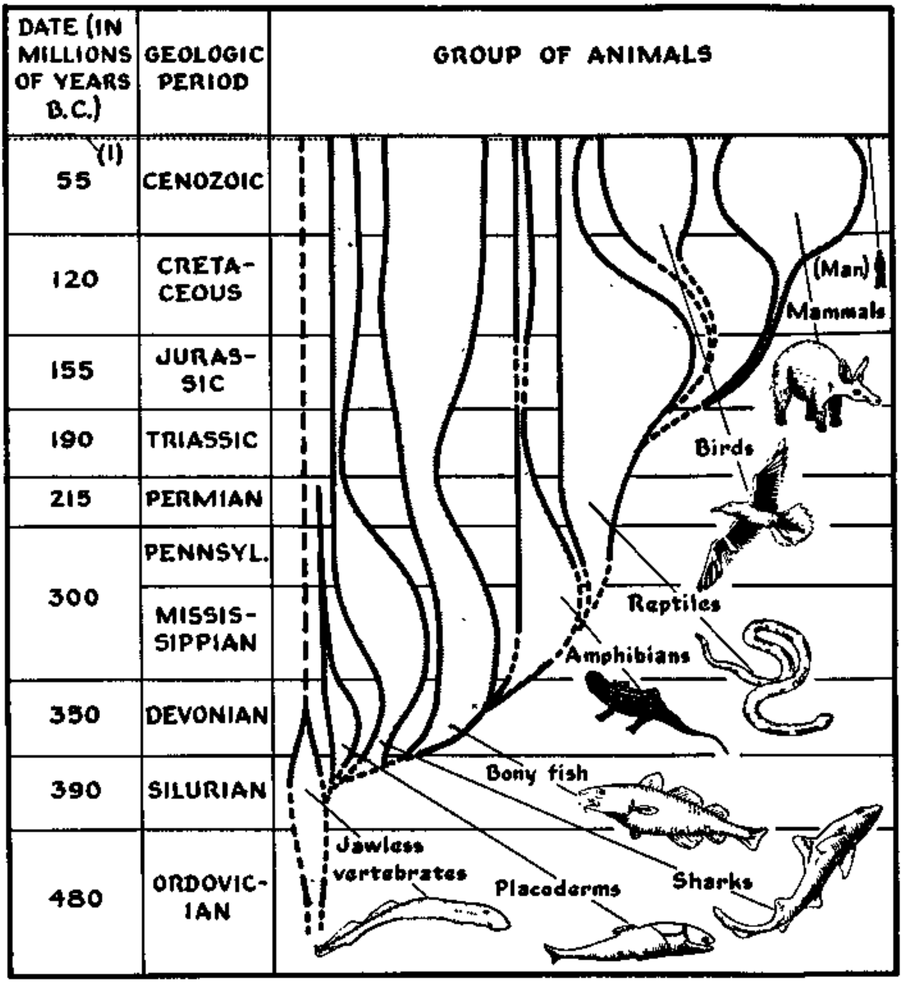


Fig. 37-3. The relative importance of various vertebrates in different geologic periods. Like all geological tables, this one reads from the bottom upward. The width of the stippled band indicates the relative importance of the group in the period. Dotted lines indicate discontinuity in the geological record, i.e., absence of known fossils in rocks of the period.

they have now become a very minor group, represented only by the hagfishes and lampreys. The placoderms flourished a bit later than the jawless vertebrates and became completely extinct by 190,000,000 B. C. At about the time of their extinction, the reptiles became the dominant forms, evolving an abundance of swimming, running, and even flying reptiles. The heyday of the Age of Reptiles saw the evolution of the dinosaurs. These later became extinct, leaving only the much less spectacular snakes and lizards of our own day. Before the reptiles were very well advanced, however, the mammals and the birds evolved from them, though they seem not to have been very abundant until comparatively recently, at the beginning of the "Cenozoic" era, about 55 million years ago. Organisms that could, by any charity of definition, be called "man" have been in existence a scant million years. Incidentally, movies and comic-strips to the contrary, dinosaurs and primitive men failed to make each others' acquaintance by about one hundred million years. Too bad to spoil a good story.

The chronicle illustrated in Figure 37-3 does not, however, carry us back as far as the geologic record permits. To extend this record, we have Table 37-1, which should, like all records of rock depositions, be read from the bottom upward. Of the beginnings of life, we know nothing for certain. It is most likely that the first forms of living things had no skeletons or hard parts and, hence, could hardly be expected to leave any records of their existence. It is only when we come to sponges and radiolaria, with their various spicules and inorganic spines, that fossilization is likely. We have no certain record of living things before 900 million years ago.

The table gives only the fewest highlights of the geological record. We know of thousands of species that evolved, flourished, and became extinct before man appeared.

223. Comparative Anatomical Evidence of Evolution

Modern evolutionary theory presents to our view a mechanism that makes evolution possible. The geologic evidence is compatible with the historical doctrine that present-day organisms are, in fact, evolved from older forms that were unlike them. As additional, circumstantial evidence of this evolution, there are a host of anatomical observations that

TABLE 37-1

THE GEOLOGIC TIMETABLE

Geologic tables of this sort are always organized to be read from bottom to top, which is the order in which the sedimentary rocks are laid down.

NAME OF ERA	NAME OF PERIOD	NOTEWORTHY FORMS OF LIFE	DATE OF BEGINNING (Millions of years B. C.)
Cenozoic	Quaternary	Man.	1
	Tertiary	Rise of birds, mammals, and flowering plants.	55
Mesozoic (Age of Reptiles)	Cretaceous	Rise of mammals and birds. Extinction of spectacular reptiles.	120
	Jurassic	Continued dominance of reptiles and conifers.	155
	Triassic	Rise of dinosaurs. First mammals. Rise of conifers.	190
Paleozoic	Permian	Appearance of primitive insects. Extinction of trilobites.	215
	Carboniferous	Reptiles appear. Extensive forests of ferns and club mosses, leading to coal formation.	300
	Devonian	Amphibians appear.	350
	Silurian	Dominant forms: primitive fishes and eurypterids (extinct). First land plants.	390
	Ordovician	First primitive fishes.	480
	Cambrian	Trilobites (extinct) dominant forms. Many mollusks.	550
Proterozoic		Evidences of sponges, radiolaria, algae.	900
Archeozoic		Presumptive origin of life. No fossils available in these earliest sedimentary rocks.	1,500-2,000

can be easily explained by the theory of evolution, but which scarcely make sense otherwise.

The external ear of man, for instance, is supplied with muscles which, in some individuals, are capable of moving the ear. In many animals, undoubtedly including the ancestors of present-day man, the ability to concentrate sounds by the movement of the external ear is important. The vestigial ear muscles in modern man unquestionably are to be explained by history rather than by function. Similarly, the appendix of

