Invertebrate Zoology. Harley Jones. Van Cleave. 1931. xiv - 282 pp. McGraw-Hill Book Company.

In writing and revising this textbook of invertebrate zoology the author has successfully avoided the mistake of writing for the sake of impressing his colleagues in the field. In the revision, stress has been taken from the taxonomic organization originally employed, while general material has been introduced such as was formerly found in textbooks of general zoology. The index reveals one brief reference to the entoderm; the ectoderm is referred to the same page while the mesoderm has a paragraph on the following page. Nematocysts are called exclusively "nettling" cells; cnidoblasts are not mentioned; neither for that matter is the coelom given a place in the index although it is mentioned at different places in the text. The echinoderms are discussed between the Molluscoidea and the Mollusca, and one finds scarcely a hint of the possibility of constructing a diphyletic organization of the animal kingdom. This text must have been found useful, otherwise a second edition would not have been called for, and a hasty survey indicates that the revised book is an improvement. —W. C. Allee.

reviewed in "Collecting Net"

July 25, 1931

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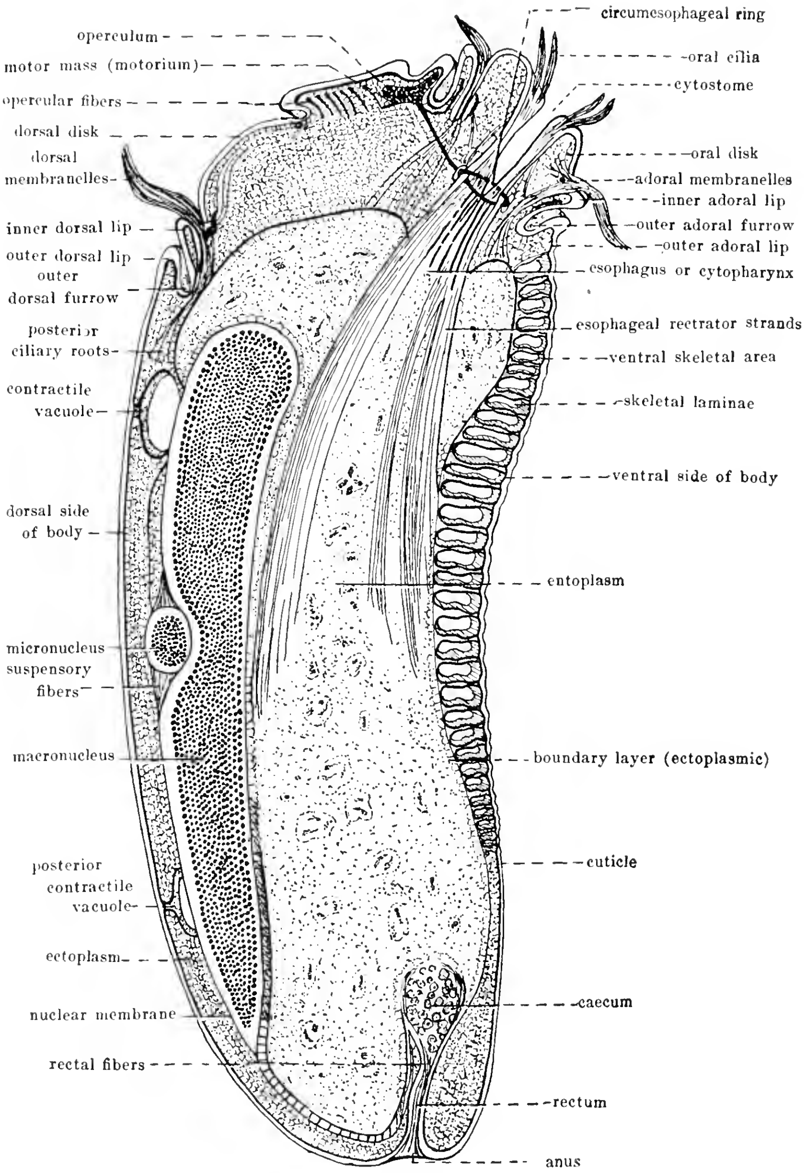

FRONTISPIECE.—Reconstruction of a sagittal section of a ciliate (*Diplodinium ecaudatum*) illustrating the extent to which specialization may proceed within the cytoplasm of a single-celled animal. (*Redrawn from Sharp.*)

INVERTEBRATE ZOOLOGY

BY

HARLEY JONES VAN CLEAVE

Professor of Zoology, University of Illinois

SECOND EDITION

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Dedicated to

HERBERT VINCENT NEAL

PREFACE TO THE SECOND EDITION

In preparing this revision, most of the chapters have been rewritten and a considerable number of new illustrations have been added. Sections on the Protozoa and the Porifera have been wholly recognized reorganized ? and the point of view and interpretations have been rather radically altered so as to bring the contents of these chapters into accord with the recent discoveries and the writings of the best recognized authorities. Six years of use of the text with undergraduate classes have revealed the fact that the original edition carried its material in too formidable a framework of taxonomic organization. Without sacrificing the standards of scientific accuracy, much material of general biological interest has been introduced into the revised edition to relieve the fault of overemphasis on morphology and taxonomy in a general invertebrate text. The severity of the taxonomic organization has been reduced further by the omission of specific sections on the orders from most of the chapters. Pertinent material formerly included under the ordinal headings has been reorganized and placed in the general discussion of the phylum or of the classes where it is less apt to become lost to the student in the intricate maze of systematic relationships of the subgroups.

To compensate for the removal of so much of the formal framework of classification from the body of the text, an outline of classification has been added at the close of the discussion for each phylum. Herein is given a terse characterization of all classes, subclasses, and orders generally recognized for each phylum. For review, for general extension of taxonomic horizon, and for a comprehensive view of the interrelationships of the various subdivisions of the phyla, these summaries give the material an organization which is easily grasped and assimilated.

Throughout the preparation of the revision, a number of advanced students in the University of Illinois have read and criticized sections of the manuscript and have generously assisted in the reading of proofs.

HARLEY J. VAN CLEAVE.

URBANA, ILL.
April, 1931.

PREFACE TO THE FIRST EDITION

An understanding of structure, development, and relationships of animals is essential as a basis for all lines of zoological study and investigation. In the early history of the teaching of zoology, a thorough grounding in these fundamental elements of the science was the chief objective of the introductory courses offered in colleges and universities. It was through an early training of this sort that most of the prominent general zoologists of the present and the preceding generations have passed. Whether they remained in the older fields of general zoology or entered as pioneers into virgin lines of investigation, this broad training gave to them an understanding of animals which could be gained by no other method.

There is a growing practice of placing major emphasis upon biological principles in the fundamental courses in college zoology. There are many arguments in support of such training based upon principles for beginners in the science. However, in such a course students frequently have so little knowledge of animals that there is but limited opportunity for them to have either a full understanding of the principles or capacity for making applications of them. Under these conditions it becomes essential that the introductory course be supplemented by a systematic study of organisms. Even in the instances where the initial course follows essentially the old type method of instruction, the number of forms covered is inadequate and should be followed by further studies.

Because of their relations to human anatomy and development and as specific material for instruction of premedical students, specialized courses in vertebrate zoology are very generally given. For students who are seeking training either as teachers or as investigators, there is fully as much need for specific courses pertaining to the invertebrates.

There have been some admirable large treatises dealing with the invertebrates, and there have been several American laboratory guides intended for such a course but there have been few books available as student textbooks. In the present work, the writer has endeavored to collate materials which will serve as a class room text and reference work at the same time. An introductory course in college zoology is assumed as a prerequisite to a course for which this book is designed as a text.

More material has been included than could ordinarily be covered in a single semester. This offers the instructor greater opportunity of selection in organizing his work than is possible when only the materials for a specific course are presented.

In zoological textbooks, it is frequently the custom to give a detailed description of a representative of each of the major groups. The writer has had a firm conviction that specific information of this nature is more readily grasped by students when they approach it through laboratory study of type forms with a mind unbiased by minute textbook descriptions.

When a highly characteristic representative of a group is described in full detail in the text, the instructor has the alternative of choosing some less characteristic or less easily available species for laboratory study or of permitting his laboratory instruction to become largely routine verification of statements set forth in the text.

By avoiding duplication in the text of materials indented for laboratory approach, it has been possible to place greater emphasis upon biological principles and generalizations in the treatment of each group.

A considerable number of my colleagues, and especially those in the University of Illinois, have rendered valuable assistance in reading and criticising portions of the manuscript and in offering suggestions during its preparation. It is a pleasure to acknowledge the very able assistance of Bernice F. Van Cleave whose criticisms of the early drafts of the manuscript and aid in reading the proofs have been of very great value.

Various publishers have granted the use of cuts or the permission to reproduce illustrations. Henry Holt and Co. and P. Blakiston's Son and Co. have supplied cuts for a considerable number of illustrations. The John Wiley and Sons, The Comstock Publishing Co., Gustav Fischer, and the MacMillan Co. have granted permission to redraw illustrations and in some few instances have furnished cuts. Acknowledgment of these courtesies is further made in the legends accompanying the text-figures.

H. J. VAN CLEAVE.

URBANA, ILLINOIS,
November, 1923.

CONTENTS

INVERTEBRATE ZOOLOGY

CHAPTER I

INTRODUCTION

This book deals with that portion of the field of zoology which concerns all animals other than those included in the single phylum Chordata. Its scope is thus expressed in negative terms, for all animals lacking a backbone are invertebrates. Early in the development of modern classification the term Vertebrata was introduced as the name of a phylum or branch to include the four highest classes of the Linnean system. Popularly, then, all animals have become recognized as either vertebrates or invertebrates. More recently, three small groups of animals, including Amphioxus, the sea squirts, and Balanoglossus, have been shown to possess characters which seem to point to definite relationships with the Vertebrata, even though they lack a vertebral column. One of these characters is the presence of a notochord, a structure which in the embryology of the vertebrates is the forerunner of the vertebral column. As a consequence, the Leptocardii, the Tunicata, and the Enteropneusta as prochordates have been combined with the true Vertebrata to form a phylum which bears the name Chordata.

Technically, then, the terms chordate and non-chordate furnish a more sound basis for distinguishing the highest phylum of animals from all the lower phyla combined, but the widespread and popular acceptance of the terms vertebrate and invertebrate have operated against the general introduction of these terms. Strictly speaking, the prochordates are invertebrates but they are not discussed in this book.

In the classification here adopted, twelve non-chordate phyla are recognized, as follows: Protozoa, Porifera, Coelenterata, Ctenophora, Plathelminthes, Nemathelminthes, Trochelminthes, Coelhelminthes, Molluscoidea, Echinoderma, Mollusca, and Arthropoda.

THE SYSTEM OF CLASSIFICATION

Primary and Subdivisions.—It should be recalled that each phylum is made up of classes, orders, families, genera, and species in descending sequence and that each primary division is capable of still further arrangement into sub- and supergroups. Thus, when a class comprises a large number of orders, it frequently becomes convenient to combine the orders within the single class into two or more groups by uniting those orders which seem to have essential features in common into a subclass or a superorder. Each major or primary group may thus have within it secondary groups of greater scope than the next-lower primary division.

Basis for Classification.—The entire system of classification of animals is based upon interpretation and judgment. There are no absolute units of measure which determine how many species or how many classes any phylum is to include. Every attempt at classification in some measure aims to express varying degrees of relationship between different organisms, and every decision regarding relationships is based upon fixed premises. Proofs of phylogenetic relationships are not procurable through direct observation, but evidences are offered in the structure and development of the individual and frequently through fossil remains of extinct forms which serve as bridges or connecting links between our modern groups. Man's knowledge of all organisms is, at best, but fragmentary. A comparison even of the known facts of structure, development, and habits of two organisms involves much interpretation in determining the relative importance which is to be ascribed to each set of facts. Some structures and organs are highly variable even among the offspring of the same parents, while other characters may be relatively fixed in members of one group and highly variable in those of another. Obviously, then, all facts are not of equal significance in determining relationship and there is no arbitrary means of predicting which are of value and which are worthless in making comparisons.

In common parlance, one organism is said to be higher or lower than another without any conscious analysis of how the decision has been reached. Such an expression, in order to carry weight, is reached only after numerous comparisons have been made and a decision has been reached as to what differences are essential and what incidental.

Primitive vs. Degenerate.—Simplicity of organization is not always a safe guide in the interpretation of relationships, for simplicity of form and structure may be either primitive or secondarily derived as a consequence of degeneracy. A tapeworm (Fig. 67) is simpler in many points of organization than a planarian (Fig. 60 *c*), because the tapeworm lacks a digestive system and special sense organs, both of which are present in the planarian. Primitively, every organism must be able to digest and assimilate its own food materials. Dependence upon some other individual for performing a process essential to life cannot be a primitive condition but is secondarily acquired and has been accompanied by degeneration of the digestive organs in perfectly adjusted parasites. The tapeworm is consequently degenerately and not primitively more simple than the planarian.

Mutability of Group Concepts.—Throughout the entire system of classification, different premises and definitions lead to wholly divergent conclusions. A group which has been considered as a class by one zoologist may be set apart as an independent phylum by another, just because the same observed facts receive different interpretation and the same terms are defined differently. In elementary zoological courses, a rigid system of classification is frequently taught, but the advanced student must sooner or later appreciate the fact that group concepts are man-made devices adopted for man's convenience in his discussions of organisms which seem to be related. Shift of emphasis or new facts and new interpretations play an important part in formulating any scheme of classification, for, after all, group concepts are constructed to include organisms and are not necessarily expressions of natural laws with which the organisms must of necessity agree.

The Law of Priority.—Scientific names of the larger subdivisions of the animal kingdom are subject to considerable differences in usage, for there are no fixed rules governing the acceptance or rejection of names pertaining to phyla, classes, and orders. In contrast with this, the use of names for species, genera, and families is definitely controlled by rules or laws. An International Commission on Zoological Nomenclature was established by the International Zoological Congress (1895) to formulate a code of rules or laws governing the problems of naming animals. One of the basic principles of this code has been the law of priority. According to this law the valid name of a genus or of a species can be only that scientific name under which it was first described, provided that the name is binomial and has not been used previously for some other animal. The same specific name may be used for any number of different animals belonging to different genera.

The tenth edition of Linnaeus' Systema Naturae was published in 1758. Since the appearance of this work marks the first general application of binary nomenclature in zoology, this date has been accepted by the International Commission as the starting point for application of the law of priority.

It frequently happens that after certain generic and specific names come into general use some one discovers that an earlier writer had applied a different binomial name to the same animal. Then the generally accepted name has to be dropped in favor of the prior name. Confusion and inconvenience frequently result from the application of this law but it seems to be the only safe means whereby scientific names may be accepted.

It also frequently happens that a generic name has been used previously for some other genus of animals and in this instance only the earliest use of the name stands as valid, for the second time the name is used it is considered as a homonym. The name Trichina was applied to a parasitic worm in 1835, but in 1830 the same name had been assigned to a genus of insects. It therefore became necessary to rename the worm, and even after the name Trichina came into very general and popular use the worm was renamed Trichinella.

Since the name of a family is formed by adding the suffix *-idae* to the stem of the name of the type genus, family names are also governed by the same laws which govern the use of generic names.

Phylogenetic Relationships.—The arrangement of animal groups in a list or in a book of necessity follows a sequence which places the lowest at one end and the highest at the other. Frequently, this arrangement carries with it the idea that classification intends to express a linear relationship of all forms, that each group has arisen from or has evolved from the one preceding. Such a hypothesis was held by some of the early zoologists, but the more commonly accepted idea of today postulates that our present-day animals are not directly related but that two groups bear closer or more distant relationship to each other chiefly through an extinct form which is an ancestor of both. Thus, for example, among the flatworms the Turbellaria are regarded as the most primitive class in the phylum Plathelminthes, while the Trematoda are considered as a higher class. This does not mean that trematodes had their origin from the turbellarians but probably signifies that both trematodes and turbellarians had a common origin through some ancestral group of past time which was neither trematode nor turbellarian.

Thus, instead of a linear arrangement illustrating the modern idea of phylogenetic relationship of the animal groups, this relationship is best expressed as a branching treelike structure (Fig. 1) in which the various groups are represented by the branches. Closely related groups would be represented by a forking of a common ancestral branch. One point wherein the tree comparison may not be carried too far is that many of the branches connecting modern-day forms are dead or extinct. Through the field of paleontology we have an imperfect picture of these connecting branches in the records left as fossil animals—imperfect because there are so many groups like the naked Protozoa and the worms of which but few fossils are known. Because of the significance of these extinct animals in considering our modern fauna, attention is directed to some of the more important fossil forms throughout the body of this book. The necessity of considering our fauna as a product of the animal life of the past makes it seem advisable to include here a reference table showing the sequence of some of the more important geological periods with some of the dominant forms of life characteristic of each.

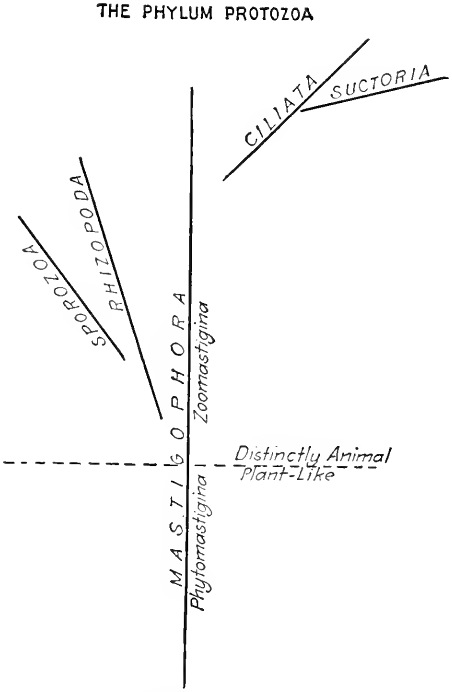

FIG. 1.—Phylogenetic arrangement of the classes in the phylum Protozoa.

Geologic Chronology for North America

(Slightly modified from Lull)

Eras	Major divisions	Periods	Dominant life
Psychozoic			Age of man
Coenozoic	Quaternary	Glacial	
	Tertiary	Late Tertiary	Age of mammals
		Early Tertiary	
Mesozoic	Late Mesozoic	Epi-Mesozoic interval	Rise of archaic mammals
		Cretaceous	Extreme specialization of reptiles
		Comanchian	
	Early Mesozoic	Jurassic	Rise of birds and flying reptiles
		Triassic	Rise of dinosaurs
Paleozoic	Late Paleozoic or Carboniferous	Epi-Paleozoic interval	Extinction of ancient life
		Permian	Rise of land vertebrates, modern insects, and ammonites
		Pennsylvanian	Rise of insects and primitive reptiles
		Mississippian	Rise of echinoderms and sharks
	Middle Paleozoic	Devonian	Rise of amphibia
		Silurian	Rise of scorpions and lung fishes
	Early Paleozoic	Ordovician	Rise of corals, nautilids, and armored fishes
		Cambrian	Rise of shelled animals and dominance of trilobites
Late Proterozoic	Algonkian		Age of primitive marine invertebrates, but very few fossils known
Early Proterozoic	Neolaurentian		
Archeozoic	Paleolaurentian		No fossils; probably only single-celled organisms

REPRODUCTION IN INVERTEBRATES

Many of the early naturalists believed in spontaneous generation of life, that is, that non-living matter gives rise to living organisms continuously. As early as the seventeenth century Redi and some other leaders in science advanced evidences that the more complex organisms cannot originate in this manner. It is only within the past century, however, that the spontaneous generation of the lower organisms was finally discredited and disproved. That all life comes only from living things was only then established as an axiom. Power of reproducing its like is an inherent property of protoplasm which sharply differentiates it from all lifeless matter. Though all forms of life possess this power of reproduction, the detailed steps in the genesis of new individuals are far from uniform throughout the animal kingdom. Of the varied methods of reproduction encountered among animals, common features permit them all to be classified as either asexual or sexual. Any reproductive process which involves the genesis of new individuals through the functioning of specialized cells, termed the gametes or germ cells, is *sexual.* Conversely, any reproductive process which does not involve the functioning of germ cells is *asexual.*

Asexual Reproduction.—In the simplest forms of animal life, the body of a single individual becomes divided into two or more parts each of which by the growth processes assumes approximately the size of the original organism which produced it. This kind of reproductive process wherein no germ cell functions is termed asexual and depends upon the power of part of an organism to reproduce the whole (Figs. 2 to 4). If the products resulting from such a division of the body are approximately equivalent, the term fission is applied to the process. Fission is further recognized as simple or binary (Fig. 2) and multiple (Fig. 3) depending upon whether two or numerous individuals result. In binary fission, the direction of the dividing plane is frequently indicated by specifying whether the fission is longitudinal or transverse. Fission is characteristic of many Protozoa and occurs in isolated instances through many metazoan groups, but in the latter asexual reproduction through the formation of buds is more frequent. In budding (Figs. 4 and 36), a relatively small part of the body of a parent individual becomes modified as a starting point of a new individual. Only after development has gone to certain stages is the bud recognizable as similar to

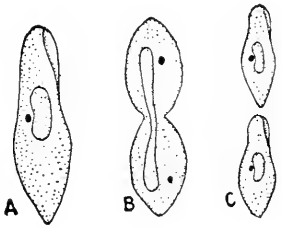

Fig. 2.

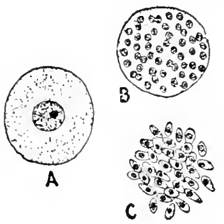

Fig. 3.

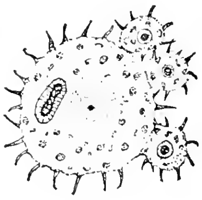

Fig. 4.

Figs. 2–4.—Diagrams to illustrate the methods of asexual reproduction: 2, binary fission in Paramecium; 3, multiple fission or spore formation in a protozoan; 4, budding in Acanthocystis.

the parent. Ultimately, the bud may separate from the parent and become an independent organism, or, in some instances, it remains attached permanently and successive generations retain bodily connection, thereby producing a colony.

Buds usually occur on the external surface of the parent individual, but in some instances groups of cells within the body become surrounded by a membrane and form what are designated as gemmules or internal buds. Typically, these are highly resistant bodies which are liberated by the disintegration of the body of the dead parent and as resting gemmules tide the species over times and conditions which are unsuited for a vegetative period. The gemmules of sponges and statoblasts of the Polyzoa are among the best examples of internal buds or gemmules. In both origin and structure, these are multicellular.

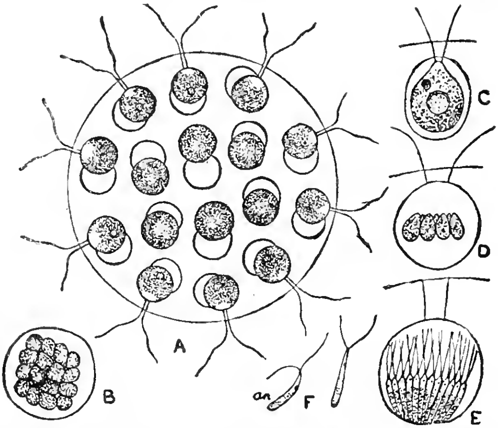

FIG. 5.—*Eudorina elegans* Ehrenberg. *A*, adult colony, ×475; *B*, daughter colony produced by division of one of the cells of *A*, ×730; *C–E*, development of spermatozoa from a mother cell; *F*, spermatozoa. (*From Shull, LaRue, and Ruthven after West and Goebel*).

Sexual Reproduction.—There are relatively few Metazoa which rely upon asexual reproduction exclusively. More frequently a process involving the specialization of cells for reproduction is encountered. Any cell specialized for this purpose is designated as a gamete or germ cell, and reproduction through such an agency is termed sexual reproduction. Even among the Protozoa (Fig. 5) germ cells are encountered. Despite their relative simplicity in organization, there are comparatively few protozoans for which a complete developmental history is known. For some of the most commonly known forms, ignorance of anything beyond an asexual multiplication has led to a widespread belief that simple division is the only means of reproduction. However, in the Protozoa which have been thoroughly investigated, it has been found that an asexual cycle (schizogony) is frequently followed by a sexual cycle (sporogony). Presence of a complicated life cycle, involving an alternation of generations, has thus been established for some single-celled creatures (see Fig. 29).

Specialization of Gametes.—In its most characteristic form, sexual reproduction involves the complete fusion of two specialized gametes to form a zygote (Fig. 6). In some instances, however, the fusing cells are termed isogametes because they seem to be alike in form and function. Though isogametes have considerable significance in hypothetical discussions of the origin and differentiation of sex cells, they are of relatively infrequent occurrence among animals. Even in some instances in which fusing gametes are indistinguishable in size the two react differently to cytological stains and thus give evidence of a probable differentiation even though morphological differentiation is lacking.

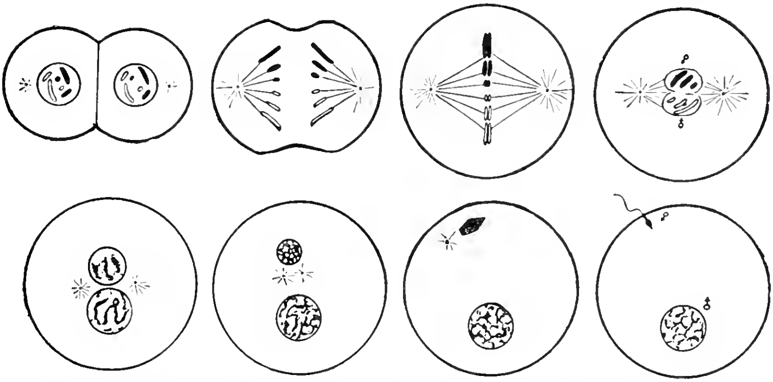

Fig. 6.—Diagram of fertilization and cleavage. It is assumed that maturation of the egg has been completed before the entrance of the spermatozoon. (*After Sharpe*).

The gametes of most animals show two distinct lines of differentiation. The enlargement of the cell through accumulation of yolk or deutoplasm is characteristic of macrogametes or egg cells. In some instances, the ovum does not contain all of the stored food material but is accompanied by special storage cells as yolk cells or follicle cells. Special protective envelopes or shells are frequently developed about the egg cell. The male germ cell or microgamete is usually very minute and represents a specialization for effective locomotion.

In many kinds of animals, but a single type of germ cell is produced by any given individual. Those which produce macrogametes or ova are designated as females, while those which produce microgametes or spermatozoa are called males. When both kinds of germ cells occur in the body of the same individual such a one is said to be hermaphroditic. Usually this condition involves the presence of two distinct gonads but in some molluscs there is a hermaphroditic gonad which produces both eggs and spermatozoa.

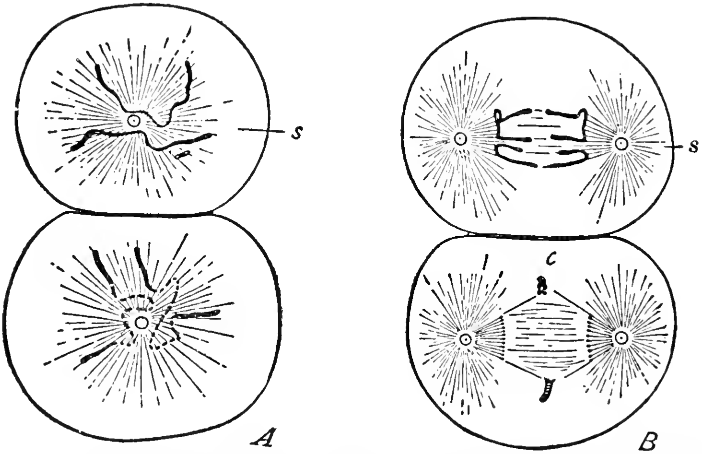

Fig. 7.—Two cell stage in development of the egg of *Ascaris megalocephala*, showing chromatin diminution in somatic cells. Germ cells are derived from blastomere marked *s* which retains all of its chromatin. (*After Boveri*).

Early Isolation of Germ Cells.—Long before germ cells become functional they are readily distinguishable from the other cells of the body. The exact point at which this differentiation of germ cells from somatic cells is accomplished has been determined for only a few animals but in these instances the cells destined to form the gametes are distinguishable at a remarkably early period in development of the young. In *Ascaris megalocephala*, a nematode of the horse, the first division of the fertilized egg (Fig. 7) separates two cells only one of which (*s*) retains all of its chromatin intact. Portions of the chromosomes in the other cell are cast off into the cytoplasm. It is only from the cell with unaltered nuclear content that the germ cells have their origin. But even in this instance the separation of germ cells from somatic cells is not so direct as this narration might imply. In each of about the first five divisions of the cell with its full complement of chromatin one of the two resulting cells undergoes a chromatin diminution but at the end of the fifth or sixth cleavage the germ plasm has been isolated and in all subsequent divisions every blastomere gives rise to either somatic or germ cells.

In several other instances, it has been noted that the cells which later produce the gametes are distinguishable early in embryonic life. In insect embryos, the cells from which the gametes are formed are distinctly larger than the somatic cells. Thus in the fly Miastor, the primordial germ cells (Fig. 8 *gc*) are readily distinguishable from the somatic cells (*cl*) early in the cleavage of the egg.

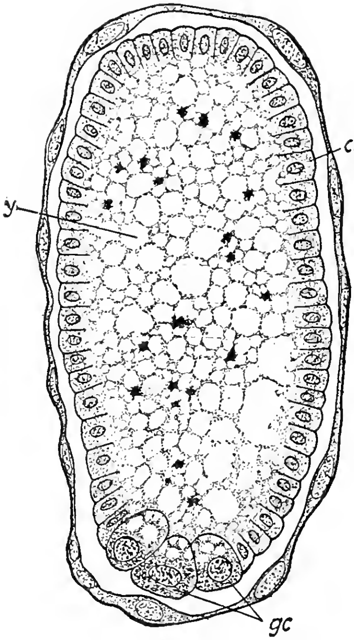

Fig. 8.—Development of a centrolecithal egg of the fly Miastor. Blastula stage showing germ cells (*gc*) at posterior extremity readily distinguishable from the other blastomeres (*cl*). (*From Shull, LaRue, and Ruthven after Hegner*).

Gametogenesis and Fertilization.—Even though the cells which later go to form the gametes are early distinguishable from the somatic cells, they must pass through a complicated series of changes before they are capable of union in fertilization. These changes are collectively termed gametogenesis or, in the male, spermatogenesis and in the female, oogenesis (Fig. 9 *B-D*). Three periods are recognizable in gametogenesis: a multiplication period wherein the relatively small number of primordial germ cells is greatly augmented; a growth period, which involves fundamental changes in the nuclear organization of the cell and in relative size; and finally a maturation period during which the chromosomes in the gametes are reduced to one-half the number characteristic of the somatic nuclei. The modified nuclear division resulting in a reduction of number of chromosomes is known as meiosis. The chromosome number in cells which have not undergone maturation is said to be diploid, because each cell contains two sets of chromosomes, one of which is derived from its male parent and the other from the female parent. Following maturation, the gametes are said to have the haploid or reduced number of chormosomes.

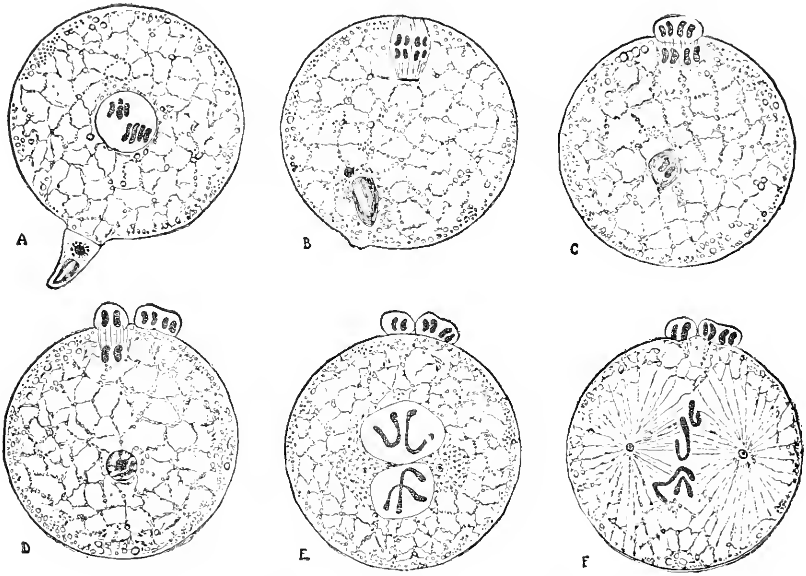

Fig. 9.—Maturation of the egg and fertilization in Ascaris. *A*, spermatozoon about to enter egg; *B*, spermatozoon inside egg; egg nucleus in anaphase of first maturation division; *C*, completion of first polar body; *D*, late anaphase in formation of second polar body; *E*, masturation of egg completed, male and female pronuclei, each with two chromosomes, meeting; *F*, formation of first cleavage spindle from centrosome of spermatozoon, with two paternal and two maternal chromosomes in late prophase. *(From Sharpe after Hertwig).*

The reduction in chromosome numbers is in preparation for fertilization or the union of two gametes to form a fertilized egg or zygote (Fig. 9). By this reduction phenomenon the fertilized egg, and consequently all of the cells resulting from its mitotic division, retain a constant number of chromosomes from generation to generation. Through fertilization a sperm cell with the haploid number of chromosome unites with an egg cell with the haploid number to form a zygote whose nuclear composition is diploid.

In the maturation process, two kinds of chromosomes are usually distinguishable. These are the ordinary chromosomes, which are designated as the autosomes, and others which differ from them both in appearance and in behavior and are termed the sex-chromosomes or heterosomes.

In some instances, the immature germ cells of each sex have a pair of sex-chromosomes. Typically, the sex-chromosomes of the female are both alike and are called the X-chromosomes. On the other hand, in the immature germ cells of the male one of the sex-chromosomes is frequently smaller than the other and is designated as the Y-chromosome. Under these conditions the autosomes of the maturing male germ cells are distributed evenly and equally among the mature cells, but the sex-chromosomes become segregated so that any individual cell in addition to its autosomes contains either an X- or a Y-chromosome but never both. In the male, then, half of the sperm cells contain the Y-chromosome but no X, while the other half contain an X-chromosome but no Y. Every mature egg cell contains the autosomes and a single X-chromosome. Fertilization of an egg cell by a spermatozoon containing the Y-chromosome produces a zygote from which only a male could develop, but fertilization by a spermatozoon with an X-chromosome produces a zygote from which only a female could develop.

The Y-chromosome may be entirely lacking in some species. Under these conditions, there are two kinds of male sex cells formed: one with the autosomes plus an X-chromosome, the other with autosomes alone.

While the dimorphism in the germ cells is usually characteristic of the male, there are some instances recorded, as in the birds, in which all of the male germ cells are alike, but the female germ cells show chromosome differences.

Composition and Cleavage of Zygote.—Except for the possibility that one of the fusing germ cells may have one more chromosome than the other, the two gametes contribute equally to the chromatin content of the zygote. The cytoplasm of the zygote is that contained in the mature egg except for a practically insignificant amount brought in by the entering sperm cell. The stored food material, which provides the energy requisite to the life processes of the embryo, is furnished by the deutoplasm of the egg cell, except in those forms which have accessory yolk cells accompanying the egg and those which receive nourishment from the parent individual. The so-called middle piece of the sperm cell contains a centrosome. Barring some very unusual circumstances, this centrosome brought in by the male pronucleus forms a mitotic spindle within which the chromatin of both the male and female pronuclei becomes commingled. The mitotic division of the fertilized egg which ensues is followed by cleavage of the surrounding cytoplasm. Through a continued sequence of mitosis and cleavage, large numbers of cleavage cells or blastomeres are formed.

Cleavage Patterns.—The relative size and arrangement of these blastomeres is greatly influenced by the amount and distribution of the stored material within the egg. If the yolk is evenly distributed, the egg is said to be homolecithal and it undergoes a complete cleavage resulting in the formation of numerous cells, all of which are practically uniform in size. However, deutoplasm is heavier than the surrounding cytoplasm, and in many instances tends to accumulate at the vegetative pole of the egg. The term telolecithal is applied to such an egg. Yolk serves as a mechanical obstruction to the paths of the cleavage planes. Consequently, if the vegetative pole is heavily yolk laden, cleavage is restricted to a disc of cytoplasm at the animal pole. However, in some telolecithal eggs, the entire cell cleaves, but, since the mitotic spindle tends to take a position in the center of the cytoplasm of the cell, spindles will be formed nearer the animal than the vegetative pole and as a consequence the resulting cells are unequal in size. The cells at the animal pole are much smaller than those at the vegetative pole. Some arthropod eggs have the yolk collected in the center and are therefore said to be centrolecithal. Cleavage in such an egg is restricted to the layer of cytoplasm surrounding the yolk (Fig. 8) and is referred to as superficial cleavage.

The blastomeres resulting from cleavage of the fertilized egg assume various arrangement patterns. In some groups of animals, the blastomeres fail to follow any orderliness in their formation and arrangement. Instances of this sort are designated as indeterminate cleavage. This condition stands in sharp contrast with that found in some other groups, the members of which have cleavage processes so orderly that it is possible to predict with exactitude the direction which successive cleavage planes will take. Determinate cleavage, as this is called, renders it possible to trace the history of each blastomere, to follow through a cell lineage the succession of blastomeres, and to tell what organ or structure of the larva or adult is ultimately to be formed from any given blastomere. This recognition of a fixed arrangement of the cells is especially characteristic of annelids and molluscs (Fig. 10). The annelidan cross and the molluscan cross are terms which are applied to the fixed cleavage patterns characteristic of these respective groups. The orderly processes which give rise to fixed relations of the cells of the embryo are carried throughout the entire life of some organisms, for scattered through the various phyla there are examples of animals which in the adult stage possess an absolutely fixed number of cells or of nuclei in all or in part of the organs of the body. Such a condition is spoken of as cell constancy or nuclear constancy.

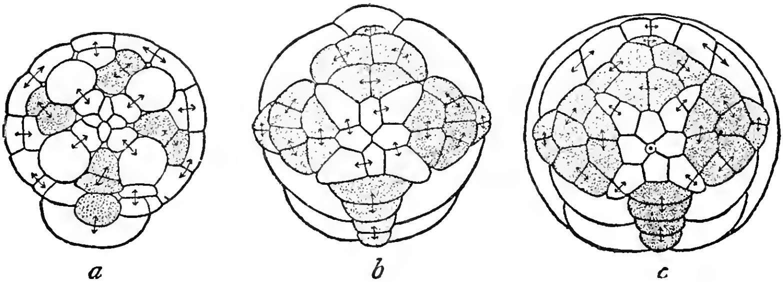

FIG. 10.—Diagrams showing cleavage pattern in Mollusca and Annelida. *a*, blastomeres of Nereis (*after Wilson*); *b* and *c*, blastomeres of Crepidula. The stippled cells form the Molluscan Cross. The four unshaded cells at the pole of the embryo are termed the apical cells, while the unshaded cells radiating from these comprise the Annelidan Cross. (*After Conklin*).

Blastula and Gastrula.—All eggs pass through a stage called the blastula wherein the blastomeres are usually arranged in a single layer. Typically, the cells surround a central fluid-filled cavity, but in centrolecithal eggs the fluid-filled cavity is replaced by a solid yolk mass. The cells in certain regions of the blastula multiply more rapidly than the surrounding cells. Typically, in the homolecithal egg this unequal growth causes part of the wall of the blastula to be forced within the blastula cavity as an inpocketing or invagination. This stage in development is termed a gastrula and is composed typically of an outer layer of cells, the ectoderm, and an inner layer, the entoderm, which surrounds a central cavity, the gastrula cavity or archenteron. Primitively, this archenteron is in communication with the exterior through an opening, the blastopore. A gastrula such as that just described occurs only in the homolecithal type of egg. In telolecithal eggs, with total cleavage, the small blastomeres at the animal pole multiply much more rapidly than do the heavily yolk-laden vegetative cells. As a consequence, the cells from the animal pole grow down and surround those of the vegetative pole which thereby become the entoderm, while the small surface cells are recognizable as ectoderm. In such a gastrula, there is no archenteron within the entoderm. Gastrulation by this method is termed epibolic gastrulation. In telolecithal eggs with only partial cleavage, a modified invagination occurs through a shoving in of cells near the edge of the cleavage disc. As mentioned above, blastula formation in the centrolecithal eggs gives rise to a layer of cells arranged around the central yolk mass. In later development, each cell of this blastula undergoes a cleavage parallel to the surface of the egg. Thereby a two-layered condition or a gastrula is attained and the process is spoken of as delamination.

Mesoderm and Later Development.—The addition of the third body layer, the mesoderm, between the ectoderm and the entoderm is one of the most conspicuous and most significant features in later development of all animals above the coelenterates. Development from this point onward is subject to so many individual differences that few general statements may be made. In many of the more generalized groups, the attainment of the gastrula stage marks the beginning of an independent existence. By means of cilia the larva has the power of movement and through the blastopore food is taken into the archenteron where it is digested and assimilated. However, in many groups and especially in terrestrial and fresh-water forms, the individual is carried far past the gastrula stage while still confined within the egg membranes. In the extreme of such cases, the individual which emerges from the egg is essentially like the adult except in size and stage of development of the reproductive organs. Throughout its development, the young of such a form would be referred to as an embryo. On the other hand, if the individual produced from the egg lacks some structures characteristic of the adult and possesses others which are lost in later development, the young is ordinarily termed a larva. Many different larval forms are encountered in the various invertebrate groups but these are so numerous and have such diverse forms that descriptions of them will be given in the discussion of the groups in which each type belongs. It should be mentioned, however, that these larval stages are frequently considered as having great phylogenetic significance. Groups having fundamentally similar larvae are usually considered as having developed from a common ancestral form, for there are many evidences supporting the law of biogenesis which states that ontogeny is a brief recapitulation of phylogeny.

Parthenogenesis is sexual development without fertilization. The eggs of many kinds of animals undergo a modified type of maturation and are then capable of development without fertilization. It is not uncommon for parthenogenesis and true sexual reproduction to alternate in the life cycle of the same species. The parthenogenetic habit has become thoroughly established in some species of animals. Frequently, in such instances, males are extremely rare and there are some species which reproduce parthenogenetically in which males have never been observed.

Paedogenesis and Polyembryony.—The gonads of some individuals become functional before the body reaches adult form. In some of the dipterous insects (flies of the genus Miastor, for example), the larvae become precociously mature and as maggots produce mature eggs. These eggs undergo parthenogenetic development within the body of the larva and a new generation of larvae is produced within the body of each. This type of precocious parthenogenetic development is termed paedogenesis.

It has been demonstrated that in some instances a single fertilized egg may give rise to more than one individual. This condition, which has been termed polyembryony, occurs in both invertebrates and vertebrates and is especially characteristic of some insects. This power of development of an entire individual from a portion of an embryo calls to mind the fact that experimentally the blastomeres of many of the marine invertebrates may be isolated and each blastomere thus separated forms a complete individual.

Breeding Habits.—Regarding breeding habits, numerous different conditions exist. In the Protozoa and among many lower Metazoa, isolated gametes are set free into the surrounding medium and fertilization occurs entirely apart from the bodies of the parent individuals. Motility, at least of the male gametes, and chemical emanations from the female gamete bring the two germ cells together and thus insure fertilization. Under such conditions, the larva or young of Metazoa passes through its embryological stages until it is capable of independent maintenance. Among many Metazoa, this stage is reached with the gastrula, for at this time the larva contains organs differentiated sufficiently to enable it to ingest and utilize food from the outside world. For its metabolism prior to this time, the embryo has been dependent upon the food substances stored within the egg. Correlated with increase in quantity of stored food material within the egg, the young of many species undergo complete development upon the materials thus furnished, as mentioned above, and never lead an independent larval existence.

Frequently, the eggs are fertilized while still within the body of the female. This may involve a copulation whereby sperm cells are deposited within the body of the female by the male through some sort of intromittent organ, or, in some instances, as in the rotifers and leeches, sperm cells are united in groups called spermatophores which penetrate the body wall of the female. Parts of the body of the female may be modified as a seminal receptacle for receiving the sperm cells from the male, though fertilization of the eggs may be deferred for some time, even several years, after copulation has taken place. In hermaphroditic forms, there are several distinct methods of fertilization. Reciprocal copulation (Fig. 78), whereby sperm cells from one hermaphroditic individual fertilize the eggs of the other, occurs in many instances. Self-fertilization is also encountered in some hermaphroditic organisms.

Birth Habits.—When eggs are discharged before cleavage has begun, the species is said to be oviparous. Frequently, the egg is retained within the body of the female until the young is fully formed and the larva emerges from the egg membranes before it leaves the body of the parent. This condition is designated as viviparous. Any condition intermediate between these two extremes is termed ovoviviparous. In this condition, the egg has at least started to divide before it leaves the body of the parent. In popular, and sometimes in scientific, usage the term oviparous is applied to any condition in which the female brings forth eggs, regardless of the stage of development of the contained ovum or embryo. The term ovoviviparous is in this instance restricted to that condition in which the embryo is liberated from the egg membranes just before it leaves the maternal body.

General References

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CHAPTER II

PHYLUM PROTOZOA

The Cell as an Individual.—The Protozoa represent the simplest organization of animal protoplasm to form independent units or individuals. Though in the typical examples the individuals comprise single cells (Figs. 15, 19, 20), the cytoplasm of these cells has undergone various lines of differentiation and specialization. Thus these cells are far from simple or "undifferentiated" when considered from the point of view of adaptation for numerous different functions (see Frontispiece). The chief point of distinction between the cell of a protozoan and one of a many-celled animal (metazoan) lies in the fact that in the former all of the functions of a living animal are executed by a single mass of protoplasm. Any specialization for different functions in the single cell must be restricted to specialization of a part within that cell. On the other hand, the Metazoa are composed of numerous cells, groups of which have become specialized for limited functions. Consequently, for the rest of the functions characteristic of living matter these cells of limited function in the Metazoa become more or less dependent upon the other cells united with them to form an aggregate termed an individual. It thus becomes obvious that differentiation in Protozoa usually involves specialization of the parts within a single cell, while in the Metazoa entire cells become specialized for limited functions. In this light it is readily understood that "undifferentiated" as applied to a protozoan cell does not imply "unorganized" for the organization found there is frequently much higher (see Frontispiece) than in many kinds of metazoan cells which have undergone histological differentiation (Figs. 37–46).

Protozoa as Non-cellular Organisms.—Since the concept of the Protozoa as simple organisms has led to such widespread misunderstanding of the true nature of these complicated, though minute, animals, some protozoologists have chosen to consider Protozoa as non-cellular. The advocates of this position hold that the body of a protozoan with its specialized regions represents a mass of protoplasm which has undergone modifications for varying functions though the body of the protoplasmic mass has never become divided into cellular units.

Some other workers prefer to retain the morphological comparison of a protozoan as a single cell while they draw their contrasts on the side of differences in physiology or function. In his "Biology of the Protozoa" Dr. Calkins has well expressed his view in the words:

> . . . while a single protozoan is to be compared structurally with a single isolated unit tissue cell of a metazoan as a bit of protoplasm differentiated into cell body, or cytoplasm, and nucleus, it is a very different unit physiologically. In its vital activities it should be compared not with the unit tissue cells, but with the entire organism of which the tissue cell is a part . . . it is still a cell and at the same time a complete organism performing all of the fundamental vital activities within the confines of that single cell.

The complexity of structure within a single-celled protozoon is well illustrated in the figure of Diplodinium which faces the title page of this book. The multiplicity of specialized parts in this animal does not permit one to think of it as a simple organism.

Metazoan Tendencies.—There is no broad gap separating the simple, single-celled Protozoa on the one side from the Metazoa on the other. Many Protozoa, especially among the Mastigophora and Ciliata, show distinct tendencies toward specialization of cells. Frequently, the cells resulting from the division of a single one remain attached, thus forming a group which functions as a unit and is termed a colony (Fig. 5). Within such a group only part of the cells may retain the powers of reproduction while the others carry on all of the remaining functions for the colony. This marks an early separation of two kinds of cells, the germ cells as distinct from the body or somatic cells (Fig. 5). Separate germ cells or gametes occur in many different kinds of Protozoa, in fact it is not uncommon for two different kinds of gametes to make their appearance in this group as microgametes (male germ cells) and macrogametes (female germ cells), but in all these instances all of the somatic cells remain similar. Thus, there is a finely graded series of changes which connects the single-celled condition and the colony bearing only one kind of somatic cells and one or more types of germ cells. Most zoologists agree that this marks the limit of histological differentiation in the Protozoa.

If histological differentiation of the somatic cells occurs, the organism is recognized as a metazoan.

Definition.—An inclusive definition of the Protozoa might be given as follows: The Protozoa constitute that phylum of the animal kingdom which includes all single-celled animals and cell aggregates in which there is no histological differentiation of the somatic cells.

Organization.—Because of their small size, Protozoa were entirely unknown to the early scientists. Their study dates from the introduction of the microscope. Most of the early observers maintained that Protozoa are made up of complete systems of organs such as are found in the higher animals. Dujardin denied the presence of organ systems. Definite comparisons with single cells of the Metazoa were first made by de Bary as early as 1843 but it was left for von Siebold (1848) to describe them as unicellular.

In lax usage, the term organ is still used in referring to those parts of the protozoan cell which have become adapted to special functions. More correct usage restricts this term to cell groups. Accepting this limitation, it becomes necessary to designate differentiated structures in Protozoa as cell organs or organellae. This distinction has led to a rather common usage of terms such as cytostome (cell mouth), cytopyge (cell anus), cytopharynx (cell pharynx), in referring to the organellae of Protozoa.

The five classes of this phylum differ so widely in structure and degree of specialization of parts that little may be said that would apply equally to all animals included here. While most Protozoa are small in size, the plasmodia of the Mycetozoa may cover a surface several inches in diameter. At the opposite extreme stand the Sporozoa, many of which pass through a spore stage in which the individual is less than 1 micron in diameter. These represent about the smallest cells known in the animal kingdom.

The cytoplasm of a protozoan cell is usually divided into a covering ectoplasm and a more distinctly granular internal mass, the endoplasm. Within the ectoplasm, there are extreme differences in organization, for in some instances it is reduced to an extremely thin layer while in others it is stratified into several distinctly separable regions. In the Microsporidia, and some other forms, no differentiation of the cytoplasm into layers has been demonstrated.

Habitats.—Protozoa are encountered in extremely diverse habitats. All classes, with the exception of the Sporozoa, have numerous species which occur as free-living organisms in both fresh and salt water. Soil-inhabiting species are not uncommon.

Many species are widely distributed over the face of the earth wherever conditions favorable for their existence are found. This broad distribution seems to be associated with the power of entering into an inactive state during which the body is surrounded by a protecting wall. This encysted condition may come as part of a definite life cycle or may result from inhospitable conditions, such as the evaporation of the water in which active specimens are living. In this state the inactive cysts may be carried extremely great distances by the wind or other agencies of distribution. Encysted forms are excellent examples of suspended animation, for when the cysts fall into favorable conditions the cyst wall is lost and the protozoan becomes active after its period of dormancy. By this means many species have attained almost cosmopolitan distribution, so that students in Europe, Asia, Africa, and South America find in their pools and lakes many of the same species that North American students encounter. Forms of the open ocean and of the deep seas seem to be more restricted in their distribution. Even different regions in the same ocean may yield characteristically different lists of protozoan fauna. The limitations of distribution in the ocean are even more striking when we consider that certain species live only at the surface of the water while some genera have never been discovered anywhere except in the extreme depths of the seas.

Many forms occur as cysts in the soil but some, especially rhizopods and flagellates, remain active in ordinary garden soil and are thought to be important because they feed upon bacteria of the soil. Little is known of the actual role of Protozoa in connection with the problems of soil biology. While active Protozoa doubtless feed upon important soil bacteria, no one has yet proved that they exert an injurious effect upon the soil.

The parasitic habit has become the exclusive condition among the Sporozoa, but in each of the other classes the same habit is encountered to a greater or less degree. Some species have the faculty of leading either an independent or a parasitic existence, as opportunity is presented to the individual animal. Especially in tropical countries the diseases of man and of his domestic animals are very frequently the result of protozoan parasites. Malaria, sleeping sickness, dysentery, Rocky Mountain spotted fever, Texas fever are some of the diseases for which the causal agent is a protozoan.

Food Habits.—In food habits, the Protozoa display great diversity. Many of the chlorophyll-bearing Mastigophora are plantlike in their metabolism. Under the influence of sunlight their chlorophyll synthesizes food substances in a purely plant-like manner. These forms in which the food is built up from simple compounds by the processes of photosynthesis are designated as autotrophic.

Most of the Protozoa are holozoic in their metabolism and require complicated organic compounds as foods. These organic foods may be ingested as solid particles either through the action of pseudopodia as in Amoeba and other Rhizopoda or through a cytostome as in Paramecium and many other ciliates and many flagellates. In the endoplasm, these solid food particles undergo digestion in food vacuoles before they are assimilated. In the instances just cited the food material may be either living or dead plant or animal matter. However, in some species the predaceous habit is rather firmly fixed. Thus Didinium lives largely upon paramecia the bodies of which it ingests through a highly specialized cytostome located at the tip of a proboscis. The Suctoria through their hollow tentacles are enabled to suck out the protoplasm from other organisms and utilize it as food.

Organic matter may be absorbed through the body surface in many Protozoa. This is especially true of forms which lack a cytostome. These organisms dependent upon the absorption of elaborated food stuffs may be either parasitic upon living organisms or may utilize decomposing organic matter. In the latter instance, they are said to be saprophytic.

Cultures.—Under usual conditions, Protozoa are present in stream, pond, or lake water in relatively small numbers. Various factors in the environment cooperate in keeping the numbers of any given species from becoming excessive. If individuals of a given species multiply unusually, forms which feed upon this species, or depend upon it in other ways, will naturally increase, thereby tending to reduce the excessive numbers. Thus the "balance of nature" works here even as among the higher forms of life. If food is present in excess and natural enemies are lacking, the balance is broken and immense numbers make their appearance. This is what happens when an infusion or culture medium, rich in food material, is allowed to stand in the laboratory to produce a protozoan culture.

There is a tendency for the forms appearing in laboratory cultures to follow a regular though not absolute sequence in the order of their appearance. The first forms to become abundant are frequently minute flagellates (monads). According to the observations of Woodruff these are followed in succession by the Ciliata: Colpoda, Hypotrichates, Paramecium, and Vorticella. Only in very old cultures following the foregoing series did he find Amoeba in relative abundance.

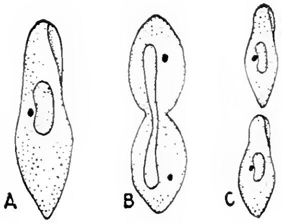
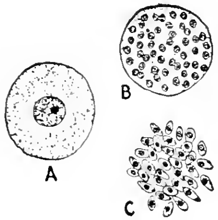


Fig. 11.



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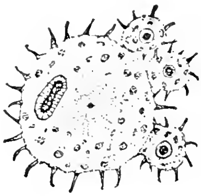

Fig. 13.

Figs. 11–13.—Diagrams to illustrate the methods of asexual reproduction. 11, binary fission in Paramecium; 12, multiple fission or spore formation in a protozoan; 13, budding in Acanthocystis.

Though most species of the free-living, fresh-water Protozoa will reproduce in laboratory cultures, there are some which refuse to do so and though abundant in the plankton are not found in laboratory cultures. Examples are some of the dinoflagellates and ciliates of the family Tintinnidae.

Reproduction.—Various forms of reproduction are encountered in this group. The one most frequently found is that of binary fission. In this process, the nucleus usually undergoes an indirect division and this is followed by constriction and finally separation of the cytoplasm to form two new individuals (Fig. 11). Commonly, structures become duplicated in the dividing individual before fission is completed. Fission not uncommonly occurs when individuals are in an inactive or encysted state. A type of multiple fission (Fig. 12) is characteristic of some groups of Sporozoa and Mycetozoa. In this instance, the nucleus undergoes a series of divisions. Each of the nuclear masses thus formed becomes surrounded by a layer of cytoplasm and upon the rupture of the original cell wall numerous small cells, called spores, are liberated.

In the indirect nuclear divisions mentioned above, there are frequently one or more points wherein the process differs from mitosis as it occurs in metazoan cells. When the centrosome occurs within the nuclear wall, the entire process of division may be accomplished without the disappearance of the nuclear membrane. Frequently the chromatin is present as one or more large bodies which are termed karyosomes. These constrict and divide without chromosome formation, in a manner somewhat resembling amitosis. The term promitosis has been applied to this primitive type of indirect nuclear division to distinguish it from the more elaborate mitosis.

In some flagellates and rhizopods the chromatin is not confined to a nucleus but is spread more or less uniformly throughout the cytoplasm. Such distributed chromatin granules have been observed by some investigators to form minute secondary nuclei (as in Actinosphaerium) which become the nuclei of conjugating gametes.

Because of the important role that chromosomes have assumed in discussions of heredity in the Metazoa, much interest has centered around a discussion of the nature of chromatin masses in Protozoa. Some investigators maintain that in many species of Protozoa definite chromosomes appear in specifically characteristic numbers.

Many Protozoa have a definite life cycle more intricate than a simple succession of fission states. Frequently, this cycle involves two distinct types of adult individuals: sporonts, which give rise to gametes, and schizonts, which give rise to asexual individuals. There may thus be an alternation of generations involving two distinct types of developmental cycle: a cycle of sporogony, during which gamete formation and fertilization occurs, and one of schizogony, during which no sexual process is involved. These alternating cycles in the free-living forms are correlated with environmental conditions, especially seasonal changes, while in the parasitic species thay are frequently correlated with change of host. In the malarial organisms (Fig. 29), for example, schizogony continues during development of the organism in the vertebrate host and sporogony involving the fertilization of gametes is restricted to the sojourn of the parasite in the body of the mosquito.

Budding (Fig. 13) differs from fission chiefly in the relative sizes of the resulting parts. In fission, two or more approximately equivalent parts result from the partition of one individual. Through budding, on the other hand, the identity of a parent organism is retained, for the buds arise as smaller outgrowths from the body of the producing individual.

Conjugation in the Protozoa involves either the temporary or permanent fusion of two or more individuals of the same species. A simple type is found in the fusion of the cytoplasm of a number of individuals to form a plasmodium, as in the Mycetozoa. More frequently the nuclei are involved in either a permanent fusion resulting in true fertilization or a temporary fusion involving an exchange of nuclear material.

Endomixis.—An intricate process of nuclear reconstruction without the fusion of individuals occurs in some Protozoa. Details of this phenomenon, which is termed endomixis, have been observed especially in Paramecium by Doctors L. L. Woodruff and Rhoda Erdmann. They found that in Paramecium the macronucleus gives off budlike fragments at regular time intervals and that these fragments are absorbed in the cytoplasm. While the macronucleus is being broken up, the micronucleus undergoes a series of divisions, differing in detail in the different species but resulting in the formation of eight products. In *Paramecium caudatum*, which has a single micronucleus, a series of three divisions produces the eight micronuclear bodies; while in *P. aurelia*, which has two micronuclei, only two divisions of the micronuclei occur. Part of the eight micronuclear bodies disintegrate while of the remainder some form micronuclei, others macronuclei. Thus wholly new nuclear equipment is formed from a portion of a micronucleus after a manner strikingly similar to the nuclear reorganization following conjugation. In *Paramecium caudatum*, endomixis occurs at regular intervals of about 60 days, while in *Paramecium aurelia* the period is approximately 30 days.

In some other ciliates endomixis has been observed but in these it usually occurs during an inactive period of encystment.

Heredity in the Protozoa.—Studies on heredity in the Protozoa have been distinctly hampered by the lack of conclusive information on the entire life cycle in all but a relatively few species. Some forms, as far as known, reproduce by simple division. Here, obviously, any mechanism for inheritance would be simple indeed. On the other hand, those species which undergo conjugation possess all of the possibilities for recombinations of nuclear material from two parents which characterize the highly complicated mechanism of biparental inheritance in the Metazoa. Intermediate between these two extremes lie those species in which endomixis occurs. This process, with its striking similarity if not full equivalence to parthenogenesis in the Metazoa, introduces the possiblility of recombinations of the gene-bearing chromatin within the body of the single individual.

Many types of bodily change have been recorded among Protozoa, seemingly due wholly to environmental changes such as those in the medium, in temperature, etc. Even certain types of mutilation are passed on to the progeny for a limited number of generations. But the evidence is fairly conclusive that here, as in the Metazoa, changes originating during the life of the individual are not permanent. When abnormal individuals produced by a changed environment or by mutilation are returned to normal surroundings the body eventually assumes its characteristic form.

Extensive work on selection has been carried on by H. S. Jennings and others who have found that a single individual of a "wild" population may contain a great number of hereditary characteristics stored up in the single individual through its past history of chromatin interchange during conjugation. When such wild individuals are isolated and their offspring are reared under uniform conditions, extremely diverse individuals may be secured, evidently the result of recombinations of characters. For one species of Paramecium, Jennings discovered eight distinct races each reproducing its own kind.

Colony formation frequently results from incomplete separation of cells following division. The products of rapid division may remain in union for a short time to form a temporary aggregate which ultimately separates into its individual cells, or they may remain permanently associated to form a colony. The connections and relationships between the individuals of a colony are highly varied. The cells of the colony, regardless of their arrangement, usually have connections of protoplasm passing from one to another. By this means communication between the cells is carried on readily and the actions of the individual cells are coordinated so that the group behaves as a unit.

The individual cells in many colonies are not bound closely together but are loosely associated by protoplasmic connections (Fig. 14) or by individual stalks of attachment. The appearance of unity is greatly strengthened in many colonies by the presence of a regularly shaped gelatinous mass (Fig. 5) in which the cells are embedded. Branching or arboroid colonies (Fig. 14) frequently occur in the Peritricha and in some Mastigophora. Highly developed colonies (Fig. 5) are common in the Mastigophora, especially among the Euglenoidea. Because of the similarity between various mastigophoran colonies and the cleavage and blastula stages in the development of Metazoa, this group has frequently been cited as the one most directly in line with metazoan phylogeny. However, some workers are inclined to the view that while colony formation is less characteristic of the Ciliata, specializations found there demand consideration in any discussion of the phylogeny of the Metazoa.

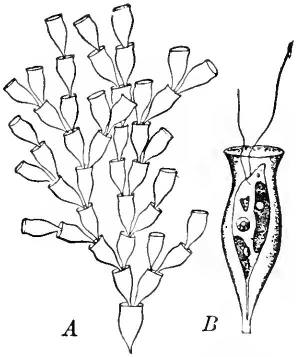

Fig. 14.—One of the colonial Chrysomonadina, *Dinobryon sertularia* Ehrenberg. *A*, arrangement of cells in treelike colony; *B*, individual in its cuplike sheath. (*From Shull, La Rue, and Ruthven after Kent*).

The general plan of classification by Doflein has been adopted in the present work. In this system, relationships are more clearly shown than in the older systems which involve recognition of four equivalent classes. In the remainder of this chapter, the following subphyla and their included classes are discussed:

- Subphylum I. Plasmodroma.
  - Class 1. Mastigophora.
  - Class 2. Sarcodina.
  - Class 3. Sporozoa.
- Subphylum II. Ciliophora.
  - Class 4. Ciliata.
  - Class 5. Suctoria.

SUBPHYLUM PLASMODROMA

In the subphylum Plasmodroma are assembled all Protozoa which never develop cilia, while the subphylum Ciliophora includes those which have cilia at least during part of their existence.

Class Mastigophora

The presence of one or more flagella is practically the only character common to all Mastigophora. More than superficial examination is necessary to distinguish some Mastigophora bearing numerous flagella from ciliates, and on the other hand the boundary between Mastigophora and Sarcodina is obscured through the presence of temporary flagella on some of the Sarcodina and of pseudopodia on some of the Mastigophora (Fig. 15). In addition to these confusing relationships with other classes of Protozoa, there are some forms which are so distinctly plantlike that they are claimed alike by zoologists and botanists. Body shape is far from constant in many forms, the degree of constancy depending upon the character of the body surface. In some, the pellicle is either wanting or so thin as to permit of free amoeboid movements. Limitation to change in shape is secured in some by the presence of supporting structures of organic matter such as the axostyle (Figs. 21 and 22).

FIG. 15.—*Mastigella vitrea.* (*After Goldschmidt*).

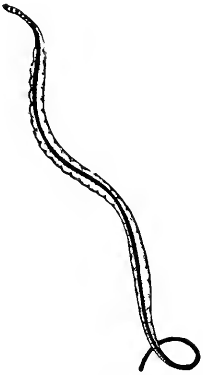

FIG. 16.—Isolated flagellum of Euglena showing axial filament within surrounding sheath. (*After Bütschli*).

Each flagellum (Fig. 16) consists of a firm axial filament, part of which is encased in a more fluid contractile sheath. Distally, this filament extends a short distance beyond the sheath and constitutes an "end piece." Proximally, the axial filament continues through the cytoplasm to the blepharoplast, though in some instances the basal granule from which the flagellum arises may be separate from the blepharoplast and connected with it only by a delicate thread, the rhizoplast. There is thus developed a system of centers associated with the base of the flagellum, connected by fine protoplasmic fibers. The name kinetic elements has been applied to this system in the belief that it controls or directs the activity of the flagellum. In most of the parasitic, but lacking in the free-living flagellates, there occur one or more masses of deeply staining substance known as the parabasal body (Fig. 21) associated with the kinetic elements. These are thought to be a store of material to be used by the kinetic elements in their functioning. Kofoid and his followers refer to this whole group of blepharoplast, nucleus, rhizoplasts, and parabasal body as a neuromotor apparatus.

Among the more characteristic Mastigophora, the flagella occur at the anterior extremity. If they are directed forward and by their movement pull the body along, they are called trachella; if they are directed backward and by their movement propel the body ahead, they are designated as pulsella. The trachella are the more common type. In many Mastigophora, flagella arising at the anterior extremity are directed backward along the side of the body as trailing flagella. These may be either free or fused with the side of the body as an undulating membrane as in the Trypanosomes (Fig. 23).

Even in some chlorophyll-bearing Mastigophora there is a cytopharynx, though it is not always functional for ingestion of solid food. Contractile vacuoles usually empty into the cytopharynx, either directly or through communicating canals and reservoirs.

A single nucleus is usually present, though in some of the parasitic forms there may be two (Giardia, Fig. 21) or many nuclei, as in members of the family Calonymphidae, parasitic in termites.

On the basis of relationships and general methods of metabolism, the Mastiogophora may be divided into two subclasses. The distinctly plantlike forms are included within the Phytomastigina, while the ones displaying more pronounced animal characters are grouped within the subclass Zoomastigina.

Subclass PHYTOMASTIGINA

Members of this subclass have one to four flagella located at the anterior extremity. The cytoplasm is usually very finely granular, not heavily vacuolated, and without distinct boundary between ectoplasm and endoplasm. Typical members of this group (Fig. 17) possess chromatophores, frequently brown or yellow in the lower forms and green in the higher. Especially in the latter, chlorophyll is found. While members of this subclass are characteristically capable of manufacturing their own food, there are but few which are entirely lacking in power of taking in either fluid or solid foods. Contractile vacuoles are usually present in the fresh-water forms either as a simple pulsating vacuole or as a more highly complicated system of vacuoles and reservoirs. Division is usually by longitudinal binary fission.

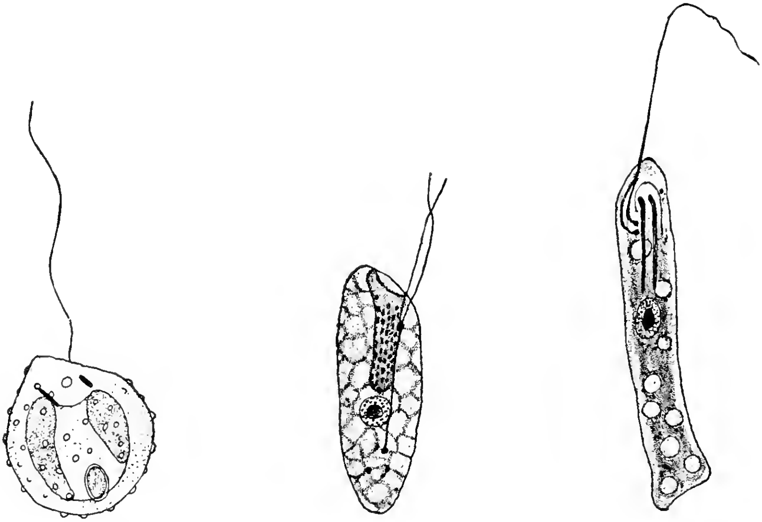

FIG. 17. FIG. 18. FIG. 19.

FIGS. 17–19.—Typical examples of Phytomastigina. 17, Chromulina showing chromatophores and a distinct shell (*redrawn from Hofender*); 18, *Chilomonas paramecium*, a form without chloroplasts, common in laboratory cultures (*redrawn from Doflein*); 19, *Peranema trichophorum*, a species with a long flagellum, only the tip of which vibrates (*redrawn from Doflein*).

In most cases the cell organs become duplicated before separation of the body begins. In some species of Euglena, "division cysts" are formed, and in these instances reproduction does not occur during motile stages but only after the flagellum has been cast off and the individual has entered a quiescent phase. Many of the members of this subclass have but a delicate pellicle or lack it entirely and are thus capable of extreme changes in body form as exemplified in the peristaltic or "euglenoid" movements of the bodies of Euglena and some of its colorless allies, Astasia and Peranema (Fig. 19). In contrast with these stand the dinoflagellates some of which have distinct shells made of a substance closely allied to cellulose, covering the entire body.

The members of this subclass include forms of extremely diverse size. While some species are only about 2 microns in length, others, such as the Noctiluca, one of the organisms causing phorphorescence in the ocean, reach as much as 1.5 mm. in diameter.

This subclass includes the much discussed Volvox family, the most plantlike of all Protozoa. Members of this family illustrate all the important steps in colony formation and in the history of reproduction. In Spondylomorum, reproduction is wholly asexual, each of the sixteen cells of the colony by fission producing a new colony. In Gonium, while asexual reproduction occurs, a zygote may result from the permanent union of isogametes. Male and female sex cells occur in Pandorina, Eudorina (Fig. 5), and Volvox, the colonies of some species of the last two being sexually differentiated into male and female colonies.

The subclass Phytomastigina includes five orders, which are listed and some of the distinctive characteristics given in the table of systematic arrangement of the Protozoa at the close of this chapter. Though motile flagella are characteristic, many species of Phytomastigina have the ability to discard their flagella and still live an active life. In this immotile state, feeding and reproduction may continue normally and there is no impervious wall formed as in instances of encystment. In many of these plantlike flagellates the surface cytoplasm of the cell has the ability to secrete a gelatinous substance which passes through the pellicle and forms a matrix surrounding the cell. Frequently the cells resulting from division remain associated. Then the whole mass becomes enclosed as a colony in a gelatinous matrix, only the flagella extending through it to the outside.

Another type of surface secretion results in the deposition of cellulose or other materials to form a shell or test surrounding all or part of the cell body. In some instances these tests are highly ornamented and frequently they are composed of plates joined together in specifically characteristic arrangement and number so that species, in the dinoflagellates for example, may be differentiated on the characters furnished by the test.

The plantlike flagellates are very widely distributed in both fresh and salt water. Many genera of the dinoflagellates are exclusively marine and in this group is now included the large Noctiluca noted for its phosphorescence. Most of the Volvox family are limited to fresh water where they occur as conspicuous elements of the plankton, frequently so abundant as to impart distinctive colors, odors, and tastes to the water. One family includes species, especially of the genus Chrysidella, which live symbiotically within the bodies of other animals and are the "yellow cells" of the Radiolaria and Foraminifera. While some members of this subclass live as parasites on or in other animals, most of the hosts are invertebrates, and hence as parasites they have been relatively unimportant and have received little attention.

Subclass ZOOMASTIGINA

The Zoomastigina include the orders of flagellates the members of which are distinctly animal in their nutrition or receive their food by absorption. Hence in food habits they are classed as holozoic and saprozoic. Chlorophyll and chromatophores, so characteristic of the Phytomastigina, are lacking in this subclass, consequently the autotrophic method of nutrition is lacking. The kinetic and locomotor elements are very highly specialized especially in the parasitic forms. Colony formation is common, particularly the arboroid type. There are no instances in which fertilization is definitely known. Fission may occur in either a free-swimming or an encysted state, and multiple fission may result in the formation of a number of individuals within the membrane of the original cell. Encystment is practically universal.

Some of the most important members of the Mastigophora belong here because of the prevalence of the parasitic habit in the Protomastigina. Four orders are recognized in this classification, though authorities differ in the number and grouping of the forms within this subclass. The orders are not clearly defined units but some probably represent groups of convenience.

The simplest members of this subclass show confusing mixtures of flagellate and rhizopod characters, for forms like Mastigamoeba and Mastigella (Fig. 15) possess numerous pseudopodia and a permanent flagellum.

The minute monads and the colonial Anthophysa are frequently encountered in laboratory cultures. A delicate collar surrounds the base of the flagellum in the choanoflagellates in such close mimicry of the collared cells of sponges (Fig. 50 *B*) that some zoologists have seen a possible origin of the sponges from these choanoflagellates.

Chilomastix (Fig. 20), Giardia (Fig. 21), and Trichomonas (Fig. 22) are genera which have species living very commonly as intestinal parasites of man and represent unusual degree of development of a neuromotor apparatus.

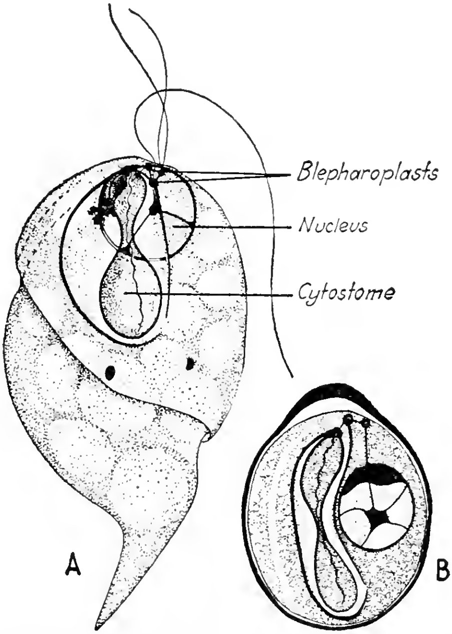

FIG. 20.—*Chilomastix mesnili* (Wenyon). *A*, active stage; *B*, encysted. (*After Kofoid and Swezy*).

Flagellates living in the gut of termites represent the most highly specialized members of the Mastigophora and the most bizarre types of protozoan structure. Their bodies are so closely set with flagella that they were originally considered as ciliates. In the bodies of their hosts, according to the discoveries of L. R. Cleveland (1923), they digest the wood eaten by the termites. The symbiotic interdependence between the flagellates and their host is revealed by the fact that the Protozoa die if the termites are deprived of wood and the termites are unable to subsist on wood diet if freed of the flagellates. Trichonympha, Teretonympha, and Stephanonympha are representative genera of these peculiar flagellates. In the last-named genus are at least 100 nuclei and similar duplication of the groups of kinetic elements.

Trypanosomes (Fig. 23) occur as blood parasites in all classes of vertebrates. In some instances, they are restricted to a single vertebrate host species and in so far as has been observed these are harmless to the host. Such is the condition which exists between the rat host and its normal parasite *Trypanosoma lewisi* which occurs in rats all over the earth. This species is transmitted from one rat to another by the rat flea. The trypanosomes are taken into the stomach of the flea when blood is sucked from an infected rat. The trypanosomes penetrate the tissue cells of the flea and undergo multiple fission. After considerable change in form they penetrate into the rectum of the flea and are passed out with the feces. Reentrance into the rat is not by the bite of the flea but occurs when the rat licks its fur.

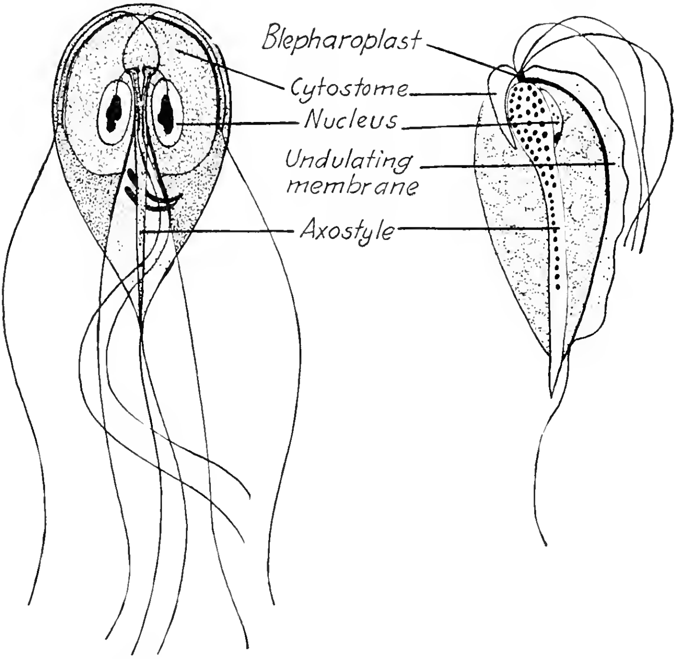

Fig. 21. Fig. 22.

Figs. 21 and 22.—Typical parasitic Zoomastigina showing, especially, the organization of the neuromotor apparatus. 21, *Giardia microti* Kofoid and Christiansen. Parabasals are two curved, dark bodies behind the axostyle. (*After Kofoid and Christiansen*). 22, *Trichomonas augusta* Alexieff. (*After Kofoid and Swezy*).

In contrast with the non-pathogenic *T. lewisi* stand some other species of the same genus which produce fatal diseases in man and other animals in Africa and South America. *T. gambiense* and *T. rhodesiense* are the organisms responsible for the true sleeping sickness in man. A single genus of fly known as the tsetse fly (Glossina) transmits the trypanosomes to man. Rhodesian sleeping sickness (transmitted by *Glossina morsitans*) is more virulent than the Gambian variety (carried by *G. palpalis*). One of the great difficulties experienced in control measures is the fact that the trypanosomes seem to live normally in the bodies of antelope and other game animals which thus serve as reservoirs for the spread of the disease. When the tsetse fly sucks the blood of an infected person, the trypanosomes undergo development in the salivary glands of the fly and when they reach the infective stage are injected into the blood of other human hosts by the bite of the fly. The part of the cycle in the invertebrate host is thus radically different from that of *T. lewisi*. In the blood of an infected man the trypanosomes are never present in large numbers. They are found in lymphatic glands and in the cerebrospinal fluid. Infection is accompanied in its early stages by fever, enlargement of lymphatic glands and spleen, anaemia, and wasting of the body. The lethargic condition which generally precedes death, giving rise to the name "sleeping sickness," accompanies the invasion of the central nervous system by the trypanosomes.

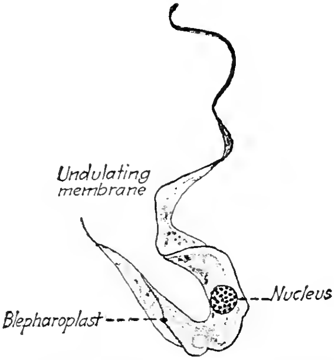

FIG. 23.—*Trypanosoma theileri* (Bruce), from blood of a cow. (*After Lühe*).

In addition to human sleeping sickness, Chagas' disease in South America is due to a trypanosome. Many species attack domestic animals, while others have been recorded from fishes, Amphibia, reptiles, and birds. The genus Leishmania is likewise important because of the human diseases Kala-azar and oriental sore produced by some of its species.

The spirochaetes represent a group of organisms of very great importance and yet of highly problematical relationships. Some investigators have thought that they are protozoans related to the typanosomes, but in structure, in habits, and in reactions they seem to be more closely related to the bacteria. *Treponema pallidum*, the spirochaete which causes syphilis, is one of the most important representatives of this group. Some of the species of the genus Spiroschaudinnia produce a disease in man known as relapsing fever.

In his "Biology of the Protozoa," G. N. Calkins (1926) rules the spirochaetes out of the Protozoa, "as their main characteristics place them much closer to the bacteria than to Protozoa. Their transverse division and spore formation through coccoid bodies are not duplicated amongst flagellated Protozoa, but are distinctly Spirillum-like."

Class Sarcodina

The Sarcodina usually lack a true cell wall, though in many instances skeletons or other protective coverings have been developed. The cytoplasm is characteristically more fluid than in other classes of Protozoa. The majority of Sarcodina are floating forms tending toward spherical body shape, but creeping forms attain flattened bodies or become cylindrical.

Pseudopodia are the most characteristic feature of the Sarcodina in spite of the extremely different appearances which these structures may present in the various orders. In most instances, pseudopodia serve both for locomotion and for the ingestion of food. No less than four types of pseudopodia are generally recognized by students of Protozoa: axopodia, myxopodia, filopodia, and lobopodia. In the order named these represent progressive modification from motile, ancestral flagella. Each axopodium (Fig. 24 *C*) is provided with an axial filament arising from a kinetic element in the endoplasm. The filament is invested by a sheath of ectoplasm endowed with powers of streaming back and forth along the filament. Thus structurally there is very close agreement between an axopodium and a flagellum. Myxopodia (Fig. 24 *B*) lack an axial filament but possess a core of denser protoplasm. When they come in contact they tend to fuse forming a mesh or network of cytoplasm as in the Foraminifera. Filopodia lack all axial structures and consist of a wholly homogeneous cytoplasm. Lobopodia (Fig. 24 *A*), the form of pseudopodia encountered in Amoeba, are the most transitory type. For their formation they are dependent wholly upon the fluidity of the protoplasm.

The nucleus is frequently single, though binucleate or multinucleate individuals are common in some orders. The nuclei in these latter are essentially similar rather than manifesting the functional differentiation which is characteristic of the macro- and micronuclei of the ciliates.

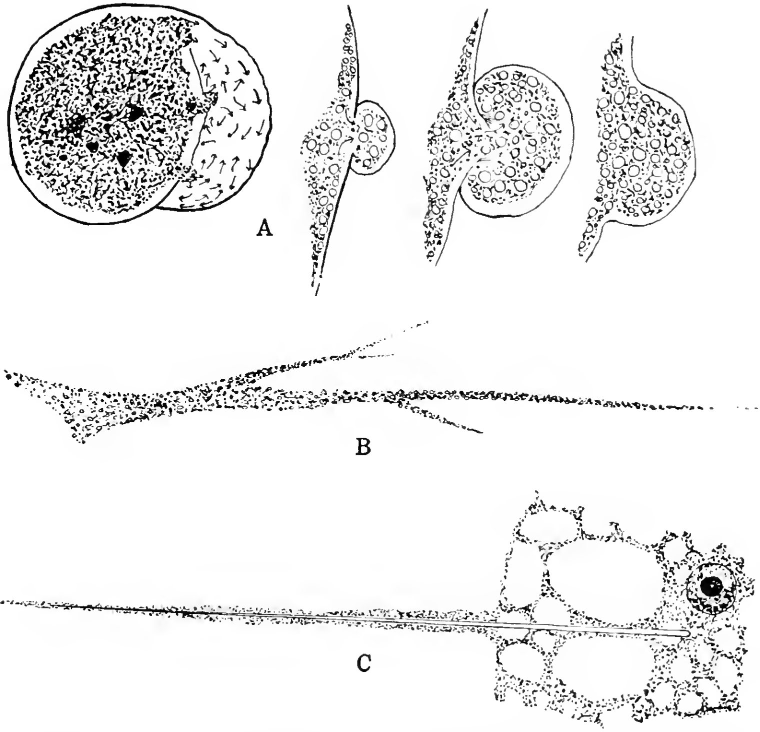

Fig. 24.—Types of pseudopodia. *A*, eruptive types of lobopodium; *B*, myxopodia of Foraminifera; *C*, axopodium of Heliozoa. (*Redrawn from Calkins*).

Binary and multiple fission and budding are all represented in the types of reproduction among the Sarcodina, and some forms pass through a definite life cycle involving conjugation (Arcella). The relatively simple organization of the Rhizopoda has led many students to assume that only a simple cleavage of the cell is involved in the reproductive process. It is probable that simple fission is not the sole phenomenon in the ontogeny of many forms. Encystment, so common a phenomenon in fresh-water and parasitic Sarcodina, has not been observed in Foraminifera and Radiolaria, the two chief groups of marine forms.

Many important parasites, especially among the Amoebae and Mycetozoa, occur in this group. The Radiolaria (Fig. 25) and Foraminifera (Fig. 26) have been of great importance because of the part played by their shells in the formation of sedimentary rocks.

Subclass Actinopoda

The Heliozoa and Radiolaria are united to form the subclass Actinopoda. The first of these are chiefly fresh-water forms, the latter exclusively marine. As chiefly floating forms, the members of this subclass are many of them spherical, with pseudopodia of lobose type or with axopodia. A dense cortical layer of the cytoplasm so characteristic of Amoeba is lacking in the Actinopoda. The cytoplasm is highly alveolar and in the fresh-water forms (Heliozoa) bears one or more contractile vacuoles in the ectoplasm. A sharp separation of ectoplasm and endoplasm is marked in the Radiolaria by a chitinous membrane called the central capsule (Fig. 25 *A*). The cytoplasm within the central capsule contains one or many nuclei, while the extracapsular ectoplasm is devoid of nuclei and is differentiated into more or less specialized zones. Minute openings in the capsular membrane permit of communication between the ectoplasm and endoplasm.