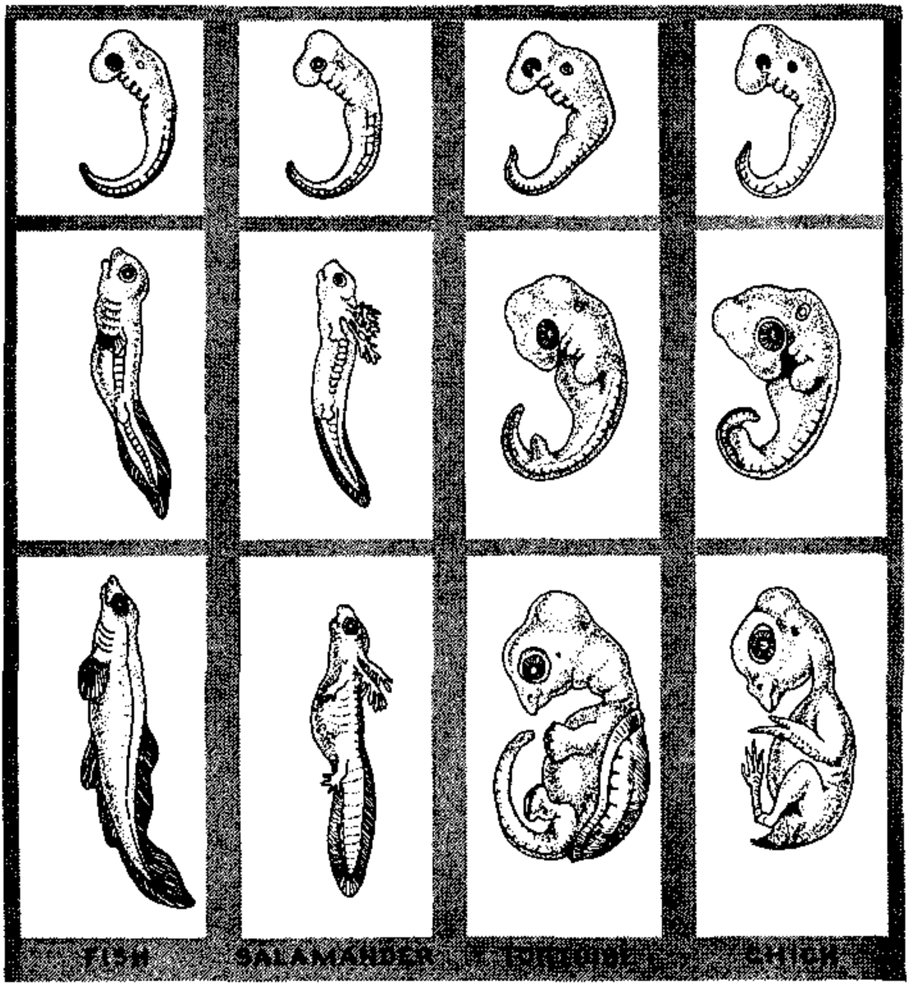
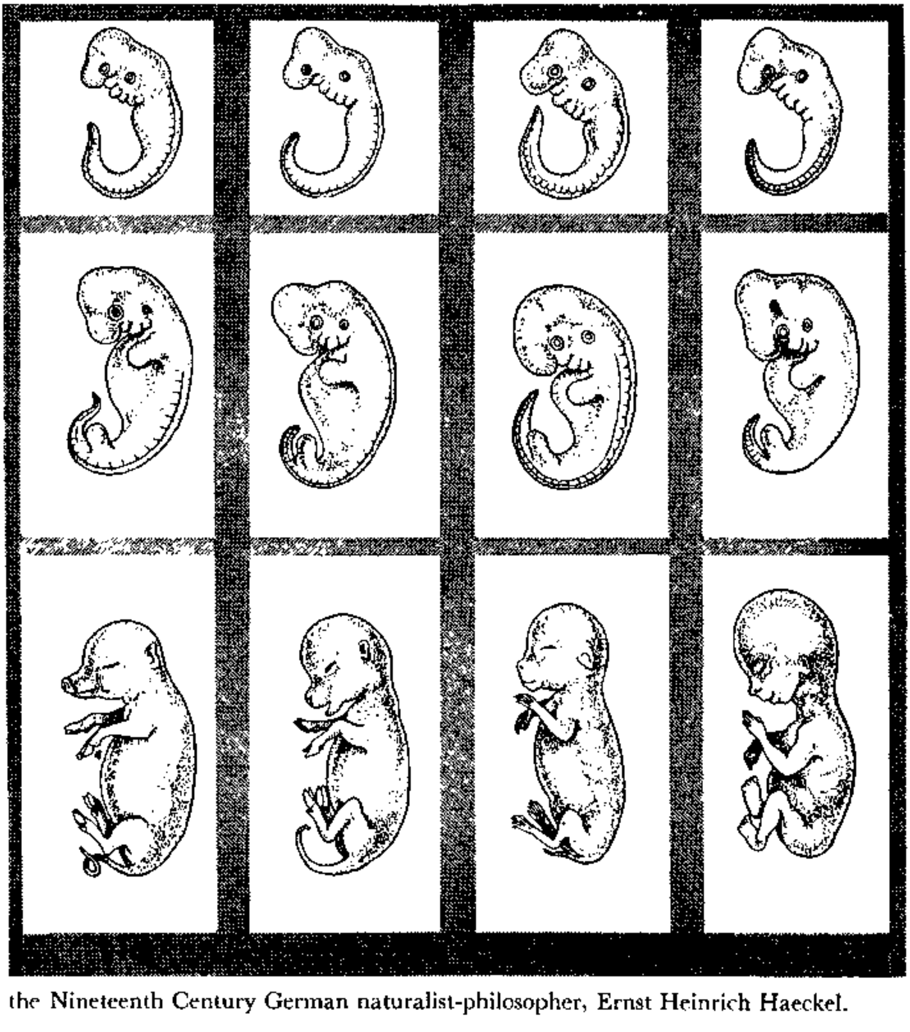


Fig. 37-4. Comparable embryonic stages of various vertebrates, as reported by

the large intestine (Fig. 8-8) is probably a remnant of the days when our ancestors were entirely herbivorous and had need of a fermenting chamber for their difficult-to-digest cellulosic food.



the Nineteenth Century German naturalist-philosopher, Ernst Heinrich Haeckel.

Again, there are present in some of the large blood vessels of the body simple valves that serve to prevent the backward flow of blood. Some of the veins that horizontally encircle our mid-region possess such valves, whereas the leg veins returning blood from the lower regions do not. This distribution can scarcely be explained by function because the former, horizontally running veins do not need them, whereas the lack of valves in the leg veins may lead to enlarged, or *varicose*, veins. However, from an evolutionary standpoint, the present anatomy is understandable. Our ancestors walked on all fours, and in such a position, valves in the circumthoracic veins would be functional, since these vessels would be in a vertical plane in such an animal. But the leg veins would have less need for valves than they have now that we walk erect.

These are but a very few of the multitudinous anatomical evidences of evolution. The proper appreciation of the extent to which **comparative anatomy** corroborates the theory of evolution can be gained only by the detailed study that constitutes the science of that name.

224. Embryological Evidence of Evolution

Developmental anatomy likewise lends support to the theory of evolution. The nature of the evidence is best appreciated by a close inspection of Figure 37-4, in which are assembled different embryonic stages of various vertebrates. Notice that in the earliest stages all these embryos are very much alike. As they mature, they diverge from each other in appearance. Those animals which are (on other grounds) held to be closely related retain their resemblances longest in the embryonic stages. For example, the evidence clearly indicates that birds evolved from reptiles; notice the close resemblance between their embryos. During the embryonic development of an organism, many structures appear to start out to be one thing and end up as something quite different. Notice, in the first row of figures, that all of the embryos show external signs of gills. Only in the fish are typical gills developed. In man, part of the presumptive gill structures become part of the middle ear.

Facts such as these have led to the promulgation of the so-called **Law of Recapitulation,** which, in its modern form, can be stated thus:

> **In its embryonic development, an organism passes through some of the developmental stages of an organism lower than it in the evolutionary scale, developing similar embryonic structures which, however, may have different fates.**

This law implies a corollary: *The more closely related two species are, the longer will the embryonic development of the two run parallel.*

225. Chemical Evidence of Evolution

In protoplasm, the most characteristic class of chemical compounds are the proteins. It is possible that many of the similarities of the protoplasm of different species are due to the possession of similar, perhaps identical, proteins. It is certain that different protoplasms have some proteins that are different. It is suspected that *the protoplasm of each species includes at least one unique protein.* There is no proof for this statement, but it is a useful working hypothesis.

The ordinary methods of chemical analysis are inadequate to distinguish proteins. For this purpose, one must use the antigen-induced antibodies described in Chapter XXX. Through the use of the antigen-antibody reaction, it has been shown that **the more closely related two species of organisms are, the more similar are their proteins.** The proteins of a great many plant and animal species have been subjected to comparative study and, from these chemical data, have been constructed evolutionary family trees that prove to be very similar to the family trees constructed on the basis of morphological considerations. For example, the specific proteins we call "A," "B," "M," "N," and "Rhesus" (see § 185-§ 187) have been found in various apes, but not in other mammals such as dogs and cows. On the basis of the evolutionary scheme, this makes sense.

Probably related to chemical similarity is the phenomenon of susceptibility to specific diseases. Contagious diseases, to be discussed in the next chapter, are caused by specific kinds of microbes. A given species of microbe can infect only a limited number of organisms. In general, the organisms that it can infect are fairly closely related species. For many bacterial species, the organisms need be only in the same class (Mammalia). This is fortunate, of course, for it makes possible the use of guinea pigs and rats in the study of human diseases. Few organisms can infect both cold-blooded and warm-blooded groups. Sewage laden with typhoid bacteria can be poured into a river without the slightest harm to the fish, though it can infect a whole city of humans downstream. The most specific forms of infective agents are the viruses, submicroscopic, possibly nonliving, but self-multiplying, proteins. Viruses are usually infective only for a single species, or closely related species, which fact has, until recently, made research into human virus diseases (such as poliomyelitis and "colds") difficult because, frequently, only expensive monkeys and apes could be used as experimental hosts. A new technique which makes virus research more promising is described below.

There is evidence that the gradual differentiation of species that occurs during embryology involves not only the visible morphology (see again Fig. 37-4) but also the invisible chemical architecture. Correlated with this is the fact that a disease organism that will multiply in only a few closely related adult species will multiply in the embryos of many species. If the ability of a disease organism to grow in a host is in some direct or indirect way related to the chemical constitution of the host—and this seems a reasonable assumption—then the loss, during embryological development, of an animal's ability to act as host to a disease organism is evidence of the gradual development of chemical specificities in the host.

Of all disease organisms, a virus (if it is an organism) is the most specific. However, making use of the fact that embryos are far less specific in their effect on viruses than are adults, it has been found possible to grow mammalian disease viruses in the embryos of birds, which are quite distantly related forms. Since fertile hens' eggs are readily available in quantity, the **embryonated egg** method of cultivation of viruses has proven a great boon to experimental work with viruses (see Fig. 37-5).

226. The Genetic Explanation of Circumstantial Evidence

Granted that each organism produces many structures and chemical substances that make sense only on an evolutionary hypothesis, there still remains a point that needs explaining. Why should an organism possess a structure or chemical that it does not need? Why should it pass through a stage which, logically, has no relationship to its adult requirements? Will not natural selection eliminate individuals that do such "foolish" things?

In the early days of modern evolutionary theory, a great deal of nonsense was written about recapitulation (§ 224). The phrase "racial memory" was used by some to explain the phenomena. By its definition, such a concept was outside the realm of provability or disprov-

Fig. 37-5. Growing viruses in chick eggs. Inoculation (A) and several days' incubation (B) yield a heavily infected embryo (C) from which the virus can be harvested. (Reproduced by courtesy of Parke, Davis and Company's *Therapeutic Notes.*)

ability, hence, was what modern philosophers call "non-sense" and no concern of rational man. We will try to avoid such a pitfall in discussing the significance of the various circumstantial evidences of evolution. Can anatomical and chemical relics, and embryological recapitulation be explained in terms of what we know of genes?

If "neutral" genes are involved—that is, genes that have no selective value, plus or minus—a fairly simple explanation is possible. Once a neutral gene is produced by mutation, it may, in a small population, because of the random fluctuation effects (§ 217), rise to any frequency. If the population later becomes large, the gene frequency will thenceforth remain constant (Hardy-Weinberg Law). Such an explanation fits the known distribution of the blood-group proteins (A, B, etc.) which have no known selective value. With suitable modification, this explanation may also explain the survival of neutral characteristics that were of survival value to remote ancestors.