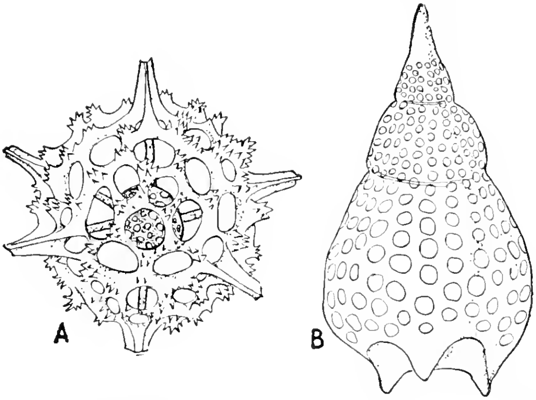

Fig. 25.—Two characteristic forms of radiolarian shells. (*After Haeckel*).

Silicious skeletons of marvelously intricate design (Fig. 25 *A*) or simple latticework cover the body in some members of this subclass, though others may be naked or provided with varying arrangements of spicules, spines, and plates.

Reproduction involves binary fission, budding, and multiple fission. In the Radiolaria the spores formed in the endoplasm within the capsular membrane may be similar (isospores) or dissimilar in size (anisospores). Though these spores appear to be gametes, definite information on this point is lacking.

Food consists largely of living organisms captured by lobose pseudopodia.

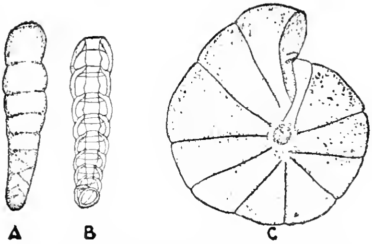

FIG. 26.—Shells of Foraminifera. *A*, *Siphogenerina striatula; B*, *S. columnellaris*, seen in longitudinal section; *C*, *Cyclamina orbicularis*, side view. (*After Cushman*).

Subclass RHIZOPODA

The amoeba-like forms (Fig. 27), the Foraminifera (Fig. 26), and the slime molds are the most characteristic representatives of this subclass. All forms of pseudopodia excepting the axopodia are found but rarely combined in the same individual. A test is very commonly present. It may be of pseudochitin to which other material such as silica are cemented or may consist of calcium carbonate laid down between two chitinous membranes as in the Foraminifera.

The genus Amoeba, so commonly met in elementary zoological laboratories has many relatives that live a parasitic existence in the bodies of numerous invertebrate and vertebrate hosts. The majority of these dependent amoebae are either harmless parasites or commensals, though *Endamoeba histolytica* (Fig. 27) and one or two other species cause dysentery in man.

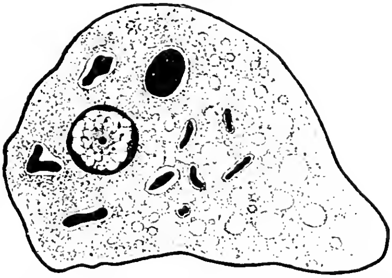

FIG. 27.—*Endamoeba histolytica* in vegetative state. (*Redrawn from Hegner*).

Some shelled rhizopods such as Arcella, Euglypha, Centropyxis, and Difflugia are apparently but amoebae that have acquired houses and are hence included in the same order (Amoebida). In contrast, the Foraminifera (Fig. 26) have anastamosing pseudopodia and shells showing varying degrees of complexity. The foraminiferan shells are of extremely diverse natures but usually closed at one pole and open at the other. In form, the shell ranges from a simple, single chamber (Monothalmia) to complex series (Fig. 26 *B*) of spirally arranged chambers (Polythalmia). Growth of the latter is through the periodic formation of new chambers of increasing dimensions. Foramina serve to communicate between the various chambers of the shell, all of which are filled with protoplasm. As the protoplasm increases in bulk, it protrudes beyond the limits of the old shell and a larger chamber is added to the chambers previously formed. Pseudopodia of different types protrude through either a single opening or numerous small apertures. In some of the smaller forms, the shell is almost wholly of organic material formed by the protoplasm. More commonly, silicious or calcareous matter is also present, and frequently foreign bodies are incorporated directly into the substance of the shell. Chalk deposits, the nummilitic limestones, and various other sedimentary rocks have been formed largely of the fossil shells of Foraminifera.

Members of the suborder Polythalmia (Fig. 26) are exclusively marine. The shells, which are of extremely diverse types, may be either pure lime or partly of organic matter. Those of some fossil forms are relatively immense in size (*Psammonyx vulcanis*, 5 to 6 cm.). Some idea of the rate of reproduction of these forms may be gained from the fact that chalk deposits many feet in thickness are composed almost exclusively of their shells (Biloculina). In Norfolk, England, the chalk measures have an average thickness of 1,450 feet. It is reported that nearly 50,000,000 square miles of ocean bed is covered with a globigerina ooze.

The slime molds are frequently considered as fungi, but though they are border-line forms between plants and animals the structure and development of the vegetative body gives proof of close relationship with other rhizopods. The young stages are small amoeboid forms which may, by direct transformation, develop a flagellum. Transition between these two stages is accomplished very readily. Both reproduce by ordinary fission and each has the power of ingestion of solid food material and absorption of organic fluids. The flagellate form may become a microcyst from which either the flagellate (myxoflagellate) or the amoeboid (myxamoeba) form may emerge.

Logs, stumps, and fallen leaves in moist woodland are especially favorable places for discovering sporangia of slime moulds in all their diversity of beautiful forms and pleasing colors. Though most have no direct economic importance, *Plasmodiophora brassicae* is parasitic upon cabbage and related plants.

Class Sporozoa

The Sporozoa are Protozoa without locomotor structures in the adult stage. While representing great diversity of structure, habitats, and life cycle, they all agree in having the parasitic habit firmly established and in reproducing by spores which are usually enclosed in a firm shell. In some instances, especially where alternation of hosts is introduced, the spore shell may be wanting and in still other instances more than one spore may be included within a single shell. Alternation of generations is widely distributed in this group. Sporozoa are usually intracellular parasites, at least during the early stages in development. In most instances the spores give characters more readily available for identification than do the vegetative stages. Nutrition is exclusively by absorption through the body surface.

Representatives of many groups ranging from Protozoa to mammals serve as hosts to sporozoan parasites. Pathological conditions in the host frequently result from infection by these parasites. The organisms which cause malaria (Fig. 29) are by far the most important members of this class.

Subclass Telosporidia

In members of this subclass spore formation occurs only at the end of the vegetative period and sporulation results in the destruction of the vegetative individuals. Typically, the adult stage has a single nucleus but in some a multinuclear stage is found. Infection of a new host is through a stage called a sporozoite which is usually an intracellular parasite. The sporozoite either develops directly into a sexual individual or first passes through an asexual multiplicative cycle. Following fertilization, spores are formed which give rise to the sporozoites.

The gregarines, the Coccidia, and the malarial organisms are the chief representatives of this subclass. Of these the gregarines live in invertebrates exclusively, being found chiefly in arthropods and annelids where they dwell as parasites in the lumen of the digestive tract and of glands opening into it. Typically the gregarine body is divided into an anterior protomerite and a posterior deutomerite separated by an ectoplasmic septum. Of these only the latter bears a nucleus. Frequently, especially in the young stages, there is an outgrowth of the protomerite carrying various structures for attachment to the host. This is termed the epimerite. Since no mouth opening is present, all food is absorbed directly through the body wall. A myoneme layer within the deeper region of the ectoplasm renders body movements possible.

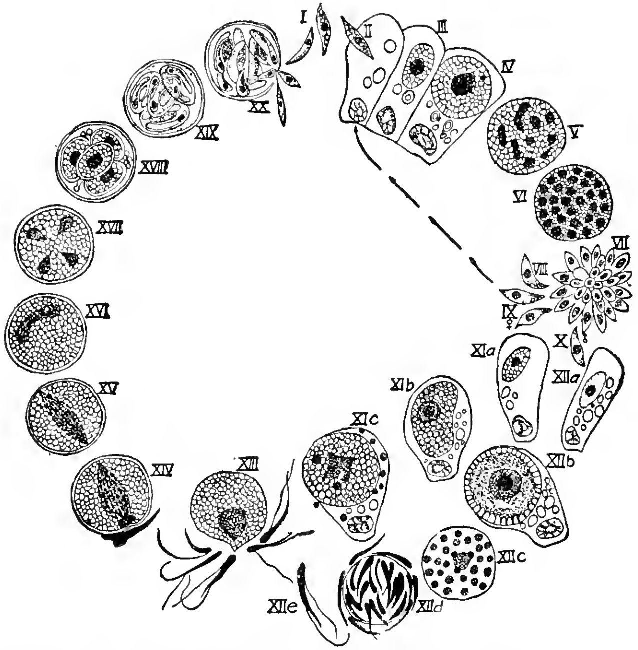

FIG. 28.—Life cycle of *Eimeria schubergi*. Stage V to VIII, a period of schizogony; XI*a* and XII*a* beginning of development of male and female gametes in sporogony period of the cycle. (*From Shull, La Rue, and Ruthven*).

The Eugregarinaria are the typical gregarines which in their life cycle involve only a propagative phase. This suborder is usually subdivided into two groups, the cephaline gregarines which bear an epimerite at least in the early developmental stages, and the acephaline gregarines which never possess an epimerite. The cephaline gregarines, of which there are numerous genera and species, occur chiefly in the alimentary canal of arthropods. Gregarina, Stenophora, and Leidyana are a few of the numerous genera. The acephaline gregarines are chiefly coelom parasites, either lying free in the coelom or sometimes within organs located in the coelom. Monocystis from the sperm sacs of oligochaet worms is the typical genus.

The Coccidia (Fig. 28) dwell typically within the epithelial cells and are wholly lacking in powers of locomotion. Both vertebrates and invertebrates are subject to attack and one species of the genus Isospora parasitizes man.

The Haemosporidia live chiefly in the red blood corpuscles of vertebrates and are thus different in habits from the lumen-dwelling gregarines and the epithelial tissue-inhabiting Coccidia. As a typical example of the group stand the organisms (*Plasmodium vivax, P. malariae, Laverania falciparum*) which are the causal agents of malaria. The life cycle involves both schizogony and sporogony.

The amoeboid organisms of malaria, called schizonts (Fig. 29; 1 to 7), occur in the erythrocytes of persons afflicted with the disease. Each schizont grows until it almost fills the corpuscle (6). Then spore formation takes place and upon rupture of the corpuscle numerous spores or merozoites are liberated into the blood stream, ready, if they escape the attack of the leucocytes, to enter new erythrocytes and thus continue an auto-infection through an indefinite period. The chills characteristic of the disease are coincident with the periods of sporulation.

Following a series of these asexual generations, the spore upon entering a corpuscle produces a gametoblast (9*a*, 9*b*). In later development, each gametoblast develops into either a single female gamete or a group of male gametes. Further development of these gametoblasts depends upon their being taken into the body of a mosquito of the genus Anopheles which secures them with the blood of a malarial patient. The mosquito is not able to transmit malaria to a new human host immediately following the introduction of the organisms into the body of the mosquito. It is only upon completion of the sexual cycle (13 to 27) of the parasite within the tissues of the insect that the bite of the mosquito may transmit the disease. In the stomach of the mosquito, each microgametoblast gives rise to a number of motile microgametes (15*b*). Each of these upon fusion with a macrogamete (16) forms an ookinete or zygote (17). The zygote penetrates the wall of the stomach and becomes encysted (18). While in this condition sporoblasts are formed and each of these gives rise to numerous spindle-shaped sporozoites (25). These are liberated into the body cavity of the mosquito (26) and are

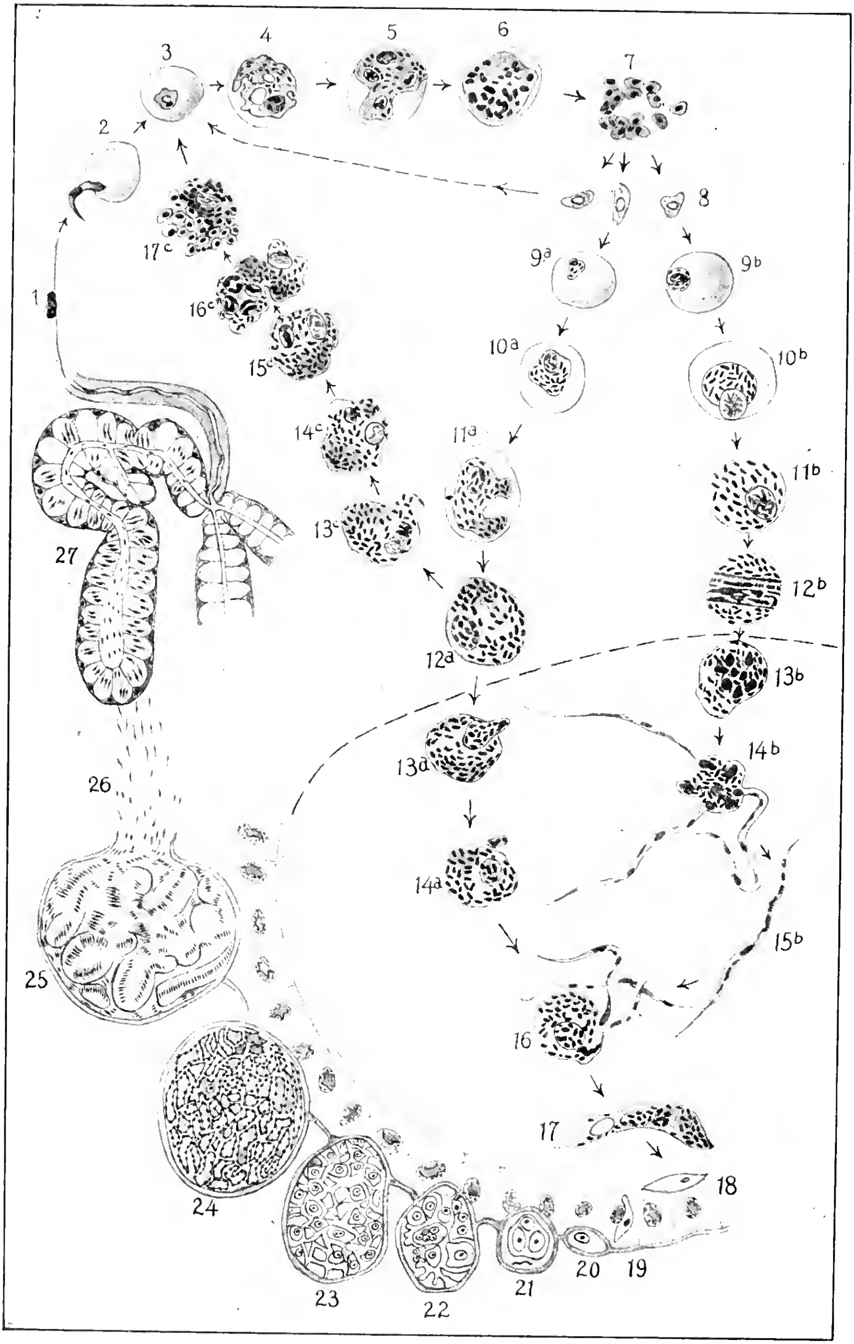
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Fig. 29.

carried by the circulatory system to various parts of the body including the salivary glands (27). From this location they are able to pass along the hypopharynx and thus are introduced into the blood stream of any human being bitten by the mosquito.

Several different kinds of malaria are distinguishable both from clinical evidence and from morphological and developmental differences of the causal organisms. Spring tertian or benign malaria, of which *Plasmodium vivax* is the cause, is characterized by the presence of a fever recurring on alternate days. The quartan type of malaria, which is caused by *P. malariae,* is distinguished by fevers with two-day intervals between attacks. Infections of *Laverania falciparum* produce malignant or pernicious malaria with daily recurrence of the fever.

Subclass NEOSPORIDIA

Members of this subclass are multinuclear in their adult stage. Spore production is continued over a considerable period of time so that in any one individual, spores in different stages of development are to be found. Unlike the Telosporidia, spore formation does not bring the life of the individual to an end. Spore formation is indirect, for the body forms a number of sporoblast mother cells. These in turn give rise to the sporoblasts which become transformed into the spores.

The Neosporidia include the Myxosporidia parasitic almost exclusively on fishes, Microsporidia in insects but occasionally in fishes, and the Sarcosporidia in muscle cells of mammals. Of the Myxosporidia many species invade the gills, integument, and muscles of fishes producing conspicuous cysts filled with minute spores. The Microsporidia have considerable economic interest, for the pebrine disease of silkworms is a serious menace to the silk industry and the Nosema disease attacks honey bees.

FIG. 29.—Life cycle of *Plasmodium vivax*, the tertian malarial parasite. Stages 1–12 and 13*c*–17*c* in human blood stream; stages 13*a*–14*a*, 13*b*–15*b*, and 16–27, in body of mosquito. 1, the infecting stage for man, the sporozoite; 3–7, stages in schizogony resulting in the formation of merozoites (7). 9*a*–12*a*, formation of macrogametocyte; 13*a*–14*a*, maturation of microgamete. 9*b*–12*b*, formation of microgametocyte; 13*b*–15*b*, maturation of the microgametes. 16, fertilization; 17, zygote or ookinete. 18–25, stages in development within cysts in stomach wall of mosquito; 26, sporozoites liberated from cysts making their way through the body fluids to the salivary glands of the mosquito (27), where they are ready to infect a man bitten by the mosquito. 13*c*–17*c*, stages in formation of merozoites from macrogametocyte which fails to leave the human body. 9*a* and 9*b*–(25) are stages in sporogony. (*From Lühe after combinations of drawings by Grassi and Schaudinn*).

Pasteur's name is closely associated with the Microsporidia because of his discovery of the cause and means of control of pebrine.

The Myxosporidia have bivalve spores which usually contain one, two, or four polar capsules in addition to the amoeboid body called the sporoplasm (Fig. 30). The polar capsules are observable in fresh material without previous treatment. Two nuclei are found in the sporoplasm. The vegetative stage (Fig. 31) occurs either as a tissue parasite or in cavities. In the cavities the trophozoite forms plasmodia of various shapes. The tissue-inhabiting forms are usually oval, rounded, or elongated and may be either free or encysted. Spores are formed in the endoplasm of the plasmodial trophozoite.

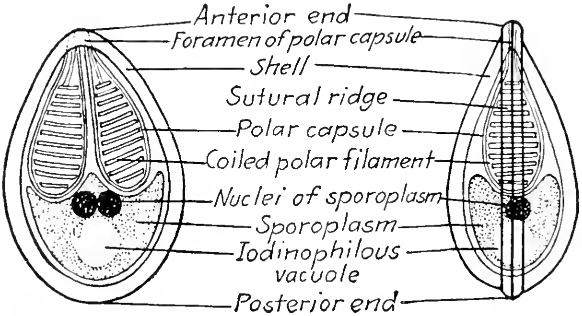

FIG. 30.—Diagrammatical front and side views of a Myxobolus spore. (*After Kudo*).

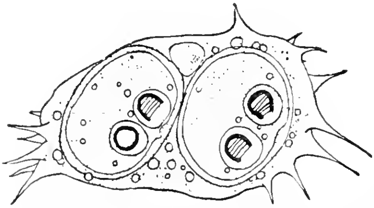

FIG. 31.—Vegetative stage of a myxosporidian, *Leptotheca ohlmacheri*. (*After Kudo*).

Gall bladder, uriniferous tubules, and urinary bladder of fishes are common seats of infection by the free organ-inhabiting forms, while gills and muscles of fishes are especially favorable tissues for the encysted forms. Cysts, which may attain a diameter of several millimeters, result from the hypertrophy of host tissues surrounding what was originally a single parasite. By endogenous budding of this parasite, spores in all stages of their development are being produced continuously. Leptotheca, Myxidium, Myxobolus, Henneguya, and Chloromyxum are characteristic genera.

In the Microsporidia, each spore contains a single polar capsule which is observable only after treatment with proper reagents.

Sarcosporidia occur in the muscles of various mammals. The encysted form reaches a length of several millimeters and finally becomes a mass of sickle-shaped spores in clumps separated from each other by partitions. Detailed structure of the spore is not known. The encysted forms of the genus Sarcocystis within the muscles of mammals have long been known under the name of Miescher's corpuscles, but the complete life cycle is not understood.

SUBPHYLUM CILIOPHORA (INFUSORIA)

The subphylum Ciliophora includes all Protozoa which possess cilia at least through part of their active life, and in typical instances the nuclear material has become separated into two specialized bodies, one controlling the generative processes (the micronucleus) and the other directing the general activity of the cell (the macronucleus). Instead of referring to this condition as binucleate, it is more proper to consider the nucleus as dimorphic, for the micro- and macronuclei combined perform the functions ordinarily exercised by the single nucleus of metazoan cells and of those Protozoa which have single nuclear bodies. In some degenerate forms (Opalina and Ichthyophthirius) there is no distinction of micro- and macronuclei, for two or more similar nuclei occur. There are two classes within this subphylum: the Ciliata, in which cilia are retained throughout life, and the Suctoria, in which cilia are lost after the young individuals become attached to some object.

Class Ciliata

As mentioned earlier in this chapter the ciliates represent a degree of complication of parts (see Frontispiece) not found elsewhere even in the differentiated metazoan cells. It has been maintained by some that the body of the ciliate with its specialization and differentiation of the nuclei represents a differentiation analogous to the separation of somatic and germ cells in the Metazoa. Though the Mastigophora are commonly cited as the protozoan group through which relationships with the Metazoa are traced, there is considerable evidence that this phylogenetic significance is at least shared by the Ciliata.

Both free-living and parasitic forms are common. Though the cell is commonly covered by a pellicle or cell wall, there are definite openings for the ingestion of food and discharge of waste. A cytostome leads through a cytopharynx down into the endoplasm and a cytopyge for the elimination of solid waste is present though usually not observable except at the time of elimination.

The Cytoplasm.—The cytoplasm is divided into an ectoplasm and an endoplasm of which the former comprises a number of rather sharply differentiated regions not uniformly encountered in the various groups. The alveolar layer is the outermost and is marked by a striated appearance due to the arrangement of the alveoli of the cytoplasm. Beneath this lies the trichocyst layer in which the spindle-shaped trichocysts are embedded with their tips at the surface ready for discharge as long, stiff organs of defense. A contractile layer underlies this one. It consists of myonemes which ordinarily run parallel to the rows of cilia. Between or external to the myonemes are found the basal granules from which the cilia take their origin as they pass between the alveoli of the alveolar layer to the outer surface. A spongy zone of ectoplasm traversed by fluid-filled spaces and channels overlies the endoplasm and with the contractile vacuoles and their associated radial canals represents an excretory layer.

The endoplasm is less highly organized. It comprises a fluid cytoplasm within which are contained the nuclei, mitochondria, Golgi apparatus, and various inclusions such as food and water vacuoles, excretory granules, and sometimes symbiotic algae.

Trichocysts, commonly associated with the ectoplasm, have their origin in the endoplasm and later migrate to their peripheral location. Trichites are elongated rods usually surrounding the mouth, apparently giving support and protection to the body. Similar supporting rods are frequently combined to form a tube known as a pharyngeal basket leading from the mouth into the endoplasm.

The Nuclei.—The macronucleus is extremely variable in shape, while the micronucleus is usually a single rounded mass. In the Peritricha, the macronucleus is frequently a long ribbon-shaped structure and in the Heterotricha it usually assumes a distinctly beaded or moniliform condition. An exceptional distribution is found in the genus Trachelius the members of which have a single large macronucleus and thirteen micronuclei. The number of micronuclei is not constant even for the species within the same genus. Thus in Paramecium, the common species *P. caudatum* has a single micronucleus, *P. aurelia* has two, *P. polycarium* has four, and *P. multimicronucleata* may have as many as eight. In spite of its importance in normally directing reproductive processes, the micronucleus is not an absolute essential in cell life, for amicronucleate races of Paramecium, Didinium, and other ciliates have been cultured for long periods.

Reproduction is by binary fission, usually in the free state but in some forms accompanying encystment. Preparatory to fission the micronucleus divides by mitosis and the macronucleus by amitosis. In several ciliates, chromosomes of a fixed number have been observed in the dividing micronucleus though never in the macronucleus. Mouth and other structures are frequently duplicated in the dividing individual before fission is completed.

Conjugation of varied forms occurs in this group. It always results in reorganization of the protoplasm involving the absorption of the macronucleus by the cytoplasm and reorganization of a new macronucleus and micronucleus from products of a fertilization nucleus. The old idea of conjugation as essential to prevent senescence has been shown to be unfounded, for Woodruff has carried a race of Paramecium through 11,000 generations without opportunity for conjugation. This he accomplished by keeping isolated individuals under observation and removing one after each body division.

In the Peritricha, of which Vorticella is an example, a modified form of conjugation between. a microconjugant and a macroconjugant occurs. By two or three successive divisions, some individuals produce four or eight microconjugants which after acquiring an aboral ring of cilia become free-swimming. One of these microconjugants fuses with an ordinary individual, which is the macroconjugant. In brief, the micronucleus of the microconjugant undergoes division to form eight parts of which seven degenerate and only one persists. Later, this one divides into two. During this same time the micronucleus of the macroconjugant has divided into four parts of which three degenerate and the remaining one redivides to form two nuclei. In both conjugants, the macronucleus has undergone disintegration. In each conjugant, one of the two pronuclei which originated from the micronucleus disappears. The remaining nucleus of the microconjugant passes over into the cytoplasm of the macroconjugant and fuses with the single nuclear mass remaining there. As a consequence, the macroconjugant now has a fusion nucleus and the microconjugant which now has no nucleus drops off and disintegrates. The nucleus of the remaining individual divides into eight parts of which one becomes a micronucleus and the other seven macronuclei. Through a series of divisions of the micronucleus and fission of the cytoplasm, seven individuals ultimately result from the conjugation.

Endomixis, comparable to parthenogenesis of the Metazoa, has been discussed earlier in this chapter.

Arrangement of Cilia.—On the basis of arrangement of the cilia, five orders of ciliates are recognizable. The cilia on the body surface are primitively arranged in meridional bands radiating from a terminal mouth (as in Prorodon) but in many forms the mouth has shifted its position, and with it the arrangement of body ciliation becomes more complicated. The cilia which are not fused in bands or tufts are usually in meridional or spiral arrangement and occur either in furrowlike depressions or each cilium within the center of a small depression. In Paramecium, these depressions are hexagonal or rhombic. At the angles of these polygons and in the middle of some of the sides are located the points of the trichocysts. Each cilium is composed of a firm axial filament covered by a sheath of more fluid contractile substance. The filament takes its origin from a basal granule and in many instances minute fibrils extend inward from the basal granules to the wall of the macronucleus. Various modifications of cilia occur. Non-motile tactile bristles have the same general structure as the typical motile cilium. In the pharynx of many ciliates, all the cilia of a row become fused to form an undulating membrane or several adjoining rows may fuse to form a membranelle. In the Hypotricha, tufts of cilia are fused to form brushlike structures called cirri.

FIG. 32.—Diagram showing wave motion of cilia. (*After Verworn*).

Movements of cilia are coordinated by a system of fibrils which comprise a neuromotor system. These fibrils have been most highly specialized and most thoroughly studied in some of the Hypotricha—Euplotes, for example (Fig. 34). Cilia which have not been modified to form membranelles or cirri move in rhythmic waves (Fig. 32) along the rows of unmodified cilia.

In many forms, such as Vorticella, which is attached by a stalk, the cilia create water currents carrying food to the animal and do not ordinarily produce locomotion. Under such circumstances dissemination of the species is accomplished during the reproductive period when individuals break loose from their stalks and for locomotion use cilia which are formed at this time only.

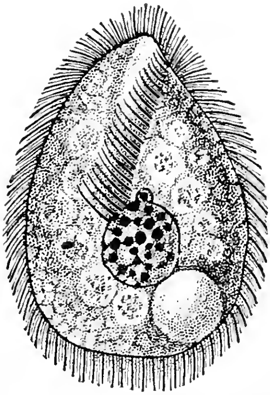

FIG. 33.—*Balantidium minutum* Schaudinn. (*After Schaudinn*).

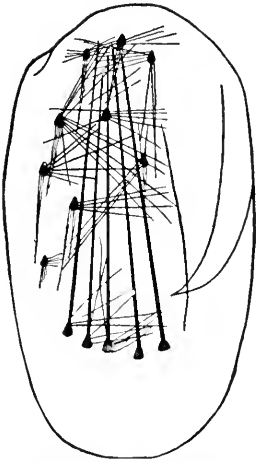

FIG. 34.—Neuromotor system in *Euplotes harpa*, showing system of fibrils connecting the cirri. (*After Prowazek*).

Class Suctoria

The Suctoria are characterized by the complete lack of cilia in the adult stage and the presence of tentacles by means of which other organisms are captured and the protoplasm drawn into the body of the suctorian. Cilia occur on the body of the free-swim-

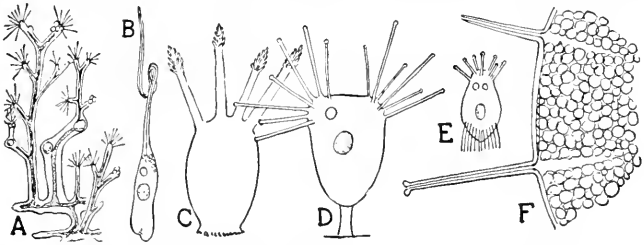

FIG. 35.—Suctoria (*after various writers*). *A*, colony of Dendrosoma; *B*, Rhyncheta; *C*, Ophryodendron; *D*, Tokophrya; *E*, ciliated young of Sphaerophrya; *F*, diagram of capitate and styliform tentacles arising from ectoplasm. (*From Hertwig's Manual of Zoology by Kingsley, Courtesy of Henry Holt and Co.*).

ming larva (Fig. 35 *E*) but are lost when the animal assumes the adult form after becoming sessile. The tentacles are hollow, usually terminating in a suckerlike knob. The macronucleus is extremely variable in form. In some colonial representatives its branches extend throughout the branches of the colony. A micronucleus has never been demonstrated for some suctorians. Binary fission, so common in the Ciliata, is rare in the suctorians. Both external and internal buds are of common occurrence. The embryos when liberated are furnished with bands of cilia for locomotion. Conjugation, in nature similar to that found in Ciliata, may take place either between similar individuals or between a fixed individual and a free-swimming bud, suggesting the condition found in the Vorticella. Podophrya, Acinetá, Ephelota (Fig. 36), Tokophrya, and Dendrosoma are typical genera.

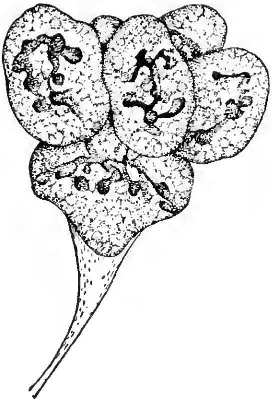

Fig. 36.—A suctorian (*Ephelota bütschliana*) with five daughter buds. (*After Calkins*).

Interrelationships of the Classes of Protozoa

The Protozoa represent the simplest present-day organization of animal life. It is probable, however, that at one time there existed simpler living substance which would be considered animal in nature. This most primitive form of life was probably more homogeneous in its make-up, for morphological differentiation of the nucleus and cytoplasm and regional differentiation of the cytoplasm such as we find in even the simplest Protozoa have probably resulted from long periods of progressive evolution.

There are numerous evidences that plant life existed on the earth before animals came into being. The Mastigophora, through the Phytomastigina, display unquestioned relationships with the members of the plant kingdom (Fig. 1). Because of this fact some biologists consider the Mastigophora as the most primitive class of the Protozoa.

On the other hand, the rhizopod organization is, on the whole, less intricate than that of the Mastigophora or of any other protozoan. Consequently, on the criterion of simplicity of organization, some consider the Sarcodina as the most primitive class of the phylum. It remains as a possible explanation that the Sarcodina represent the simplifying effects of a regressive evolution. In their vegetative stages, the Sporozoa show convincing evidences of rhizopod affiliations through the presence of pseudopodia and in their general organization. Sporozoa probably had their rise through some ancestral form of our present-day Sarcodina.

In the Ciliophora is encountered the highest morphological and physiological differentiation found in Protozoa. Without doubt this subphylum stands at the apex of protozoan evolution. The Suctoria have been given off as a side branch from the main ciliate stem, as evidenced by the fact that suctorians, in their development, pass through a ciliated larval stage.

Questionable Protozoa.—In discussing the Mastigophora, attention was called to the fact that many of the Phytomastigina possess characters which point to plant affinities as well as animal relationships. The problem of assigning such forms to either plant or animal kingdom depends upon establishing definite criteria for separating these two kingdoms. The zoologist confronts a much more difficult task when he comes to consider some of the extremely minute bodies which have been named as possibly the causal agents of certain diseases. In some such instances there is yet no ground for proof that the bodies under discussion are actually living cells. Thus the Negri bodies found in the nervous system of animals suffering from hydrophobia are thought by some to be degeneration products of diseased cells, while others believe them to be protozoan cells. Similarly, for many diseases, minute bodies which in their behavior resemble Protozoa more closely than bacteria have been observed, though they defy actual assignment to any known group of the Protozoa. The bodies associated with Rocky Mountain spotted fever, trench fever, and typhus fever, so very minute that they pass through filters, are considered as Protozoa by some workers but there is no general agreement as to their classification.

As pointed out previously, the spirochaetes have been shuffled back and forth between the Protozoa and the bacteria because of the lack of decisive characters that would compel them to be lined up with one group or the other. This problem of the relationships of the lower plants and animals is far from settled.

In fact, at the present time many bacteriologists are now maintaining that bacteria may belong to the animal kingdom.

Outline of Classification

Phylum Protozoa.—Single-celled animals or cell aggregates in which there is no histological differentiation of somatic tissues.

A. **Subphylum Plasmodroma.**—Protozoa lacking cilia throughout life.

I. Class Mastigophora.—One or more vibratile flagella.

a. **Subclass Phytomastigina.**—Plantlike flagellates.

1. Order Chrysomonadina.—One or two flagella; small; frequently with pseudopodia; yellow-brown chromatophores; spore formation in cysts. *Dinobryon* (Fig. 14), *Chromulina* (Fig. 17), *Chrysopyxis*, *Uroglena*, *Synura*.

2. Order Cryptomonadina.—One or two flagella; small; constant body form; yellow, brown, blue, or green chromatophores; chiefly marine. *Chilomonas* (Fig. 18), *Chrysidella*, *Cyathomonas*, *Cryptomonas*.

3. Order Dinoflagellata.—Two flagella, one usually in circular furrow; yellow-brown chromatophores; test usually present; chiefly marine. *Ceratium*, *Noctiluca*, *Peridinium*, *Gymnodinium*, *Haplozoon*.

4. Order Euglenoidina.—Relatively large; one or two flagella; green or red chromatophores or wanting; complex vacuole system; usually a cytostome; chiefly fresh-water. *Euglena*, *Phacus*, *Peranema* (Fig. 19), *Astasia*, *Trachelomonas*.

5. Order Phytomonadina.—Two flagella; green or yellow chromatophores; colony formation characteristic; sex differentiation in all degrees. *Chlamydomonas*, *Gonium*, *Spondylomorum*, *Pleodorina*, *Pandorina* *Eudorina*, *Platydorina*, *Volvox*.

b. **Subclass Zoomastigina.**—Animal-like flagellates; no chromatophores; no chlorophyll; vacuole simple; kinetic and locomotor elements highly differentiated.

6. Order Protomastigina.—One to few flagella; pseudopodia common; one nucleus. *Mastigamoeba*, *Mastigella* (Fig 15), *Actinomonas*, *Dimorpha*.

7. Order Protomonadina.—One or two, rarely three, flagella; one nucleus; minute; many parasitic. *Trypanosoma* (Fig. 23), *Leishmania*, *Crithidia*, *Monas*, *Bodo*, *Bicosoeca*, *Anthophysa*.

8. Order Polymastigina.—Few to many flagella; one, two, or many nuclei; many parasitic in digestive tract; colony formation unknown. *Giardia*, *Chilomastix*, *Stephanonympha*, *Dinenympha*.

9. Order Hypermastigina.—Many flagella; one nucleus; parasitic in insects; highly specialized. *Lophomonas*, *Joenia*, *Trichonympha*.

II. Class Sarcodina.—Usually lack cell membrane; floating or suspended forms or with pseudopodia for locomotion.

a. **Subclass Actinopoda.**—Unusually spherical; typically floating; axopodia; highly alveolar.

1. Order Heliozoa.—Stiff, radial pseudopodia; frequently openwork skeleton. *Actinophrys*, *Actinosphaerium*, *Acanthocystis* (Fig. 4), *Clathrulina*.

2. Order Radiolaria.—Shell or spicules; central capsule; exclusively marine. *Acanthometra*, *Acanthosphaera*, *Sphaerocapsa*.

b. **Subclass Rhizopoda.**—Pseudopodia without axial filaments; typically creeping.

3. Order Proteomyxa.—Naked; pseudopodia reticulose or filose. *Nuclearia*, *Vampyrella*.

4. Order Mycetozoa.—Terrestrial or semiterrestrial; plasmodium formation. *Arcyria*, *Stemonitis*, *Dictydium*, *Comatrichia*.

5. Order Foraminifera.—Typically myxopodia; often complex calcareous shells. *Globigerina*, *Allogromia*, *Polystomella*, *Rotalia*, *Cyclammina* (Fig. 26), *Siphogenerina* (Fig. 26).

6. Order Amoebida.—Naked or simple, one-chambered shell; lobopodia or filopodia. *Amoeba*, *Endamoeba* (Fig. 27), *Pelomyxa*, *Arcella*, *Difflugia*, *Centropyxis*, *Euglypha*.

III. Class Sporozoa.—Exclusively parasitic; reproducing by spores; locomotor structures lacking in adult condition.

a. **Subclass Telosporidia.**—Spore formation at close of trophic stage only; intracellular parasites during part of life cycle.

1. Order Gregarinida.—In lumen of arthropods and annelids. *Gregarina*, *Monocystis*, *Stenophora*.

2. Order Coccidiomorpha.—Typically intracellular. *Isospora*, *Eimeria* (Fig. 28), *Haemogregarina*, *Leucocytozoon*.

b. **Subclass Neosporidia.**—Reproduction throughout trophic stages.

3. Order Cnidosporidia.—Sporoblast bivalve, containing one or more polar capsules; important pathogenic parasites of invertebrates and vertebrates. *Myxobolus* (Fig. 30), *Leptotheca* (Fig. 31), *Myxidium*, *Nosema*, *Glugea*.

4. Order Sarcosporidia.—Muscle of vertebrates, particularly mammals. *Sarcocystis*.

B. **Subphylum Ciliophora.**—Protozoa having cilia at least in some stages.

IV. Class Ciliata.—Simple or compound cilia throughout vegetative life.

1. Order Holotricha.—Generally with uniform body cilia; lacking a specialized zone of membranelles. *Prorodon*, *Opalina*, *Coleps*, *Didinium*, *Dileptus*, *Colpoda*, *Colpidium*, *Paramecium*, *Lacrymaria*.

2. Order Heterotricha.—Body covered with fine cilia; left-handed oral spiral of membranelles. *Balantidium* (Fig. 33), *Stentor*, *Spirostomum*, *Bursaria*, *Nyctotherus*.

3. Order Oligotricha.—General body ciliation lacking; adoral cilia usually a complete ring of membranelles, the only organ of locomotion. *Halteria*, *Strombidium*, *Tintinnus*, *Tintinnidium*, *Entodinium*, *Diplodinium*.

4. Order Hypotricha.—Flattened dorsoventrally; motile organs on ventral surface only; oral membranelles in left-handed spiral. *Kerona*, *Urostyla*, *Uroleptus*, *Stylonychia*, *Oxytricha*, *Euplotes*.

5. Order Peritricha.—Typically stalked; oral cilia in right-handed spiral; body cilia rarely present. *Vorticella*, *Cyclochaeta*, *Trichodina*, *Cothurnia*, *Zoothamnium*, *Carchesium*, *Epistylis*, *Opercularia*.

V. Class Suctoria.—Cilia confined to buds or embryos; adults bear tentacles for sucking and piercing; usually attached by a stalk. *Dendrosoma* (Fig. 35 *A*), *Tokophrya* (Fig. 35 *D*), *Sphaerophrya* (Fig. 35 *E*), *Podophrya*, *Acineta*, *Ephelota*, *Rhynchaeta*, *Ophryodendron* (Fig. 35 *C*).

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CHAPTER III

INTRODUCTION TO THE METAZOA

In the foregoing chapter, attention has been called to the tendencies which some Protozoa display toward the specialization of their cells. Most of this specialization is expressed in increased complexity of intracellular organization. In some instances, however, groups of cells, termed colonies, act as the unit or individual. Within colonies some of the cells frequently become specialized as gametes for reproductive purposes but all of the somatic cells remain alike. In the Protozoa, any specialization of somatic cells affects all equally, so there is no differentiation.

It seems probable that the Metazoa must, at some time, have originated from protozoan ancestors, but all evidences of the means of this transition have been lost and both Protozoa and Metazoa have gone far along independent lines of evolution since the Metazoa came into existence. The lack of fossil forms bridging this gap is not surprising, for both the Mastigophora and the Ciliata, through the ancestors of which this genesis might have taken place, have no hard parts which could be preserved as fossils.

There are a few present-day animals which have been termed the Mesozoa because they have been considered as intermediate between Protozoa and Metazoa, but their simplicity is probably due to degeneracy, as is shown in the section of this chapter devoted to them.

Embryology frequently offers a clue to and outlines the steps in phylogeny (recapitulation theory). All Metazoa, in their development, typically pass through a single-celled stage—the fertilized egg. This fact readily furnishes the basis for an analogy of metazoan origin from the single-celled organisms. In the development of the fertilized egg into the adult organism, there is a time when large numbers of fundamentally similar cells (the blastomeres) are produced through the partition of the single cell. It is only in later development that these cells through histological differentiation assume different forms and come to perform diverse limited functions. This subject of histological differentiation, which marks off the Metazoa from all Protozoa, is discussed in the second section of this chapter. A brief discussion of the organ systems of the invertebrates concludes the chapter.

A. The Mesozoa

A small group of relatively simple many-celled animals composed of a layer of ectoderm cells covering a single or several entoderm cells has frequently been considered as standing intermediate between the Protozoa and the Metazoa and has consequently been termed the Mesozoa. The phylogenetic significance which has thus been attached to this group is a subject regarding the tenability of which very grave doubts are justifiable, for all of the more important representatives of the group are internal parasites. It seems probable that their simplicity of organization is an accompaniment of degeneracy directly traceable to adaptation to the parasitic existence. Not even the known facts regarding the development of these forms aid in pointing out relationships with any other group of organisms.

The Dicyemidae and the Heterocyemidae include species which are parasitic in cephalopods, while Rhopalura, which represents the Orthonectidae, lives as a parasite in various invertebrate hosts.

B. Histological Differentiation

Differentiation of Tissues.—As emphasized in the foregoing chapter, all Metazoa differ from the Protozoa in that the cells of the former become specialized for restricted functions, that is, undergo histological differentiation. Certain groups of cells become similarly specialized for carrying out one specific function more effectively than that function may be executed by unmodified protoplasm. Such a group of similarly specialized cells is termed a tissue. A tissue is made up not only of units of cytoplasm and their contained nuclei, but frequently the cytoplasm forms substances which are essential in the effective functioning of the tissue. These substances, which are termed plasmic products, may be either inconspicuous or so prominent that the cells which produce them are obscured.

Classification of Tissues.—Since the function of a tissue is one of its most important characteristics, the classification of tissues is usually built around this character. Even though differentiation leads along numerous different lines in the metazoan body, the general results are so nearly uniform in different animal groups that but four chief classes of tissues are commonly recognized, namely; epithelium, connective tissue, muscle tissue, and nervous tissue.

In addition to these chief classes of tissues, many other kinds are recognizable but often these are modifications of one or more general classes. Thus the nettling cells of a Hydra or the pigment cells of a squid may be considered as special classes of cell differentiation. But since these special types of cells are rather readily referable to an epithelium or a connective tissue or one of the other types, there is no distinct advantage in creating additional classes of tissues.

Both form and structure of an organism depend upon the grouping of the component tissues. Thus both morphology and physiology go back for their final basis to the study of the several tissues and frequently to the form and structure of the individual component cells.

EPITHELIAL TISSUES

Definition and Classification.—Any tissue which covers a surface is called an epithelium. Phylogenetically, tissues of this class are the most primitive, for the coelenterates are essentially nothing but epithelial in structure. In like manner, in individual development among all the Metazoa, the first division of labor for the cells of the embryo occurs with the formation of the gastrula stage when nothing but surface coverings is present.

Form vs. Function.—Varied forms of cells and sundry functions occur in tissues in this group. If an epithelium comprises but a single layer of cells, it is termed simple, while an epithelial layer two or more cells in thickness is designated as stratified epithelium. The form of the component cells leads to the use of such descriptive terms as cuboidal, columnar, and squamose, but, since function is a much more important criterion for classification, epithelia are grouped as protective, formative or glandular, ciliated, communicative or sensory, and germinal.

Ciliated and Flagellated Epithelium.—Even in the gastrula stage of ontogeny some or all of the cells are frequently provided with cytoplasmic threads, the movements of which are primarily for locomotion. Ciliated or flagellated cells as a means of locomotion are only infrequently found in adult metazoans but do occur in the flatworms (Fig. 62), the rotifers (Fig. 72), and molluscs (Fig. 91). More frequently, however, cilia and flagella on epithelia of Metazoa produce movements of the medium (Fig. 37) rather than affect locomotion. Thus in the sponges the flagellated cells produce the water currents which carry the food supply. The same is true of the ciliated mantle and gills of the mussels.

Protective Epithelium.—Because of their location on external surfaces epithelia are frequently modified for a protective function. Stiff fibrils in the cytoplasm (Fig. 38) and thickenings of the outer margin of the cell are two means whereby mechanical protection is secured. Frequently, an external epithelium may form extracellular materials which are deposited in a layer or in a succession of layers over the surface of the body. The cuticula characteristic of so many invertebrates is thus produced by an underlying epithelium which is frequently termed a hypodermis. In many instances, inorganic salts are deposited in this cuticula until a shell-like armor of resistant plates is formed.

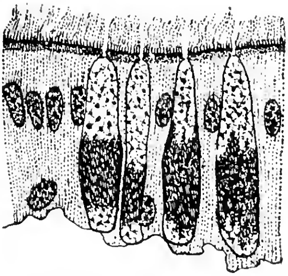

Fig. 37.—Glandular and ciliated epithelium showing unicellular glands in entoderm of earthworm, *Eisenia rosea*. (*After Schneider, courtesy of Gustav Fischer*).

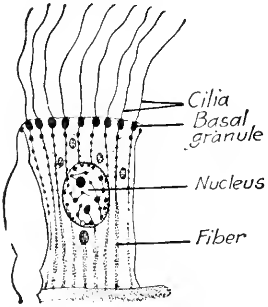

Fig. 38.—Protective epithelium from a flatworm, *Planocera folium*. (*After Schneider, courtesy of Gustav Fischer*).

Glandular or formative epithelium represents one of the commonest modifications of this class of tissue. Even in the gastrula stage the entoderm of the embryo has begun to be specialized as a glandular tissue and the cytoplasm and its inclusions render the entoderm obviously different from the ectoderm. Cells scattered singly through an epithelium may become specialized as gland cells, as in the case of the mucous cells (Fig. 37) of the earthworm. Frequently, these unicellular glands become enlarged and through elongation the single cells extend down into the underlying tissues much deeper than the ordinary epithelial cells which surround them.

Flat surfaces or large areas of an epithelium may become differentiated for a glandular function, as in the foot of Hydra, but in most instances specialized glands require an increased surface for their functioning as secretory or excretory organs, and consequently areas of glandular epithelium become invaginated either as a simple tube or as a series of branched tubes and chambers the walls of which are composed of gland cells. A duct usually keeps such a compound gland in communication with the surface from which the gland cells were originally invaginated.

Sensory or Communicative Epithelium.—Naturally, the only communication which an organism may have with the outside world is through its surfaces. Consequently, any sensory mechanism must be associated with the surface of the body and is therefore epithelial in origin. Sensory cells located in the epithelium have communication with nerve endings through which they are able to transmit stimuli to the central nervous system. Hairs or bristles on the surface of epithelial cells render them especially susceptible to touch stimuli, so isolated cells or groups of cells thus modified form various tactile organs. An association of pigment with epithelial cells having rich nerve supply usually signifies an optic organ of some type and is designated as a retina. Balancing organs or statocysts (Fig. 39) are usually modified epithelia specialized for receiving tactile stimuli through the movements of a body called a statolith or an otolith.

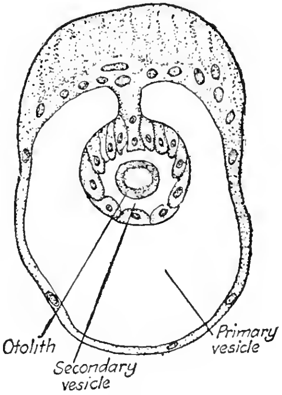

FIG. 39.—Statocyst of Gonionemus. (*Orig.*)

Germinal Epithelium.—Germ cells of all Metazoa have their origin in an epithelium. In many of the groups, the presence of a germinal epithelium is readily observable. In some of the simple Metazoa, as, for example, the coelenterates, the germ cells may arise as modifications of epithelial cells which are not even necessarily grouped to form a gonad. The gonads of many groups are bounded by an epithelium, the cells of which transform into the germ cells. Morphologically, the female germ cells become differentiated from ordinary epithelial cells chiefly through the addition of deutoplasm or yolk and in many instances through acquiring additional membranes. On the other hand, the male germ cells become highly modified and undergo extensive rearrangements of their parts, chiefly as an adaptation for more effective movement.

CONNECTIVE OR SUPPORTING TISSUE

Definition.—Tissues which fill in between and connect other tissues, give support to them and to the body in general, are grouped under the general category of connective or supporting tissues. It has been shown that the individual cells in their form and function give the chief character to epithelial tissues, but in the connective tissues plasmic products are usually the most conspicuous elements. In some tissues these products are intracellular as in the spicules formed by certain cells of the sponges. Fat or adipose tissue results from an accumulation of oil or fat droplets within the cytoplasm until they coalesce to form a single large drop around which the cytoplasm of the cell is spread in a thin, attenuated layer.

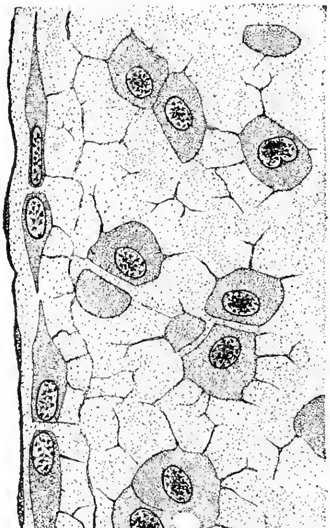

FIG. 40.—Cartilage of an adult squid. (*From Dahlgren and Kepner, courtesy of The Macmillan Company*).

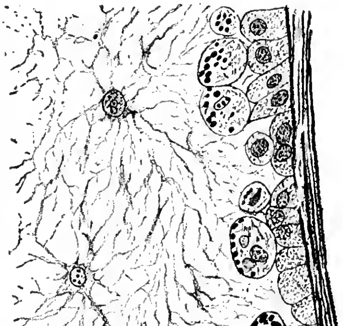

FIG. 41.—Portion of a section of *Cerebratulus marginatus*, showing much branched connective tissue cells. (*After Schneider, courtesy of Gustav Fischer*).

More frequently, the plasmic products are intercellular. In such instances, the cells of a connective tissue are embedded in a non-protoplasmic matrix the specific nature of which may be highly variable. In its simplest condition, this matrix is composed of a gelatin-like mass within which the cells are embedded to form a homogeneous or gelatinous connective tissue (Fig. 40). Frequently fibrillae are formed within the gelatin (Fig. 41) giving greater firmness. Depending upon the arrangement of these fibrillae, their composition, and composition of the matrix, several kinds of connective tissue are recognizable, as, for example, fibrous connective tissues, elastic tissue, cartilage, etc.

MUSCLE TISSUE

Movement is an inherent property of all protoplasm. Even in the Protozoa, portions of the cytoplasm frequently become altered as fibers for movement more effective than that which characterizes undifferentiated, viscous protoplasm. These partial specializations of the protozoan cell for movement are termed myonemes. Partial differentiation of cells for contraction are not infrequent in the Metazoa. The inner margins of the ectoderm cells of Hydra contain contractile threads within the cytoplasm, and consequently the covering cells of the Hydra are frequently termed epithelio-muscular cells. In the nematodes, the mesoderm cells forming the innermost layer of the body wall undergo a partial differentiation to form a series of longitudinal muscle fibers. The peripheral parts of these mesoderm cells become specialized for contraction while an undifferentiated mass of cytoplasm containing the nucleus protrudes into the body cavity.

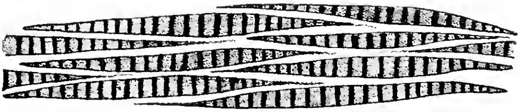

FIG. 42.—Muscle fibers from subumbrella of jellyfish. *Carmarina hastata.* (*After Schneider, courtesy of Gustav Fischer*).

Frequently, mesenchyme cells become elongated or spindle-shaped and develop myofibrils within their cytoplasm. Such cells when grouped together form the commonest type of smooth muscle tissue.

Striated muscles occur even in forms as low as the medusae (Fig. 42), where they remain on the surface of the body. They usually originate as epithelial cells. The nuclei of cells which are to form striated muscle undergo a series of divisions without subsequent division of the cytoplasm. In the cytoplasm of the polynuclear cells thus formed, numerous fibrils make their appearance. The fibers are surrounded by a sarcoplasm containing the nuclei, and the whole muscle element is covered with a sheath which is termed the sarcolemma. Each fibril is composed of two different kinds of substance, one called the isotropic substance which does not stain readily, and another, the anisotropic substance which is doubly refractive and stains deeply. The two substances alternate regularly along the fibril, and in adjoining fibrils they are in alignment so that in stained preparations under the microscope a bundle of fibrils has a cross-striped appearance. Peculiar groupings of fibrils occur in some muscle cells (Fig. 43).

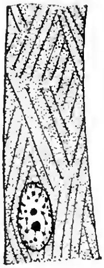

FIG. 43.—Muscle fiber from adductor muscle of mussel, *Anodonta mutabilis*. (*After Schneider*).

NERVOUS TISSUE

Irritability, or the power of reacting to stimuli, is inherent in all protoplasm but even in the single-celled Protozoa it has been shown that parts of the cytoplasm become specialized as a neuromotor apparatus. Such specialization has been demonstrated for some of the ciliates in which it seems probable that stimulation is propagated along certain tracts or fibrils more efficiently than through undifferentiated cytoplasm. In most Metazoa, a nervous system is developed for transmitting sensory and motor impulses through the linking together of highly specialized nerve cells or neurons. Nervous impulses are propagated through a plexus of scattered cells in the hydroid stage of the coelenterates.

Characteristically, a nerve cell consists of a nucleated cell body of cytoplasm from which one or more cytoplasmic processes are given off. There is a definite polarity in nerve cells. A given fibril propagates an impulse in only one direction. When there are several cytoplasmic processes from the cell body of a neuron those which transmit the impulse inward toward the cell body are termed dendrites. Normally, but a single process carries impulses outward from the cell body and this process is called a neurite or an axon.

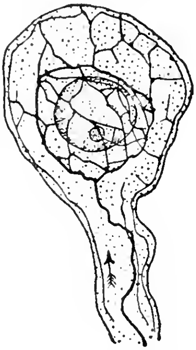

FIG. 44.—Neurofibrillae in ganglion cell of a leech. (*After Apathy*).

In most of the higher Metazoa, the nerve cells are grouped into masses which are called ganglia. The neurites and dendrites form part of the fibrous portion within the ganglia and continue in groups out from the ganglia as important constituents of the nerves of the peripheral nervous system.

By very special histological technic the cytoplasm of a neruon and its processes is shown to contain various fibrillar structures (Fig. 44). It is thought that nerve impulses are transmitted along these fibers rather than through the general cytoplasm. In addition, much of the cytoplasm of nerve cells contains deeply staining granules or masses of questionable significance, which are termed the tigroid bodies. Frequently, a region within the cytoplasm of the cell body directly continuous with the cytoplasm of the axon is devoid of tigroid bodies. This implantation cone, as it is sometimes called, is so marked in

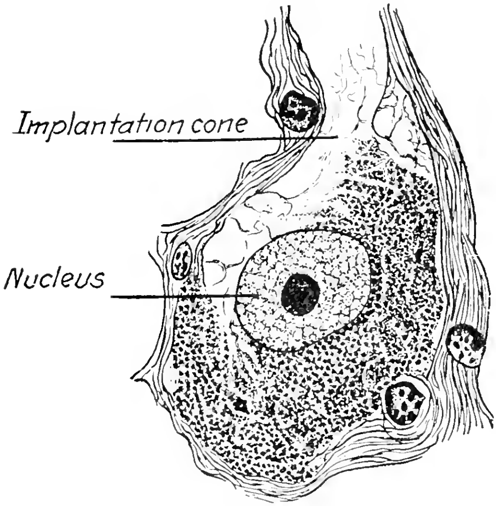

FIG. 45.

FIG. 46.

FIG. 45.—Nerve cell from ganglion of crayfish. (*After Dolley*).

FIG. 46.—Neuroglia cells from nerve cord of earthworm, *Eisenia rosea*. (*After Schneider*).

arthropods that sections of nerve cells (Fig. 45) have the appearance of being highly vacuolated.

Interspersed between the neurons and fibers of a ganglion are varying amounts of mesodermal connective tissue and a highly modified type of ectoderm cells (Fig. 46) which are called neuroglia. The neuroglia cells of invertebrates usually have some portion of the cell body on the surface of the ganglion, while a fiber-bearing, supporting portion extends between the nervous elements of the ganglion.

In function, structure, and origin, nervous tissue and the sensory epithelium discussed earlier are intimately associated.

Morphological Changes in the Nucleus

In the foregoing discussion, attention has been focused upon the changes in the form and structure of the cytoplasm and of the plasmic products which are involved in histological differentiation. Omission of the nucleus from this discussion does not imply that it is not concerned in differentiation. There are, however, few conspicuous changes in form or appearance of the nucleus in comparison with the radical changes in the extranuclear portions of the cells. As the controlling center of most of the activities of the cell, doubtless the nucleus must have varying functions depending upon the line along which the cell is specialized, but there are few reflections of this in the morphology of the nucleus. The nuclei in some highly active tissues become irregular or even much branched but these morphological changes seem to be correlated with rate of activity rather than with actual differentiation of the nucleus in a particular kind of tissue.

C. The Organ Systems

Just as the individual cells in the many-celled animals become dependent one upon another through histological differentiation so also do the individual tissues become interdependent. Few tissues function as utterly isolated units, for they become combined in groups which are known as organs. These organs are the readily recognizable morphological units of which the metazoan body is composed. All of the tissues which form an organ cooperate in the performance of some function. Obviously, not all tissues in an organ function to the same extent, but usually one kind of tissue becomes the dominant or essential tissue and is aided in carrying out its functions by the other tissues of the same organ.

Thus, in a digestive organ the essential process of digestion is made possible through the presence of glandular epithelia which form substances necessary for the digestion of food. The epithelia are frequently aided in this function by cooperative muscles under whose action the content of the digestive tract is kept agitated so that all of the food material comes into contact with the digestive fluids produced by the epithelia.

When identical or similar organs are grouped for the performance of the same or related functions, such a complex is termed an organ system. All of the activities which characterize the living animal are so fundamentally interrelated that the numerous organs and tissues of the metazoan body are capable of being grouped under a relatively small number of systems. Yet these major organ groups, the systems, have their interrelations and function not as independent units but as a correlated whole—the organism or the individual.

Throughout the following sections of this book constant reference is made to the digestive, circulatory, respiratory, excretory, locomotor, reproductive, and nervous systems. The organs of which each system is composed in the various phyla and classes are not necessarily identical in structure or origin, for frequently the same function is carried on by conspicuously different organs in different groups. A brief discussion of the modifications of the several organ systems is given here, but for a full understanding and appreciation of this discussion, the student should again read this section after having completed the laboratory study of a number of metazoan forms.

The Digestive System.—The power of transforming non-living food substances into living matter or protoplasm is a distinctive property of all living organisms. This is not accomplished by a direct transmutation or by a simple act of endowing the food with life. Since living protoplasm is in a liquid or semiliquid state the process of digestion or liquefying of food is the essential first step in the transformation of food into living matter. In some degenerate forms of animal life which have become adapted to a purely parasitic existence, as, for example, the tapeworms and the Acanthocephala, food taking is restricted to the direct absorption of liquids by the cells of the body. Organs of digestion are entirely wanting in such instances, for the entire digestive process is performed by the organs of the host.

In some of the Protozoa and in a few of the Metazoa, solid food substances are taken directly into the protoplasm of the organism. These ingested particles, though within the protoplasm, remain foreign to it until they have undergone physical and chemical changes which render them capable of assimilation by the protoplasm. This type of digestion is termed intracellular digestion. Among the sponges and some of the flatworms, in addition to the Protozoa, the entire digestive process is intracellular.

Ontogenetically, the archenteron of the gastrula stage represents the first organ specialized for digestion. In many animals, the larva upon reaching the gastrula stage is an independent organism capable of self-maintenance. Food taken through the blastopore of such a gastrula is rendered liquid through the action of secretions formed by the entoderm cells. Thus the gastrula cavity becomes a space within which intercellular digestion takes place and is termed an archenteron or primitive digestive system.

Among the Metazoa, there are some animals in which the digestive system of the adult never reaches a state of complexity appreciably higher than that of the archenteron. Among the Coelenterata, the polyp of the Hydrozoa is essentially similar to the archenteron, for it is a simple entodermal sac with but a single opening, the mouth. In many other coelenterates, there is a beginning of a separation of the distributive function from the central digestive cavity. Thus in the jellyfishes, the gastrovascular system consists of a central cavity from which a peripheral system of pouches or canals passes to the outlying parts of the body and thereby aids in the distribution of the digested food.

In most of the Metazoa above the coelenterates, the blastopore of the gastrula is not retained, as the mouth of the adult for the blastopore closes during development of the embryo and for a time the entodermal digestive tube is but a sac without communication with the outside. Communication is later established by an infolding of the body-covering at the anterior extremity to form an ectodermal antechamber to the entodermal digestive sac. Such an entodermal digestive sac with a single opening lined with ectoderm (the stomodaeum) is characteristic of the Turbellaria.

In the nemertines and in all organisms higher than the flatworms, there is characteristically a second ectodermal invagination to meet the entoderm. This second ectodermal invagination is normally located at the posterior extremity as a proctodaeum terminating in an anal aperture. Forms in which both stomodaeum and proctodaeum occur are said to have a complete digestive system. In its simplest condition, this consists of a continuous tube the extremities of which are ectodermal and the true digestive middle portion of which is formed of, or at least is lined with, entoderm. Most of the highly developed digestive systems represent only modifications of this simple tubular condition. Different regions become modified for limited functions. With these specializations, changes both in form and in structure arise and regions such as esophagus, stomach, and intestine are marked off. Jaws or organs for the comminution of food are frequently developed in the stomodaeum. Glands grow out from the walls of the tube and remain attached to the digestive tract only through ducts. Muscles, connective tissue, and vessels of the circulatory system become associated with the entodermal tube to form a more highly complicated digestive system. In some instances, the proctodaeum receives the ducts of the reproductive system and is then termed a cloaca.

Circulatory System.—Whether digestion is intercellular or intracellular, the products of digestion are directly available to only part of the cells of the body while the remainder of the cells must rely upon some agency external to themselves for furnishing them with the materials essential for anabolism. In some of the simpler Metazoa, this is accomplished by direct transfer of the materials from cell to cell, but in the highly complicated organisms such transfer is not possible because some cells are so far removed from the organs where digestion takes place. In such instances, a special system for the distribution of digested food has made its appearance as a specialized circulatory system.

Many steps in the development of complexity of the circulatory system are observable in the different animal groups. It has already been pointed out that the gastrovascular system of coelenterates serves for both digestion and distribution but even in this phylum many steps in the differentiation of the two systems are found. Trematodes and Turbellaria among the flatworms also represent the condition of a combined gastrovascular system.

In its simplest form, as exemplified by the hydroid polyp, this system is a simple sac or pouch, the walls of which are formed of two layers of cells, the ectoderm and the entoderm. The most distant cells of such an organism are so slightly removed from the store of digested food material that distribution is by direct transfer from cell to cell. In the medusae of the same phylum, the digestive sac is relatively small and located near the center of a much enlarged body within which transfer from cell to cell is not so readily possible. Under these conditions a distributive system arises, intimately associated with but somewhat distinct from the digestive system. The tubes or pouches of such a gastrovascular system mark the beginnings of a separate system for circulation.

Among the coelomate animals, digested food materials frequently pass through the wall of the digestive tract into the coelomic cavities where it becomes recognizable as the body fluid. Only in the simple coelomate animals is this fluid entirely free within the body cavities, for it becomes more or less confined within a system of definite channels comprising the vessels of the circulatory system. When the fluid is continuously within vessels, the system is termed a closed system, but when in any part of its course the fluid is emptied into the body cavity or into sinuses the system is designated as an open circulatory system. Muscles become associated with at least part of the vessels which then function as a pumping organ or heart. In many invertebrates, the most conspicuous pumping organ is the vessel, or part of the vessel, which lies dorsal to the digestive tract, but hearts are frequently located in other regions or the body, as, for example, the gill hearts of molluscs and the modifications of the circular vessels in the annelids.

In some instances, notably in the molluscs, the heart becomes differentiated into various chambers. Those which receive the blood are termed auricles and those which force the blood out into the vessels are called ventricles. The heart presents an interesting instance of independent or parallel development in invertebrates and vertebrates. A three-chambered heart is fairly common in the molluscs, while the fishes have but a two-chambered heart.

Respiratory System.—The energy manifested by a living organism results largely from the union of oxygen with protoplasm and its contained food substances. Highly complicated organic compounds are oxidized or broken down into simpler waste substances, thereby transforming the potential energy of the complex chemical compounds into the kinetic energy of the living organism. The term respiration is applied to the process of admission of oxygen into living protoplasm and the subsequent giving off of carbon dioxide. More strictly this process should be termed aerobic respiration, for there are some organisms which obtain their energy release in the total absence of oxygen and these are said to undergo anaerobic respiration. Since aerobic respiration is by far the more common, the term respiration when not modified is usually taken to mean this type.

Respiration is a process essential for the existence of every living cell, yet in the many-celled metazoans respiration as a cellular process becomes masked or lost sight of through the introduction of organs which facilitate the process for the entire organism. Since the respiratory process involves an exchange of oxygen and carbon dioxide, any surface which serves for this exchange must be moist and delicate in order to permit a diffusion of the gases. In animals which are diploblastic, as the coelenterates, conditions for respiration are not essentially different from those found in the single-celled Protozoa, for practically every cell has a surface exposed to the water through which the gases may diffuse. Even in some of the coelomate animals, such as the earthworms, the body surface provides an area sufficient for the respiratory exchange but in these as well as in all the higher animals the body fluid plays an important part in that it absorbs or loosely combines the gases within the body.

In many animals, the body surface is unable to supply all of the cells with oxygen because of insufficiency or because of dryness which inhibits diffusion. Special organs for respiration have been developed in all such forms. Roughly, in invertebrates, these modifications may be classified as gills, tracheae, book-lungs, and lung sacs.

Of gills, there are two distinctly different kinds, blood gills and tracheal gills. The former usually consist of portions of the body wall drawn out into thin filaments or thin lamellae the cavities of which are continuous with the body cavity and are filled with body fluids or contain blood vessels through the walls of which the respiratory exchange takes place. Tracheal gills are evaginations or invaginations of the body wall within which or around which air tubes or tracheae are distributed. Gills occur on almost any part of the body, wherever their function may be carried out.

Tracheae are invaginations of the body wall to form a system of air tubes which carry atmospheric oxygen directly to all parts of the body in insects. The intimate structure of the tracheal system is discussed in greater detail in Chapter XV.

In the arachnids, an invagination of the body wall leads into an organ called a book-lung, the walls of which are composed of much-folded delicate membranes through which oxygen is taken from the air-filled cavity of the book-lung and carbon dioxide is given off.

In some molluscs, the cavity which ordinarily bears gills lacks these structures and has become secondarily modified as a lung sac into which atmospheric air is periodically admitted and from which the air bearing carbon dioxide is ejected.

Excretory System.—As a result of katabolic processes, wastes are formed within every living cell. The carbon dioxide mentioned above is only one of the important waste substances. Water, ammonia, urea, and other nitrogenous compounds accumulate within the living protoplasm. Many of these wastes are soluble in water and tend to diffuse through the walls of the cells.

In many of the Protozoa, contractile vacuoles facilitate the collection and elimination of these wastes. Among the coelenterates and the Porifera, direct diffusion through the cell surfaces into the surrounding water suffices for the elimination of these katabolic products. In the Metazoa, the first specialization for their elimination is the protonephridial system of flatworms, rotifers, and trochophore larvae. This system consists of a series of tubules associated with flame cells. Such a system may be provided with an enlarged excretory vesicle within which the excretory matter accumulates before it is discharged through the excretory pore.

A great many of the coelomate animals have a metanephridial system which picks up excretory wastes from the coelomic cavities and from the body fluid. The unit of structure in such a system is essentially a funnel-like nephrostome which communicates with the outside by means of a tubule. The nephridia are paired organs segmentally arranged in annelids, while in the Crustacea they are considerably modified in form and are limited to one or two pairs.

A group of thin-walled Malpighian tubes communicates with the intestine of insects and discharges excretory wastes from the body fluid into the digestive canal.

Reproductive System.—In some Metazoa, the gonads or essential organs of reproduction are the only organs involved in the reproductive process. Thus, in the coelenterates, the germ cells are dehisced directly from the body surface or into the gastrovascular cavity. Ducts which lead from the gonads to the exterior are present in most other Metazoa. These, and other accessory organs, comprise the reproductive system. The gonads may be single, paired, or multiple. Frequently, a gonad becomes subdivided into follicles, each of which has more or less the appearance of an independent organ.

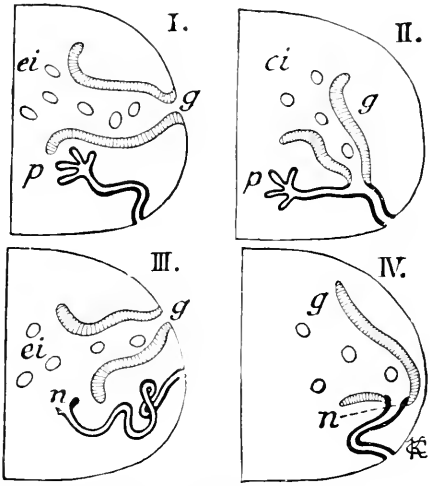

FIG. 47.—Different relations of nephridia and sexual ducts in chaetopods (*after Goodrich*). I, hypothetical primitive condition, gonoducts (*g*) and protonephridium (*p*) independent; II, ciliated grooves discharge into duct of protonephridium as in Phyllodoceids and Goniads; III, ciliated grooves and metanephridium (*n*) open independently as in Dasybranchus; IV, ciliated grooves open into canal of metanephridium as in Syllids, Spionids, etc. (*From Hertwig's Manual of Zoology by Kingsley, courtesy of Henry Holt and Co.*).

When each individual bears the organs of but one sex, the species is said to be dioecious. Very frequently among the invertebrates a single individual may produce both eggs and sperms and is then said to be hermaphroditic or monoecious. Hermaphroditism commonly results from the occurrence of a full set of gonads and accessory organs for each sex in the body of the same individual but in some snails both eggs and sperms are formed in the same gonad, which is therefore designated as a hermaphroditic gonad.

In most instances, the ducts which carry the germ cells from the ovaries and spermaries are at least in part (Fig. 47) derived as modifications of excretory ducts. In the marine annelids the varied relations of ducts for elimination of waste and liberation of germ cells are well illustrated. In some forms the gonoducts and the excretory ducts are wholly independent (Fig. 47, III), while in other forms the gonoducts or ciliated groove may become united with either a protonephridial tube (II) or a metanephridium (IV).

Vasa deferentia of the male are usually directly continuous with the gonads, while the oviducts of the female have communication with the ovaries only through the body cavity. A portion of the oviduct of the female is frequently enlarged as a uterus within which the eggs are held for either a brief time or through the full period of the development of the embryos.

Following copulation, sperm cells are frequently stored within the body of the female in a receptaculum seminis from which they escape to fertilize the eggs which are produced over a considerable period of time. The vitellaria are also accessory glands of the female. They furnish nutritive materials and in some instances supply the substances of which the eggshell is formed. In many animals, there are no separate vitellaria and frequently in these only a portion of the ovarian cells become functional ova, while others act as nurse cells or follicle cells which supply the ova with additional reserve food material.

Copulatory organs are of common occurrence. An intromittent organ known as the cirrus is frequently characteristic of the male. This may be a modification of the terminal portion of the vas deferens or, as is often the case, may be purely accessory structures such as spicules or appendages modified to aid in the transfer of sperm. Clasping organs are especially characteristic of the males of some arthropods, and in the same group ovipositors are frequent accessories of the female system.

Locomotor System.—Numerous specialized structures for locomotion are encountered in the single-celled organisms. Cilia, flagella, pseudopodia, and myonemes are characteristic partial differentiations of cells for movement. The first two of these especially are carried over into the Metazoa as modifications of epithelial cells for locomotion or the production of movement. Many larval Metazoa perform locomotion by means of cilia exclusively, but the flatworms and the rotifers represent the highest adults in which locomotion results from ciliary action. In the Metazoa, movements and locomotion more frequently result from the activity of contractile fibers which represent different degrees of specialization or differentiation of muscle cells. In some instances, there are scattered contractile elements, but more commonly the contractile elements are associated to form continuous sheets or bundles of muscles.

The dermomuscular sac of flatworms represents a definite stage in the development of a locomotor system. Alternate contraction and relaxation of the longitudinally and circularly directed fibers in such a sac produce successive shortenings and elongations of the body. As a consequence locomotion results. When hard skeletal parts make their appearance, groups of muscle cells become attached to these hard parts and with fixed points of attachment perform more effective movements. Even the setae of an earthworm serve for muscle attachment and aid in locomotion, thereby suggesting an extremely early stage in the differentiation of a locomotor skeleton. The exoskeleton of the arthropods is the most highly organized locomotor skeleton found in the invertebrates.

Nervous and Sensory System.—Histological elements differentiated for transmission of nervous impulses assume sundry forms of organization in the metazoan body. The hydroid or polyp stage of the coelenterates is usually provided with a scattered or diffuse arrangement of nerve cells, but in all of the Metazoa above the coelenterates the nerve cells are grouped to form definite tracts of nerve tissue. In these tracts occur not only the cell bodies of the neurons and cytoplasmic fibers with their specializations as already described but also supporting elements of which the neuroglia cells are the most important. Usually, there is a tendency for the cell bodies of the neurons to become massed in certain parts of the nerve tracts. These regions are designated as ganglia.

The nervous systems of medusae are interesting in that they exhibit a series of steps toward the centralization of the nervous system. In the hydromedusae, a nerve ring without any differentiation of ganglia parallels the margin of the bell. In the scyphomedusae, the nerve ring has become more specialized and shows localization of the cell bodies to form ganglia.

Among metameric animals, there is a tendency for ganglion formation in each somite, but this primitive scheme is in many instances altered by the fusion of two or more successive ganglia to form a single mass. This tendency is especially pronounced in the anterior region of the body where a single prominent ganglion, the brain, is located.

In many of the worms, two or more lateral nerve cords pass through the body, while in some of the annelids and in the arthropods these have been fused to form a single chain of ganglia ventral to the digestive tract. An examination of a cross-section of such a nerve cord, however, usually furnishes evidences of its double nature.

That portion of the nervous system which contains the ganglia and consequently is the controlling center for directing the activity of the organism is designated as the central nervous system, while from it fibers and bundles of fibers pass to the various parts of the body as a peripheral nervous system. Largely through the latter are the sense organs brought into relationship with the central nervous system. A sympathetic system in some of the higher arthropods controls the activity of some of the internal organs.

As has been pointed out, there are numerous modifications of epithelial tissues for receiving stimuli and transmitting nervous impulses to the central nervous system of the invertebrates. Concerning many of these sensory organs our knowledge is but fragmentary, for they are organs which have no counterpart in the human body and consequently direct knowledge of their functions is beyond the scope of human experience. In some instances, their functions may be inferred from the location and the mechanics of their structure and through the reactions of the organism when the organ in question is stimulated.

Tactile organs are very commonly developed as hairs or bristles from the surfaces of epithelial cells, or, as in the case of bristles of arthropods, they may be formed as outgrowths of specialized cells. Tactile organs may be scattered fairly uniformly over the surface of the animal, but sometimes specific organs are especially adapted for receiving tactile stimuli, as, for example, the tentacles of coelenterates, worms, and snails and the antennae and palpi of insects and crustaceans. In many such instances, other sensory organs are associated with those of touch. Thus the olfactory organs of insects are commonly found on the antennae along with other sensory organs of uncertain function. In some instances, the antennae are provided with hairs which seem to be associated with an auditory function.

Both taste and olfactory organs of the invertebrates are rather simple in their organization. They are especially developed in the insects, where they frequently occur as a sac or depression within which there is a bristle or conelike projection.

Organs of sight, hearing, and balance are frequently much more highly organized than those organs previously mentioned. The association of pigment with sensory epithelial cells frequently denotes the presence of a retina or some sort of structure for reception of light stimuli. Yet there are some organisms, such as the earthworms, which respond to light stimulation without having any specialized sense organs for the reception of light stimuli. Pigment spots near the bases of the tentacles in many jellyfishes are usually thought to have a light-percipient function and in some instances even have lenslike bodies associated with them.

In the turbellarians, there are eyes in which the sensory epithelium forming the retina has undergone considerable specialization, and in many of the marine annelids highly complicated optic organs are found. The highest development of an invertebrate eye is found in cephalopods, the eyes of which very closely resemble those of vertebrates, though the two seem to have no phylogenetic relationship but apparently have arisen independently of each other.

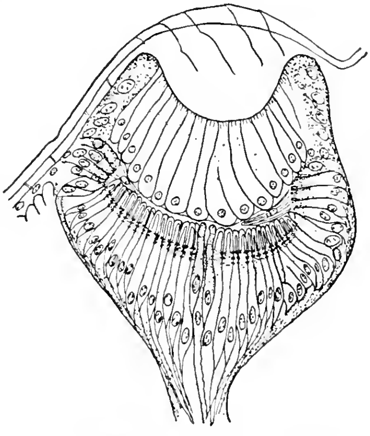

FIG. 48.—Median ocellus of Acilius. (*After Patten*).

Compound eyes are highly characteristic of arthropods. A compound eye is composed of an aggregation of similar elements called ommatidia the number of which is indicated by the facets or rounded or hexagonal markings on the surface of the eye. Each ommatidium is bounded externally by a biconvex cornea beneath which is located a fluid or a solid conelike lens. Beneath this are one or more chitinous rods termed the rhabdomes. Pigment cells surround each ommatidium and nerve fibers pass off from the base of the rhabdomes.

The term ocellus is frequently taken as synonymous with a simple eye, but from point of view of structure there are two very distinctly different types of ocelli. Those of one type, exemplified by the median ocelli of insects (Fig. 48), are but little less complicated than the compound eyes, while the lateral ocelli are much simpler.

The simple, unpaired median eye of the lower crustaceans shows many features in common with the eyes of the flatworms.

There are numerous modifications for auditory and balancing functions in invertebrates but most of these are recognizable as some sort of otocyst or statocyst (Fig. 39), which depends upon the movement of a free or suspended body, the otolith or statolith, against the walls of the vesicle for stimulating the central nervous system and causing the organism to right itself. In some of the insects is found a highly specialized auditory organ in which a tympanum receives sound waves and transmits the stimulus through an underlying space to the nerve endings in the sensory epithelium.

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CHAPTER IV

PHYLUM PORIFERA

The word sponge usually calls to mind the sponges of commerce which are only one type of the skeletal remains from animals belonging to the phylum Porifera. A mass of parenchymatous tissue penetrated by numerous pores covers this framework in the living animal. The living commercial sponges, though slimy to the touch, have a fairly solid fleshy body which is described by one author in the following manner: "In appearance and consistency and the manner in which it cuts with a knife, a living sheep's-wool sponge is not unlike a piece of beef liver, perforated with holes and canals." Sponges vary so much in shape that little can be said regarding their form. Without exception, they are attached to some object and have lost powers of free locomotion. Along with the lack of locomotor powers there is the correlated lack of nervous tissue. In fact, there are no specialized organs of any kind in the sponges.

Distribution.—Sponges live under the most varied conditions of aquatic existence from polar regions to the tropics and in both salt and fresh water, but they seem to be more influenced by conditions of the immediate environment than by mere geographical location. Some species are characteristic of the shore lines, even flourishing between tide marks, while others live only in the greatest depths of the ocean. Only a single family (Spongillidae of the class Demospongia) has become adapted to life in fresh-water, but in the species of this family distribution is so much facilitated by the reproductive buds or gemmules that most of the genera are practically cosmopolitan.

Fossil sponges appear in all strata of the Earth's crust back to the Cambrian but even the oldest fossils are fairly closely similar to forms of today, so they throw little light upon the problem of the origin of sponges.

Cell Layers.—The cell layers of the sponges offer but little opportunity for comparison with the remainder of the Metazoa. The main bulk of the body consists of a solid mass of mesoderm cells. The cells covering the surface of the body and those lining the internal cavities have an entirely different history from the ectoderm and entoderm cells of other many-celled animals. For this reason many zoologists maintain that the sponges represent a line of development wholly independent of all the higher animals and consequently set off the sponges from the Metazoa, applying to this phylum the rank of a separate subkingdom, the Parazoa. Certain chambers inside the sponge are lined with flagellated cells which, because of their location and function in capturing and digesting food, have frequently been considered as entodermal cells. In Fig. 49, the location of the flagellated cells is indicated by the hairlike parallel lines. In the course of embryological development these flagellated cells have been shown to arise from those cells of the embryo which in normal development give rise to the ectoderm. In fact, in the protozoan genus Proterospongia (Fig. 50 *B*), which is thought by many to be like the ancestor bridging the gap between the flagellate Protozoa and the sponges, the collared flagellate cells are found on the outside of the body.

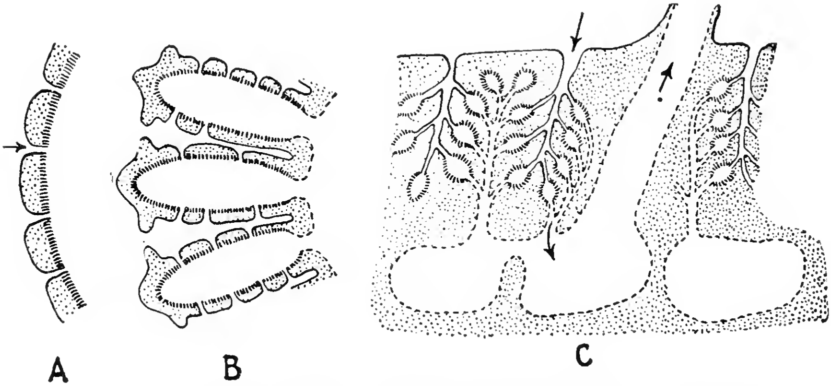

Fig. 49.—Morphological types of sponges. *A*, Ascon type; *B*, Sycon type; *C*, Leucon type. (*From Korschelt and Heider*).

Morphological Types.—Three types of sponge structure are usually recognized (Fig. 49). In the simplest sponges, of the Ascon type (*A*), the body is a thin-walled sac having a single large opening, the osculum, at one extremity and numerous minute incurrent pores through the body wall communicating with a central cavity. This central cavity, which is frequently called a stomach, is lined with flagellate cells, but since digestion is intracellular the cavity is not a true digestive cavity and therefore not a stomach. Opening and closing of the pores leading into this flagellated chamber are under control of the animal. When the pores are open, the action of the flagella causes water currents bearing food material to pass through the flagellated chamber and out through the osculum. During this passage, food is removed from the water and ingested by the cells. Leucosolenia and Olynthus are examples of this simplest type of sponge organization.