If the genes are not neutral, other genetic facts must be drawn upon. Intensive research has led to these two generalizations:

1. Every structure, substance, or function is the result of the interaction of many genes.
2. Although each gene probably causes only one primary action (e.g., production of one enzyme that has one action), this action, affecting the entire complex organism, may produce many secondary effects. (Just as one chemical, say adrenin, injected into the body, may produce quite different effects in different parts of the body.)

A structure that has survival value is probably the result of the interaction of many genes, each of which has many effects. Some of the secondary effects will probably be of value, too. (If too many were of negative value, the responsible genes could not survive.) When, in the course of evolution, the primary structure ceases to have survival value, not all the genes contributing to its formation can be eliminated because some of them have other effects that are of positive survival value. And so the structure (or substance, or function) persists in a more or less modified form long after it has ceased to have survival value in the adult. Thus, we have ear muscles and muscles for making goose-pimples in adult humans, and as embryos, we start to develop gill arches but then "change our minds" and develop middle-ear bones instead.

Along such lines, geneticists feel, must the persistence of structures be explained. The explanation is, at present, hypothetical. But, as we learn more of what genes are and what they do, we should be able either to prove or disprove the hypothesis. It is, therefore, a scientific hypothesis and worth keeping in mind.

QUESTIONS AND PROBLEMS

37-1. What is a fossil? Explain how fossils are dated.

37-2. Which is more reliable, relative dating or absolute dating of rocks?

37-3. About how long has man been in existence?

37-4. What is the oldest record we have of living things?

37-5. How would you explain the existence of goose-pimples in man? (This is not easy!)

37-6. What is the Law of Recapitulation?

37-7. Yellow-fever virus can be grown in adult men, certain adult monkeys, but not in adult chickens. It can, however, be grown in embryonic chicks. How can this fact be explained? What bearing does it have on the theory of evolution?

37-8. What *may* be the genetic explanation of vestigial structures such as the ear muscles, the appendix, and the valves in horizontal veins?

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Chapter XXXVIII

Evolution and Disease

227. Evolution and "Progress"

The modern doctrine of evolution was born into a world in which the idea of progress was already well established. It was natural that the two ideas should have become wedded in the popular mind, that the evolutionary series "from amoeba to man" should have been regarded as a progression from lower to higher forms. (Man, his own judge, labeled himself "higher," of course.) Geologically speaking, an amoeba (or things much like it) undoubtedly appeared on the earth long before man. But does this mean that the one evolved *from* the other? A statement of this sort implies a straight-line relationship that facts do not support. The evolutionary course of development cannot be accurately compared to a chain (cf., "the missing link") but to a multitudinously branching tree with the tips of the branches representing present-day forms and with the more central parts of the tree conceived dimly, ghostlike, since they represent forms that are now extinct, for the most part. If man has evolved "from" the amoeba, so has a flatworm, a water flea, a starfish, and a parasitic roundworm.

There is no reason for supposing that evolution has occurred in a predetermined direction. In every phylum of plants and animals, there are some parasitic species. The parasitic species in any phylum unquestionably arose from free-living species in the same phylum and not from parasites of "lower" phyla. Unconsciously equating evolution with progress, biologists often speak of the evolution of tapeworms from free-living flatworms as a "degenerate evolution," or "degeneration"; and of the tapeworms as being "degenerate flatworms." Such phrases are best considered to be no more than figures of speech. A tapeworm can do things a planarian worm is incapable of doing, namely, succeed in living and reproducing in the intestine of a man. Since the ancestors of the flatworms could not do this, one should hardly speak of the evolution of the tapeworm as a "backward evolution." It is probably best not to think in terms of "forward" and "backward," of "progress" or "degeneration." Organisms evolve into environmental niches that are available to them; to say more is to run a grave risk of speaking nonsense.

228. Each Species an Environment

We tend to think of each living thing as being surrounded by an environment that is nonliving—the air, the sunshine, etc. But, when we reflect on the matter, we realize that this simplification is not true, that the environment of every species includes many living things. In part, living things act by modifying the physical factors of the environment. Plants that can live only in moist shady places, e.g., many ferns and mosses, find such environments ready-made for them in a forest. The environment they require can be defined mostly in terms of nonliving factors which living things happen to modify. A much closer identification of living things with the environment is found in the example of the moth and the *Yucca* (§ 220) in which each species constitutes an indispensable part of the environment of the other. Every instance of symbiosis involves such an identification.

Not only *may* a species be a living part of the environment of some other species, but it is almost inevitable that it *will* become such. Every living species is made of complex organic substances that are rich in energy. Since the protoplasms of various species exhibit basic similarities (§ 164), the protoplasm of one species can be rather easily turned into the protoplasm of another—more easily, at any rate, than can most nonliving material. By its mere existence, each kind of living thing figuratively invites a predator or a parasite to exploit it. Each species constitutes a challenge to a potential parasite; it offers an opportunity of survival to the organism that can penetrate its defenses and utilize its protoplasm. That such a challenge is always met is attested by the fact that every living thing ever studied has been found to support at least one parasite and, in most cases, at least one parasite that is restricted to the one host species. The temptation of a free meal is not resisted by nature.

The free meal may be gobbled up by either a predator or a parasite. What is the difference between the two? Roughly speaking, we think of predators as eating the prey from the outside while parasites devour it from within. This difference, coupled with the Pyramid of Protoplasm principle (§ 200), means that, although a predator may be much larger than its prey (and often is), a parasite is necessarily smaller. If a parasite occupies its typical location, inside the body of the host, its physiology is very likely to be quite different from that of a predator. Recall that, in the process of digestion (Chap. VIII), complex protoplasm is broken down to the building blocks amino acids, fatty acids, glycerol, and simple carbohydrates. Since all protoplasm is made of these same building blocks, it is obvious that the particular source of the building blocks will not make much difference to a predator. An antelope-eating lion can grow just as fat on mice—if he can get enough mice. The limited range of predation of each predator species is determined, one might say, by economics. He eats anything that is worth his while bothering about. Predators are seldom restricted to one or even a few species of prey. (Though, in exercising choice, a predator is guided more often by inherited instinct than by personal experience and reason. A rabbit could probably survive perfectly well on a diet of meat. But he does not have the physical equipment for catching meat on the hoof and, concomitantly, he has instincts that direct him toward eating plant material.)

Among parasites, specialization is the rule. A parasite is usually restricted to one or a few species. Liver flukes (§ 126) occur in many different species of vertebrates, but a given species of liver fluke is usually restricted to only a few species of hosts. So it is with tapeworms and many other parasitic worms. The species-specificity of parasitic bacteria and viruses is often even more extreme. Most bacteria that cause human disease can live in only a few other animals. Some parasitic viruses seem to be restricted to man. The poliomyelitis virus grows naturally only in humans, though scientists have persuaded it to grow in a few other kinds of mammals.

A genuine parasite that lives inside the body of another organism has an opportunity to take in protoplasm that is relatively unmodified by digestive processes. If we extend the architectural analogy, instead of taking in building blocks (amino acids, etc.), a parasite takes in whole sections of the protoplasmic edifice—facades, rooms, wings, towers, so to speak. The parasite is almost always dependent on these prefabricated units, since it is unable to build the whole structure from mere building blocks.

229. Adaptations of the Parasite

Imagine a free-living species of bacteria that "decides" to become a parasite of man. What changes will the changed mode of life entail, *for the bacteria?* We cannot answer this question with certainty because we have never witnessed the change from one mode of life to the other. On the experimental side, no one has succeeded in changing a free-living species to a parasitic one. This very lack of success becomes suggestive in the light of other observations cited below.

In the soil, there are hundreds of species of bacteria that can live if furnished with a single amino acid as food. If our picture of the unitary nature of protoplasm is correct (§ 164), these microbes can synthesize all the vitamins and necessary proteins from simple amino acids. In so far as laboratory workers have checked this prediction, it has been found to be true.

What of the disease-producing, or **pathogenic,** microbes? It has been found that, for pathogenic bacteria, a simple medium such as one containing a single amino acid will not at all suffice in culturing them. Instead, when the culture of parasitic bacteria was first attempted, it was found to be necessary to furnish the parasites with such complex mixtures as whole blood or macerated brain tissue. When chemists tackled the problem of growing the parasites in a medium containing only known substances ("*a well-defined medium*"), it was found that whole blood, brain tissue, etc., could be dispensed with only if a very complicated mixture of many amino acids and many vitamins was furnished them. Different species of parasites had to be furnished different vitamins and amino acids. Almost without exception, **parasitic microbes are unable to carry out many of the syntheses essential to life.** They can survive only because their hosts furnish them with the substances they need, that is, with "prefabricated units" instead of mere "building blocks."

Is this incompetence of the parasite due to failure to evolve from parasitism to independence, or to "degeneration" from a free-living condition? Since parasites are very species-specific, and since the host species have, in any case, been on the earth only a short time (e.g., 1,000,000 years in the case of man), we must suppose that we are dealing with degeneracy (unless we espouse the too-easy explanation of complete spontaneous generation).