The Sycon (Fig. 49 *B*) differs from the foregoing chiefly in the fact that the central cavity is lined with pavement epithelium and the flagellated cells have withdrawn to small radial chambers or ampullae embedded in the thickened wall. The central cavity is now a distinct cloaca with which each ampulla communicates by means of a small opening called the apopyle. As the name implies, the radial chambers are arranged radially about the cloaca. Alternating with the radial chambers are the incurrent canals which pass from the exterior inward toward, but not into, the cloaca. Minute openings, the prosopyles, communicate between the incurrent canals and the adjacent ampullae, thus allowing water currents bearing food material to pass through the radial chambers, into the cloaca and out through the osculum. Grantia and Sycon are two typical genera whose representatives are built upon the Sycon plan.

As they acquire greater bulk, some sponges reach a size wherein direct communication between the ampullae and the exterior and cloacal surfaces is no longer possible. Intricately branched incurrent and excurrent canals establish these surface relations for the deeply embedded ampullae (Fig. 49 *C*). Sponges of this character are of the Leucon type and are typified by such genera as Leucilla and Oscarella.

Physiology of Sponges.—Regardless of the type, all sponges are fundamentally alike in their methods of securing food. Movements of the flagella in the flagellated chambers produce water currents through the canal system of the sponge. Food particles entering the flagellated chambers are ingested by the cells, and the process of digestion is wholly intracellular. From the incurrent streams of water the sponge derives its nourishment and its oxygen for respiration while the same water stream as it leaves the body by way of the osculum carries the metabolic wastes.

Reproduction.—Asexual reproduction through budding is common in sponges. By this means masses of individuals are produced thereby forming colonies. These colonies may be either groups of distinctly separable individuals with only a common region near the base, or they may be so intimately fused as to render the recognition of individuals impossible. Sponges possess great power of regeneration. In the commercial sponge fisheries, advantage is taken of this fact and small fragments are planted and allowed to grow before harvesting.

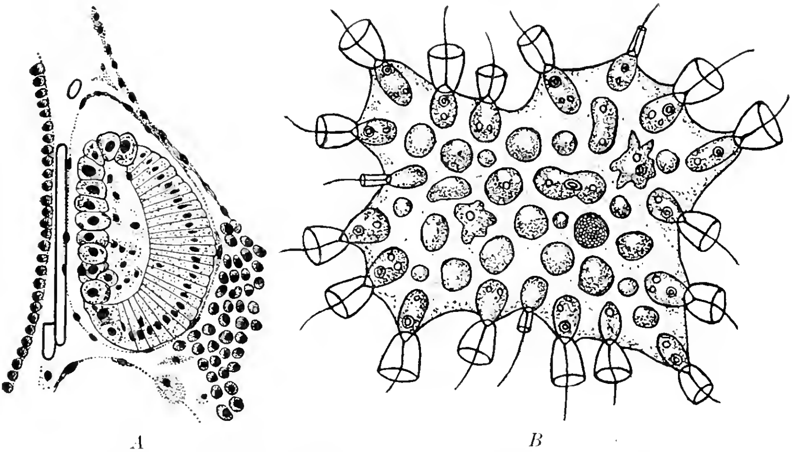

Fig. 50 *A*.—Embryo of Grantia. Blastula stage within embryonic chamber of parent individual. (*After Dendy*).

Fig. 50 *B*.—Proterospongia, showing collared flagellate cells. (*Redrawn from Kent*).

Gemmule formation is another type of reproduction found in fresh-water sponges. Groups of cells called gemmules or internal buds become separated from the surrounding tissues by confining membranes. These gemmules are capable of withstanding desiccation and other adverse circumstances which are fatal to the living sponge and are therefore of great importance in the life cycle of sponges.

Sponges are usually hermaphroditic, but since in any individual the germ cells of the male usually mature before those of the female they are said to be protandrous. Eggs are fertilized within the parent and there undergo segmentation (Fig. 50 *A*). The formation of the germ layers and the transformation of the larva present conditions wholly unlike these found typically in the Metazoa. The blastomeres resulting from cleavage of the fertilized egg become arranged as an ovoidal blastula (Fig. 50 *A*) one pole of which is rounded and the other flattened, but from this point onward conditions are not in harmony with the usual plan of embryonic development. The cells at the more pointed pole become extremely granular, while those at the opposite pole become much elongated and each develops a flagellum. The large columnar cells grow down and partly enclose the mass of granular cells. At about this stage, the larva breaks through the embryonic chamber in which it has developed and by way of the osculum uses the flagella to swim freely in the water. Upon leaving the embryonic chamber of the parent, the granular cells which have up to this time been partially invaginated into the blastocoel come to lie on the surface of the embryo. The larva is now an ovoid body one pole of which consists of flagellated cells and the other of granular cells. In other invertebrate larvae, the ciliated or flagellated cells are the ones which remain on the surface of the body and form the skin. Hence they are called ectoderm cells. But in the sponges the flagellated cells have a different future and later come to lie inside the body. This free-swimming larval stage is called an amphiblastula. Cells which are the forerunners of the mesoderm occur in the cavity of the amphiblastula. After a day or more of free-swimming existence the amphiblastula settles down with the pole bearing the flagellated cells in contact with some object. The flagellated cells become invaginated to form a cavity within the granular cells and from these the collared flagellate cells develop. The system of pores and canals and the osculum later make their appearance, thus laying down the general form and organization of the sponge, though the details of arrangement of the parts take considerable time for growth and development.

During the period of transformation from the larva some of the mesenchyme cells from the interior of the larva break through the layer of granular cells and become distributed over the surface. These apparently mesodermal cells of the larva thus form the body covering, adding another unparalleled chapter to the history of sponge development, for in no other instance is there a record of the skin of an animal being formed from mesoderm.

Skeleton.—The skeletal structures (Fig. 51) which give the chief character to the Porifera are spicules formed by mesoderm cells called scleroblasts. Characteristically each of the large spicules of the mature sponge starts as a microscopic crystal within the cytoplasm of a scleroblast but as the spicule grows it ultimately extends the limits of the mother cell and breaks out from its walls. In some other instances spicules are formed by the combined action of a group of scleroblasts.

In the classification of sponges, the nature and form of the skeletal structures are of great importance. Spicules may be formed of either calcareous or silicious material in a great variety of patterns. A network of a substance called spongin (Fig. 51, 1) is another type of supporting structure formed by cells called spongioblasts. This spongin, which is closely allied to silk in its chemical composition, may appear either alone or along with silicious spicules.

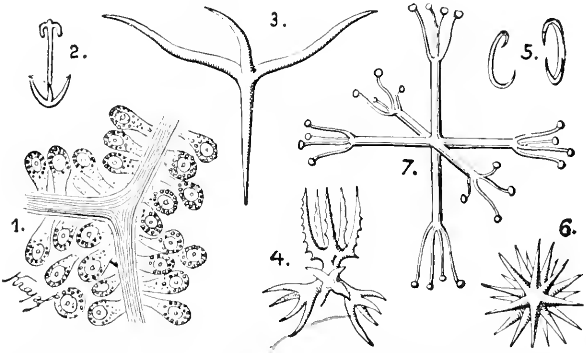

FIG. 51.—Skeletal structures of sponges (*after Schulze and Maas*). 1, spongin fiber surrounded by spongioblasts; 2–7, different types of spicules. (*From Hertwig's Manual of Zoology by Kingsley, courtesy of Henry Holt and Co.*).

Economic Importance.—Aside from the market value of sponges gathered for domestic use and utilization in the arts, sponges have relatively little direct value. They have no important enemies, but many kinds of crustaceans, worms, and other animals find shelter within their canals and some species of sponges have been found only on the bodies of other animals, especially crabs, where they apparently hold a symbiotic relationship. The spicules seem to afford a great measure of protection, for practically no animals feed upon sponges. Some of the boring sponges do damage to the shells of molluscs into which they burrow for protection.

OUTLINE OF CLASSIFICATION

Phylum Porifera.—Many celled; body penetrated by pores communicating with one or more internal chambers or canals, at least one of which is lined with collared-flagellate cells. Skeleton a framework of inorganic spicules or of organic fibers or both. Aquatic.

I. Class Calcarea.—Ocean dwellers, in shallow water; chiefly radial in form; spicules of carbonate of lime, simple or triradiate.

1. Order Homocoela.—Gastral epithelium a single sac. *Clathrina, Leucosolenia.*

2. Order Heterocoela.—Gastral epithelium lining canals or chambers around a central cloaca. *Grantia, Leucortis.*

II. Class Hexactinellida.—Deep-sea forms; chiefly radial in form; skeleton a network of silicious spicules. *Hyalonema, Euplectella.*

III. Class Demospongia.—Marine and fresh water; skeleton of spongin or of silicious spicules or both, sometimes wholly lacking; canal system complicated.

1. Order Tetraxonida.—Typically tetraxon spicules. *Geodia, Plakina.*

2. Order Monaxonida.—Typically simple spicules. *Cliona, Suberites, Spongilla, Carterius, Ephydatia.*

3. Order Keratosa.—Spongin; no true spicules. *Euspongia, Aplysina.*

4. Order Myxospongia.—Without skeleton. *Oscarella.*

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CHAPTER V

THE COELENTERATES AND CTENOPHORES

A. PHYLUM COELENTERATA

Coelenterates are diploblastic, radially symmetrical animals, usually bearing tentacles and provided with nettling cells. In fundamental structure, the bodies are but slightly modified from the plan of arrangement of the gastrula stage which occurs in the embryology of all higher Metazoa. Because of their form, Cuvier included them along with the echinoderms in his type Radiata. Extreme differences in structure preclude the possibility of uniting these two groups on the basis of superficial agreement in disposition of their parts. The echinoderms have a true body cavity or coelom in addition to the digestive cavity. In the coelenterates, however, only one cavity is found. Phylogenetically, this single cavity represents the gastrula cavity from which in higher forms of life both digestive cavity and body cavity arise during later development. Since, in the coelenterates, these two cavities are not differentiated, Leuckart suggested the name Coelenterata which they now bear, carrying with it the idea of lack of specialization of coelom from the enteron.

Morphological Types.—Body form among the coelenterates is usually referable to one of two types, the hydroid or polyp form and the medusoid or jellyfish form. While these two forms are clearly differentiated one from the other, in fundamental structure they are essentially alike. In each, tentacles are usually present and function in grasping food and bringing it into the mouth. These tentacles, and in some instances the body also, are supplied with nettling cells which are tubular threads coiled within a small bladderlike structure. As a means of defence or of offence, these threads are discharged from the nematocysts with a force sufficient to carry them even through the chitinous body covering of small crustaceans introducing into the wound an irritating fluid. By their use, some coelenterates, the Portuguese man-of-war for instance, are capable of inflicting painful injury even to man.

The term polyp, which is applied to the hydroid individual, is derived from the Latin name of the cuttlefish (Polypus) because of a superficial resemblance between the two animals.

Cell Layers.—The body wall is composed of an external layer of cells called the ectoderm and an internal layer lining the gastrovascular cavity called the entoderm. Between these lies a non-cellular, gelatinous substance termed the mesoglea. The extent and importance of this mesoglea in the various coelenterates varies extremely. In hydroids it is commonly a very delicate, inconspicuous layer, while in jellyfishes it has become the most conspicuous as well as the most bulky part of the whole organism. Structures having their origin in either ectoderm or entoderm tend to pass into the mesoglea, thus rendering it more highly complicated and causing it to partake of the nature of a definite mesoderm. The extreme of this tendency is found in the Ctenophora, a group which is frequently included as a class of the Coelenterata but here recognized as an independent phylum.

Tissues and Organs.—In degree of differentiation, the medusoid represents much the higher type. Structures frequently either wanting or of low organization in the hydroid individuals are well represented in the medusae even of the same species. Muscle occurs as a partial differentiation of epithelial cells in hydroids of the Hydrozoa and Scyphozoa but sheets and bundles of muscle tissue are recognizable in the medusae. Specialized sensory organs are almost exclusively associated with the more distinctly centralized nervous system of the medusoid forms. In these, organs of equilibrium appear in extremely diverse stages of development, representing conditions varying from simple, exposed, modified tentacles or sensory clubs to the highly complicated statocysts with accessory protective vesicles (Fig. 39). The reproductive organs typify the lowest degree of specialization, for no ducts or other accessory sexual organs of any sort accompany the gonads.

Modifications of the Digestive System.—In its most primitive condition, the coelenteric or gastrovascular cavity of coelenterates is a simple bag with a single opening, the mouth. This is the condition in the polyp of the Hydrozoa. In the medusae, there are frequently diverticula from the central chamber of the digestive system which provide greater space for the digestion of food and serve for the delivery of digested food material to the more distant parts of the body. In many instances, these diverticula have the form of definite vessels, called the radial canals, which may be united at their distal ends by a common vessel termed the circumferential canal. Further complication of the digestive system is found in the Anthozoa wherein a definite infolding of ectoderm projects for some distance from the mouth opening into the digestive chamber as an esophagus. In this same group, the cavity becomes divided by a series of partitions called mesenteries or septa which provide additional surface for the processes of digestion and assimilation of the food material.

Metagenesis.—Both types of individuals described above occur in the course of the life cycle of the Hydrozoa and the Scyphozoa. An asexual hydroid generation gives rise to a sexual medusoid generation. This condition of direct alternation between two generations of different type has been termed metagenesis. The occurrence of hydroid and medusoid forms in the developmental cycle of a single species has not been understood long. It is, then, not surprising that all of the earlier treatises considered the hydroid and medusoid generations, even of the same species, as belonging to distinct and independent groups of the animal kingdom.

Habitat.—In habits, the coelenterates are chiefly marine, though Hydra, Protohydra, Cordylophora, and a few rare medusae occur in fresh-water habitats.

At the seashore, the anemones and the colonial hydroids are among the most interesting animals on pilings, on seaweeds, and on rocks, while the fragile bodies of the free-floating jellyfishes with their play of colors and graceful pulsations are the most conspicuous of the free-floating plankton organisms. Because of their size and abundance, coelenterates are among the most prominent of the organisms which render the ocean phosphorescent.

Food Relations.—Most coelenterates feed upon microscopic organisms which are captured by the tentacles and killed by the nettling cells. Fishes and crustaceans of considerable size are included in the food of some of the jellyfishes, however, and even the minute fresh-water hydras at times feed upon newly hatched fish. In turn, the soft bodies of coelenterates frequently fall prey to other animals in spite of the protective nature of the nettling cells. The discovery of nettling cells in some flatworms and molluscs threw some doubt upon the nematocysts as distinctive organs of the coelenterates but it is now known that the nettling cells acquired their unusual location when coelenterates were used as food.

Class Hydrozoa

The Hydrozoa are coelenterates usually having an alternation of generations of which the hydroid is frequently the more conspicuous. The hydropolyp lacks longitudinal folds of the entoderm and the mouth opens directly into the coelenteric cavity. The hydromedusa, when present, has a smooth bell margin; the concave surface is partially enclosed by a membrane, the velum, which extends inward from the edge of the bell. In the members of this class the gonads may be borne either on the radial canals or on the manubrium. The germ cells are expelled from the gonads directly through the surface of the body.

Life History.—The life cycle of Obelia serves well to illustrate metagenesis as it occurs in the Hydrozoa. The hydroid colony starts as a single polyp which, by continued budding, produces a series of individuals alternating along a common stalk. Such a colony is attached to some object by means of a rootlike structure termed the hydrorhiza. In a young colony, all of the individuals are alike and all function as vegetative zooids. Starting near the base of the colony, reproductive individuals begin to make their appearance. These are sac- or vase-shaped zooids, termed gonangia, budded off in the axils between the vegetative individuals and the common stalk. Each gonangium is composed of a central core upon which buds are formed. As development proceeds, these buds display medusan characters and upon reaching full development become detached and emerge from the open end of the gonotheca as free-swimming jellyfish. The medusae produce germ cells which, upon fertilization, undergo cleavage to form a ciliated larva, termed a planula, but little higher in organization than the gastrula. After a short period of free existence the planula becomes attached to some object and transforms into a hydroid through the development of a circle of tentacles and of a hydrorhiza. From this single zooid, an entire colony is produced through repeated budding.

While budding is the usual method of reproduction during the asexual generation of Hydrozoa, it occurs but rarely in the medusoid generation. Sarsia and a few other genera are peculiar in that young jellyfishes are budded from the manubrium or from the margin of the bell at the ends of radial canals.

The Gonophore and Its Reduction.—An individual among the coelenterates which bears the gonads is termed a gonophore. Ordinarily, this is a free-living medusoid individual (Fig. 52 *A*) with gonads either on the manubrium or on the radial canals of the gastrovascular system. In some representatives of the class Hydrozoa, the medusoid generation is lacking. This condition is usually the result of a process which is designated as gonophore reduction. Usually, the gonophores have their origin as products of asexual reproduction from the hydroid individuals. Under ordinary circumstances, they undergo development to a certain stage while still attached to the hydroid and are then liberated.

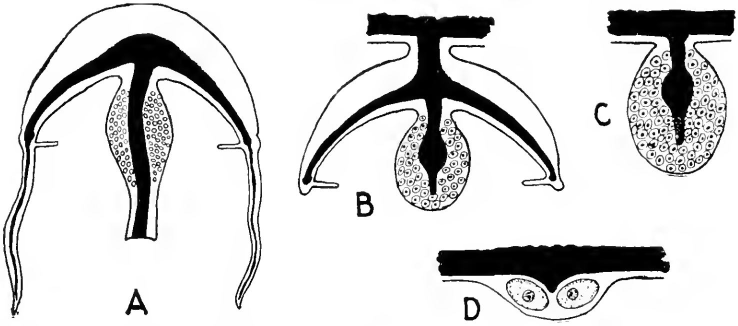

FIG. 52.—Gonophore reduction. *A*, free gonophore, an independent medusa; *B*, a medusa which remains permanently attached to hydroid colony and fails to develop either tentacles or mouth; *C*, still further reduction of gonophore to a simple manubrium (the spadix) surrounded by gonads; *D*, gonads produced around a slight entodermal rudiment of the manubrium as in Hydra. (*After Kingsley*).

In some instances, however, freedom is never gained, then the gonophores remain permanently attached to the parent hydroid (Fig. 52 *B-D*) and organs essential to the independent existence of the gonophore fail to develop to a functional stage or degenerate entirely. By the selection of different examples, a finely graded series of steps in the degeneration of the medusoid may be secured. A greatly reduced gonophore comprises little more than an ectodermal bag within which the germ cells are arranged about a core of entoderm called the spadix. The spadix represents the remains of a degenerated manubrium. The term sporosac is applied to such a reduced gonophore (Fig. 52 *C*) attached to the body of a hydroid individual. In some species of Corymorpha, medusae-bearing gonads are formed. Though the medusae pulsate in futile fashion for several days, they never break away from the parent polyp. The ultimate in gonophore suppression is found in members of the genus Hydra, wherein the gonads occur in the ectoderm with practically no remnant of spadix or other medusoid remains (Fig. 52 *D*).

Suppression of the Hydroid.—In contrast with the gonophore reduction discussed above stands the suppression of the hydroid generation characteristic of representatives of the order Trachylinae. In these, development of the medusa proceeds directly from the larva derived from the fertilized egg without the intervention of the polyp generation.

Polymorphism in Hydrozoa.—The original plan of two body forms alternating in the life cycle of the Hydrozoa has become much modified in members of one order called the siphonophores (Siphonophora). These are free-floating or swimming colonial forms in which the parts have become so interdependent and so highly specialized for limited functions that it becomes difficult to distinguish whether the individuals of the colony are hydroid or medusoid.' A continuous tube of the digestive system connects all the individuals of a colony and each performs but a limited service for the entire colony. One individual consists of only an air-filled bladder or pneumatophore (Fig. 53 *A*), which regulates the position of the colony at or beneath the surface of the ocean. Nectocalyces, or swimming bells (*B*, *C*), frequently occur just below the float and provide the colony with a means of locomotion. These are lacking in one of the most widely known siphonophores, the Portuguese man-of-war (Physalia), whose greatly enlarged pneumatophore acts as a sail. The remainder of the colony consists of feeding zooids *H*, dactylozooids as sensory organs *F* and *G*, sporosacs *E*, bracts or organs of defence *D*, and batteries of nettling cells *I*. The individuals are so completely interdependent and are so highly specialized for carrying on limited functions for the colony as a whole that the colony is frequently

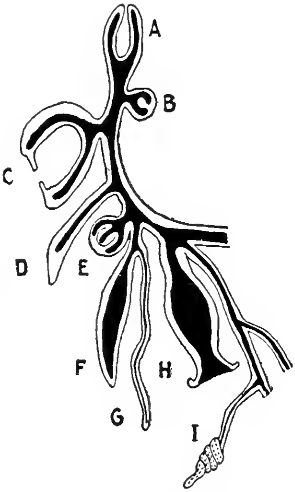

FIG. 53.—Diagram of a siphonophore colony (Physophorida). *A*, pneumatophore; *B*, *C*, swimming bells; *D*, protective zooid; *E*, sporosac; *F*, *G*, dactylozooids; *H*, feeding polyp; I, nettling cells. (*After Claus*).

likened unto a single individual with organ systems resembling those found in higher Metazoa.

Dimorphism.—A condition of two unlike forms in the same generation is not unusual in the Hydrozoa. This condition is most commonly encountered as the specialization of vegetative and reproductive zooids in the same colony as described for Obelia. Dimorphism of a less common type occurs in the stag-horn coral Millepora, wherein gasterozooids provided with mouth and tentacles and dactylozooids lacking the mouth are associated in the same colony. Neither of these represents the gonophore generation, for rudimentary jellyfishes of both sexes are produced, usually in chambers within the coral-like skeleton of the colony.

Histological Differentiation.—As was stated in the introductory discussion of the characters of the phylum, the medusa represents a higher type of differentiation than is found in the hydroid polyp. Scattered nervous elements and sensory cells characteristic of the polyp are replaced by a centralized nerve ring with which statocysts and light-percipient organs are associated in the hydromedusa except in the Anthomedusae, which are without statocysts. Hertwig has called attention to the fact that no less than eight distinct lines of differentiation occur in the ectoderm cells of the hydromedusa. There are myoblasts, nerve cells, indifferent cells, sensory cells, cnidoblasts, gland cells, pigment cells, and germ cells. Since a number of these are represented by several distinct types of histological differentiation, as, for example, the several distinct types of sensory and gland cells, these simple diploblastic animals become more highly organized than is ordinarily understood.

Body Covering and Skeleton.—An investing membrane surrounds some hydroid forms (Obelia) but is wanting in others (Hydra, Tubularia). This investing membrane may be either a delicate perisarc covering all or only part of the zooid or, in some instances (Millepora) part of a massive calcareous skeleton. The expansion of perisarc around a vegetative zooid is termed a hydrotheca, while that around a reproductive zooid is termed a gonotheca.

Class Scyphozoa

The Scyphozoa are coelenterates having an alternation of generations of which the medusoid is the more conspicuous.

Medusae of the Scyphozoa are often less that an inch in diameter, though one species of Cyanea on the Atlantic coast is said to reach a diameter of 7 feet across the bell and to have tentacles 120 feet long. The scyphopolyp or scyphistoma when present is distinguishable from the hydropolyp through the presence of four longitudinal folds of the entoderm called the taeniolae. In the development of the medusae, these form the gastral tentacles or phacellae. When the germ cells leave the gonade they are liberated into the gastrovascular cavity, not directly to the exterior as in the Hydrozoa. The scyphomedusa lacks a velum, has a more or less notched margin, and bears entodermal gonads. While Scyphozoa are usually dioecious, some genera are hermaphoroditic. Form and structure of the medusa are more readily understood when the development has been outlined.

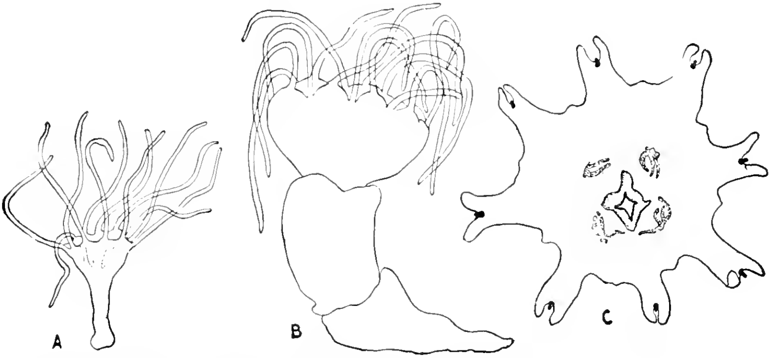

FIG. 54.—Larval stages in the development of Aurelia. *A*, scyphistoma; *B*, strobila; *C*, ephyra. (*Orig.*).

Life History.—The medusae of Aurelia produce germ cells, which, upon fertilization, undergo cleavage and develop into a ciliated larva called a planula. After a brief free existence, the planula becomes attached to some object and transforms into an individual superficially like a Hydra, to which the names scyphistoma (Fig. 54 *A*) or scyphopolyp have been applied. By a series of transverse constrictions, the scyphistoma becomes separated into a pile of saucerlike structures (Fig. 54 *B*) and in this stage is called a strobila. As the constrictions become deeper, a series of ephyrae become detached from the strobila. At the time of their liberation, each ephyra (Fig. 54 *C*) has eight prominent armlike projections arranged radially about the margin of the body. Growth of the medusa from this ephyra involves a rather conspicuous metamorphosis. The eight arms mentioned above mark off eight radii of the mature jellyfish. The four radii passing through the angles of the mouth are known as the perradii, the other four as the interradii. Axes falling between the bases of the eight arms of the ephyra are designated as the adradii. By more rapid growth of the adradial zones the notches of these regions become filled up, thus giving the young jellyfish a slightly crenated circular outline. The marginal tentacles make their appearance in the adradial regions.

Though alternation of generations described for Aurelia is the customary type of development among the Scyphozoa, in some genera a free-swimming medusa develops directly from the fertilized egg. True asexual reproduction does not occur in the medusa of Scyphozoa.

Body Form.—There is great diversity in form of body among the Scyphozoa. Aurelia has a flattened, saucer-shaped bell while some of the genera from the tropics have almost cubical bodies (Cubomedusae). The cubical appearance is heightened by the presence of only four tentacles on the margin of the bell. Some of the relatives of the Aurelia lack marginal tentacles altogether and in the members of the suborder Rhizostomae a series of folds around the manubrium bear eight small mouths in addition to the one at the end of the manubrium. Members of the genera Haliclystus and Lucernaria have the aboral surface drawn out as a peduncle by which the animal becomes attached. In these same genera, marginal tentacles are lacking but the bell is drawn out into eight arms each of which is provided with a cluster of diminutive tentacles.

Class Anthozoa

All organisms belonging to this class conform to a polyp form of organization. The anthozoan polyp differs fundamentally from the characteristic hydrozoan polyp in the presence of an ectodermal esophagus and of longitudinal partitions called septa or mesenteries (Fig. 55) partially dividing the gastrovascular cavity. Well-developed bands of muscles are found in connection with the septa. The mesoglea contains numerous cells, thus having the appearance of a simple connective tissue and supplying firmness and a fleshy consistency to the body in many forms. Both solitary and colonial forms occur in this exclusively marine group of almost universally sessile organisms. Examples of the solitary forms are the sea anemones and of the colonial forms are the corals, gorgonians, sea pens, and sea pansies.

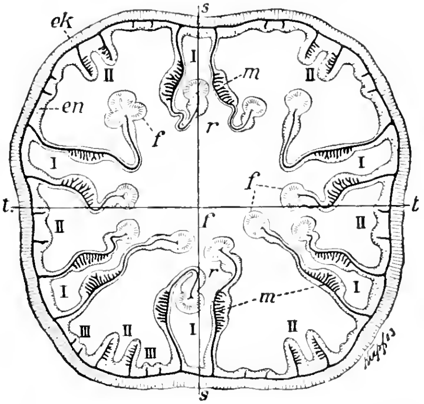

FIG. 55.—Section of a young sea anemone. *ss*, sagittal plane; *tt*, transverse axis; *I*, *II*, *III*, septa of first, second and third orders; *ek*, ectoderm; *en*, entoderm; *f*, mesenterial filament; *m*, muscle; *r*, directive septa. (*After Boveri, from Hertwig's Manual by Kingsley, courtesy of Henry Holt and Co.*).

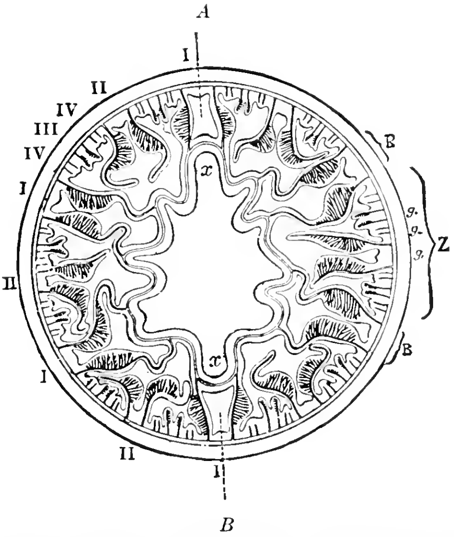

FIG. 56.—Transverse section of Zoantharian. *AB*, plane of symmetry; *x*, siphonoglyphe. (*From Hertwig's Manual by Kingsley, courtesy of Henry Holt and Co.*).

Anthozoa occur in greatest abundance in tropical seas where their skeletal remains build massive coral reefs.

Digestive System.—The mouth is usually oval or slit-like and leads through an inturned tube of ectoderm, called the esophagus, into the gastrovascular cavity. Like the mouth, this esophagus is usually compressed so that a sagittal axis is recognizable marking off a biradial symmetry. In some instances, one or two grooves run the length of the esophagus at the poles of the sagittal axis. These grooves (*x*, Figs. 56, 57) are termed the siphonoglyphes. The esophagus extends only part way from the oral toward the pedal surface. It is held in position by the primary septa (Fig. 55, *I*), folds of entoderm and mesoglea which extend from the body wall inward to meet the esophagus and thus at the oral extremity completely divide the gastrovascular cavity into a number of pockets or chambers.

Number and Arrangement of Septa.—Since each chamber of the gastrovascular cavity continues beyond the body proper into a tentacle, there is usually a direct relation between the number of chambers and the number of tentacles. In addition to the primary septa, many others reach only part way toward the esophagus. These are of varying lengths and on the basis of their length and order of development are termed secondary, tertiary, and so forth (Fig. 55, *II*, *III*). The number of primary mesenteries is of considerable importance in distinguishing the various orders of the Anthozoa. In the Alcyonaria (Octocoralla), there are eight septa. In practically all representatives of this order, the muscle ridges of all septa are directed toward the same pole of the sagittal axis. Edwardsia is an exception to this rule and marks a step in transition from the Alcyonarian to the Zoantharian (Hexacorallan) type, for in Edwardsia the position of the muscles on one pair of septa at one pole of the sagittal axis is reversed. The Zoantharia usually have one pair of primary septa at each pole of the sagittal axis and two lateral pairs on each side of the body. The two pairs lying in the main axis (Fig. 55 *r*) are called the directives. The muscle ridges on these face outward, while in all the remaining pairs the ridges of one pair face each other. In development, the primary septa are the first to appear. Between these, come the secondary and later the tertiary septa. With the increase in number of septa, there is usually a corresponding increase in number of tentacles, but this correlation is not absolute.

Other Organs.—In addition to muscles, the gonads, mesenterial filaments, and acontia are important structures associated with the septa. The germ cells, which have their origin in the ectoderm, come to lie in the mesoglea near the free margin of the septa. The ruffled free margin of each septum is edged with a thickened mass of epithelial cells called the mesenterial filament, thought to be of use in holding and compressing food particles, thereby aiding in digestion. Near the pedal disc, these mesenterial filaments are frequently modified to form long threadlike organs, the acontia, which are provided with numerous nettling cells. Through the mouth or through minute pores in the body wall the acontia are thrust to the outside of the body where they serve as efficient defensive organs.

Reproduction.—Most Anthozoa, with the exception of the sea anemones, possess some sort of skeletal structures, either as solid deposits formed by the zooids or as spicules in the colony wall. These structures are of such diverse natures in the different groups that they cannot be described here.

Sexual development involves the formation of a planula through cleavage of the fertilized egg. The planula, after a brief free-swimming life, settles down and undergoes a transformation to the polyp form. Budding is of common occurrence and gives rise either to separate individuals or to colony formation.

Subclass ZOANTHARIA

Sea anemones, true stony corals, and black corals are examples of the Zoantharia which may be recognized from other Anthozoa by the presence of numerous simple or unbranched hollow tentacles. The corals are colonial, while the anemones occur as solitary polyps. The esophagus is provided with two siphonoglyphes and the gastrovascular cavity bears numerous paired mesenteries, typically occurring in multiples of six. Except for the directives (mentioned above) the septa are arranged in pairs with the muscle bands of each pair facing one another. Edwardsia is an exception with its eight mesenteries and sixteen or more tentacles. Various other modifications of the rule occur in other representatives of this subclass.

There is great diversity in extent of development of skeletal material in this subclass. Skeletal structures are lacking in the sea anemones, the stony corals develop massive calcareous skeletons, while the black corals have a branched, hollow axial skeleton of horny material lacking lime spicules.

Subclass Alcyonaria

Eight feathered tentacles and eight single mesenteries (Fig. 57) characterize members of this subclass which are also frequently referred to under the name Octocoralla. Colonial forms, frequently with polymorphism of the individuals, are common. Budding to form a colony is usually stoloniferous.

As in the preceding subclass, here also we find diversity in skeletal structure. Horny or solid calcereous rods give form and support to the colonies of sea fans (Gorgonians) and precious coral, while only clustered spicules occur within the tissues of the sea pens and sea pansies.

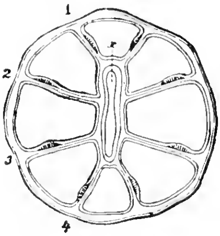

Fig. 57.—Transverse section of an Alcyonarian. (*From Hertwig's Manual by Kingsley, courtesy of Henry Holt and Co.*).

B. PHYLUM CTENOPHORA

The Ctenophora have very commonly been considered as a class of the Coelenterata. The absence of marginal tentacles, lack of netting cells, centralization of the nervous mechanism, and transformation of the mesoglea into a mesoderm mark the chief arguments in favor of considering the ctenophores as an independent phylum. The most striking external feature is the presence on the surface of the body of eight meridional bands of swimming combs or plates (Fig. 58) each of which is composed of a linear series of short rows of cilia.

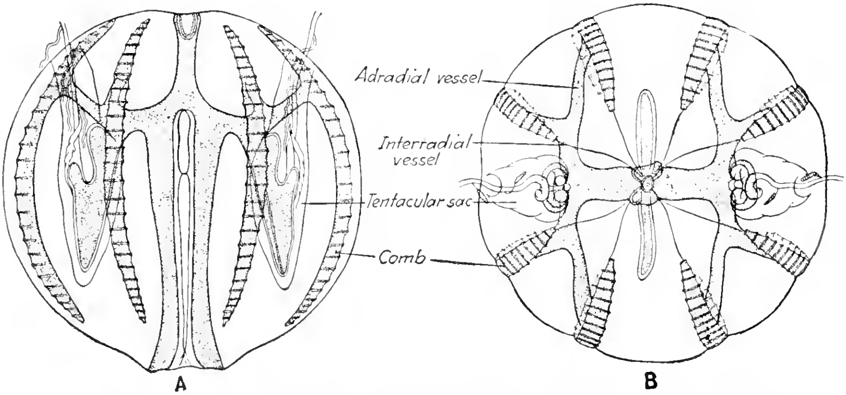

Fig. 58.—A ctenophore, *Pleurobrachia rhododactyla* Agassiz. *A*, lateral view *B*, aboral view. (*After L. Agassiz*).

Two tentacles arising in lateral ectodermal depressions or pockets are characteristic of most representatives of this phylum. At the aboral pole occurs a slight depression within which is located a single otocyst. In the transverse plane this depression is continued as two narrow ciliated areas called the polar plates.

Body form is not constant throughout the group. Many individuals are ovoid, others have a somewhat shortened dorsoventral axis, and still others are drawn out into a narrow band.

The nettling cells characteristic of coelenterates are wanting in the ctenophores. In their place structures called adhesive cells occur upon the tentacles.

Digestive System.—The mouth leads into a tube called the stomach, but since it is ectodermal in origin it is more properly a stomodaeum. This stomach opens into an entodermal sac, the funnel. The stomach and funnel are both flattened with the broad axis of one at right angles with that of the other. From the funnel are given off laterally two perradial vessels each of which divides dichotomously to form the four interradial vessels, (Fig. 58 *B*). By another dichotomous division these form the eight adradial vessels each of which communicates with one of the meridional vessels directly underlying the rows of combs. Each perradial vessel gives off a branch called the paragastric canal, which runs parallel to the stomach and ends blindly. At its aboral extremity the funnel gives off a funnel vessel which, after forming two or four branches, proceeds to the aboral pole and there empties through two or more openings called the excretory pores.

Development.—Ctenophores undergo direct development from the fertilized egg. There is no alternation of generations. One of the most interesting facts regarding the development of the egg is that the materials for the formation of the adult structures seem to be definitely arranged within the egg even before the first cleavage. Evidence of this has been gained from the fact that injury to or removal of a bit of the cytoplasm leads to the formation of a ctenophore lacking in some organ or structure such as the reduction in number of combs or loss of a part of the digestive system.

Classes and Orders.—On the presence of or lack of tentacles, two classes are recognizable: the Tentaculata and the Nuda. Of these, the former includes three orders and the latter a single order, the Beroida. Members of the order Cydippida (Pleurobrachia, Hormiphora, etc.) have ovoid or pear-shaped bodies bearing two tentacles arising from tentacular sacs or sheaths and into which they may be retracted. The Lobata includes those which have two large oral lobes and numerous minute lateral tentacles. In the young, two large tentacles are present but in later stages only their bases are present and these are without a sheath. Venus' Girdle (Cestus) is an example of the order Cestida members of which have the body much compressed in the vertical plane. Representatives of the order Beroida lack tentacles and the wide mouth and gullet occupy most of the animal.

OUTLINE OF CLASSIFICATION

A. Phylum Coelenterata.—Diploblastic; radially symmetrical; bearing tentacles and nettling cells; a single gastrovascular cavity with one opening; no anus; aquatic.

I. Class Hydrozoa.—Alternation of generations typical; medusa with velum; polyp without entodermal folds.

1. Order Leptolinae.—Hydroid fixed.

a. **Suborder Anthomedusae.**—Polyp without theca; gonads on manubrium; *Hydra*, *Clava*, *Cordylophora*, *Coryne*, *Tubularia*, *Bougainvillia*, *Hydractinia*.

b. **Suborder Leptomedusae.**—Polyp with theca; gonads on radial canals. *Obelia*, *Gonionemus*, *Campanularia*, *Sertularia*, *Aequorea*, *Plumularia*.

2. Order Trachylinae.—Medusa develops directly from egg.

a. **Suborder Trachymedusae.**—Tentacles on bell margin; gonads on radial canals. *Petasus*, *Trachynema*, *Liriope*, *Campanella*, *Aglantha*.

b. **Suborder Narcomedusae.**—Tentacles arise from aboral surface of bell some distance from margin; gonads on manubrium. *Cunina*, *Aeginopsis*, *Cunoeantha*.

3. Order Hydrocorallina.—Massive calcareous exoskeleton. *Millepora*, *Stylaster*.

4. Order Siphonophora.—Pelagic; colonial with marked polymorphism. *Physalia*, *Velella*.

II. Class Scyphozoa.—Usually alternation of generations; medusa without velum; gastric tentacles; polyp with four entodermal folds.

1. Order Stauromedusae.—Conical or vase-shaped medusa; no marginal sense bodies. *Tessera*, *Halielystus*, *Lucernaria*.

2. Order Peromedusae.—Cup-shaped medusa; four interradial sense bodies. *Pericolpa*, *Periphylla*.

3. Order Cubomedusae.—Cuboidal; four perradial sense bodies. *Charybdea*.

4. Order Discomedusae.—Saucer-shaped medusa; eight or more otocysts.

a. **Suborder Semostomae.**—Four large perradial arms surround mouth. *Aurelia, Cyanea.*

b. **Suborder Rhizostomae.**—No marginal tentacles; many mouths. *Stomolophus.*

III. Class Anthozoa.—Polyp only; esophagus; mesenteries.

A. **Subclass Zoantharia.**—Numerous mesenteries and tentacles.

1. Order Actinaria.—Solitary; no skeleton. *Metridium, Sagartia, Cribina, Cerianthus, Edwardsia.*

2. Order Madreporaria.—Colonial; calcareous skeleton. *Astrangia, Orbicella, Meandrina, Coeloria, Favia, Madrepora, Porites.*

3. Order Antipatharia.—Colonial; treelike horny skeleton. *Antipathes, Cirripathes.*

B. **Subclass Alcyonaria.**—Eight mesenteries and branched tentacles.

1. Order Alcyonacea.—Skeleton of spicules or small, irregular bodies; axial rod lacking. *Tubipora, Alcyonium.*

2. Order Gorgonacea.—Treelike; calcareous or horny skeleton. *Gorgonia, Corallium, Euplexaura.*

3. Order Pennatulacea.—Colony with one end usually buried in sea-bottom. *Renilla, Pennatula, Ptilosarcus.*

B. **Phylum Ctenophora.**—Eight meridional bands of ciliated plates; adhesive cells; centralized nervous system; pelagic.

I. Class Tentaculata.—Typically with two aboral tentacles.

1. Order Cydippida.—Body ovoid or pear-shaped; two retractile tentacles arising from aboral tentacular sacs. *Pleurobrachia, Mnemiopsis.*

2. Order Lobata.—Two large oral lobes; no tentacular sacs; numerous lateral tentacles. *Bolinopsis, Deiopea.*

3. Order Cestida.—Ribbonlike; two tentacular sacs and numerous lateral tentacles. *Cestus.*

II. Class Nuda.—No tentacles; no oral lobes.

1. Order Beroida.—Laterally compressed; gullet occupies most of interior of body. *Beroe.*

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(See general references at close of Chapter I)

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CHAPTER VI

PHYLUM PLATHELMINTHES

The Plathelminthes comprise a phylum of wormlike animals with bodies usually flattened, devoid of body cavity, and lacking true segmentation. The bulk of the body is composed of a mass of connective tissue termed parenchyma within which the various organs are embedded. Externally, this is covered by either a ciliated epithelium or a non-cellular cuticula. A body musculature is present, the fibers of which are usually circular, longitudinal, and diagonal in arrangement. Frequently, in addition, fibers are also found penetrating the body from dorsal to ventral surfaces. The nervous system usually consists of two or more longitudinal strands which, near one end of the body, bear a pair of ganglia called the brain. In many instances, the longitudinal nerve trunks are connected by cross-commissures which give the system a ladderlike appearance.