The next question that arises is this: if all parasitic species have arisen from free-living species, why are they so universally incompetent to produce their own essential protoplasmic constituents? The significance of this remarkable parallelism was first pointed out in 1936 by the British bacteriologist, B. C. J. G. Knight. A certain answer to the problem cannot be given in our present state of ignorance but, utilizing the reasoning that underlies the theory of evolution, we can point out:

> *First: If* a species is parasitic, it can "afford" to lose some of its synthetic abilities. If, among the members of a free-living species, there appears a mutant which cannot synthesize an essential constituent of protoplasm, this mutant will probably be at a selective disadvantage competing with the normal cells. However, among the members of a parasitic species, an incompetent mutant of this sort would *not* be at a selective disadvantage. Is this factor sufficient to account for the nearly universal parallelism of parasitism and synthetic incompetence? It has been suggested that:
>
> *Second: If* a species is to be a successful parasite, it *may have to* lose some of its synthetic abilities. In any living body, the parasite always encounters environmental resistance, e.g., antibodies. Whether an invader is to survive or not may be a touch-and-go matter. If it spends a great deal of its time synthesizing all its own building blocks, it may be overwhelmed by the body's defenses. But, by divesting itself of some of its normal synthetic processes and taking advantage of the ready-made food all around it, it may be able to outstrip the defensive agents. Or, perhaps, the truth may be slightly different; perhaps a parasite with great synthesizing abilities is possible but does not long remain unchanged because, as soon as a nutritionally less competent mutant is produced, it is more efficient in the host en-

vironment and ultimately replaces the original organism through the action of natural selection.

The above explanation is only a verbal one, but it is widely believed that we may soon be able to give a more specific statement of it. The principle involved has application beyond the realm of microbes. Parasitic worms (Chap. XVI) have lost many of the morphological features, e.g., eyespots, of their undoubted ancestors. Loss of structures and functions is common in parasites belonging to many phyla. In general, we may say that **any major structure or function which is no longer of use to the species will eventually degenerate.** This principle explains the degeneration of eyes in cave-dwelling forms of salamanders, crayfish, crickets, etc. It is a principle that must be invoked with care, hence, the insertion of the cautious adjective, "major." We must be careful not to imply that *any* feature possessed by a species has survival value. There are many minor characters in every species—for instance, the finger ridges of man—whose selective value is difficult to establish or even imagine.

230. The Nature of Viruses

With but few exceptions, there is a parallelism between the parasitism of a microbe and its synthetic incompetence. Of all the disease-producing microscopic things, the most incompetent are the viruses. Coupled with this incompetence is complete, obligatory parasitism. No free-living virus has ever been found.

The first discovery of viruses was made in 1892 by a Russian botanist, Iwanowski, who was studying a disease of tobacco plants called **tobacco-mosaic disease.** Although the disease was clearly infectious, that is, it could be passed from one plant to another in an indefinite series of transfers, Iwanowski could not find any microbe capable of causing the disease. But when he took a soup made of ground-up tobacco leaves and passed it through a filter the pores of which were so fine that bacteria could not get through them, the experimenter found that the filtrate which he collected still contained something that could cause the disease. This filtrate contained nothing that was large enough to be seen by the most powerful microscopes then available. The infectious agent in the filtrate could not be grown on any nonliving materials in a test tube. Reproduction could occur only in living tobacco leaves.

At first, it was thought that one of the most important characteristics of a virus was its size—the fact that it was "filter-passing" whereas bacteria were not. With further study, it has been found that there are some viruses so large that they cannot pass through a filter that will permit the passage of some bacteria. Furthermore, the property of being invisible in the microscope has become less meaningful since the invention of the vastly more powerful **electron microscope.** We have, today, pictures of many of the viruses taken with this instrument (Fig. 38-1). The electron microscope uses electrons instead of light waves to develop an image.

The remaining property of viruses—nonculturability in nonliving media—is now considered the most important one. Hundreds, or likely thousands, of attempts to grow viruses in nonliving soups and jellies have met with failure. No matter how complete a diet of vitamins and amino acids is furnished to a virus, it cannot grow. It seems to be unable to make a single substance that is a constituent of, or that is required by, protoplasm. Only within a living, metabolizing cell can virus particles multiply.

Since every virus is completely dependent on some other organism, should we say that the virus is really an organism? How does a virus differ, for instance, from red blood cells, which also multiply, but always inside a living body? In other words, is the virus a living organism? This question has intrigued biologists since the discovery of these strange entities. The difficulty of the question has increased since W. M. Stanley and others have succeeded in crystallizing some of the viruses, including the tobacco-mosaic virus. Crystallizability is an important test of chemical purity. If a substance is chemically pure, it should be possible to obtain it in the crystalline state. Is a virus which has been obtained in the form of crystals a pure substance? Many scientists think so.

Living things exhibit metabolism. Does a virus exhibit metabolism? Metabolism—which is hard to define—involves measurable changes in the composition and amounts of substances that surround a living organism. The proteins we call viruses cause no changes in the nonliving medium that surrounds them when they are separated from living cells. And when a virus is inside a living cell, how are we to know whether

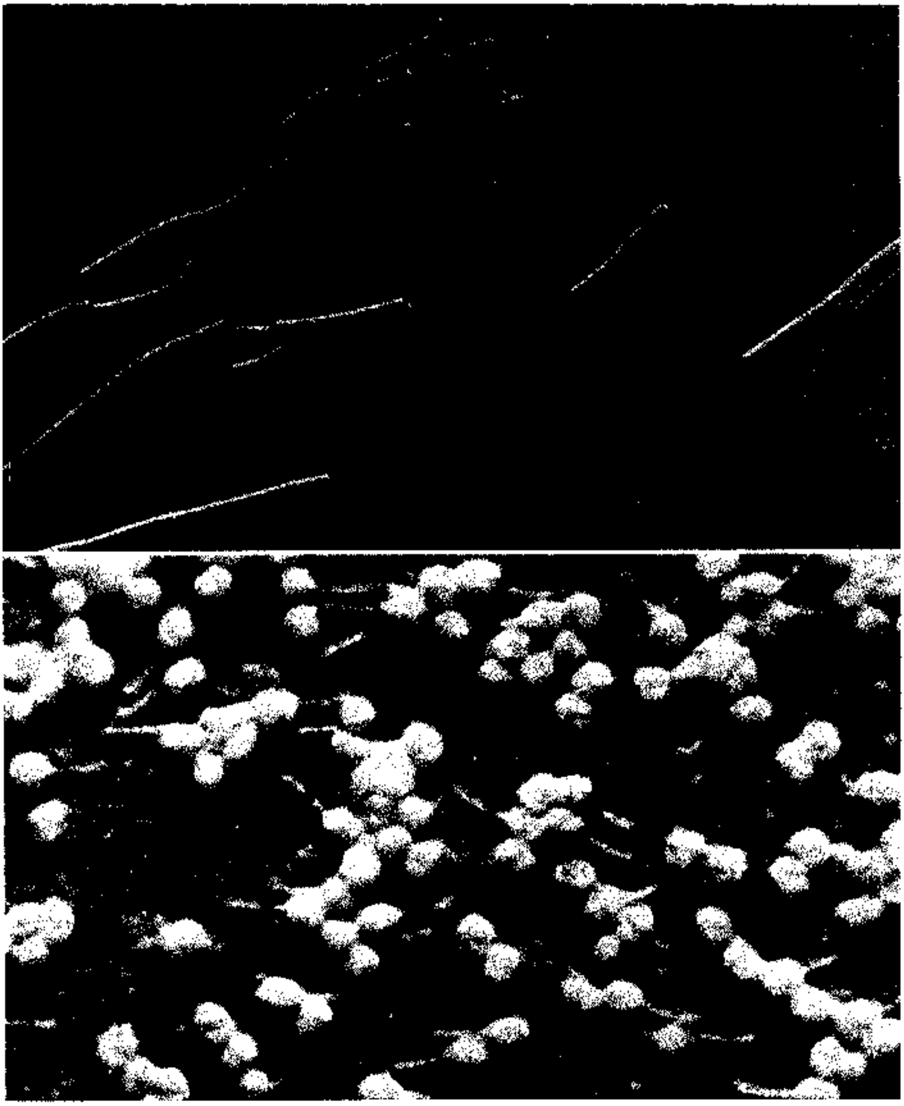

Fig. 38-1. Electron micrographs of two viruses, the tobacco-mosaic virus above; and a *bacteriophage*, i.e., a bacteria-eating virus, below. Magnification of both approximately 85,000 ×. (Courtesy of Dr. Ralph W. G. Wyckoff and the National Institutes of Health.)

it—the virus—is carrying out metabolic activities? The metabolism of the host cell confounds any measurements.

The fact that a virus is an apparently pure chemical substance that exhibits no demonstrable metabolism inclines us to call it nonliving. The fact that it can (in a suitable environment) reproduce itself indefinitely makes us want to call it living. To some speculators, one argument has seemed more potent than the others. Agreement is not easy to reach because we are not dealing with questions of the *facts about viruses*—these are unambiguous—but with the question of *the definition of life*. How are we to define life? Is metabolism, or reproduction, or the possession of a complex structure, a necessary part of the definition of life? In a matter of definition, there is no right or wrong. There is, at best, only some agreement among specialists. Where there is no agreement (as in this case), it is best to maintain a suspended judgment. Fortunately, research does not have to await a universally satisfactory definition. Investigations may even be stimulated by a disagreement at the definition level, provided the true character of the disagreement is recognized.

231. Coevolution of Host and Parasite

The origin of the disease *syphilis* is a matter of dispute, but it appears certain that it did not exist in Western Europe until shortly after Columbus discovered America. For the first decade or so of its existence, it was an exceedingly vicious disease with a high mortality. Gradually the severity of the disease decreased until, today, it is a disease that kills very few in its first stages. The seriousness of the disease (and it is still serious) is now due mostly to its delayed effects—heart disease, degeneration of the central nervous system, and other effects that may appear twenty to forty years after the initial infection.