Typically, the digestive system is composed of an ectodermal pharynx and a mesenteron, for the proctodaeum is lacking. Exceptions to this are found in the cestodes, which lack all evidence of a digestive system, and in the nemertines, which have a complete system terminating posteriorly in an anus. A few species of trematodes possessing an anus have also been described. Excretion is by means of a system of tubules, the protonephridia, which ramify throughout the body and end in minute structures called the flame cells.

Most of the flatworms are hermaphroditic. The reproductive organs consist not only of the primary organs or gonads but to them are added many accessory organs and glands not found in lower organisms. There is great diversity in methods of reproduction in this phylum. The usual bisexual method is frequently supplemented by fission, budding, and parthenogenetic development.

Form, habits, and details of structure differ so profoundly in the members of the various classes that few features beyond those already mentioned are held in common by all members of this phylum.

Interrelationships of the Classes.—The Turbellaria (Fig. 60) represent the most generalized group of the Plathelminthes. Modifications in the classes Trematoda and Cestoda represent, chiefly, adaptation to the parasitic habit. Extreme development of organs of generation and fixation (Fig. 63 *A*) and reduction of locomotor organs, sensory apparatus, and other structures characteristic of free existence characterize these two parasitic groups.

The nemertines are very commonly considered as the highest class of the flatworms. It is coming to be very generally recognized, however, that they are more closely allied to the higher worm groups.

Development.—Some of the flatworms, especially the fresh-water Turbellaria and the monogenetic termatodes, undergo direct development from the fertilized egg. More commonly, metamorphosis is involved. There are numerous different types of larvae characteristic of the various flatworm groups. Müller's larva with eight lobes, the margins of which are outlined by a continuous band of cilia, occurs in many polyclads. This seems to represent a primitive type of larva from which many others have been differentiated.

The pilidium of nemertines characteristically undergoes a complicated metamorphosis during which but a portion of the larva is utilized in the transformation to the adult form while the remainder is cast off.

Development in the trematodes frequently involves an alternation of generations. The generation which lives in snails, and is usually considered as larval (Fig. 65 *A*-*C*), undergoes a parthenogenetic cycle of reproduction, while the adults of the same species reproduce the first larval stage (Fig. 65 *A*) by means of fertilized eggs.

In addition to the sexual forms of reproduction leading to formation of larvae mentioned above, many of the flatworms reproduce asexually. Some species of Turbellaria undergo transverse fission (Fig. 62). In some of the fresh-water planarians (Fig. 61) this seems to be the chief if not the only means of reproduction. This method of naturally reproducing an entire individual from a portion of another rests upon the development of power of regeneration.

Relationships to Other Phyla.—Through the Ctenophora and the Turbellaria, the two phyla Coelenterata and Plathelminthes seem to have a fairly close phylogenetic relationship. Musculature, nervous system, and reproductive organs which have their origin as purely epithelial structures in the lower coelenterates become associated with the mesoglea in the higher coelenterates and transform this layer into a true mesoderm in the Ctenophora. This trend of development and specialization of the mesoderm is carried still further in the highly organized parenchymatous body of the Plathelminthes.

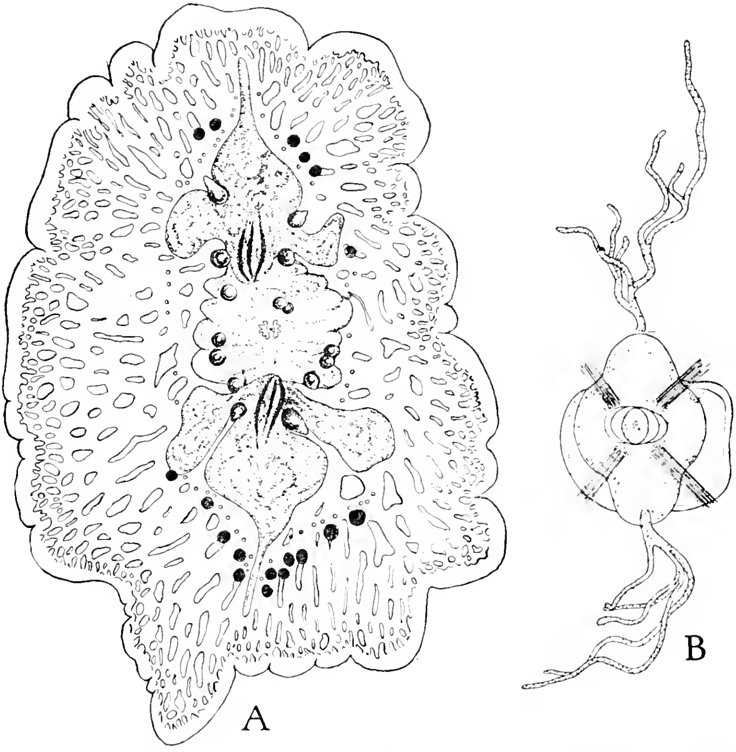

FIG. 59.—*A*. Coeloplana adult in dorsal view. *B*. Larva of Coeloplana directly after hatching. (*Redrawn from Komai*).

There are some organisms which show striking combinations of flatworm and ctenophore characteristics. Coeloplana and Ctenoplana are two such genera to which unparalleled phylogenetic significance has been attached. Coeloplana in its general form (Fig. 59 *A*) resembles a flatworm, but on its dorsal surface it bears a sense organ like the one found in similar position on the ctenophores. The dorsal tentacles and the tentacular sacs likewise resemble those of a ctenophore. Furthermore, in its life history Coeloplana passes through larval stages which bear ciliated combs (Fig. 59 *B*) of a form which have been thought to be distinctive of the ctenophores. Ctenoplana closely resembles Coeloplana except that it carries the rows of combs through to its adult condition. Thus Coeloplana resembles a flatworm and Ctenoplana a ctenophore, while each combines confusing characteristics of both groups.

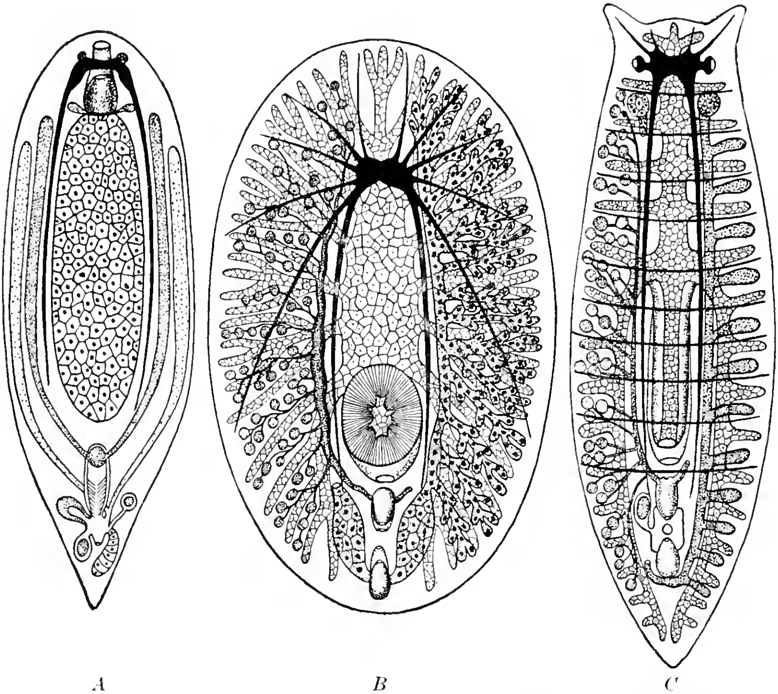

FIG. 60.—General organization in the three classes of Turbellaria. *A*, a Rhabdocoel; *B*, a Polyclad; *C*, a Triclad. The nervous system is shown in black; digestive system in cell outlines and nuclei; *A*, testes closely stippled, yolk gland coarsely stippled, ovary at posterior extremity on right; *B* and *C*, male reproductive system stippled on left side of body, female organs on right. (*From von Graff*).

Class Turbellaria

The Turbellaria range in size from minute, microscopic forms to some which attain several inches in length. The polyclads and triclads are usually distinctly flattened and in outline range from disc-shaped to lanceolate and long ribbonlike forms. Among the rhabdocoels is found even greater diversity of form. Some are spindle-shaped, while others are distinctly flattened. The ectoderm is covered with cilia (Fig. 62) which by their movement produce a smooth gliding locomotion. Currents produced by these cilia are responsible for the name of the class. Turbellaria are mostly free-living, aquatic organisms, though some have acquired the parasitic habit and others have become adapted to living in or on moist soil.

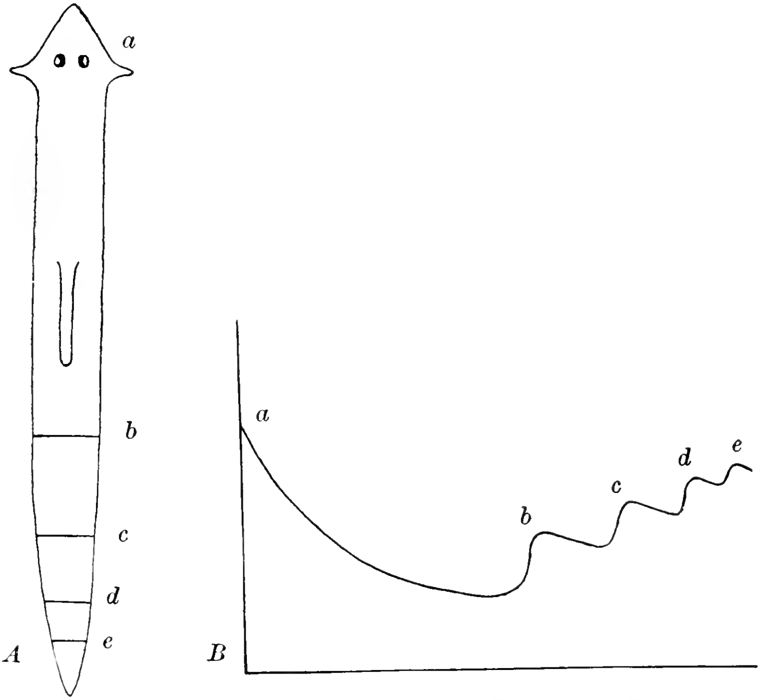

FIG. 61.—Axial gradient in Planaria. A, Planaria showing location of incipient heads; B, curve showing rise in metabolic gradient at levels marked in A. (*Redrawn from Child*).

Axial Gradient.—When two new individuals are formed from parts resulting from either natural or accidental separation of the body of a planarian in a transverse plane, there is always a tendency for the front piece to produce a tail and the hind one a head. In planarians which normally divide by fission, the posterior end of the body represents additional potential individuals even before there is any evidence of separation. Professor C. M. Child has given experimental proof of this. In his physiological studies he found that the head end of the worm has the highest rate of metabolism. This rate tends to decrease in the region behind the head. The term axial gradient has been applied to this physiological differentiation of regions along the axis of the body. When a certain level is reached (Fig. 61) the rate of metabolism shows a sudden increase. This point on the axis of the body coincides with the region where fission would first take place, and the sudden increase in rate of metabolism marks the location of a new incipient head. Behind this point Dr. Child found in long individuals a series of regions showing alternation between regions of increased and diminishing rates of metabolism. Each rise in metabolic rate marks the location of a potential new head.

The Orders.—A pharynx and blind intestine comprise the digestive tract of the turbellarians. The muscular pharynx is frequently enclosed in a pocket within the body and in feeding is thrust out like a proboscis.

Upon the nature of the intestine the three orders are distinguishable. Among the Polycladidea (Fig. 60 *B*), the mesenteron consists of a central space from which numerous branches pass into the parenchyma. These branches become greatly subdivided and frequently anastomose. In the Tricladidea, three main branches (Fig. 60 *C*) lead off from the pharynx, one directed anteriorly and two posteriorly. Each of these has numerous lateral diverticula which nearly reach the margins of the body. In the Rhabdocoelida, the mesenteron (Fig. 60 *A*) forms a simple sac-shaped or rodlike intestine. The so-called Acoela lack a cavity in the mesenteron which has been described as a digestive parenchyma.

Nervous System.—A simple, linear type of central nervous system is characteristic. In the Polycladidea, there is a considerable plexus of nerve branches with a brain near the anterior extremity and a few main trunks. The triclad central nervous system is essentially a pair of lateral nerve trunks which pass posteriorly from the brain with irregular transverse commissures. In some forms (Gunda), these connecting branches are so regular that they constitute a distinctly ladder type of system. The rhabdocoel nervous system is distinctly similar to that of the triclad type. Highly specialized sensory organs are not common in the Turbellaria. Eyes of a simple type are usually found above the brain. In the polyclads, these occur in large numbers and may also be developed along the margins of the body. In the triclads, a single pair of eyes is usually present, as is also the case with the rhabdocoels, though these last may have two pairs or even a single eye. The sense of touch is very highly developed in the Turbellaria and tentacles are frequently found, but the entire body is also highly sensitive, rendered so especially by the presence of sensory hairs.

Reproduction.—Except for some rhabdocoels, the Turbellaria are hermaphroditic. The reproductive organs differ considerably in the different orders. In most of the fresh-water forms, the eggs undergo a simple, direct development but some of the polyclads have a more complicated developmental cycle. The larval polyclad is called a Müller's larva. Asexual reproduction by transverse fission occurs in some rhabdocoels, frequently in the event of rapid fission, giving rise to a complex chain of individuals. Such a condition is shown in Fig. 62 in which the order of formation of the successive individuals is indicated. Similar chains are potentially present in the planarians, which undergo fission as shown in Fig. 61 and described in the section on axial gradients.

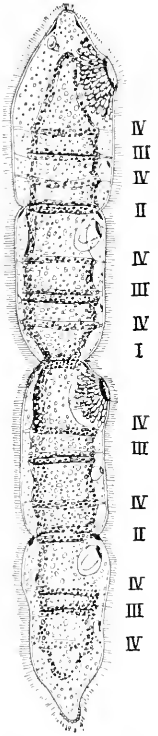

Fig. 62.—A Rhabdocoel (Microstomum) in the process of fission into sixteen zooids. Roman numerals indicate the order of the fission planes. (*After von Graff*).

Class Trematoda

The trematodes or flukes are exclusively parasitic, living either as ectoparasites upon or as endoparasites within the bodies of various animals. Since parasitism is an acquired and not a primitive mode of life, the bodies of all trematodes are more or less modified as an accompaniment of the parasitic habit. Simplicity of structure in this class denotes degeneracy and not primitive simplicity. While there are no free-living forms, most trematodes in their fundamental structure present clear evidences of close relationship with the Turbellaria. They vary from less than one millimeter to several centimeters in length.

A cuticula, frequently supplied with spines, covers the body surface of all adult trematodes, while some larval forms (Fig.

65 *A*) possess a ciliated covering. The epithelium characteristic of the body covering of the Turbellaria has become profoundly modified in this group and the cells are scattered through the underlying parenchyma.

Most flukes are hermaphroditic and the conspicuous reproductive organs are of prime importance in the classification of the group (Fig. 66 *A*). A few, the Schistosomes (human blood flukes), for example, are unisexual. Suckers, hooks, and spines are developed in varying combinations for securing attachment to the host. The number and arrangement of these structures are of particular significance in the grouping of the trematodes. Two subclasses, Monogenea and Digenea, are recognized.

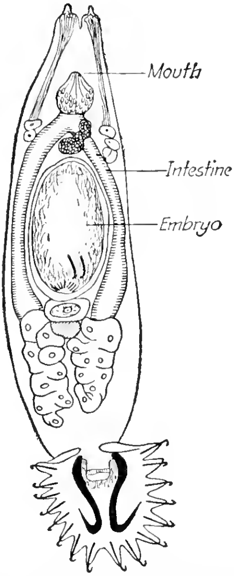

Fig. 63 *A*.—*Gyrodactylus elegans*, a monogenetic trematode. (*After Lühe*).

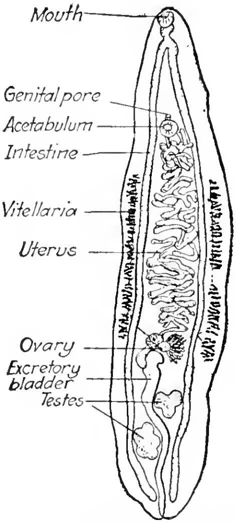

Fig. 63 *B*.—*Opisthorchis felineus*, a digenetic trematode. (*After Stiles and Hassall*).

Subclass MONOGENEA

The monogenetic trematodes are usually external body parasites but in some instances they have migrated inward to locations such as the mouth cavity, the respiratory organs, the cloaca, or the urinary bladder which are in direct communication with the body surface. The chief organ of attachment (Fig. 63 *A*) is usually located at the posterior extremity and consists of varied forms of sucking discs and combinations of hooks and spines. These hermaphroditic individuals produce eggs which undergo direct development without complicated larval changes and without alternation of hosts. The young parasites may immediately attach themselves to the body of the host which sheltered the parent fluke.

Two orders are recognized on the basis of structure of the posterior organ of fixation. In members of the order Monopisthocotylea (Gyrodactylus (Fig. 63 *A*), Dactylogyrus, Ancyrocephalus, Nitzschia), this posterior organ is a single structure provided with extremely varied combinations of hook and spines for attachment to the skin or gills of fishes. In the Polyopisthocotylea (Microcotyle, Polystoma, Diplobothrium, etc.), each individual bears two or more posterior suckers supplemented by hooks or spines. Skin and gills of fishes and body surface, urinary bladder, and pharynx of amphibians and reptiles are the chief seats of infestation by representatives of this second order.

Subclass DIGENEA

Almost all of the Digenea are internal parasites which require at least two hosts for completion of the life cycle. Instead of the direct development characteristic of the monogenetic trematodes, the digenetic forms always pass one generation or more in a mollusc before the stage capable of living inside the final host is attained. There is thus an alternation of generations accompanying an alternation of hosts. Man and his domestic animals act as hosts for numerous species of the digenetic trematodes, hence they hold much of interest for the student of medical zoology.

Digenetic trematodes are provided with one or two suckers the anterior of which usually surrounds the mouth opening. Conspicuous chitinous hooks, so common in the Monogenea, are lacking in the Digenea, though relatively smaller spines are of common occurrence. The ventral sucker, or acetabulum, is usually near the middle of the body, though in some instances it is entirely wanting (monostomes). From the mouth the digestive system continues backward as a single tube which divides to form two lateral branches, the ceca, for digestion and distribution of the food. Some forms seem to depend entirely upon absorbing their nutriment from the host directly through the body surface. The excretory system is highly characteristic. This consists of a series of finely branching tubes following a definite pattern of arrangement distinctive for each family of flukes. At the posterior end of the body the tubes empty into a median bladder. Each collecting tubule terminates distally in a flame cell the most characteristic feature of which is a tiny tuft of cilia extending into the lumen of the tube.

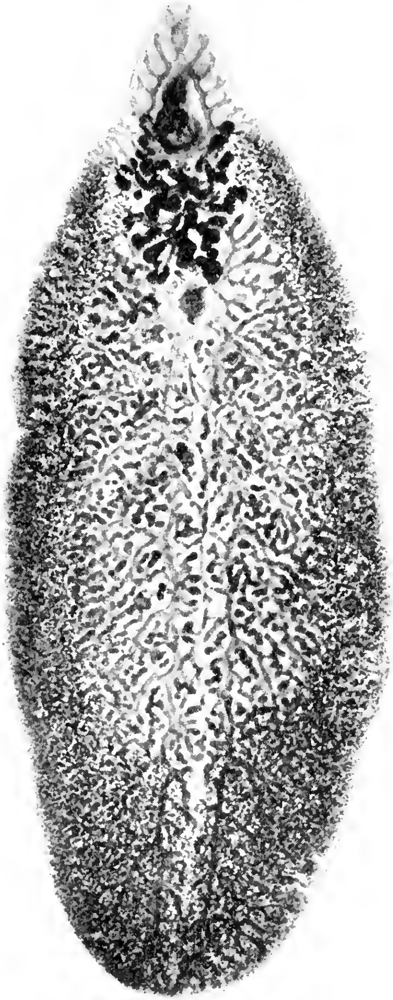

Fig. 64.—Photograph of a sheep-liver fluke stained and cleared for microscopic study. (*Orig.*).

In the adult worm (Fig. 66 *A*), the male reproductive organs consist normally of two testes which communicate with the genital pore through the vas deferens and a cirrus. The female organs comprise an ovary of variable form from which an oviduct leads through a modified region called the ootype into the uterus. Between the ovary and the ootype the oviduct may receive two canals, one from the vitelline receptacle and the other from the Laurer's canal and the receptaculum seminis. As ova pass from the ovary down the oviduct, spermatozoa from the receptaculum seminis and yolk and shell material from the vitelline receptacle pass with them into the ootype. Here each fertilized ovum and a number of yolk cells become surrounded by a shell to form an egg. The ootype is a modified portion of the oviduct in the region of the so-called shell gland or Mehlis' gland. The vitelline material which supplies both the yolk cells and the substance of the shell is produced in glandular bodies, the vitellaria, usually distributed along the margins of the body (Fig. 64), and communicating with a vitelline receptacle by means of smaller tubules which combine to form two transverse ducts.

Life Cycle.—As an illustration of the developmental cycle of the Digenea, that of the sheep-liver fluke, *Fasciola hepatica* (Fig. 64), has been chosen. The adult flukes live in the bile ducts of the sheep's liver where, by their presence and by their munching off portions of the lining of the ducts, they produce a diseased condition known as liver rot. As eggs are discharged from the parent fluke, they pass down the bile duct into the intestine and out of the body of the host along with the feces. The embryo within the eggshell develops into a small ciliated larva known as a miracidium (Fig. 65 *A*) which is released from the shell only when surrounding conditions are proper. In swampy ground or following a heavy dew or rain, this miracidium is enabled to swim in search of a suitable snail before the trematode can go further in its development. Upon coming in contact with a snail of suitable species, the miracidium makes use of a small boring spine on its anterior extremity to penetrate the soft tissues of the snail and comes to lie in the liver of the snail. Here it undergoes a transformation, becoming a bag-shaped structure called a sporocyst (*B*). Parthenogenetic reproduction occurs within the sporocyst to form numerous individuals called rediae. Each redia (*C*) is a simply organized individual possessing a pharynx and tubular intestine in addition to a single birth pore through which young are discharged. Within each redia develops either a new generation of rediae or individuals of another type termed cercariae.

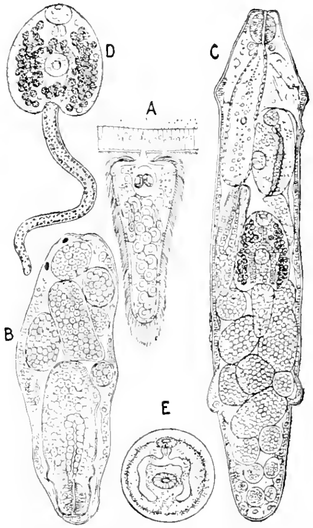

Fig. 65.—Stages in the development of the sheep-liver fluke (*Fasciola hepatica*). A, miracidium; *B*, sporocyst; with rediae developing internally; *C*, redia, with second generation of rediae and cercariae; *D*, free cercaria; *E*, encysted cercaria. (*Mostly after Thomas*).

A cercaria (*D*) is a minute fluke which in addition to the rudimentary organs of the adult contains also a strongly developed posterior tail for locomotion. The cercariae leave the body of the snail and for a time are free-swimming creatures. Finally the cercaria crawls onto vegetation where after losing its tail it becomes surrounded by a calcareous cyst wall (*E*). In this condition, it remains inactive until the plant bearing the cyst is taken into the stomach of a sheep or other suitable animal. Under the digestive action, the young fluke is liberated from the cyst and occurs free in the digestive tract. As it passes into the intestine, its chance of ever reaching maturity rests upon the discovery of the opening of the bile duct and migration through it into the liver. The successful individual becomes established in the bile passages where after a few weeks of growth it has reached adult size and begins to produce eggs, thus closing the cycle.

In the foregoing instance the cercaria enters its vertebrate host in a purely passive manner. Similarly some of the most dangerous human flukes, especially in the Orient, are taken into the digestive tract in an encysted state. In contrast, the blood flukes belonging to the genus Schistosoma have active cercariae which gain entrance to the human body by penetrating the skin.

In so far as is known, a mollusc is essential for the development of all digenetic trematodes. Frequently, other hosts are added, either as essential links in the life cycle or as faculative adaptations, until the complete developmental cycle involves a number of different species which act as host to a single parasite.

Class Cestoda

Like the trematodes, all cestodes are parasitic but through fundamental structures show marked relationships with the less highly specialized representatives of this phylum. The only sure criterion for the separation of Cestoda from other parasitic flatworms is their entire lack of a digestive system. While the typical cestode is made up of a chain of segments or proglottids and a scolex for attachment to the host, there are some, the monozoic cestodes or Cestodaria, in which the body is composed of but a single unit. Though these latter are usually not more than a few millimeters in length, the segmented forms frequently attain a length of several meters and may be divided into several thousand proglottids.

Unsolved Problems.—The question of the orientation of the cestode body has never been decided with certainty. Many zoologists maintain that the scolex is the anterior extremity of the chain because here the chief nervous centers are found. Other investigators contend just as stolidly that since in development from the larval stage the scolex is at the posterior extremity of the larva this scolex must represent the morphological posterior extremity of the adult chain. Another question upon which there is just as radical division of opinion is that upon the determination of what constitutes an individual. Is the entire chain an individual or a colony of individuals? Continuity of nervous and vascular systems throughout the chain with some modifications at the extremities not found in the individual proglottids presents evidences of unity of the entire chain. On the other hand, since the reproductive organs are about the only structures remaining in the proglottids, complete duplication of these in each proglottid gives support to the argument that each proglottid is an individual, groups of which have remained united to form a colony as a result of incomplete separation following asexual reproduction to form the chain.

Organization.—That part of the strobila which is located between the scolex and the proglottids is frequently not divided into segments but as a more or less sharply defined region is termed the neck. This is the budding zone where new proglottids are being formed. Thus in age the scolex is the oldest, then come the proglottids in order from the free extremity toward the neck. Few structures are evident in the neck and in the small proglottids most recently formed, for there is a gradual and progressive development of the organs (organogenesis) representing all stages between the fully formed organs of the terminal proglottids and the merest traces of fundaments in the proglottids just behind the neck. The sexual organs of the terminal proglottid are the oldest and consequently mature first. Upon reaching full maturity, the gravid proglottids are frequently severed from the remainder of the strobila.

In many genera the tapeworm continues to live and to produce more proglottids indefinitely just as long as the scolex and neck region remain attached to the wall of the digestive tube of the host.

Peculiarities of Chain Formation.—In some forms (Ligula), there are no partitions between the proglottids but the organs are duplicated successively in an undivided body. A secondary strobilization is known to take place in some cestodes wherein the original proglottids undergo a secondary subdivision, each giving rise to a number of proglottids which may eventually separate as independent strobila. One proglottid in each new chain becomes modified as a pseudoscolex.

Subclass CESTODARIA

The Cestodaria or monozoic cestodes rather closely resemble trematodes, but the lack of digestive organs necessitates their inclusion as a subclass along with the true cestodes. There is no sharp differentiation between scolex and proglottids in the Cestodaria, and but one set of reproductive organs usually occurs in each individual. They occur in both marine and fresh-water hosts. Members of the genus Archigetes become mature in oligochaetes, Gyrocotyle in the spiral valve of elasmobranchs, and Caryophyllaeus, Glaridacris, and Amphilina in the body cavity or digestive tract of fishes. The organ of attachment is variously modified.

Subclass CESTODA (*s. str.*)[1]

The polyzoic cestodes include all the typical tapeworms which have a scolex followed by a succession of organs usually divided in chain fashion into a series of proglottids. These cestodes reach the adult state in the digestive tract of vertebrates, every class from fishes to mammals serving in the capacity of host. There is no restriction to a single type of larval host as in the digenetic flukes, for a wide variety of both invertebrates and vertebrates act as host for larval tapeworms.

Reproductive Organs.—Each proglottid is furnished with a complete set of reproductive organs (Fig. 66 *B*), and in some instances two sets occur in each. The male organs consist of from one to more than a hundred testes (Fig. 67) embedded within the parenchyma and connected by vasa efferentia and vas deferens with the cirrus which communicates with the outside. The genital ducts of both sexes usually open in a common genital pore which is either on the lateral margin of the proglottid or

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[1] *Sensu stricto* indicates that a word is used in a limited or restricted sense. In this instance the word Cestoda is used for the entire class, but in a restricted sense the same word is used to designate the true cestodes from the Cestodaria.

on the ventral surface. When it is marginal there is no necessary regularity in its disposition, for in adjacent proglottids it may be either on the same or on opposite margins. In cestodes which have two sets of genital organs, the pores occur on both lateral margins of each proglottid.

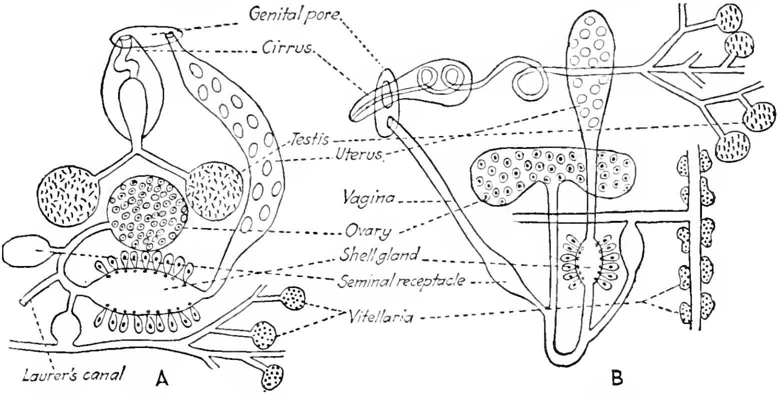

FIG. 66.—Diagrams showing the fundamental plan of organization of sexual organs in *A*, trematodes; *B*, cestodes. (*Orig.*).

The arrangement of the female organs differs greatly in the different genera. The vagina opens through the common genital pore and in addition in some instances the uterus has an independent orifice to the exterior. A typical arrangement (Fig. 67) is as follows: The vagina, as it passes through the proglottid,

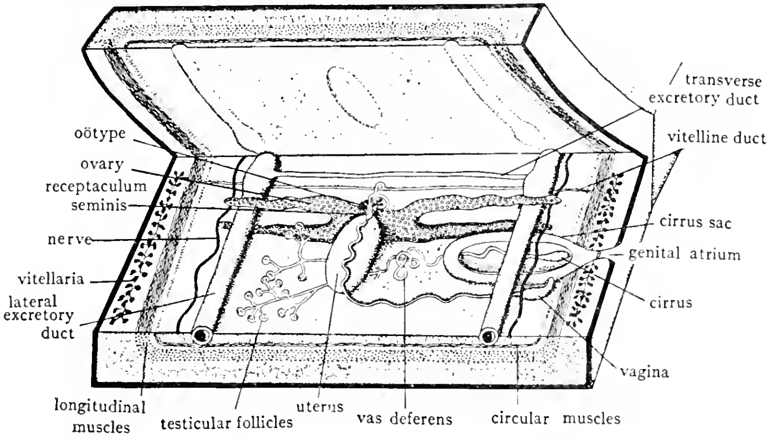

FIG. 67.—Stereogram showing arrangement of organs in a proglottid of a fish tapeworm (Thysanocephalum). (*After Causey*).

bears a dilated portion for the storage of sperm cells called the receptaculum seminis or seminal receptacle. As the duct continues beyond this receptaculum it receives two side branches, the oviduct which connects it with the ovary and the vitelline duct which communicates with the vitellaria or vitelline glands. The oviduct frequently bears a modification called the oocapt for forcing the eggs along their course. When eggs and spermatozoa meet, fertilization occurs. The fertilized eggs and the substance from the vitelline glands pass into a structure similar to the ootype of the trematodes in the region of the shell gland. Here shells are formed around the eggs which are then passed on into the uterus. In older proglottids, the uterus frequently develops egg-filled pouches which occupy practically the entire volume of the proglottid. Eggs are rarely discharged from the uterus, for more frequently the entire egg-filled proglottid is liberated and carried out of the body of the host.

Other Organs.—The nervous and excretory systems extend the length of the strobila and parts in individual proglottids do not represent complete units. Ganglia located in the scolex send nerve trunks backward through the proglottids, usually as two lateral branches fairly close to the lateral margins of the body. Specialized sensory organs are wholly wanting. Parallel to the longitudinal nerve trunks run the main canals of the excretory system. These in turn receive smaller canals the branches of which ramify through the parenchyma and terminate in flame cells.

Reproduction.—Several different methods of development occur in the Cestoda. Typically, the egg undergoes a cleavage within the shell to form an embryo, bearing six minute hooks, called an onchosphere. The onchosphere may in some instances be provided with cilia for locomotion (as in Diphyllobothrium, the fish tapeworm of man), but more frequently it is borne within embryonic membranes as an immotile body. Upon introduction into a suitable host, the onchosphere develops into a larval form differing with the various groups of the cestodes. Among the lower cestodes, which live chiefly in fishes, this larva is a small solid body called a plerocercoid (Fig. 68 *A*). A larval stage called the cysticercus or bladderworm stage (*C*) is found among the higher cestodes. The name cysticercoid is applied to larval forms (*B*) which seem to be intermediate between the plerocercoid and the cysticercus.

The taeniae which dwell in man have a cysticercus, while one of the commonest tapeworms of dogs (Dipylidium) and of rats (Hymenolepis) have a cysticercoid larva. Some of the worms having a cysticercus undergo asexual reproduction in the larval stage, developing several scolices within a single bladder (genus Coenurus) or at times budding off a series of daughter cysts each with one or more scolices (genus Echinococcus).

Life History.—As an illustration of cestode development the life cycle of *Taenia saginata*, the beef tapeworm of man, will be outlined. The mature individual of *Taenia saginata* occurs in the intestine of man. As the older proglottids become gravid, they become detached from the end of the chain and pass out of the body along with the feces. These isolated proglottids have independent powers of movement and may crawl away from the feces onto grass or other vegetation where they might be taken into the stomach of a grazing cow, along with the grass. In the stomach of the cow, the walls of the proglottid are digested away and the shells of the embryos open, thus liberating the onchospheres in the digestive cavity of the cow. Each onchosphere by the action of its hooks bores into the wall of the digestive tract and may enter the blood stream by which it is carried to remote parts of the body. Especially in the muscular and connective tissues, the onchospheres come to rest and undergo a transformation to large saclike structures, the cysticerci, each bearing an inverted scolex. Each cysticercus is surrounded by a cyst wall formed by the action of the surrounding host tissues. Here it lies without going further in its development unless introduced into the body of another animal which is suitable as a host. Cysticerci in thoroughly cooked infected beef are harmless. If beef containing the living cysticerci is eaten by man, the digestive action liberates the cysticercus from its confining cyst,

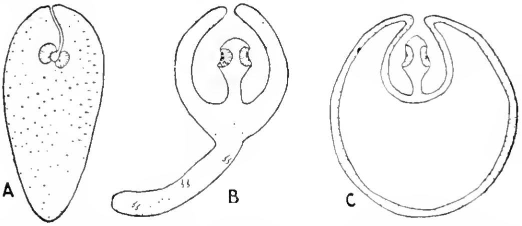

FIG. 68.—Schematic drawings of cestode larvae. *A*, plerocercoid; *B*, cysticercoid; *C*, cysticercus. (*Orig.*).

the inturned scolex becomes everted and secures attachment to the lining of the alimentary canal of the new host. The scolex is not affected by the digestive processes of the host but the cyst appended to its free extremity disintegrates, leaving only the scolex and neck which, through growth, produce the entire strobila.

The Scolex.—The scolex shows great diversity in form. In members of the order Pseudophyllidea, the scolex is usually provided with two longitudinal sucking grooves (Marsipometra, Bothriocephalus, Abothrium, Ligula), though some instances these are highly modified (Bothrimonus) and occasionally are united to form an unpaired terminal adhesive organ (Cyathocephalus). The scolex in members of this order is usually unadorned except in Triaenophorus which bears conspicuous chitinous hooks and in the primary scolex of Haplobothrium which bears four proboscides, therein resembling the Trypanorhyncha. Members of the order Trypanorhyncha, which occur chiefly in the digestive tract of marine fishes, have a proboscis of varied form provided with four terminal, long, cylindrical proboscides covered with minute spines (Tetrarhynchus). In the order Tetraphyllidea are included cestodes with a scolex bearing four cuplike bothria or suckers and with each proglottid bearing numerous vitelline follicles (Proteocephalus, Corallobothrium). The order Cyclophyllidea includes forms having four cuplike or saucer-shaped suckers and usually a terminal organ between the suckers termed a rostellum. In this order, the vitellaria are usually posterior to the ovary and occur in a single compact mass. This order of numerous families includes most of the cestode parasites of the higher vertebrates (Taenia, Anaplocephala, Hymenolepis, Dipylidium, Davainea, and many other genera).

Class Nemertinea

The nemertines are usually included as a class under the Plathelminthes because of their agreement with other flatworms in: (1) structure of the nervous system, (2) presence of a protonephridial excretory system, and (3) the strong development of the mesoderm which renders the body highly parenchymatous. On the other hand, they differ from other flatworms in: (1) the specialization of a vascular system so that distribution of nourishment is not cared for by a combined gastrovascular system, (2) the development of an anal opening at the posterior extremity of the digestive tract, and (3) the presence of a closed sac, the proboscis sheath, which surrounds the proboscis and by some is considered as representing the beginning of a coelom. In attempting to show relationships with the coelomate animals, this last point is of considerable importance. Other workers have thought that the cavities of the gonads of nemertines are really coelomic sacs.

Nemertines are chiefly marine, living usually in burrows in mud or sand, and in some species attaining a length of 90 feet. Some of the smaller forms inhabit fresh water or live in moist soil. The body surface is ciliated and frequently brilliantly colored. Numerous mucous glands produce secretions which may form a tube within which the animal dwells. The body wall contains an outer circular and an inner longitudinal layer of muscles which are so effective that a worm which is 15 feet or more when fully extended may shorten to less than 2 feet in length.

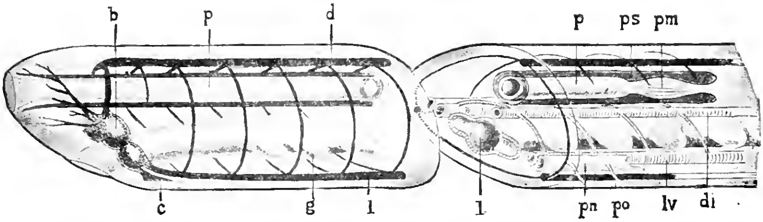

Fig. 69.—Diagram of a nemertine. *b*, brain; *c*, ciliated pit; *d*, dorsal nerve trunk; *di*, dorsal blood vessel; *g*, gastric ceca; *i*, intestine; *l*, lateral nerve trunk; *lv*, lateral blood-vessel; *p*, proboscis, retracted; *pm*, proboscis muscles; *pn*, protonephridial tube; *po*, its opening; *ps*, cavity of proboscis sheath. (*After Kingsley, courtesy of Henry Holt and Co.*).

The proboscis (Fig. 69) is one of the most characteristic structures of the nemertine. This is a hollow muscular tube turned into the body at the anterior extremity and when thus inverted extends far back through the body within a saclike cavity called the proboscis sheath. By contraction of the fluid-filled sheath, the proboscis is everted and thrust out from the anterior part of the body. At the tip of the extruded proboscis, there is frequently a sharp-pointed stylet which, of course, is at the extreme posterior end of the proboscis when it is retracted and inverted within the sheath. Retraction of the everted proboscis is accomplished by means of a retractor muscle which runs from the tip of the proboscis to the base of the sheath. Abundant nerve supply indicates that the proboscis is highly tactile, but it is also an organ of defence. When extruded, it coils around the prey and at the same time a viscid secretion from the proboscis sheath prevents the prey from escaping.

The mouth is located at the anterior extremity of the body or just ventral to the opening of the proboscis sheath. The tubular ectodermal esophagus opens into the tubular intestine (mesenteron) which usually has paired lateral diverticula along its course to the anus. The anus may be either at the posterior extremity or in some instances the digestive tract does not enter the tail region.

Reproduction.—The sexes are usually separate. The gonads, which are lateral in position, occur between the intestinal diverticula. Each ovary or spermary is a saclike organ which usually opens on the dorsal surface by a pore. Both eggs and spermatozoa are discharged from the body through the pores, and fertilization takes place outside the body of the worm. Cleavage of the fertilized egg usually results in the formation of a helmet-shaped larva known as the pilidium. Cilia occur on the lapets at the lower margins of this larva and also in a patch at the opposite pole known as the apical plate. The apical plate is the chief nervous center of the larva. Development of the adult from this larva involves a complicated metamorphosis. By the growth of two infoldings of the ectoderm, a part of the body containing the digestive system of the larva is surrounded and cut off from the remainder of the body. In later development, these ectodermal infoldings form the body wall of the adult worm and only the parts of the larva enclosed by them are utilized in the production of the young worm, for the remainder of the larva is cast off during the metamorphosis. In some instances, development is direct, without involving the pilidium, while in still others a reduced creeping pilidium, frequently termed Desor's larva, takes its place.

Vascular System.—Typically, the vascular system has three main longitudinal trunks, two lateral and a median dorsal vessel which lies between the intestine and the proboscis sheath. Transverse loops connect the two lateral vessels. The fluid contained in this system is usually colorless. This is the first instance in the animal kindgom where the function of distribution is taken over by an independent system, for in lower forms the functions of digestion and distribution are performed by a gastrovascular system.

Excretory System.—The excretory system consists of two longitudinal tubules which run parallel to the lateral vessels of the circulatory system and through their course give off small branches which terminate in flame cells. Either a single pore or several pores communicate with the exterior.

Nervous System.—The central nervous system consists of a pair of ganglia from which two lateral and one median dorsal nerve pass backward through the body. Details of structure and arrangement of the nerve trunks differ considerably in the different orders. In some instances (Protonemertini), the nervous system remains in the superficial layers of the body external to the musculature. A pair of ciliated grooves on the sides of the head, frequently called cerebral organs, are closely connected with the brain and have a sensory function. Eyes and tactile organs are usually developed.

Outline of Classification

Phylum Plathelminthes.—Triploblastic, wormlike animals; without body cavity; lacking true segmentation.