Why has syphilis become a less severe disease? What accounts for this evolution? We can see two possible explanations:

1. Syphilis has constituted a selective factor in the environment of men. Those men whose resistance was higher than the average have produced more children than those who were less able to resist it. Differential reproduction ultimately produced a more resistant race of men.

2. The syphilis organism itself has been selected for benignity. If some mutants of the organism produced a very severe form of the disease, the affected host might perish before he could pass the microbes on to the next victim. On the other hand, strains of the microbe

that incapacitated their victims only slightly would have a better chance of being transmitted to other humans.

Probably both types of evolution have occurred together. We can speak of such evolution as coevolution of host and parasite. Such evolution could explain the observed fact that a disease is generally more severe when it is new than it is several centuries later. It is important to realize that **it is not to the advantage of a parasite to be pathogenic.** The milder the effects a parasite produces, the better chance it has to survive. Old, well-established parasites generally produce relatively benign diseases, or none at all.

QUESTIONS AND PROBLEMS

38-1. Nutritionally speaking, what are the differences between a predator and a parasite?

38-2. What explanation has been given for the parallelism of parasitism and lack of synthetic abilities? Distinguish carefully between facts and speculations.

38-3. What may happen to useless structures and metabolic reactions in the course of time? Why?

38-4. Are there any structures and functions possessed by some animal or plant that are probably functionless? Can you give examples?

38-5. From the descriptions in the Bible, it would appear probable that leprosy was once a more severe disease (for the individual) than it is now. If this is true, can you give a reasonable explanation of the fact?

38-6. Syphilis today generally kills the sufferer only after a score or more years, after the breeding age is past. Would you expect natural selection to continue to operate to make the disease more benign? Explain.

38-7. Is a virus a living organism? Discuss this question in a critical way.

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Chapter XXXIX

The Origin of Life

232. The Autotroph Hypothesis

Man has speculated for thousands of years about the origin of life. His speculations have produced some notable religious works as well as a welter of scientific and pseudoscientific hypotheses. We do not, today, know the answer. We do, however, have a fairly clear view of the problem. Among scientific hypotheses, the two leading ones will be presented here.

First, we must define two terms now commonly used in discussions of nutrition. An **autotroph** (Greek *autos*, self; *trophos*, one who feeds) or **autotrophic organism** is an organism that feeds itself, that is, one *that does not have to be furnished organic food* from the outside. Green plants, which can live on CO_2, H_2O, and miscellaneous inorganic salts, are autotrophs. A **heterotroph** or **heterotrophic organism** (Greek *heteros*, different, other) is one that must be fed organic food. All mammals, for instance, are heterotrophs.

If life had a unique origin, which came first, an autotroph or a heterotroph? (That is, a plantlike thing, or an animallike thing?) The argument for autotrophs as the first organisms runs as follows:

1. All living things are made of organic material which they must either make themselves or be furnished from the outside.
2. Only autotrophs can make organic material. (The heterotrophs

merely alter it and pass it from one organism to another. Recall Chap. XXXII).

3. In the absence of autotrophs, there would be no organic matter.

4. Hence, there must have been autotrophs on the earth before heterotrophs could have existed.

233. The Heterotroph Hypothesis

The Autotroph Hypothesis seemed almost self-evidently excellent until modern nutritional research disclosed a fundamental weakness in it. In discussing the relation between nutrition and genes (Chap. XXVII), we pointed out that there is an *inverse* relationship between simplicity of nutritional requirements and complexity of genetic make-up. There seems to be a minimum material of which all, or nearly all, organisms are made, a material we call protoplasm. An organism which makes all the constituents of protoplasm itself has more genes, that is, it is more complex, than an otherwise similar organism that cannot synthesize some of these constituents itself, and so is dependent on outside sources for the missing substances. It is, therefore, apparent that when we say that autotrophs preceded heterotrophs in the development of the living world, we are, in effect, saying that the more complex organisms came before the less complex. At best, for life to have originated at all seems a highly improbable, perhaps one should say miraculous, event. To suppose that a very complex form of life came before simple forms is to compound improbabilities.

But a hypothesis that heterotrophs must have come before autotrophs can hardly be established merely by pointing out difficulties in the way of the Autotroph Hypothesis. The argument for the Autotroph Theory implies the existence of difficulties in the way of any Heterotroph Hypothesis. Can we state, and answer, these implied difficulties?

The third statement in the Autotroph Hypothesis (§ 232) contains the crucial point: "In the absence of autotrophs, there would be no organic matter." We give unconscious assent to this statement because of our awareness of the carbon cycle as it exists on the earth today. (See Chap. XXXII). Because of the activities of diverse organisms, carbon is continually broken down to carbon dioxide. The carbon in carbon dioxide is returned to the cycle only through the intervention of autotrophs. Hence, the autotrophs seem essential. In their absence, we think all organic carbon (if any) would soon be degraded to carbon dioxide.

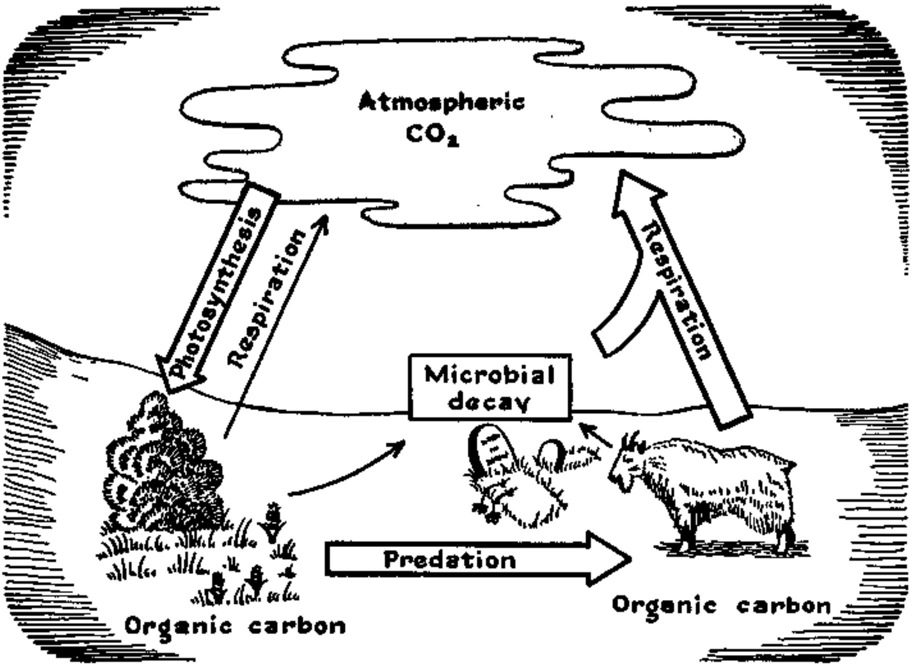

Fig. 39-1. Every arrow pointing toward carbon dioxide represents the activities of living things.

However, it is necessary to look again at the carbon cycle (Fig. 39-1). The degradation of organic carbon to the inorganic compound, carbon dioxide, is not a spontaneous process. *It is brought about by living organisms.* By the respiration of plants and animals and putrefactive microbes, organic compounds are degraded to carbon dioxide. In the absence of living organisms, this does not happen. It is perhaps our language that is at fault, its structure that subtly misleads us. Usage to the contrary, organic compounds do not decay; they *are decayed*—by living organisms. **If there are no living organisms around, organic materials will endure.**

In the beginning, then, if any organic matter could be formed (by whatever means), it could endure, thus making possible heterotrophic life at the outset. The next question is this: Is there any way that organic matter can be formed except through the actions of living things?

Under present-day conditions on the earth, the nonliving production of organic matter is of questionable importance. However, laboratory experiments show that when a mixture of carbon dioxide, ammonia, and other gases is irradiated with ultraviolet light, organic compounds are formed. Everyone knows, of course, that the sun's rays include large amounts of ultraviolet light. There are also reasons to believe that, in past geological eras, considerable quantities of carbon dioxide and ammonia were present in the earth's atmosphere. In times past, then, organic compounds could have been formed in the absence of living things. And in the absence of living things, organic matter could have persisted.

This, the bare essentials of the Heterotroph Hypothesis, seems reasonable enough. When, however, we try to clothe it more fully, we run into difficulties that we cannot, at present, explain away. The hypothesis, however, is young. It is a hypothesis that has grown up gradually, so it is not possible to assign a definite authorship and time to it. One of the earliest explicit formulations of it was given by an Englishman, J. B. S. Haldane, in 1928. A fuller statement of it was made about ten years later by a Russian, A. I. Oparin. Further meaning to the hypothesis has been given by the American, N. H. Horowitz, utilizing modern concepts of the nature of genes and of protoplasm. No one is yet satisfied with the hypothesis, but it shows promise of further development.

What sort of entity was the first living thing? If we are to adhere to the scientific principle of making a minimum hypothesis, we must hypothesize the simplest thing imaginable that could justifiably be called alive. Of the things we know today, a virus is the simplest thing that may be called alive. It does not have a cell membrane or any known morphological complexity. The simplest viruses are pure chemical compounds, proteins, that are self-reproducing when in a suitable environment. We suspect that the first "living" thing was something like a virus. In the thousands upon thousand of organic compounds floating in the hypothetical primeval organic soup, there may have been produced, by interaction of chemicals, some proteins. And among these proteins, there may have been produced some proteins that could have organized the other compounds floating around in the soup into proteins like themselves—in other words, self-reproducing proteins.

Improbable? Yes. That random physical and chemical reactions could produce anything as complex as a protein, let alone a self-reproducing protein, is, we suspect, very improbable. With billions of molecules present, there might be much less than one chance in a million of its happening in the interval of a human lifetime. But, in the origin of life, there may have been many thousands of human lifetimes for the improbable to happen. The world originated about two thousand million years ago. We have records of living things only for the last five hundred or thousand million years. There must have been a long period of time during which there was ample opportunity for the improbable to happen.