- I. **Class Turbellaria.**—Ciliated; chiefly free-living.
  - 1. **Order Polycladidea.**—Many branches to digestive tract; marine. *Planocera, Leptoplana, Stylochus.*
  - 2. **Order Tricladidea.**—Three main branches to digestive tract, one anterior and two posterior. *Planaria, Bdelloura, Dendrocoelum.*
  - 3. **Order Rhabdocoelida.**—Digestive tract a simple sac. *Microstomum, Stenostomum, Prorhynchus.*
- II. **Class Trematoda.**—Parasitic; non-cellular cuticula covers body; suckers for attachment; alimentary canal present.
  - *a.* **Subclass Monogenea.**—Ectoparasitic; development direct; suckers and hooks for attachment.
    - 1. **Order Monopisthocotylea.**—Posterior attachment organ single. *Gyrodactylus, Dactylogyrus, Nitzschia.*
    - 2. **Order Polyopisthocotylea.**—Posterior attachment organ double or multiple. *Polystoma, Microcotyle, Sphyranura.*
  - *b.* **Subclass Digenea.**—Endoparasitic; alternation of generations and alternation of hosts; one or two suckers.
    - 1. **Order Gasterostomata.**—Anterior sucker imperforate; mouth on midventral surface. *Bucephalus.*
    - 2. **Order Prostomata.**—Anterior sucker surrounds mouth which is at or near anterior tip.
      - a. **Suborder Aspidocotylea.**—Oral sucker wanting or poorly developed; ventral sucker powerful disc. *Aspidogaster, Cotylaspis.*

b. Suborder Monostomata.—No ventral sucker. *Notocotylus, Cyclocoelum.*

c. Suborder Strigeata.—Usually two suckers; cercaria fork-tailed. *Strigea, Schistosoma*

d. Suborder Amphistomata.—Acetabulum terminal or subterminal, highly developed, posterior to reproductive organs. *Gastrodiscus, Diplodiscus, Allassostoma, Watsonius.*

e. Suborder Distomata.—Oral and ventral sucker present; acetabulum usually anterior to reproductive organs. *Fasciola, Fasciolopsis, Opisthorchis, Paragonimus, Clonorchis, Telorchis, Pneumonoeces.*

III. Class Cestoda.—Parasitic; body covering a cuticula; no digestive system; scolex for attachment.

a. **Subclass Cestodaria.**—Body not divided into proglottids; a single set of reproductive organs. *Gyrocotyle, Archigetes, Amphilina, Caryophyllaeus, Glaridacris.*

b. **Subclass Cestoda.**—Body usually divided into proglottids; reproductive organs oft repeated.

1. Order Pseudophyllidea.—One terminal or two opposite sucking grooves. *Abothrium, Bothriocephalus, Diphyllobothrium, Sparganum, Marsipometra; Ligula, Cyathocephalus, Triaenophorus.*

2. Order Trypanorhyncha.—Two or four suckers and four hook-covered protrusible proboscides on scolex. *Tetrarhynchus.*

3. Order Tetraphyllidea.—Four sucking cups; in fish and reptiles. *Dinobothrium, Proteocephalus, Corallobothrium.*

4. Order Cyclophyllidea.—Four cuplike suckers and an apical organ of varied form. *Taenia, Hymenolepis, Echinococcus, Anaplocephala, Dipylidium, Davainea.*

IV. Class Nemertinea.—Ciliated; proboscis and proboscis sheath, dorsal to mouth; blood system; digestive canal complete; aquatic.

1. Order Protonemertini.—Nervous system outside the muscles; no stylet. *Carinella.*

2. Order Mesonemertini.—Nervous system in muscles; no stylet. *Cephalothrix.*

3. Order Metanemertini.—Nervous system inside muscles; usually with stylets. *Stichostemma, Geonemertes.*

4. Order Heteronemertini.—Several layers of muscles; nervous system in muscles; no stylet. *Lineus, Cerebratulus.*

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CHAPTER VII

PHYLUM NEMATHELMINTHES

The Nemathelminthes or roundworms are threadlike or cylindrical worms which have a body cavity and lack segmentation. The body is covered with a heavy cuticula. Highly developed sensory and locomotor organs are wholly lacking. Reproduction is invariably sexual, and in the course of direct development distinctive free larval stages are lacking. Since the splanchnic layer of the mesoderm is wanting, the body cavity is not a true coelom but is termed a pseudocoel. Three classes are usually recognized as belonging to this phylum, the Nematoda (or threadworms), the Gordiacea (or hair snakes), and the Acanthocephala (or spiny headed worms). There is considerable doubt as to the correct location of the Acanthocephala in the system, for evidences indicating flatworm relationships are not wanting. The three classes differ so fundamentally in structure that it seems best to offer individual treatment of the groups rather than discuss characteristics of the phylum further.

Class Nematoda

The nematodes or nemas, as they are frequently called, have characteristically elongated, cylindrical bodies (Fig. 70 *B*) covered by a resistant cuticula. They occupy almost every conceivable habitat capable of supporting life. Fresh-water, marine, and soil-inhabiting species are extremely numerous and as parasites both of plants and of animals they are of high importance. In length, they range from a fraction of a millimeter to more than a meter. There are no appendages and no segmentation, though in some free-living forms striations, cuticular scales, or bristles may give a superficial appearance of segmentation.

Histology.—In section, the body wall is seen to be composed of an external non-cellular layer, the cuticula, directly beneath which lies the subcuticula or hypoderm. A layer of partially differentiated muscular cells lines the outer wall of the body cavity and comprises the chief bulk of the body wall. Each of these epithelio-muscular cells has only a small portion of its bulk differentiated into contractile substance lying next to the subcuticula, while the remainder of the cytoplasm, containing the nucleus, protrudes as a rounded mass into the body cavity.

This muscular layer is not a continuous lining of the body cavity, for it is interrupted by slight breaks in four regions which are designated as the dorsal, ventral, and lateral lines. The fairly conspicuous thickening of the subcuticula which stands in the middle of each lateral surface is known as a lateral line. Less pronounced intrusions of the subcuticula occur also in the middorsal and midventral lines. In the lateral lines are borne the ducts of the excretory system. Near the anterior extremity of the body, these are united and communi-

FIG. 70 A.—The nervous system of a nematode. (*After Brandes*).

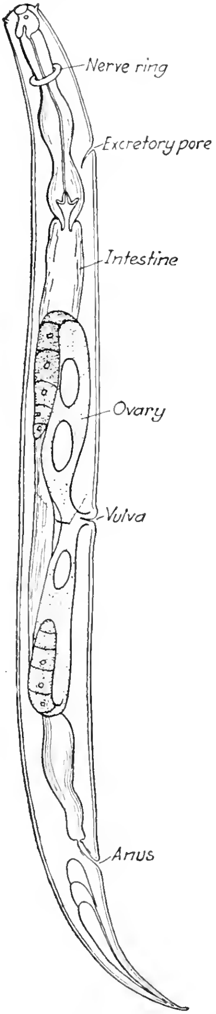

FIG. 70 B.—Semidiagrammatic drawing of a female free-living nematode. (*After Jägerskiöld*).

cate with the exterior through a single excretory pore on the ventral surface of the body. In the dorsal and ventral lines are found the two main longitudinal nerve trunks (Fig. 70 *A*) which connect with a nerve ring near the anterior extremity of the body. From this same ring are given off a number of smaller longitudinal branches, some extending forward and others a short distance backward.

Digestive System.—The digestive system is practically a straight tube (Fig. 70 *B*) with a mouth at the anterior extremity and the anus on the ventral surface slightly in front of the posterior tip. The mouth is usually surrounded by liplike organs and, in the case of parasitic forms, frequently bears chitinized structures for grappling the host tissues. Behind the mouth, there frequently occurs a muscular esophagus with an especially conspicuous pharyngeal bulb. The stomach-intestine continues posteriorly from the esophagus as a usually flattened tube. In the male, the genital ducts open into the posterior region of the digestive tube which is thus transformed into a cloaca.

Reproductive Organs.—The male is usually recognizable by its smaller size and frequently by the more pointed and curved posterior extremity. From the cloaca of the male, copulatory spicules are frequently protruded. Reproductive organs in the sexes are very simple in structure, for normally they consist of a gonoduct which is directly continuous with the gonad. This tube in the male is usually single, while in the female (Fig. 70 *B*) it is frequently bifurcated with the opening of a single vagina occurring on the ventral surface of the body. In some forms, the ducts and gonads are extremely long and coiled throughout the greater part of the length of the body, while in others they are a single straight rod.

The eggs of the horse Ascaris (*A. megalocephala*) have provided one of the most widely used materials for the intimate study of chromosomes and of the mechanics of mitosis and cleavage. The works of Boveri, Bütschli, and zur Strassen on the eggs of Ascaris stand as classics in the field of cytology.

Method of Reproduction.—Nematodes reproduce only sexually. Eggs are fertilized within the oviduct of the female and are discharged either before development has proceeded far or are retained until the young are fully developed. In some instances, the eggs are not laid but are retained in the body of the female until the young have left the egg membranes and are thus brought forth viviparously. Parthenogenesis occurs in some instances, as mentioned below.

Life Cycles.—A number of extremely interesting and important facts are connected with the developmental cycle of the parasitic nematodes. Some species are parasitic throughout their entire life (Trichinella and blood Filariae), while many are free-living for at least part of their existence (hookworms as larvae, Mermis as adults). Still others are facultative parasites living either free or parasitic as opportunities are offered. Of this last condition, *Rhabditis bufonis* serves as an excellent example. The young of this species live in mud where they undergo sexual reproduction, both males and females being found. Larvae produced by these sexual individuals may continue to produce in the same manner as the parents, or in case they find their way into the lungs of a frog they become established as parasites and develop only parthenogenetically. The parthenogenetic eggs pass out with the feces and in the mud again pass through the dioecious phase of the life cycle as free individuals.

Ascaris lumbricoides is a large worm, about 8 inches long, which lives in the intestines of man and the pig. Though the Ascaris in these two hosts look exactly alike, experiments so far indicate that larvae hatched from a worm living in a pig fail to develop normally in man, and *vice versa*. Until very recently it has been assumed that infestation by this species is by direct introduction of the young into the digestive tract of a new host individual where it becomes established immediately. Recent investigations have demonstrated that the larvae of these ascarids, when introduced into the digestive tract of a new host individual, undergo extensive migration through the organs and tissues of the body, reaching the final position only after having passed by way of the circulatory system into the lungs. Heavy infestations by these larvae cause serious pulmonary disorders, as the larvae penetrate the lung tissues and travel by way of the respiratory passages into the mouth and down the digestive tract to the intestine, where they reach maturity.

After entering the host the female requires only about 2 months to reach maturity. Some idea of the danger of this species as a human parasite may be gained from the fact that a single female has been found to give off 200,000 eggs daily with a total production of 27,000,000 eggs by a single worm. The eggs are very resistant, for the heavy shells prevent even strong chemicals from penetrating and injuring them. There are evidences that eggs of Ascaris may remain alive in the soil for a period of 5 to 6 years. This adds very greatly to the difficulty of eradicating Ascaris.

Extensive migrations are also carried on in the body of the host by the hookworms (Ancylostoma of the Old World and Necator of the New World). The adult worms, which cause very serious loss of blood and affect the entire body of the host, occur in the intestine of man where the thin-shelled eggs are produced and eliminated along with fecal matter. In the soil, the young worms hatch and feed for a while on the fecal matter. A new skin forms beneath the old one, which is finally shed, and the larva enters upon the second period of its life. After another molt, the larva is ready to infest a new host individual. This it does either by entering the body along with contaminated water or food or by active penetration of the skin. Hands and feet are the chief inroad for the larvae, which attack the skin exposed to the soil and follow along hair follicles or between epidermal scales to the lymph spaces. Once in the lymph stream they are carried passively to the subclavian, thence to the heart, and on with the blood stream to the lungs. Here the larvae leave the capillaries, enter the air sacs, and wander through the bronchi, up the trachea into the esophagus, and down through the stomach to the intestine where they become attached to the wall by means of their specially adapted sucking mouth. About 7 to 10 weeks from the time the larva enters the skin, eggs begin to appear in the feces, indicating that the worms have reached maturity and the life cycle is thus completed.

Still a different condition is found in the life cycle of *Trichinella spiralis*. There are two distinct stages in the parasitism by this worm: the sexually mature worm which occurs in the digestive tract and the encysted larvae in the muscles. Both sexes occur in the intestine of man and of other mammals of which the pig and rats are the most important hosts. The gravid female pierces the wall of the intestine with her posterior extremity. With the genital pore inserted in a lacteal vessel, the young are liberated and carried by the lymph and blood streams into the tissues of the host's body. It is not known to what extent this migration is active or passive. Upon reaching muscular tissue, the larvae become encysted and all further development is contingent upon the muscles containing the encysted larvae being introduced into the digestive system of some other mammal, for the larvae have no independent means of ever leaving the body of the host individual which sheltered the mature female in its intestine. The chief source of the adult worms in the human intestine is from the larvae encysted in pork, while the hog in turn receives its intestinal form through eating the viscera of other hogs in slaughter yards or from eating rats which have become infested.

Blood-inhabiting nematodes such as the Filariae are often carried from one host to another through the bite of blood-sucking insects. Some species which cause elephantiasis through the occlusion of blood and lymph vessels are carried by mosquitoes.

Free-living Nematodes.—There are numerous species of free-living nematodes representing many genera. In the genus Iota the body is covered with scales which give it a superficial appearance of segmentation. Tylenchus, Dorylaimus, Mermis, and Rhabditis are names of characteristic genera of free-living nematodes, though species in some of these genera may be parasitic.

Class Gordiacea

Superficially, the Gordiacea resemble the nematodes, but in finer details of structure they have little in common with them. Some systematists are inclined to disregard these differences and therefore include the Gordiacea as a subclass of nematodes. The adults live free in the water where the females lay strings of eggs which develop into small larvae. These larvae enter the body of some insect where they undergo development to the adult body form.

The hair snakes, so commonly found in watering troughs and in ponds and streams, are the adults of Gordiacea which have escaped from the bodies of crickets or other insects. They bear no lateral lines, and the nearly cylindrical body with blunt anterior extremity and irregularly roughened cuticula serve to differentiate the Gordiacea from the nematodes.

Gordius, Paragordius, and Chordodes are genera in this class.

Class Acanthocephala

The Acanthocephala are absolutely parasitic in habits. There is no trace of digestive organs in the mature worms and even in the development of the larva there are no specializations of the entoderm to form even a rudiment of an alimentary canal. As adults they occur normally in the digestive tract of vertebrates. The first larval host is practically always an arthropod, though young individuals have been found frequently in other hosts which probably act as intermediate hosts. In the digestive tract of the vertebrate, the acanthocephalan has an elongated flattened body form but upon removal to water or killing fluids the liquids distend the body to cylindrical form. One of the most characteristic structures is the proboscis (Fig. 71 *A*) at the

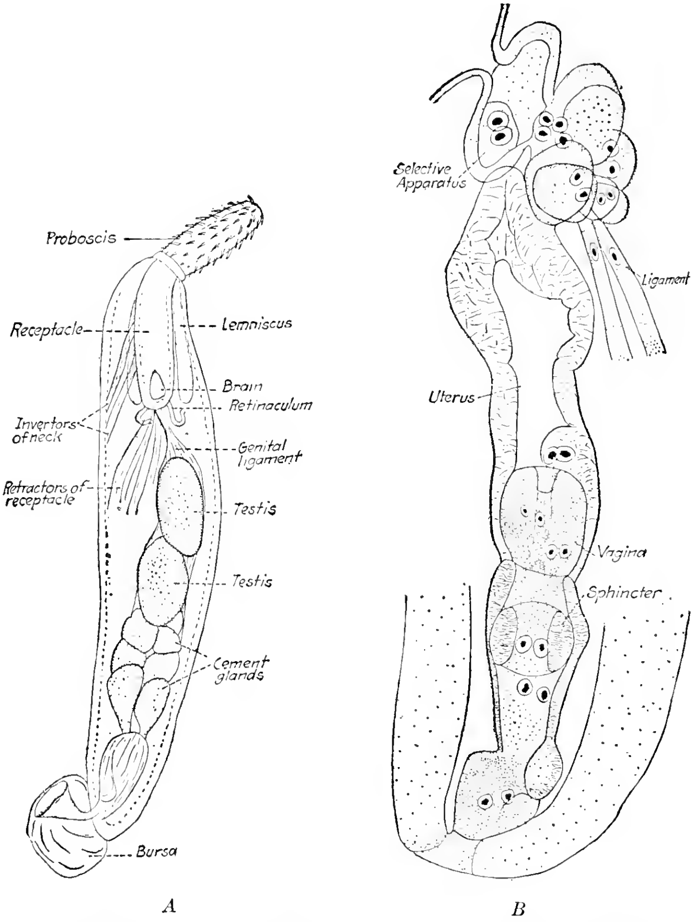

FIG. 71.—Morphology of the Acanthocephala. *A*, general organization of male of *Acanthocephalus ranae* (Schr.); *B*, interior of caudal extremity of a young female of *Neoechinorhynchus emydis*, showing genital tract. (*After Van Cleave*).

anterior extremity of the body bearing hooks for grappling into the host tissues. This proboscis is frequently capable of inversion into the anterior extremity of the body inside an organ termed the proboscis receptacle or sheath. In some instances the proboscis may be retracted within the anterior region of the body without being inverted into the receptacle.

Nuclear Constancy.—In all members of the family Neoechinorhynchidae, the individuals of each species are constructed on exactly the same plan as far as the cellular elements are concerned. Each organ and each tissue contains a definitely fixed number of nuclei in the identical positions for every member of a given species. In these forms, the size of the individual depends wholly upon the size of the component cells, for all worms of a given species are made up of the same number of cells. This is a condition wholly different from that found in some other animals, for in some species the size of the individual is dependent upon the number of cells in its body. Typical arrangement of nuclei in the organs of a single system is shown in Fig. 71 *B*.

The **body wall** is composed of an external layer of cuticula which overlies a syncitial mass called the subcuticula. This subcuticula forms by far the greatest bulk of the animal and is provided with a few rounded giant nuclei, finely dendritic nuclei, or numerous small nuclei. Two muscle layers, one with the fibers directed longitudinally and the other with the fibers directed circularly, mark the internal limit of the body wall and bound the body cavity.

At the anterior extremity of the body proper, two organs of variable shape and of undetermined function, the lemnisci, extend into the body cavity alongside of the proboscis receptacle, apparently as continuations of the subcuticula.

The **central nervous system** consists of a single ganglionic mass within the proboscis receptacle. In the different genera, this occupies a position varying from the posterior extremity of the receptacle to a point near the anterior end of the receptacle. Small branches are given off to the surrounding organs, and usually a pair of structures called the retinacula pass through the wall of the receptacle out to the body wall.

Internal Organization.—Inversion of the proboscis is accomplished by a pair of invertor muscles which run from the tip of the proboscis to the base of the receptacle through which they continue and pass on through the body cavity to an insertion on the body wall as the retractors of the receptacle.

A sheath passes backward from the posterior extremity of the proboscis receptacle as the suspensory ligament which holds the reproductive organs in place. The male organs consist of a pair of testes and a group of cement glands which communicate with the cirrus. The cirrus is contained within an evertible structure at the posterior end of the body known as the copulatory bursa. When protruded, this is a bell-shaped structure in the center of which the cirrus is located.

In the female, there is no persistent gonad. Egg masses are formed very early and after fertilization these are broken up into individual embryos each of which becomes surrounded by a series of three embryonic membranes. The hard-shelled embryos thus formed are usually ovoid or spindle-shaped in form. The embryos are held for some time within the female's body cavity which becomes filled with them. Finally, they are discharged through an apparatus known as the selective apparatus (Fig. 71 *B*) which passes them down the uterus and out of the genital pore.

All classes of vertebrates harbor these parasites. *Macracanthorhynchus hirudinaceus* found in hogs is one of the most commonly known species. The genera Echinorhynchus and Neoechinorhynchus are represented by several species in American fishes. Several genera, including numerous species, infest the intestines of birds and mammals. The genus Moniliformis occurs normally in rodents but is also at least a facultative parasite of man.

Outline of Classification

Phylum Nemathelminthes.—Body covering a cuticula; wormlike; unsegmented.

- **I. Class Nematoda.**—Complete digestive tract; lateral lines along sides of body; body cavity a pseudocoel.
  - **1. Order Trichosyringata.**—Esophagus a small tube with chitinous lining. *Trichinella, Trichostrongylus.*
  - **2. Order Myrosyringata.**—Esophagus . prominent; muscular. *Ascaris, Heterodera, Rhabditis, Strongyloides, Syngamus, Ancylostoma, Necator, Haemonchus, Filaria, Loa, Dioctophyme.*
- **II. Class Gordiacea.**—Body cavity lined with epithelium; no lateral lines; larva in insects, adult in water. *Gordius, Paragordius.*
- **III. Class Acanthocephala.**—Digestive organs lacking; always parasitic; proboscis a hook-covered introvert. *Echinorhynchus, Acanthocephalus, Neoechinorhynchus, Gigantorhynchus, Macracanthorhynchus, Moniliformis.*

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CHAPTER VIII

PHYLUM TROCHELMINTHES

Many of the higher invertebrates in their development pass through a larval stage known as the trochophore. In most instances where a trochophore is involved, it later by metamorphosis gives rise to an adult animal which in organization is fundamentally different from the simple larva. There are, however, a few organisms which in their adult state are not essentially different from the trochophore type of organization. The most characteristic of these is the group of the Rotifera. In addition to the rotifers, there is a small group of minute fresh-water organisms known as the Gastrotricha which are in some respects similar to the Rotifera. These two groups are united to form a phylum to which the name Trochelminthes is frequently applied.

By some, representatives of this phylum are thought to represent precociously mature larvae, or an instance of what might be termed phylopaedogenesis.

Class Rotifera

The Rotifera, or wheel animalcules, are microscopic animals which in fundamental structure closely resemble the trochophore. In size and superficial appearance, they might be mistaken for Protozoa and were so considered by many of the early workers. Close observation reveals in them miniature organ systems and demonstrates their true metazoan natures. Most rotifers live in fresh water though a few dwell in seas. No body of water is too large or too small for them, for tiny temporary pools frequently support a varied fauna of these minute organisms. Many are capable of withstanding desiccation and one type of eggs is highly resistant. These two facts go far toward explaining the practically cosmopolitan distribution of many species, for the dried individuals or eggs could be transported great distances or might even be carried by the winds. Some genera are commonly represented in the fresh-water plankton, others are characteristically associated with vegetation, while still others live on muddy bottoms of ponds and streams.

Gross Morphology.—The body, which is extremely variable in shape, usually consists of a trunk and a tail. In many genera a flexible cuticula covers the trunk, but in others there is a firm, shell-like covering called the lorica. The anterior extremity of the trunk is usually modified to form a structure known as the trochal disc (Fig. 72) which is one of the most characteristic structures of the rotifers. This disc bears cilia in highly variable arrangement and is capable of retraction within the anterior region of the trunk. The mobile posterior extremity is usually recognizable as a tail with some sort of adaptation for

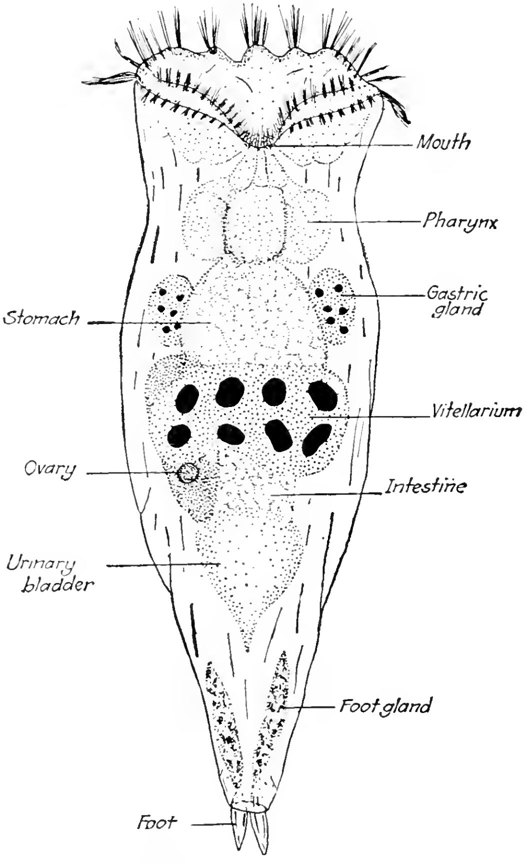

FIG. 72.—A rotifer, *Hydatina senta*, viewed from ventral surface. (*Orig.*).

attachment, though in many forms (Asplanchna, Pedalion, etc.) this is lacking. Individuals of some species are permanently attached. In this instance (Melicerta, Floscularia), they may secrete a tube or may form a case, partly of foreign matter, within which the rotifer can withdraw when disturbed. A few species form colonies by secreting a gelatinous material within which the foot of each individual becomes embedded. In free-swimming forms, the trochal disc is the chief organ of locomotion, though at times the rotifer may loop along like a leech and in some instances outgrowths from the body wall form hollow limblike appendages (as in Pedalion) by means of which the animal skips through the water.

Trochal Disc.—The plan of ciliation of the trochal disc is usually reducible to various modifications of one or two bands of cilia. In the simplest condition, a single circle of cilia edges the margin of the circular disc. Distortion of this circle at certain points results in the formation of either blunt ciliated lobes (Floscularia) or long ciliated arms (Stephanoceros) but in each of these instances the cilia are arranged in a single continuous row. In many instances, a second band of cilia is introduced parallel to the first and in some of these also the ciliated bands may become lobed. Almost always when two rows of cilia are present the mouth occurs between the two on the ventral surface of the disc. In Trochosphaera, which lacks a trochal disc, there is an equatorial preoral circle of cilia with a few cilia postoral in distribution. This condition, as well as the general internal organization of Trochosphaera, corresponds very closely to conditions found in the trochophore larvae of higher invertebrates. It is because of this close agreement that some contend that rotifers phylogenetically represent trochophore larvae which have attained full sexual development precociously.

Digestive System.—The digestive system comprises a mouth located on the ventral surface of the trochal disc, an esophagus with its elaborate mastax for triturating food, a stomach, and an intestine which opens near the posterior extremity through an anus. The mastax is highly characteristic of the rotifers but is subject to considerable modifiability of form. In many instances, there are three heavily chitinized parts discernable: an incus and two mallei, but either of these elements may be wanting. By action of the muscular esophageal wall, the parts of the mastax are worked together as an effective crushing organ which reduces the food ready for digestion, when it passes on into the stomach. A pair of digestive glands is usually associated with the stomach. Both the stomach and intestine are lined with cilia. In the genus Asplanchna, the stomach ends blindly, for there is no intestine.

Excretory System.—Coiled nephridial tubes lying in the body cavity bear flame cells at the ends of their lateral branches. These excretory tubules discharge their waste into a urinary bladder and thence into the cloaca.

Nervous System.—A single ganglion, usually located in the anterior dorsal region of the body, gives off nerves to the surrounding organs and from it a pair of lateral nerve trunks pass posteriorly to the tail. One or more simple pigment spots, and sometimes more complicated eyes, are often associated with the brain and, aside from tactile hairs, represent about the only development of sensory apparatus.

Reproduction.—Rotifers are bisexual, though usually the male is much reduced and in some instances has never been observed. At times, the male lives as a parasite on the female. Since they have no digestive organs, many males are very short lived. In describing rotifer structure, the body of the female is considered as typical. Most rotifers are oviparous or ovoviviparous, though some (Asplancha, Philodina) are viviparous. Parthenogenetic development, as commonly found here, frequently involves two different sizes of eggs, of which the larger produce only females and the smaller only males. Insemination of the female to produce fertilized eggs seems to be accomplished by perforation of the body wall at any point to introduce spermatozoa into the body cavity. Fertilized eggs thus produced differ from the parthenogenetic eggs in the possession of heavy, resistant shells and are designated as winter eggs.

Sexual Organs.—The female organs usually consist of a single ovary (two in Philodina) and a vitellarium of highly variable form, though in a few cases there are two gonads with no distinction between ovary and vitellarium. In parthenogenetic development, the young are produced within the body of the female and are usually liberated by rupture of the body wall of the parent. Winter eggs are usually carried inside the body some time before they are discharged through the oviduct and then lie dormant for a period before the young are hatched. Organization of the male is frequently simple, due to the degeneration of the digestive organs which occur as degenerate strings of tissue, near the posterior region, to which the male gonad is attached. A special copulatory organ in the form of a protrusible cirrus is often present.

Rotifers as Experimental Animals.—Because of the readiness with which they may be reared in cultures, rotifers have been widely used in the study of problems concerned with the determination of sex. For instance, in some species the ratio of males to females may be controlled directly by regulation of the temperature or by the type of food given to the parthenogenetic females.

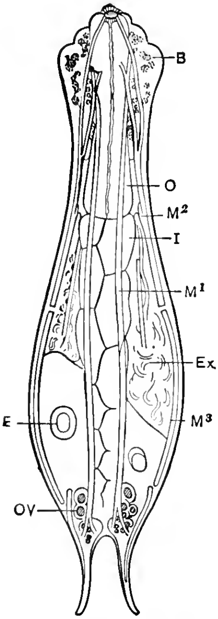

Fig. 73.—*Chaetonotus maximus*, one of the Gastrotricha, in ventral view. *Ex*, kidney; *M*, muscles; *B*, brain; *E*, egg; *O*, esophagus; *I*, intestine; *Ov*, ovary. ×400. (*After Zelinka, from Ward and Whipple's Fresh-water Biology, reprinted by permission of John Wiley and Sons, Inc.*).

Nuclear Constancy.—For a number of rotifers, it has been shown that each organ is built of a fixed number of cells or at least contains a constant number of nuclei. An especially thorough study along this line has been published by Eric Martini for *Hydatina senta*, each individual of which contains a total of 959 nuclei distributed in fixed numbers through the various organs and tissues of the body.

Class Gastrotricha

Though the Gastrotricha are here included as a class along with the Rotifera under the phylum Trochelminthes, their relationships with the rotifers are far from firmly established. Some zoologists maintain that the Gastrotricha are more directly related to the Nematoda. They are rarely more than 0.5 mm. in size and though they occur relatively frequently in protozoan and rotifer cultures, their small size and rapid movements render close examination difficult. Though widely distributed, they are restricted to fresh water.

In most instances, there is a head set off from the body proper by a slight constriction. The body is flattened on the ventral surface and convex on the dorsal. The ventral surface is furnished with two longitudinal bands of cilia near the median line, by the action of which locomotion is accomplished. The body proper may be either smooth or covered with plates, spines, or bristles. The mouth, which is borne at the anterior extremity of the head, is usually surrounded by a circle of delicate oral bristles. In addition, there are frequently lobes on the sides of the head from which groups of sensory hairs protrude.

The internal organization (Fig. 73) is relatively simple. The digestive tract runs as a straight tube through the axis of the body. In the body musculature, only a few longitudinal strands of muscle but no circular muscles have been demonstrated. The brain occupies much of the head region. The excretory organs are protonephridia.

Only females are known, yet it is uncertain whether these are truly parthenogenetic or are hermaphroditic, and the male gonads have never been observed. The ovary occupies the posterior region of the body cavity and as fully formed eggs push anteriorly in the body cavity, they frequently distort the shape of the gravid female.

Chaetonotus and Lepidoderma are the most representative genera in the North American fauna.

OUTLINE OF CLASSIFICATION

Phylum Trochelminthes.—Microscopic, triploblastic, unsegmented Metazoa; as adults usually resembling trochophore; mouth usually surrounded by cilia; aquatic.

- **I. Class Rotifera.**—A crown of cilia (corona) typically at anterior extremity; posterior extremity usually terminating in a foot or jointed tail; pharynx bears mastax.
  - *a.* **Subclass Monogononta.**—Ovary single.
    - **1. Order Notommatida.**—Mouth not near center of corona. *Proales, Notommata, Synchaeta, Polyarthra, Distyla, Monostyla, Rattulus, Diurella, Hydatina, Anuraea, Notholca, Brachionus, Schizocerca, Asplanchna.*
    - **2. Order Floscularida.**—Mouth near center of corona. *Floscularia, Microdon, Apsilus, Stephanoceros.*
    - **3. Order Melicertida.**—Two parallel wreaths of cilia with a furrow between; outer wreath always shorter. *Pterodina, Pompholyx, Pedalion, Triarthra, Trochosphaera, Melicerta, Conochilus.*
  - *b.* **Subclass Digononta.**—Two ovaries.
    - **1. Order Bdelloida.**—Fresh water. *Rotifer, Philodina.*
    - **2. Order Seisonida.**—Marine; parasitic. *Seison, Paraseison.*
- **II. Class Gastrotricha.**—Body spindle-shaped; flattened ventral surface bearing two rows of cilia; cuticular spines on back; ring of cilia(?) around mouth. *Chaetonotus, Lepidoderma.*

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CHAPTER IX

PHYLUM COELHELMINTHES (ANNELIDA)

The Coelhelminthes or Annelida comprise a number of wormlike forms which possess a coelom and are usually segmented. This group contains many of the forms included under the "Vermes" of Linnaeus and other early workers. It has been said frequently that the Vermes constituted a wastebasket into which forms which could not be placed elsewhere were dumped. Much of the advance in modern classification of the animal kingdom has centered around the recognition of groups of wormlike forms bearing common characteristics and establishing for them rank as independent phyla and classes. Thus the Plathelminthes, Nemathelminthes, Molluscoidea, and Trochelminthes have been removed from the old group Vermes and each has been elevated to the rank of an independent phylum. There yet remains an assemblage of segmented worms, arrow-worms, and gephyrean worms which seem to have enough features in common to warrant their retention for the present in a single major group of the animal kingdom. These forms, which collectively are known as the Coelhelminthes, agree in possession of a coelom and in having the nervous system of a uniform type. An excretory system is lacking in members of the class Chaetognathi and in some representatives of the other groups, but characteristically a metanephridial system is found. The Gephyrea, which lack segmentation, agree with the typical annelids in passing through a larval stage known as trochophore.

Class Chaetognathi

The chaetognaths, or arrow-worms, are small forms with body shape admirably adapted for life at the surface of the ocean where they move about with great rapidity in search of food. The body, which is almost as transparent as crystal, is usually about 15 mm. long though one species reaches a length of 70 mm. It is divided into three segments: head, trunk, and tail. Each of these divisions is separated from adjoining segments by a transverse septum, and a longitudinal mesentery divides each coelomic cavity into a right and a left part. From the sides of the head (Fig. 74) there extend a series of bristles which act as jaws in seizing prey, hence the name Chaetognathi, or bristle jaws. In preserved specimens, these jaws are frequently folded close against the sides of the head.

Swift movements are produced by muscular contractions of the body and are directed by fins which occur as outgrowths of the body wall. These are a fan-shaped tail fin and one or two pairs of lateral fins on the trunk. Some species undergo marked migrations between the surface and deeper water twice daily. In Southern California one species becomes most abundant at the surface of the ocean just after sunrise and again just after sunset. The central nervous system consists of a cerebral ganglion on the dorsal surface of the esophagus which is connected with a ventral ganglion near the middle of the trunk by two long esophageal connectives. A pair of eyes lie close behind the brain with which they are connected by a pair of nerves. Papillae scattered over the surface of the body probably have a tactile function. A peculiarly modified region on the dorsal surface just behind the head has been interpreted as olfactory.

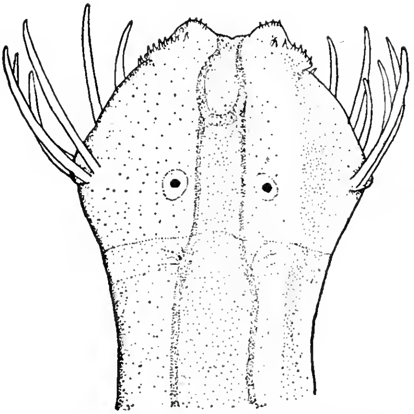

Fig. 74.—Head of Sagitta showing bristle-like jaws extended. (*Orig.*).

The individuals are hermaphroditic. Ovaries occur in the posterior part of the trunk cavity and communicate with the exterior through an oviduct on each side which opens laterally near the posterior extremity of the trunk segment. The testes are contained in the coelomic cavities of the tail segment. Spermatozoa, liberated directly into the cavity, are carried out through a delicate sperm duct which is frequently dilated near its extremity to form a seminal vesicle.

In development, the fertilized egg undergoes cleavage to form a typical gastrula. Two lateral folds of the entoderm extend down into the archenteron dividing this cavity into three parts. Of these, the two lateral cavities, lying between each fold and the body wall, later become the coelomic cavities, while the central space between the two folds constitutes the mesenteron. During the gastrula stage, two entoderm cells opposite the blastopore become recognizable as the rudiments of the gonads. By a single division, these two cells form two pairs of which the anterior pair later forms the female gonads and the posterior pair the male gonads. The young resemble the parents except in size.

Sagitta, the arrow-worm, is the most characteristic genus of the Chaetognathi of which Spadella and Krohnia are other recognized genera.

Class Chaetopoda

The Chaetopoda are among the most characteristic of Coelhelminthes. Metamerism is sharply marked. The coelom is divided into successive chambers by transverse septa which correspond with the external constrictions of the body wall, and even internal organs such as nervous, excretory, and circulatory systems bear the marks of metamerism. Most of the segments bear bristles or setae which, by their number and arrangement, give a basis for classification into subclasses. In the Polychaeta, the setae occur in outgrowths of the body wall called parapodia which function as oarlike organs in swimming.

The **digestive system,** though a straight tube, usually shows specialization into regions. The mouth typically lies on the ventral surface very near the anterior extremity beneath the terminal somite called the prostomium. In the two subclasses, the prostomium is highly variable in degree of specialization. Among the Oligochaeta it is frequently a small, inconspicuous lobe with generalized sense organs similar to those found on other segments of the body, while among the Polychaeta it more frequently bears highly specialized tactile organs and eyes.

The **circulatory system** consists of at least two main longitudinal trunks, one dorsal and the other ventral, connected by lateral vessels in each segment. Frequently, additional longitudinal vessels occur. Some of the lateral vessels in the anterior region of the body are specialized as pumping organs or hearts. These, with the dorsal vessel, propel the blood through the system by their pulsations.

The **central nervous system** consists of a ventral chain with a ganglion in each segment. This chain, which is really composed of two fused cords, frequently shows its double nature in its ladder-like appearance, and in cross-section the arrangement of cells and fibers give still further evidence. In the anterior region of the body, the two cords separate to pass around the pharynx on the dorsal surface of which occurs the largest ganglion, called the suprapharyngeal ganglion or brain.

Excretion is by means of metanephridia in the adults and protonephridia in larvae of forms which have the trochophore. Characteristically, each somite is provided with a pair of metanephridia the funnel or nephrostome of each of which is attached to the posterior septum while the tubule penetrates the septum and passes into the cavity of the adjacent somite before opening to the outside through the nephridiopore. Modified nephridial ducts (Fig. 47) are frequently utilized for the discharge of the germ cells. Primitively, separate ducts called ciliated grooves or coelomoducts serve for the discharge of the germ cells, but these frequently become associated with the nephridia, the tubules of which then becomes the gonoducts.

Embryology.—Annelid eggs undergo cleavage of determinate type which results in the formation of a definite pattern in the arrangement of the blastomeres. From polar view the cells are arranged in the form of a cross. So characteristic is this pattern (Fig. 10) that the term annelidan cross has been applied to it. Later development results in the formation of a trochophore except in fresh-water and terrestrial forms. The structure and transformation of this larva will be described later. Asexual reproduction is not uncommon. In some forms, there is but slight specialization of the individual somites. This condition, known as homonomous metamerism, facilitates asexual reproduction and frequently leads to the formation of a chain of individuals through the differentiation of the metameres of a single worm.

Subclass POLYCHAETA

The sexes are separate in the polychaetes. Usually, the anterior somites are rather highly specialized to form a distinct head bearing eyes and tactile organs. The somites have outgrowths from their lateral margins which are known as parapodia and serve as rudimentary appendages. Each parapodium is supported by numerous bristles or setae which are arranged in two bundles. The lobe of the parapodium surrounding the ventral bundle of setae is called the neuropodium, while that surrounding the dorsal bundle is the notopodium. In Nereis, the notopodia are supplied with numerous blood vessels and function as gills. Among other polychaetes, gills are frequently developed as long filamentous outgrowths, either along the sides of the body or restricted to certain areas. Each lobe of the parapodium frequently bears a fleshy sensory projection termed the cirrus. In some instances, dorsal scales covering the back of the worm represent modified dorsal cirri.

Dimorphism.—Among the polychaetes, two different types of individuals are frequently encountered in the same species, the atoke or sexless and the epitoke or sexual individual. Before their relationships were understood, these phases were frequently considered as distinct species and even as different genera. In some instances, the atoke (Fig. 75) has the power of budding to produce sexual epitokes which become separated as free individuals. This is the condition found in the palola worm (*Eunice viridis*) the epitoke of which appears in extreme numbers in the tropical South Seas and is relished by the Samoans as a food. The atoke remains in the corals at the bottom of the sea where it proceeds to regenerate a new posterior end.

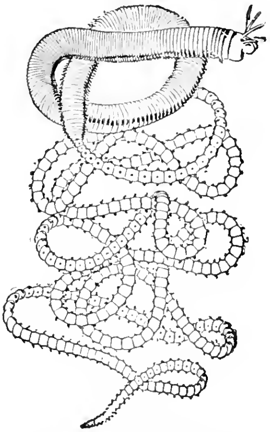

Fig. 75.—A Palola worm, *Eunice viridis* (Gray), showing differentiation of body into an enlarged atoke and a posterior epitoke. (*After Woodworth*).

In some of the common species of marine annelids there are striking differences in appearance of the immature worms and those filled with mature germ cells. These differences are so conspicuous that before they were understood, mature and immature worms of the same species were ascribed to different genera. In some species of the common clam worm (Nereis) the peculiarly modified mature specimens were given the generic name Heteronereis. When the young worms approach maturity, the segments in the posterior half of the body become storehouses for the germ cells, taking on an entirely different appearance from those of the front half of the same worm. Thus an anterior atoke and a posterior epitoke are recognizable in the body of the mature Nereis, though the two regions never become separated as in the palola worm. The most conspicuous of the changes in the epitoke region concern the parapodia. These increase in size while the original setae are shoved out and are replaced by new ones of entirely different shape and arrangement. The lobes of the parapodia develop new outgrowths which render them more effective swimming organs. Even though the parapodia of the immature Nereis seem to be admirably fitted for swimming, the worm rarely becomes pelagic except at the onset of sexual maturity.

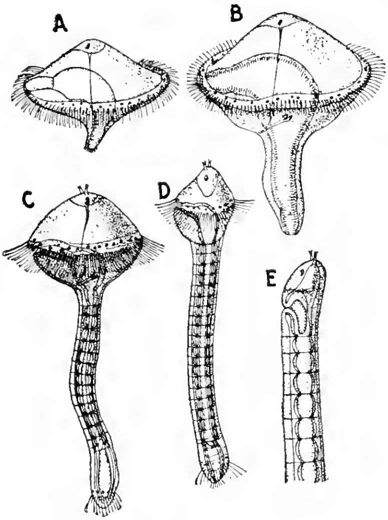

Fig. 76.—The development of Polygordius. *A*, young trochophore; *B*, elongation of posterior cone; *C*, *D*, stages in transformation of trochophore; *E*, anterior extremity of young Polygordius following metamorphosis. (*After Fraipont*).