It seems most reasonable that heterotrophs were evolved first. However, once there existed a heterotroph that could reproduce at the expense of the nonliving organic material available, there was created the danger that this primitive "organism" might "eat itself out of house and home." As various classes of organic compounds would be exhausted by primitive individual "organisms," if among these "organisms" mutant types appeared which could make their substance out of simpler compounds, these mutants would be favored in the struggle for existence. As each type of food material was exhausted, the natural advantage of an organism that could synthesize it would permit it to become the predominant type. Thus, step by step, the first heterotroph may have picked up one synthetic ability after another until, finally—perhaps just as the last of the free organic foods was disappearing—there may have emerged the first autotroph, a complex organism with many gene-produced synthesizing enzymes. Once this type appeared, the living world would be independent of a free food supply, and there would exist the possibility of evolving many new organisms, of both autotrophic and heterotrophic natures.

The argument given above is a verbal one and represents, substantially, the present stage of our conception of how life began. To carry conviction, the Heterotroph Hypothesis will have to be elaborated in terms of genes and enzymes and synthetic reactions, in other words, in terms of that imperfectly understood complex we call metabolism. We will probably not have a really satisfying theory of the origin of life until we understand the nature of life itself. We suspect that finding the answer to one of these questions will make the answer to the other obvious.

QUESTIONS AND PROBLEMS

39-1. What is the fundamental weakness of the Autotroph Hypothesis?

39-2. Why is it more accurate to say that foodstuff *is decayed,* rather than to say *it decays?*

39-3. What difficulties stand in the way of acceptance of the Heterotroph Hypothesis?

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Chapter XL

Man: Evolution in the Future

234. Biology and the Future

Man is a strange organism. In so far as we can tell, all plants and most animals live predominantly in the present. In so far as they are conscious at all, the majority of them are concerned most of the time with the here and now. The past exists chiefly as an accumulation of conditioned reflexes. Preparation for the future is usually represented only by a battery of adaptive instincts. There is no evidence that any other creature shows the overweening concern with the past and the future that is exhibited by man. *Where did we come from? Where are we going?* These questions excite the interest of every human who enjoys an intellectual life.

The first question, the question of our past, is susceptible to satisfactory and reasonably accurate answer. This question lies within the domain of history. As far back as written documents are available, the problem is the concern of historians. Beyond the written documents, the archeologist and the biologist take over. The problem of the future, however, is treated differently. There is no recognized discipline or science whose concern is the future of man. In their various times and manners, the theologist, the philosopher, the economist, the politician, and the biologist have concerned themselves with the future of man. The question is a complex one that involves the fields of all of these specialists and of others. Synthesis is desirable, but it is questionable if there is any man living who can make the needed synthesis. Each scholar gives a partial solution, valid, at best, in the phases that touch his own specialty. The future of man is enmeshed in a tangled skein of human institutions and desires. Even if we cannot, in this book, untangle the mess, we can perform the useful function of pointing out the biological threads that run through it.

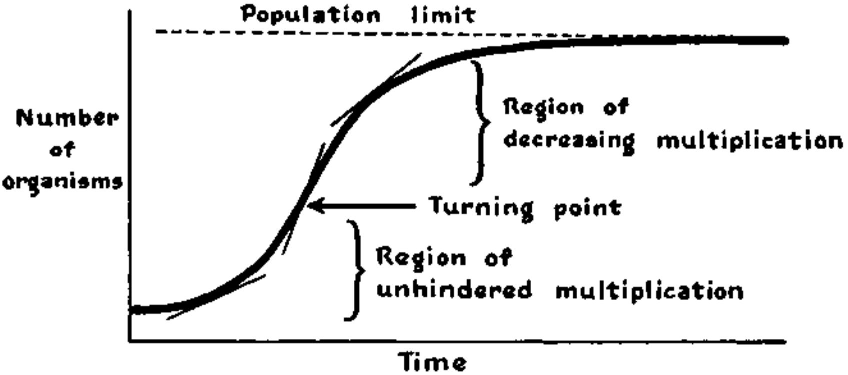

Fig. 40-1. The curve of population increase for *any* population in a constant and finite environment.

235. The Limits to Multiplication

Every species of plant or animal is capable of indefinite increase in numbers. The environment available to each species is finite. Hence, the population curve rises steeply for awhile, then bends over, and finally levels off in the familiar S-shaped curve shown in Figure 40-1, and previously discussed in § 209. Since all organisms are capable of indefinite increase, any population that is growing in a finite environment will exhibit the S-shaped growth curve. Is this true of human populations also?

In a finite environment (such as an island, under a stable social organization), a human population reaches a maximum size beyond which it does not go. Fluctuations occur, but there is an upward limit to the population size. What forces keep the human population within bounds? Some of the forces are the same as for all other plants and animals: disease and scarcity of food. In addition, there is the development of various means of self-destruction that are not universally used by other organisms, namely warfare, infanticide, and cannibalism. In the latter days of human evolution, there have appeared two controlling forces that are new to the animal world: abstinence from sexual intercourse and contraceptive measures. In summary, we may say that, in a finite environment, a population of humans is kept from surpassing a limit by these various restrictive forces: disease, starvation, self-destruction, and man's interference with his own reproduction.

The growth of human populations has differed somewhat from that of most animal populations in that it has been difficult in the past, and is still difficult, to say what the upper limit is. Man's ingenuity at wresting ever greater harvests from the soil, through the development of improved strains of plants and animals and of more efficient harvesting machines, has, in effect, from time to time, increased the extent of the available environment. Will he ultimately be held in check by the amount of sunlight falling on the earth? (See § 201.) Or by the amount of uranium available? Or by the number of square feet of earth to stand on? Or will he migrate to other planetary systems and be finally held in check by the finite size of the entire universe?

These questions, interesting as they are, are somewhat academic. Whatever may be the final limit, there is, at any moment in history, a temporary population limit determined by the industrial technology and agricultural practices current at that time. Moreover, the evidence indicates that the world's population is continuously pushing hard against this limit. In a few particular countries, the limiting forces may not be very obtrusive at the present time, but in the world as a whole, the population seems to be very close to its momentary limit, as is suggested by the fact that the deaths due to starvation and crowd diseases run into the millions every year.

236. Selective Reproduction

All species of animals and plants produce more offspring than can survive to breeding age. Or, to put it another way, not all of the adult progeny that *might* materialize do so. We may say that there are some potential offspring that do not become actual offspring. What of these "lost" potential offspring—is their loss purely a matter of chance? Do some parents have more actual offspring than others? If so, is this state of affairs due wholly to chance?

In discussing the logical basis of the evolutionary mechanism, we have already pointed out (§ 216) that variations, some of which are inheritable, are present in all species of plants and animals; and that, statistically speaking, those variants that are better suited to the environment will survive in greater proportion than those that are less well suited to the environment. Of course, nonsurvival is always *partly* a matter of chance. A green plant may just happen to grow where a cow passes by and eats it; a man may just happen to be hit by a falling airplane part. But this chance factor in survival can be ignored because, *by the definition of chance, it can have no influence on the composition of the population that survives.*

There is, also a selective factor in survival. Albino corn plants do not survive at all to produce the next generation; corn plants that have great resistance to a fungus disease will survive in greater numbers than those that have poor resistance. Selective survival will influence evolution. Each succeeding generation will have more "good" variants and fewer "bad" variants, where goodness is defined in terms of the selective factor (need for food, presence of disease organisms, etc.).

What of man? Do all varieties of men reproduce at the same rate? Is failure to reproduce attributable entirely to chance? Observations,

TABLE 40-1

NUMBER OF CHILDREN PER WIFE PAST CHILD-BEARING AGE, CLASSIFIED ACCORDING TO THE SCHOOLING OF THE WIFE. Data gathered in Indianapolis, Indiana, 1941. (Whelpton, P. K., and Kiser, C. V. *Milbank Memorial Fund Quarterly*, **21**, 221-278, July 1943.)

SCHOOLING OF WIFE	AVERAGE NUMBER OF CHILDREN
4 or more years of college	0.88
3 years of college	1.02
2 years of college	1.11
1 year of college	1.20
4 years of high school	1.13
3 years of high school	1.66
2 years of high school	1.68
1 year of high school	1.84
8 years of grade school	1.94
7 years of grade school	2.59
Less than 7 years' schooling	2.81

repeated many times and in many places, have shown that this is not the case. To quote but one set of data, we present Table 40-1, which shows that, with one exception (at four years of high school), there is a regular increase in the number of children with the decrease in the amount of the schooling of the wife. Now, people quit going to school for many reasons. The observations of school teachers and administrators indicate that intellectual inability to learn is one of the reasons. Though there are individual exceptions, men and women who complete college have, on the average, greater innate intellectual ability than those who do not complete grammar school.

Is intelligence inherited? This question presents a number of difficult problems, among them the problem of measuring intelligence. Commonly, intelligence is measured in terms of a statistic called "Intelligence Quotient," or "I. Q." for short. Ideally, the I. Q. is independent of the amount of schooling, and within a given society, among those who have had some schooling, it approaches the ideal closely enough. Studies made of the I. Q. of parents and children show that parents with higher-than-normal I. Q.'s have children with higher-than-normal I. Q.'s, on the average. Similarly, parents with low I. Q.'s produce children with low I. Q.'s. These studies do not preclude the possibility that, occasionally, stupid parents may produce a genius or intelligent parents a moron. These exceptions scarcely affect the average.

In passing, it should be pointed out that there are many people who, fearful of the possible consequences of admitting that intelligence is partly determined by heredity, would deny the role of heredity entirely, implying that "all men are created equal." There is a dull kind of safety in adopting this position because, among humans, it is difficult to disentangle environmental and hereditary factors. However, in other animals, where experimentation is possible, it has been clearly shown that there are inheritable factors that determine the limits of intellectual ability. To assert, either explicitly or implicitly, that the case is otherwise with humans is to espouse a doctrine of exceptionalism that is repugnant to scientists.

237. The Effect of Selective Reproduction

If intelligence is, in part, due to hereditary factors, and if those who are more intelligent reproduce at a lower rate than do those who are less intelligent, plainly the *average* intelligence of the population will decrease. Table 40-2 presents the results of a calculation of the rate of

TABLE 40-2

CALCULATED EFFECT OF OBSERVED SELECTIVE REPRODUCTION ON THE I. Q. OF A PARTICULAR POPULATION IN THE UNITED STATES. (FROM F. LORIMER AND F. OSBORN*, 1934)

I. Q.	FIRST GENERATION; OBSERVED PER CENT OF POPULATION IN CLASS	SECOND GENERATION; CALCULATED PER CENT OF POPULATION IN CLASS	CHANGE; PER CENT CALCULATED
140 and up	1.71	1.50	−12.3
130-139	3.25	2.88	−11.4
120-129	7.17	6.46	−9.9
110-119	11.91	11.44	−3.9
100-109	17.24	16.93	−1.8
90-99	21.28	21.64	+1.6
80-89	18.67	19.31	+3.4
70-79	12.01	12.65	+5.4
60-69	5.30	5.61	+5.8
50-59	1.46	1.59	+8.8
	In I. Q. Points	In I. Q. Points	In I. Q. Points
Median (a kind of average)	95.90	95.01	−0.89

decrease of average intelligence in a United States population, the calculation being based on the measured percentages of individuals falling within each I. Q. class and the observed rate of reproduction of the various classes. It will be observed (last column) that the percentage of the more intelligent classes decreases, while that of the less intelligent increases. The effect of this on the average I. Q. of the population will be to decrease it approximately 0.89 of a point in one generation. Other studies have led to a different value for the decrease in I. Q. due to selective reproduction, but the precise value of this figure need not concern us. In all cases, the studies indicate *that as long as our present*

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* From F. Lorimer and F. Osborn: *Dynamics of Population.* Copyright, 1934, by The Macmillan Company and used with their permission.

social organization continues, there will be a slow but continuous downward trend in the average intelligence.

The practical science—if science it be—that is concerned with the human consequences of heredity and social organization and with measures designed to perpetuate "good" heredity is called **eugenics,** meaning literally, well produced or well born. Eugenicists look with foreboding at data such as those in Table 40-2. It seems to them desirable that the intelligence of the population remain at least as high as it is now. All evidence indicates that it is falling.

If unopposed, the I. Q. of the population will continue to fall. To combat this, eugenicists have proposed various measures which can be divided into two general classes: *positive* eugenical measures, and *negative* eugenical measures. We shall take up the second first.

Negative eugenical measures are aimed at discouraging the breeding of the less-desired types of humans. The principal measure used to date has been that of sterilization of the extremely unintelligent. Many states and nations have laws which permit the sterilization of the feeble-minded. Observation has shown that, almost without exception, two feeble-minded parents can produce only feeble-minded children. There seems to be little danger of society's being deprived of something valuable by the sterilization of all feeble-minded individuals. The legal right of society to do this has been upheld in the courts.

The sterilization of the feeble-minded has been opposed for various reasons. One of the strongest reasons has been the feeling that it somehow interferes with the "rights" of the individual. In discussing this point, one must first emphasize that sterilization alters an individual in one respect only: it keeps him from having children. (See § 115 once more.) It does not prevent him from having sexual intercourse, nor lessen his enjoyment of it. The operation required is an exceedingly minor one in the case of the male and not very dangerous in the female.

Aside from the eugenic effect, sterilization of the feeble-minded has other desirable consequences. It is possible to obtain the same eugenic effect by keeping feeble-minded individuals permanently behind locked doors. The expense of this measure to society is very great, and it is usually disadvantageous to the individual. Most feeble-minded people are capable of supporting themselves, with some aid and supervision perhaps, and are much happier doing so. If they are sterilized, society benefits in three ways: (1) The individual contributes to his community, instead of acting as a drain on its resources; (2) the transmission of his deficient hereditary traits is prevented; and (3) the rearing of children in a home managed by feeble-minded parents is avoided. This last is an important point to remember when considering the possibility of a normal child being born of subnormal parents. Such an event may occasionally transpire, but this possibility seems insufficient reason for permitting feeble-minded people to procreate and bring up children.

It is difficult, on rational grounds, to object to the sterilization of the feeble-minded. One must not, however, be too optimistic about the benefits of a sterilization program. Only a few per cent of the population fall in the lower categories of intelligence. The effect of sterilizing all of the feeble-minded will not be very great; as fewer and fewer feeble-minded individuals turn up in successive generations, the effectiveness of the program will diminish. This does not constitute an argument against the program, but merely a caution against overoptimism.

More spectacular results could be obtained by preventing the breeding of the more numerous members of the subnormal classes higher than the feeble-minded. However, the nearer a class is to the normal, the less certain is it that the greater part of its deficiency is attributable to inheritable characteristics, and the less objection can be raised to an individual's breeding. The identification of the less extreme types is also less certain, and the danger of misadministration (due to error or malice) is correspondingly greater. For this reason, there has been no serious proposal, in countries not in the grip of racist doctrines, to extend negative eugenic measures above the level of the feeble-minded class. In the present state of our knowledge and ignorance, this caution is commendable.

238. Positive Eugenics

It should also be possible to raise the average I. Q. by positive eugenics, that is, by encouraging the reproduction of those individuals whose I. Q. is higher than the average of the general population. If such people can be persuaded or enabled to produce more children on the average than are produced by other members of the society, the average I. Q. may be expected to rise.

It is probable that a program of *negative* eugenics can be successfully carried out only if a society is willing to countenance mandatory laws because some of the individuals to whom the measures apply are too lacking in intelligence to recognize the problem their fertility presents. With respect to *positive* eugenics, however, a different situation prevails. The individuals who should be persuaded to produce more children are more intelligent than the average and, hence, are capable of understanding the social problems involved. A state fiat is not required. It should be possible to accomplish the desired end by individual persuasion.

It must not be supposed that the problem is a simple one. It is complicated by social organizations, social traditions, and the exigencies of competition. To state general truths: by and large, the individuals with greater innate intellectual ability go to school longer than do those with less; the longer a person goes to school, the older he is before he is self-supporting and, hence, in a position to marry; and the older a person is at the time of marriage, the fewer children he produces. There are individual exceptions, but these are general truths. These facts constitute, in a sense, the mechanism that accounts for the relative infertility of the more intelligent groups in our society.

Must intelligent people necessarily be relatively infertile? It seems clear that the fact is a result of our social organization. With different social traditions, it could be otherwise. If, to take an example, college students were supported by society or their parents to such an extent that they could afford to marry and start a family while still in school, the result would be eugenically good. In recent years, the proportion of married college students has risen. Whether this increase will be maintained remains to be seen.

In addition to late marriage, there is another factor that tends to limit the size of families in the high I. Q. group: ambition. In our strongly competitive world, young children are not economically an asset but a liability. A very ambitious man of high I. Q. is likely to put strict limits to the size of his family to insure that the necessity of supporting many offspring will not interfere with his career.

What can be done? The first thing needed is the dissemination of information. There are many very intelligent people of good education who have not had brought home to them the hereditary element in intelligence and the social consequences of their failure to reproduce. This is a problem of education. Curiously, it is the so-called "educated classes" that are most in need of this education.

Of course, more than facts, in the ordinary sense, must be involved in this education. A man of high I. Q. may be thoroughly cognizant of the facts mentioned above, and yet his actions may be unaffected by them because he lets his personal ambitions overshadow any questions of community well-being. People of this caliber will reproduce their own kind only if their consciences make them hold their ambitions partly in check. *In effect*, extreme ambition sterilizes the individual. People of greater-than-average intelligence will make possible a world in which their kind can continue to be numerically important only if they have the conscience to sacrifice other advantages and pleasures for this good.

239. What Traits Are Desirable?

It may have been noticed that all the preceding discussion has centered around intelligence, of which I. Q. is presumed to be a measure. This limitation was deliberately made in order to simplify the discussion of the principles of eugenics, but such a limitation cannot for long be imposed without dangerously oversimplifying our real eugenic problems. "Brains" are desirable—yes. But, as a less-favored person might put it, "Brains ain't everything."

Human society is bewilderingly complex, and human aspirations and abilities seem almost endless in number. The history of mankind makes it abundantly clear that the great men—however greatness is defined—are not exclusively, or even principally, men of great intelligence. What was the I. Q. of Mozart, of Schubert, of Rembrandt, or of Keats? We do not know, but their biographies suggest they were men of only mediocre intelligence, at best. But who would maintain that their contributions to humanity were trifling? Plainly, there are many sorts of ability other than that measured by the "Intelligence Quotient" tests. Inconclusive evidence, e.g., the family tree of the Bach family, indicates that some of these abilities are in part due to inheritable traits not identical with the genes that make for high I. Q. There are many professions and occupations which require, in large measure, qualities other than great intelligence. Even science which, at first glance, seems particularly to require intellectual ability, presents to those of mediocre intellect considerable opportunities for accomplishment. Admittedly, one can readily cite many great men of science who were intellectual giants—Newton, Gibbs, and Galton, to mention but three. But some of the greatest advances have been made by individuals of only mediocre intellect. Darwin, if we may judge by his school record, was such. Dalton, who first developed the modern atomic theory, seems to have been rather stupid. And Mendel, who discovered the laws of heredity, twice failed to pass the examinations given to prospective high-school teachers. In science, as elsewhere, great accomplishment is possible only to those capable of great absorption in their work. By and large, the willingness to work hard is more important than brilliance.

What is desirable? Great intelligence? Ability to work hard—but is *that* due to inheritable traits? Perhaps emotional stability is what we should breed for? Yet, what will we say of the painter, Van Gogh; the poet, Poe; or of the composer, Wagner—men who would scarcely pass any test we might set up? Perhaps good health is the desirable trait? But what of Keats, a member of a tuberculous family, who himself died of the disease; what of Chopin or of Robert Louis Stevenson, both sickly characters? Poor health is due, in part, to environment (disease organisms) and, in part, to hereditary susceptibility to diseases. Perhaps it is desirable to discourage the breeding of people who come from families in which there is clearly high susceptibility to certain diseases (such as tuberculosis), but we must realize that even lack of physical vigor is not always a disadvantage to the individual, however it may affect society.

The problem of deciding what traits are desirable is complicated by the structure and evolution of society itself. To consider only the role of intelligence, imagine what would happen if we could, by magic, make all the people in our society have an I. Q. of at least 140 beginning next Tuesday at four o'clock. Picture such people (of near genius intelligence) carrying out all the routine operations of our daily life—making change in dimestores, cleaning out sewers, driving trucks, running elevators, and watching gauges on automatic machines. Would the work of society be done the better for all this intelligence? Perhaps for a day or two, but not for long. We can safely predict that there would soon be widespread rebellion among the bored geniuses. Great intelligence is an advantage only in situations that demand it. The experience of every employer shows that it is not only important to get a man who is intelligent enough for the job, but also to avoid one who is too intelligent for it. At the present time, it seems impossible so to organize our society that it demands only one type and grade of ability. So long as a multiplicity of jobs exists, so long will a multiplicity of abilities be of value. Even were we given the power to control the breeding of men completely, it is clear that an extremely selective breeding program would lead to trouble unless the organization of society evolved at the same time and in the proper way.

240. Difficulties in the Way of a Eugenic Program

Consider the wonders that man has accomplished through the control of the breeding of plants and animals. Starting with a wild cabbage-like plant and using various selective criteria, he has produced plants as diverse as the domestic cabbage, cauliflower, Brussels sprouts, broccoli and kale (§ 215). From a single species of wild horse, he has developed the tiny Shetland pony and the two-thousand-pound Percheron draft-horse, to mention only the extremes. All the many varieties of goldfish are descended from a single stock. The same may be said of the pigeons.

Viewing these remarkable results, it was natural, in the early days of genetics, for men to become enthusiastic about the possibilities of making better men through the control of human breeding. There were proposed various eugenic programs, involving both negative and positive measures. Aside from the limited, and well-deserved, success of the negative part of the program (sterilization of the feeble-minded), no eugenic program has received appreciable public support in any of the true or so-called democratic nations. The lack of public support has been the image and, perhaps, the consequence of the lack of professional support. The most extreme eugenicists have not, for the most part, been professional geneticists. Perhaps this situation springs, in part, from a reluctance of the geneticists to think of the social consequences of their knowledge. Certainly, it arises from the geneticists' keen appreciation of the immense complexity of the problem, a problem in which their special competence is of only limited relevance.

What are the difficulties that stand in the way of a comprehensive eugenic program? We may say they are of three sorts:

1. Insufficient knowledge of the role of genes in determining human abilities.
2. Lack of agreement on desirable goals.
3. Lack of political machinery for achieving goals.

Only for the first difficulty does there seem to be an immediate prospect of removal. Acquiring positive knowledge of genes in humans is difficult because there are so few children in a family, and because men and women choose mates to suit their own tastes rather than the geneticist's needs. However, we do have complicated statistical machinery for establishing the role of genes in human inheritance. Ultimately, we shall know quite a bit about the subject. Perhaps, in another three or four hundred years, we shall know as much about human genetics as we learned about the genetics of *Drosophila* in the first five years of study.

241. The Inevitability of Selection

Confronted with a situation such as this, in which wise action is so difficult, one may naturally say, "Well, let's do nothing." In a state of ignorance, such a decision is wisdom. Unfortunately, we cannot act on this decision.

Man, whose powers of increase know no limit, lives in a world in which there are limits to the available energy and physical space. Sooner or later, depending on technological advances and on other factors, the human population will reach a limit. Some authorities think we have already reached this limit; others think that we may have another generation's grace. Already, over a million people die of starvation every year; but, perhaps, these deaths can be charged against poor transportation of food. Whatever the precise details, the logic of our situation is clear. Sooner or later, not all the children that humans are willing to procreate can survive. Either there must be a relatively painless weeding out before birth or a more painful and wasteful elimination of individuals after birth. Whatever means of elimination may be used, will the "thinning" process be carried out in a nonselective manner?

If we neglect to choose a program of eugenics, will the production of children be nonselective?

We have already given evidence (Table 40-1) that productivity is even now selective. People with low I. Q. are reproducing at a faster rate than those with a high I. Q. This may be a good or a bad thing; but it is so. Without our taking conscious action, reproduction is selective.

Though we seldom embark on conscious eugenic actions, we are constantly making decisions that have genetic consequences. Consider the matter of health. From experiments with animals, we know that there are many genes that affect the natural healthiness of an animal. In a state of nature, mutant genes that make the animals more susceptible to diseases are soon eliminated. Genes affecting health must also exist in man; in fact, we have good evidence for the existence of genes that increase the probability of the development of such diseases as tuberculosis, diabetes, and some forms of cancer. In a "state of nature," such genes would be eliminated, due to the increased death rate and, hence, lower reproductive rate of those organisms that possessed the genes.

Man, however, through medical arts, diminishes the disease-produced death rate, perhaps to the vanishing point, permitting the possessors of these genes to reproduce. Thus are the genes saved for posterity. Every time a philanthropist sets up a foundation to look for a cure for a certain disease, he thereby threatens humanity eugenically. Of course, if we have a cure for a given disease, it may not much matter if all the population is susceptible to it—so long as civilization survives. But the population is thereby made more vulnerable to extinction in times of social disorganization. For an example in point, consider diabetes (§ 111). Now that we have insulin in bottles, a diabetic is almost as well off as a normal person, except for the financial drain on his resources. A population composed wholly of diabetics could survive perfectly well—until such time as the organization of society broke down, as it might under war conditions, when there might not be enough technological organization left to effect the chemical extraction of cows' pancreases or to manufacture hypodermic needles.

Again, consider the matter of charity. When one saves a starving man, one may thereby help him to breed more children. This may be a good or a bad thing, depending on the facts. Some people maintain that very poor people are, on the average, less able and intelligent than the rich, and that their deficiencies are, in part, due to hereditary factors. Others maintain that pauperism is exclusively a matter of bad luck; or that paupers are better genetic material than millionaires. There is a need here for indisputable facts; but, whatever the facts, aid to paupers undoubtedly has genetic consequences. A more subtle form of aid to low-income groups is the graduated income tax which taxes the rich proportionally more heavily than the poor. The precise genetic effect of this may be hard to predict, but it undoubtedly has effects.

It is obvious that we have been dealing with highly controversial matters, matters which one ordinarily thinks have no place in a textbook of biology. We do not propose to discuss them further, except to stress once more the point that it is not possible to avoid eugenic action; that every time we support a charity, endow a research institute, or promulgate a new taxation scheme, our actions, whether good or bad, have eugenic consequences, however unconscious we may be of them. We cannot live in the world without acting in it.

242. Opinion vs. Knowledge

In the first chapter of this book, a distinction was made between science and the fields of human interest that are not called science—the fields of ethics and aesthetics, for instance. Such a distinction is commonly made. What one calls a science is, of course, a matter of definition. What do we mean by science? What is the distinction between, for instance, physiology and ethics?

Two characteristics are notable in the fields of knowledge we call sciences:

1. A science deals with "objective" phenomena, things that we know of through the senses.
2. The conclusions of a science are ones to which all "normal" men can agree.

The fields of endeavor that we are not willing to call sciences, as presently defined, do not possess either of the above characteristics. The discipline of ethics is built upon the concepts of "good" and "bad," concepts that clearly do not refer to anything that can be seen, heard, or felt; and the conclusions of one expert in the field are frequently seriously questioned by other experts. The discipline does not seem to be a science.

Can this deficiency be remedied? Can we make of ethics a science? Is it possible to abandon its present fundamental concepts and build a new discipline out of other concepts that refer to things that are objectively knowable, a changed discipline which yet deals in some fashion with the same practical problems that are the concern of the traditional discipline? More important, can we arrive at useful conclusions which are of such a nature as to command the sort of agreement of "normal" men that is now accorded the conclusions in the disciplines we call sciences? The desirability and importance of effecting this change in the nature of ethics becomes daily more apparent.

A generation ago, it was possible to conclude an exposition of a science on a high inspirational note, with a eulogy of the mankind that had gained so great a physical mastery of the world in so short a time. The events of the last few years have made impossible such a conclusion to an elementary textbook of science. What man has accomplished in, geologically speaking, the few seconds of his existence, is truly awe-inspiring; but what remains to be done, and the urgency of doing it, are even more *awe-ful* (in the Biblical sense). The magnitude and immediacy of the problems facing us make an admiring backward glance at our progress seem indecent. In this uncertain world, the only honest glory we may hope to gain is that which may be ours if we attack our problems with clarity and high spirit.

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