Development.—Practically all polychaetes are marine and in development pass through the trochophore stage. In organization, the polychaetes represent a more primitive condition than the oligochaetes. Though the obligochaetes are frequently simpler in structure, their simplicity is the result of degeneracy, for it seems probable that in becoming adapted to life in fresh water or to the terrestrial existence they have departed from the generalized structure and mode of development which characterize the more primitive members of the class.

The trochophore (Fig. 76, *A*) is typically pear-shaped or in the form of two cones joined by their bases, one dorsal and the other ventral in position. Surface ciliation of this larva may follow any one of a number of patterns. A tuft of cilia at the apical plate and a preoral circle near the equator of the larva are the most constant, but other bands may also appear. The digestive system consists of a mesenteron which communicates with the mouth opening through an esophagus and with a terminal anus through an intestine. The region between the digestive tube and the outer body wall is filled with a gelatinous substance through which run strands of muscle and nerve and the tubules of the protonephridial system. Near the posterior extremity of the early trochophore, there usually occur a pair of cells called the teloblasts which are the forerunners of the mesoderm. As the larva elongates, these teloblasts continue to divide, forming bands of mesoderm cells on either side of the digestive tract. With the elongation of the posterior cone of the trochophore in the transformation of the larva into the adult worm, these mesoderm bands become divided into primitive segments (Fig. 76 *C*) within which the coelomic cavities later make their appearance. The segments of the young worm thus formed are usually provided with provisional setae which are later thrown off and replaced by the permanent setae.

Both free-living and sessile polychaetes are found. Modifications of body form associated with these differences in habits have furnished a basis for the separation of two orders.

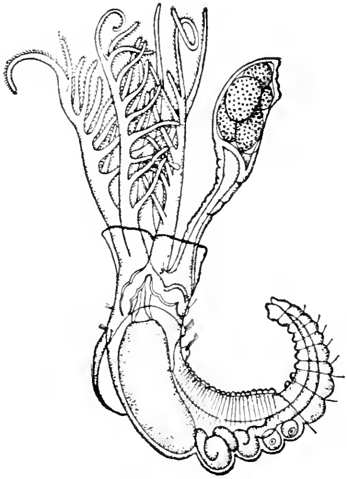

FIG. 77.—Lateral view of a serpulid worm, Spirorbis, removed from its shell. The ovoid bodies within the club-shaped operculum are developing embryos. (*After Claparède*).

Free Living.—In the order Errantia are included all of the free-swimming polychaetes with a well-developed head but with all the remaining segments practically homonomous, bearing parapodia of approximately uniform character. The pharynx is evertible and frequently bears a pair of formidable jaws which are used in capturing prey. Nereis, the clamworm, is one of the commonest examples of this order. Aphrodita has the dorsal surface so covered with bristles as to warrant the common name sea mouse. Lepidonotus bears twelve pairs of broad overlapping scales on its back. Syllis reproduces by means of lateral clusters of buds, and Autolytus undergoes asexual reproduction through the formation of buds at the posterior extremity.

Tube Dwellers.—Members of the order Sedentaria are tube dwellers. Some live in burrows in the sand (Arenicola), others form membranous tubes (Myxicola, Manyunckia), and still others live in calcified tubes within which they withdraw (Hydroides, Spirorbis) and close the opening with a modified tentacle, the operculum. The Sedentaria lack the jaws characteristic of the free-moving Errantia and display much greater diversity in structure of the anterior and posterior regions of the body. Numerous filamentous gills and tentacles frequently adorn the head and anterior body somites which usually protrude from the tube or burrow (Fig. 77), while the parts constantly encased have weakly developed parapodia. Bright colors frequently occur on the gills and anterior region of some of the tube dwellers. When such forms stick their heads from their tubes, they have all the brilliance of full-blown flowers.

Subclass OLIGOCHAETA

The oligochaetes are as characteristically terrestrial and fresh-water inhabitants, as are the polychaetes marine. In many ways, they bear evidences of degeneracy as an accompaniment of the change from marine to fresh-water or land habitat. Pelagic larvae and parapodia are entirely lacking in all members of the subclass, while gills occur in only a few forms and the sensory apparatus represents a very low stage of specialization. Setae occur in pairs, rows, or bundles but never have parapodia associated with them. The sexes are never separate. The male and female gonads occur in different segments. In the Naididae and Aeolosomatidae, asexual as well as sexual reproduction occurs.

Near the anterior end of the worm, usually not far removed from the openings of gonoducts, the body wall of a number of somites is supplied with numerous glands which in the height of sexual development form a thickened collar-like band over the dorsal and lateral surfaces of the body known as the "clitellum." This clitellum produces secretions which harden to form a capsule or cocoon for containing the eggs after they are laid. In the earthworms, fertilization is reciprocal. During copulation (Fig. 78) a spermiducal pore of each individual is opposite the opening of a receptaculum seminis of the other so that sperm cells of each individual pass into the receptaculum of the other, thereby accomplishing cross-fertilization.

Various systems of subdividing the Oligochaeta have been proposed, most of which have as a basis either the habits or structural characters correlated with aquatic or terrestrial habits.

Members of the order Microdrili are small oligochaetes of relatively few segments and usually aquatic in habits. Eyespots are frequently present.

In the order Megadrili are found the larger oligochaetes, which are commonly known as earthworms. The bodies of these contain numerous segments (Moniligaster, Perichaeta, Microscolex, Diplocardia, Helodrilus, Lumbricus).

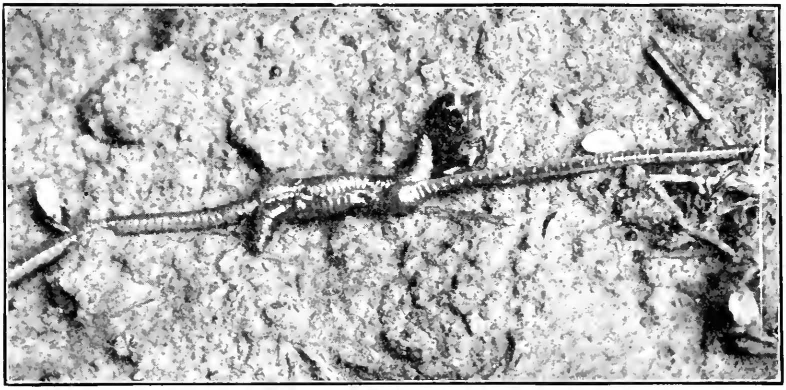

Fig. 78.—Flashlight photograph of earthworms in copulation. (*Original photo by Alvin R. Cahn*).

Class Hirudinea

The Hirudinea, or leeches, are annelids with a fixed number of somites (generally 34), but superficially each somite is subdivided by constrictions (Fig. 79) into a number of annulations, so the number of external rings does not correspond to the number of internal divisions of the coelom. The coelom is very greatly reduced but the small pouches furnish the basis for the determination of the number of somites. With the exception of one genus (Acanthobdella) leeches have no setae. The posterior extremity bears a sucker on its ventral surface and usually a second sucker is developed around the mouth. Both of these are organs of attachment, and in addition the oral sucker aids in the ingestion of food. In addition to a graceful undulating swimming, free in the water, leeches may also progress by fixing the anterior sucker to some object, then drawing the body into a loop and fixing the posterior sucker near the same spot.

Slight development of the coelom and the dorsoventral flattening of the body give leeches a distinct flatworm appearance. Segmentation, presence of a coelom, development of a clitellum, presence of a distinctly annelid type of nervous system, and general organization, however, demonstrate close relationships with the Oligochaeta. Michaelsen proposes a group Clitellata to include the Oligochaeta and Hirudinea as two coordinate

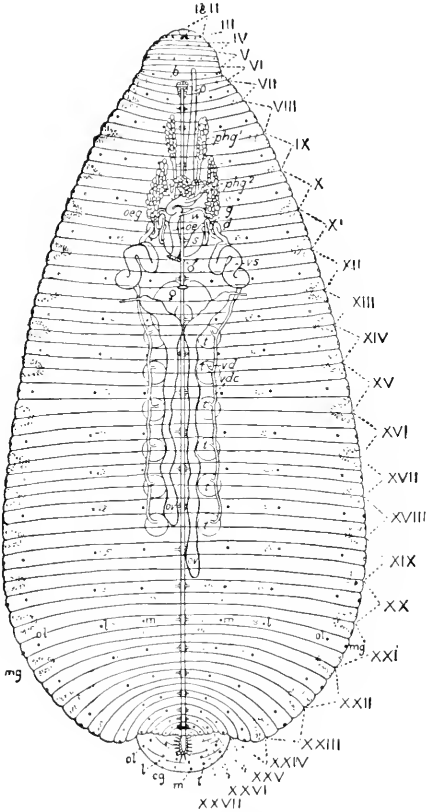

FIG. 79.—Organization of a leech, *Placobdella parasitica*. I–XXVII, somites; *phg*, pharyngeal glands; *oe*, esophagus; *s*, atrium or spermatophore sac; *v.s*, seminal vesicle; *t*, testes; *ov*, ovary. (*Redrawn from Whitman in Ward and Whipple's Fresh-water Biology and reprinted by permission of John Wiley and Sons, Inc.*).

groups. This same author suggests that leeches may be oligochaetes modified for predatory habits.

The digestive system does not lie loosely in a spacious coelom as does that of the Chaetopoda, for the coelom is largely encroached upon by a parenchyma which leaves a system of blood-filled sinuses in addition to the definite circulatory system. The terminal buccal chamber opens into a muscular pharynx which, in turn, leads by way of an esophagus into a stomach or crop. This latter may be either a straight tube or may give rise to from one to twenty pairs of lateral diverticula before emptying into the intestine. A small rectum leads to the anus on the dorsal surface near the posterior extremity.

A metanephridial system similar to that found in the Oligochaeta serves for excretion. Usually, not more than seventeen pairs of nephridia occur, for they are lacking from the somites of both extremities and from some of the clitellar somites. The central nervous system consists of a brain and a ventral chain of ganglia of which there are frequently twenty-three.

Leeches are hermaphroditic. Fertilization occurs either by reciprocal copulation or through the implantation of spermatophores on the skin. Spermatozoa escape from these and penetrate the tissues to the ovarian sacs where fertilization occurs. Development from the egg is direct. In many leeches a cocoon is formed by the clitellum for sheltering the eggs and young as in the oligochaetes. In some species, however, the eggs are carried on the ventral surface of the parent's body and even the young remain attached there for some time after hatching.

Hirudinea get their vernacular name of bloodsuckers from the fact that many species are permanent or temporary ectoparasites on the bodies of other animals. Many species, and especially the young, are predaceous in habit, feeding upon other small organisms, and resort to the parasitic habit only when opportunity is offered. Most leeches are inhabitants of fresh water, though some are marine and a few are terrestrial. Those which feed upon blood have either three jaws supplied with sharp teeth (Gnathobdellida) which lance the skin of the host or a conical proboscis evertible from the pharynx (Rhynchobdellida) for piercing. Glandular secretions from the leech hinder coagulation of the blood and render its wounds difficult to staunch.

Two orders are commonly recognized, the Rhynchobdellida and the Gnathobdellida. Of these, the former are jawless while the latter have jaws. Species of the genus Piscicola which live on fishes, Glossiphonia, and Placobdella are characteristic of the first order, while the medicinal leech (*Hirudo medicinalis*) and Macrobdella, which so commonly attacks bathers, are examples of the Gnathobdellida.

Class Archiannelida

As the name signifies, the Archiannelida seem to represent a primitive type of annelid organization which may have considerable significance in solving the problem of the origin of the higher annelids. The body, which shows only slight indication of segmentation externally, has a coelom completely divided into somites. Both parapodia and setae (Fig. 76 *E*) are lacking. The nervous system is distinctly more simple than that characteristic of other annelids, for it remains in direct contact with the epidermis and shows no centralization to form ganglia. In the genus Protodrilus, there are two ventral nerve cords connected by transverse commissures, but in Polygordius there is a single cord. Representatives of both of these genera are exclusively marine. The prostomium bears a pair of tentacles and in addition to these a pair of ciliated grooves are the only structures which seem to have a sensory function.

In the development of Polygordius, a typical trochophore (Fig. 76) occurs the formation and metamorphosis of which have been worked out in great detail.

Appendix to the Archiannelida

Dinophilus and some other simple wormlike forms are of questionable systematic position. Some zoologists maintain that they show possible relationships with the Archiannelida, while others consider them as more closely related to the Trochelminthes. Members of the genus Dinophilus are minute marine worms which live among seaweeds. The body consists of a head, five or six trunk segments, and a tail segment. The adult worm rather closely resembles the larva of marine polychaetes.

Class Gephyrea

The Gephyrea are marine worms which differ from the remaining annelids in the lack of segmentation, parapodia, and setae. Development involves a modified trochophore larva. The undivided coelom contains a complete digestive system the intestine of which extends posteriorly some distance, then coils back on itself to a dorsal anal opening toward the anterior extremity of the body. The extended anterior extremity of the body is provided with tentacles or a lobed tentacular fold within which the mouth is located. The entire anterior region is capable of inversion within the body.

A single pair of nephridia comprise the excretory apparatus and serve as gonoducts. The nervous system originates in the anterior extremity as a dorsal cerebral ganglion which is joined with the ventral longitudinal nerve cord by a pair of lateral branches. The ventral nerve cord bears no ganglia but gives off lateral branches to the body wall and to the internal organs.

Though the sexes are usually distinct, persistent gonads are not present. The germ cells have their origin in masses or ridges of cells in the lining of the body cavity and either undergo full development in this location or are discharged early into the coelom where development is completed.

Sipunculus and Phascolosoma are characteristic genera of the Gephyrea.

OUTLINE OF CLASSIFICATION

Phylum Coelhelminthes.—Coelomate worms; usually segmented.

- I. **Class Chaetognathi.**—Marine, pelagic; three segments; bristle jaws. *Sagitta, Spadella, Krohnia.*
- II. **Class Chaetopoda.**—Numerous segments with setae; ventral chain of ganglia; blood vascular system.
  - *a.* **Subclass Polychaeta.**—Parapodia; numerous setae; marine; separate sexes; no clitellum; trochophore larva.
    - 1. **Order Errantia.**—Free-swimming. *Nereis, Aphrodita, Lepidonotus, Syllis, Autolytus, Halosydna.*
    - 2. **Order Sedentaria.**—Tube dwellers. *Clymenella, Arenicola, Myxicola, Sabellaria, Hydroides, Spirorbis, Chaetopterus, Amphitrite.*
  - *b.* **Subclass Oligochaeta.**—Clitellum; no parapodia; few setae; not marine.
    - 1. **Order Microdrili.**—Small; few segments; aquatic; asexual reproduction common. *Tubifex, Dero, Nais, Chaetogaster, Aeolosoma, Pristina, Mesenchytraeus.*
    - 2. **Order Megadrili.**—Large; many segments; usually terrestrial; sexual. *Moniligaster, Perichaeta, Helodrilus, Diplocardia, Lumbricus.*
- III. **Class Hirudinea.**—Typically thirty-four somites; more annulations than somites; one or two suckers.
  - 1. **Order Rhynchobdellida.**—No jaws; introvert at anterior end. *Glossiphonia, Placobdella, Piscicola.*

2. Order Gnathobdellida.—Mouth large; usually jaws present; no proboscis. *Macrobdella, Hirudo, Haemopis, Dina.*

IV. Class Archiannelida.—Marine; no setae or parapodia; segmented internally; no ganglia in nervous system. *Polygordius, Protodrilus.*

V. Class Gephyrea.—No segmentation or parapodia; trochophore; introvert.

1. Order Inermia.—No setae; anus dorsal. *Phascolosoma.*

2 Order Armata.—Few setae; anus posterior. *Sipunculus, Echiurus.*

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CHAPTER X

PHYLUM MOLLUSCOIDEA

The phylum Molluscoidea contains three classes which agree in the possession of a ridge called the lophophore at the anterior extremity of the body bearing a crown of ciliated tentacles. The three classes: Polyzoa, Brachiopoda, and Phoronida, present so many individual peculiarities that few statements may be made that would apply equally to the organization of the members of all three. Consequently, the structure and characteristics of the individual classes will be discussed separately.

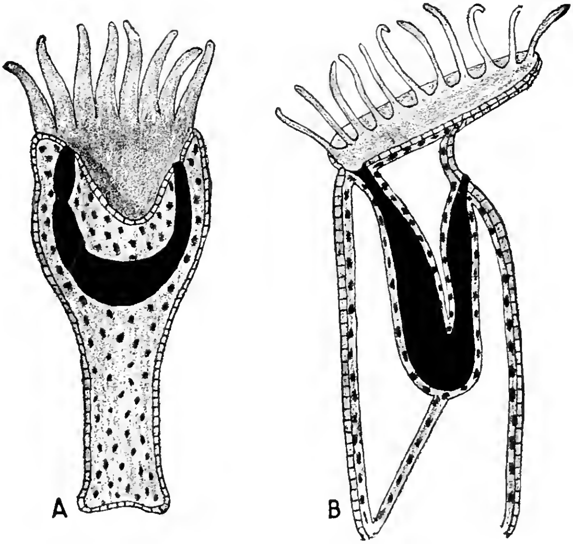

FIG. 80.—Diagrams to show contrast in general organization in; *A*, an endoproct bryozoan; *B*, an ectoproct bryozoan. The digestive system is shown in solid black. Compare the position of the anal opening in the two figures. (*Orig.*).

Class Polyzoa

Individuals of the class Polyzoa (or Bryozoa) bear very close superficial resemblance to hydroid polyps from which they are readily distinguishable because the polyzoan zooids possess a complete alimentary tract terminating in an anus near the anterior extremity of the body. The position of the anal opening with reference to the circle of tentacles serves as a basis for the discrimination between the two orders (Fig. 80), which show extreme differences in internal structure. In the order Ectoprocta, the anus occurs outside the tentacular ring, while in the Endoprocta it is within the circle formed by the tentacles. The lack of a coelom in the Endoprocta renders their relationship to the other Polyzoa open to question. Some investigators have considered that the Endoprocta possibly bear relationship to the Rotifera. The majority of the Polyzoa are colonial. The individuals of a colony are bound together by an organic connecting material. The individuals are in many instances covered with a gelatinous, horny, or calcified layer forming an exoskeleton. Polyzoa are most abundant in salt water, though a number of genera appear in fresh water.

I. ORDER ECTOPROCTA

The Ectoprocta are colonial forms which frequently attain considerable size. Individuals of a colony are variously arranged in branching pattern (Bugula, Plumatella), in flat mats (Cristatella), as encrusting layers (Microporella, Cribrillina), or as solid gelatinous masses (Pectinatella), which may attain a size of a foot or more in diameter. The individual zooids uniting to form these different types of colony assume a number of distinctly different shapes. The lophophore is capable of retraction within the anterior part of the zooid through the agency of special retractor muscles. In addition to the action of this introvert, the entire zooid is frequently able to withdraw into the interior of the colony. In some instances, either an operculum or a series of lobes is drawn into the aperture to close it when the zooid is retracted.

Modified individuals occur in many Ectoprocta. Avicularia are modified zooids shaped much like a bird's head the beak of which is capable of grasping objects and holding them until they disintegrate. The food fragments are then secured by the tentacles. Vibracularia, another type of modified individual, are long whiplike structures which, in their development, seem to be modified avicularia.

The funiculus is a double strand of tissues which passes from the bend in the alimentary canal through the coelom to the aboral extremity of the zooid. In addition to the budding which gives rise to the colony formation, sexual reproduction may also take place. Most ectoprocts are hermaphroditic. Ovaries and spermaries make their appearance either in the lining of the coelom or in the tissues of the funiculus. The gonads dehisce into the coelom where fertilization takes place. In some species special chambers, called ovicells, are provided for containing the developing embryos. Following cleavage, a free-swimming larva of variable form in different species makes its appearance. This larva undergoes a transformation to form a zooid from which a colony later develops by budding. Statoblasts, or internal buds, are characteristic of many fresh-water ectoprocts. These are surrounded by chambers which upon drying become filled with air and serve to float the statoblasts. In the fresh-water genera, Pectinatella and Cristatella, the free larval stage has been retained.

II. ORDER ENDOPROCTA

In members of this order, the anal opening occurs within the circle of tentacles. With the exception of one genus, Urnatella, the entire group is marine. The body is usually cup-shaped, enclosing at its open end a cavity called the vestibule (Fig. 80 *A*), which contains the mouth and the anus. The rim of this cavity bears the tentacles, which are capable of being withdrawn into the vestibule. The space between the alimentary canal and the body wall is filled with a gelatinous matrix. This lack of an undisputed coelom, together with the fact that the excretory system is protonephridial, furnishes ground for doubting any close relationship between the Endoprocta and the Ectoprocta. Pedicellina, Urnatella, Loxosoma are characteristic genera.

The larva formed by the endoprocts undergoes a less conspicuous transformation than that of the ectoprocts. After becoming fixed, it transforms into a zooid from which other individuals arise by budding.

Class Brachiopoda

Because of the presence of a bivalve shell, brachiopods are frequently confused with molluscs. The shell of the brachiopod is, however, composed of a dorsal and a ventral valve (Fig. 81), while the valves of the bivalve molluscs are lateral. In the brachiopods, the valves are articulated in their posterior regions and from the posterior end of the animal a stalk or peduncle for attachment is frequently developed. The valves are lined by a mantle by whose action the shell is secreted. The bristles borne in the edge of the mantle are of the same type as those found in annelids and seem to point to a relationship between brachiopods and annelids. The ventral shell in many cases bears a short beaklike projection posterior to the hinge and it is through this that the peduncle passes. The shells so closely resemble the most primitive type of oil lamp that the common name "lamp shell" is very generally applied to shells of this group.

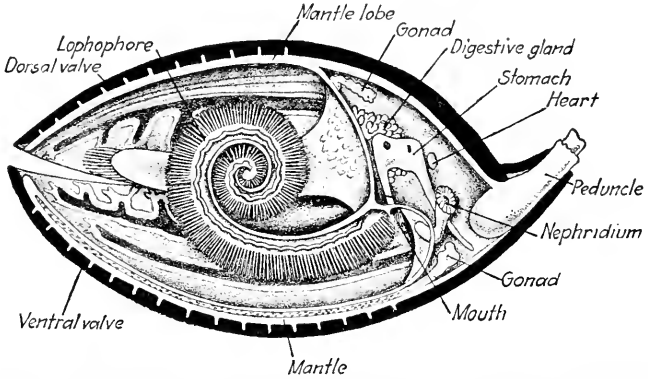

FIG. 81.—Semidiagrammatic sagittal section of a brachiopod (*Magellania lenticularis*). (*Redrawn from Parker and Haswell, with the permission of Macmillan Co.*).

In members of the order Inarticulata (Lingula, Crania, and Discina), the foregoing description does not apply, for the two valves are similar and the hinge is wanting. In the Articulata, where a hinge is present, the valves are not held open by an elastic hinge ligament as in the Acephala of the molluscs, but both opening and closing of the valves are accomplished by muscular action. Closure of the shell is by means of a pair of adductor muscles which are attached to the dorsal shell but unite to form a single muscle before reaching their insertion on the ventral valve. Two pairs of divaricator muscles pass between the ventral valve and that part of the dorsal valve posterior to the hinge. By their contraction the valves are opened. From each valve a pair of muscles known as the adjustors pass to an insertion on the peduncle. It is through contraction of these last muscles that the animal is able to shift the position of the entire body.

Much of the space within the shell is occupied by a pair of conspicuous, spirally coiled arms or lophophores. In the order Articulata, the dorsal valve frequently bears a calcareous loop which supports the lophophore. Each arm on its outer margin bears a longitudinal groove bordered by a row of small tentacles. Water currents produced by the cilia on the tentacles and in the groove carry food particles toward the mouth.

The U-shaped digestive tract consists of a mouth opening in the middle of the lophophore, a dorsally directed gullet which empties into an expanded stomach, and from this a ventrally directed intestine which ends blindly except in members of the order Inarticulata. Cilia line the entire digestive tract.

Two transverse septa divide the coelom into three somites, but the shortening of the chief axis of the body has been accompanied by a coiling of the digestive tube and consequently the arrangement of the septa is somewhat confused and difficult to observe. The coelomic cavities extend into the arms and the mantle lobes. One or two pairs of nephridia communicate with the coelomic pouches and serve as both excretory and reproductive ducts. The gonads are borne chiefly in the coelomic cavities of the mantle. The sexes are usually separate.

The brachiopods pass through a trochophore larval stage. During cleavage and embryonic development the eggs are held in brood pouches. At the time of its liberation the larva is divided into three segments. The fully grown larva becomes attached by its posterior end and from this region the peduncle develops. The large midregion or mantle segment of the larva increases in size and secretes the shell characteristic of the adult.

Brachiopods are exclusively marine. Though represented by relatively few living species, they reached an extreme state of species formation in the Silurian and Devonian periods. Terebratulina, Terebratula, and Waldeheimia are characteristic modern genera of the Articulata.

Class Phoronida

The relations of members of the single genus Phoronis have been much under discussion among zoologists. Wormlike in form, these marine organisms dwell in membranous or leathery tubes. The body is long, cylindrical, and unsegmented, at one extremity bearing numerous ciliated tentacles arranged in the form of a lophophore as characteristic of members of the phylum

Molluscoidea. Both mouth and anus occur on the extremity bearing the lophophore. The larva, which is known as actinotrocha, is a modified trochophore.

OUTLINE OF CLASSIFICATION

Phylum Molluscoidea.—Triploblastic; aquatic; lophophore bearing ciliated tentacles; anus near anterior end.

- **I. Class Polyzoa.**—Zooids small; usually colonial; alimentary canal U-shaped.
  - **1. Order Ectoprocta.**—Anus outside lophophore; coelomate.
    - *a.* **Suborder Gymnolaemata.**—Lophophore circular; chiefly marine. *Crisia, Stenopora, Bugula, Membranipora, Paludicella, Tubulipora.*
    - *b.* **Suborder Phylactolaemata.**—Lophophore horseshoe-shaped; fresh water. *Plumatella, Fredericella, Pectinatella, Cristatella.*
  - **2. Order Endoprocta.**—Anus within lophophore; no coelom. *Loxosoma, Pedicellina, Urnatella.*
- **II. Class Brachiopoda.**—Bivalve shell; marine; solitary; usually a peduncle for attachment.
  - **1. Order Inarticulata.**—Valves of shell without hinge; shell chiefly organic; anus present. *Lingula, Crania, Discina, Glottidia.*
  - **2. Order Articulata.**—Valves of shell hinged; shell limy; no anus. *Terebratula, Waldheimia, Magellania, Laqueus.*
- **III. Class Phoronida.**—Marine; wormlike; in cylindrical sand tube. *Phoronis.*

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CHAPTER XI

PHYLUM ECHINODERMA

The Echinoderma are radially symmetrical, coelomate animals with usually a subdermal skeleton of calcareous plates and a vascular system known as the ambulacral system, used chiefly in locomotion. All representatives of this phylum are marine in habits. Here are included the starfishes, serpert stars, sea urchins, sand dollars, sea cucumbers, sea lilies, and some groups which are known only from fossil remains. Of the echinoderms living at the present time, five distinct types of organization are represented, hence there are five recent classes in the phylum.

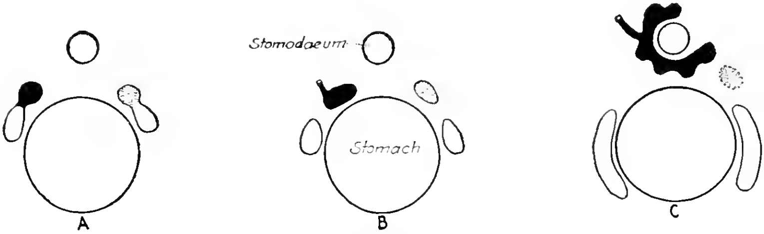

FIG. 82.—Diagrams to represent the formation of the rudiments of the coelom and of the water-vascular system in an echinoderm as viewed from the dorsal surface. Left hydrocoel rudiment in solid black; right stippled. *A*, constriction of hydrocoel rudiments from coelom; *B*, left hydrocoel acquires communication with exterior through stone canal; *C*, left hydrocoel encircles stomodaeum and buds off rudiments of five radial canals, coelomic pouches increase in size and surround the stomach. (*Orig.*).

The radial symmetry is not perfect, for some structures are distinctly bilateral in their arrangement. In the classification of Cuvier, the echinoderms were included along with the coelenterates within the group Radiata. The superficial resemblance in arrangement of parts seems to be an adaptation to the sessile habit, developed independently in these two groups, and does not indicate any phylogenetic relationship. Radial symmetry of Coelenterata is primitive, while that of the Echinoderma is only secondarily derived from a bilateral condition, as is evidenced by the marked bilaterality of the larvae. Details of the transformation from the one type of symmetry to the other will be discussed in detail.

Development of the Water-vascular System.—During early larval development, an echinoderm is distinctly bilateral in form (Fig. 84). Radial arrangement of the parts characteristic of the adult makes its appearance only following the formation of the mesoderm. Mesothelial sacs (Fig. 82) are formed as lateral outpocketings of the entoderm just as in embryos of many other groups. Both the right and the left mesoderm pouches undergo a constriction (*A*) which separates each into an anterior and a posterior sac. The posterior sacs continue to increase in size and ultimately form (*C*) the right and left coelomic cavities. The anterior sacs are the rudiments of the water-vascular system and are termed the hydrocoel sacs. The left hydrocoel acquires communication with the body wall through a tubular outgrowth (*B*), which becomes the stone canal of the water-vascular system. The right hydrocoel fails to develop but remains vestigial and finally disappears. The entire water-vascular system is thus formed from the left hydrocoel. As it increases in size, it encircles the esophagus of the larva and becomes the ring canal of the vascular system. Five radial pouches extend outward from this ring canal and as they increase in length they become recognizable as the radial vessels one of which passes along each arm of the adult. The water-vascular system thus has its origin from one of the mesodermal pouches of a bilaterally symmetrical larva which in later development assumes a radial arrangement of its parts.

The skeletal system is one of the most characteristic features of the echinoderms. Though details of arrangement and extent of development are highly variable, certain of the plates are fairly constant in their fundamental relations throughout a number of classes. The skeletal plates have their origin in the mesoderm and lie near the surface of the body directly beneath the outer body covering. Spines, frequently associated with these plates, suggest the meaning of the name Echinoderma which is Latin for spiny skin. In some instances (Echinoidea), the plates are rigidly articulated to form a continuous shell or test, unchangeable in form, within which most of the organs lie. In other classes (Asteroidea, Ophiuroidea, and Crinoidea), at least some of the plates are movable and permit of some flexibility in the parts which they cover. Among the Holothuroidea, the skeletal plates are so poorly developed that their presence in the soft body wall is restricted to minute discs and anchor-shaped bodies scattered through the tissues.

Other Organ Systems.—The locomotor and skeletal systems described above are the most distinctive of the systems found in echinoderms. There are no highly specialized organs for excretion, no definite circulatory system, and the nervous system represents a very low order of specialization. Excretion is accomplished through the action of amoebocytes in the coelomic fluid, and excretory products are liberated through gills variously located on or in the bodies of the several classes.

Like all higher Metazoa, the nervous system has its origin in the skin of the embryo, but in echinoderms it remains permanently associated with the skin and never migrates to an internal position affording greater protection. The nerve ring and its branches are of lowly organization, for there is no concentration of nerve cells to form a brain, and even ganglia are lacking. Echinoderms are well supplied with sense organs but most of them are of generalized type. Tactile organs are extremely diversified, including both ordinary and modified tube-feet and certain kinds of spines. Pedicellariae are highly sensory in addition to their function of defense. Eyes are found commonly in only the starfishes and the sea urchins. Other sensory organs will be mentioned under the various classes.

The tubular digestive system, with both mouth and anus, displays great diversity in the various classes.

The sexes are separate. The gonads are single in the sea cucumbers, but in other classes there are five gonads, each with its duct but with no other accessory organs, for the germ cells are liberated into the water for fertilization and subsequent development.

Researches on Echinoderm Eggs.—An enumeration of the researches that have been conducted upon the eggs of echinoderms would call for practically a complete history of the development of the fields of embryology and cytology. Starting with the pioneer descriptive embryology by Alexander Agassiz, we find some of the most detailed and most superbly illustrated studies on cleavage and on the larval forms that have been made for any group of animals. Hans Driesch used sea urchin eggs to test the powers of isolated cells of the embryo in the formation of a whole larva. Working on the eggs and sperms of starfish and sea urchins, Frank Lillie developed an explanation of why the sperm cell moves toward the egg cell. A specific substance called fertilizin is given off by the eggs into the water and serves as a chemical stimulus to direct the sperm cells to the eggs. The nature of the ultimate structure of protoplasm and the role of membranes in fertilization and in other life processes have been largely conducted upon echinoderm eggs. Jacques Loeb used sea urchin eggs in his carefully devised experiments on parthenogenesis to determine the factors that induce eggs to undergo cleavage without fertilization. These are only samples of the hundreds of researches in which the germ cells of echinoderms have played an important part in developing our ideas of living matter.

Orientation.—The main axis of the body extends between the oral and aboral poles. This arbitrary morphological orientation is frequently not in accord with the natural or physiological orientation as determined by the natural position of the body of the living animal. In Asteroidea, Ophiuroidea, and Echinoidea the oral surface is ventral in position, while in the Crinoidea the mouth is directed upward, and in the Holothuroidea the chief axis is parallel to the surface on which the animal rests. Typically, the parts of the body are arranged in radial manner about the main axis. In most echinoderms, the ambulacral system occupies certain radial regions of the body where the skeletal plates are perforated for the tube feet. These regions are designated the ambulacral areas, while the plates between the ambulacral areas constitute the interambulacral areas. Many of the echinoderms have on the oral and aboral surfaces series of plates which seem to be constant enough in their appearance in the various groups to be considered homologous.

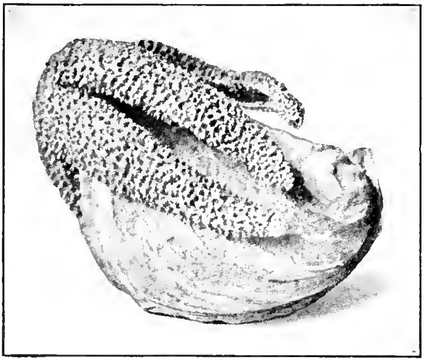

FIG. 83.—Starfish devouring an oyster. (*From Linville, Kelly, and Van Cleave, General Zoology*).

The crinoids and the extinct blastoids and cystoids are sedentary. Correlated with this habit, they possess a stalk of attachment which is a prominent morphological character in these groups. Recognition of this character is expressed in the establishing of two subphyla: the Eleutherozoa, which lack a stalk, and the Pelmatozoa, which characteristically carry a stalk.

Economic Importance.—Starfishes are among the worst enemies of the oysters (Fig. 83) and cause great losses in that industry. Most of the other echinoderms have little direct economic importance. They feed chiefly on seaweeds, and in turn some species serve as food for fishes.

SUBPHYLUM ELEUTHEROZOA

The echinoderms which are devoid of a stalk and are consequently capable of free locomotion have been assembled within the subphylum Eleutherozoa. The common starfishes (Asteroidea), the brittle stars and serpent stars (Ophiuroidea), the sea urchins and sand dollars (Echinoidea), and the sea cucumbers (Holothuroidea) are the classes included within this subphylum.

Class Asteroidea

The Asteroidea are the common starfishes. In these, the body is composed of a central disc from which usually five arms radiate. Arms may occur in multiples of five, though a few species fail to adhere to the pentagonal form. In the species which have more than five rays the extra rays are commonly added after the larva has metamorphosed to a five-rayed condition. New rays continue to bud off between the older ones until more than twenty rays are found in full-grown individuals of a number of species. A sharp differentiation of arms and disc is wanting in the cushion stars. The coelomic cavity of the disc is continued into the rays and many of the viscera thus extend into the arms. The mouth occurs on the ventral surface, in the center of a membrane called the peristome. Along the oral surface of each ray extend the tube feet, which are confined to a depression called the ambulacral groove.

Starfishes are found in all the oceans and at all depths. They dwell on the bottom, though they frequently crawl onto submerged piles and wharves. Many species live wholly in deep water, while others are readily observed in the tide pools.

Arrangement of Plates.—Each skeletal plate of the ambulacral grooves is provided with notches in the margins which articulate with other ambulacral plates. The notches in adjacent plates coincide, so the opening for each ambulacrum is between two plates. The ambulacral pores thus formed are in parallel rows. Distally, each double row of ambulacral plates terminates in a single ocular plate. This is so named because of the sense organ which it bears. The rigid body of a dried or preserved specimen gives little idea of the powers of movement possessed by the arms of the living starfish. The plates are articulated and their movements are controlled by body muscles in a manner which permits of considerable flexibility and freedom of movement in the arms. Laterally, yet on the oral surface, the ambulacral plates are bordered by a row of interambulacral plates which usually bear movable spines. A series of less regularly arranged adambulacral plates edges each row of interambulacrals.

The aboral surface of each arm is made up of a series of plates of considerably variable arrangement in different members of the group. The disc of the Asteroidea lacks the regularity in arrangement of its plates so characteristic of some other classes of echinoderms. The madreporite is the only conspicuous plate which is constant in position, and even this is variable in some species, for in these more than one madreporite occurs. Both the disc and the rays are typically covered with scattered spines. The areas between these spines are ciliated and bear numerous, small, hollow filaments, the branchiae or gills, which are direct continuations of the coelom. Through the thin walls of these gills the body fluids are able to carry on the respiratory process.

Pedicellariae.—Surrounding the body spines and scattered over the general surface of the body, there are frequently minute pincher-like organs called pedicellariae. Each of these is a small calcareous organ at the end of a strongly muscular stalk. In various species, these differ in form though two types are commonly found. In one type, the two jaws of the pinchers are articulated at their bases with a separate small calcareous body, while in another type the two jaws cross each other at their bases and continue beyond the crossing in handle-like processes where the muscles for operating the jaws are attached. Pedicellariae serve to remove small foreign bodies from the skin of the starfish and probably also serve as protection against small organisms which might attack the body of the starfish.

Plates of the Disc.—The five genital plates, which are located interradially on the dorsal surface of the disc, are perforated by the external openings of the gonoducts. The five pairs of gonads lie within the coelom at the bases of the arms. One genital plate is in most instances enlarged and perforated by numerous pores which serve for the entrance of water into the water-vascular system. In some instances, this sieve or madreporite is not single but occurs as two or more plates.

Symmetry.—In the typical condition of a single madreporite, the eccentric position of this organ is the most conspicuous external evidence of deviation from the radial type of symmetry. Since a plane passing through the madreporite and through the arm on the opposite side of the disc bisects the body, the animal is in reality bilaterally symmetrical. For convenience of reference, the arm opposite the madreporite is called the anterior arm or ray. This, and the two adjacent rays, constitute the trivium, while the two remaining rays, between which the madreporite is located, comprise the bivium.

The digestive system opens to the exterior through the ventral mouth. Small objects are ingested through the mouth; but because of the small size of the peristome, large objects cannot be taken into the body. Mussels and oysters (Fig. 83), which serve as food for the starfish, are digested outside the body through the peculiar provision which admits of the starfish everting the stomach through the mouth opening. The everted stomach surrounds large food masses and, after digesting them, is again drawn through the mouth opening into the body. A rather conspicuous constriction divides the stomach into dorsal and ventral chambers. The mouth opens directly into the ventral or cardiac chamber of the stomach while dorsal to this lies the pyloric chamber. From the cardiac chamber, a gastric pouch extends into each ray. A pair of hepatic ceca, occupying much of the space within each ray, communicate by a common duct with the pyloric chamber near the base of each arm. An intestine of minute size leads from the pyloric chamber to the aboral surface of the disc where it either opens through an eccentric anus or ends blindly. Small, branched ceca are given off from the intestine in some starfishes. The fact that these ceca undergo rhythmic pulsations suggests the possibility that they may have a function as respiratory organs.

The water-vascular system is a series of tubes or canals of which the main parts comprise a ring canal surrounding the esophagus and a series of radial vessels given off from this, one to each arm. The ring canal communicates with the exterior by way of a stone canal which opens through the madreporite. In many Asteroidea, there is but a single madreporite and stone canal, but in some two or more of these structures are present. This latter condition is frequently associated with the powers of asexual reproduction. Small tufts of tubules called Tiedemann's bodies, interradial in position, are connected with the ring canal. Within these organs the amoeboid lymph cells which occur in the water-vascular system are formed. In addition, long-stalked vesicles called Polian vesicles join the ring canal interradially in some forms of Asteroidea. To these, also, have been ascribed the function of lymph glands.

The longitudinal canal in each arm passes along the median line of the ventral surface just outside (that is, ventral to) the ambulacral plates. At the tip of each ray, the ambulacral canal ends in a single tactile organ. Most Asteroidea have four longitudinal rows of tube-feet in the ambulacral area of each arm, but in some (*e.g.*, Henricia) there are but two longitudinal rows. By opposite lateral branching, canals are given off along the course of the longitudinal canal and communicate with the tube-feet. In the typical condition of four longitudinal rows of feet, the two lateral branches arising from the same level on the longitudinal canal are of unequal length. This condition usually alternates in adjacent pairs, so on each side of the longitudinal canal a long and a short transverse canal alternate. Thus the tube-feet fall into two parallel rows on each side of the longitudinal canal. Each ambulacrum is a muscular tube which, at its inner end, bears a muscular sac called an ampulla. By contraction of the walls of the ampulla, the fluid in the tube-foot is put under compression. Relaxation of the muscles in the foot permits the tube to elongate greatly. At the same time, the hydrostatic pressure causes a cuplike disc at the end of the foot to flatten, and in case the disc comes in contact with some object it adheres to it. Shortening of the tube is accomplished by allowing the fluid to turn back into the ampulla. When several feet become attached to an object, by their concerted contraction they drag the whole body of the starfish, and in this manner locomotion is accomplished.

The Sexes and Reproduction.—Though starfishes are of separate sexes, there are no external features which distinguish the sexes. Some species have been found to reach maturity in less than a year. The gonads increase in size with the approach of the breeding season. Mature eggs are discharged directly into the water. Sperm cells, discharged by sexually mature males, are likewise set free in the water, where fertilization takes place. Total, equal cleavage gives rise to a free-swimming ciliated blastula. Following gastrulation, the rounded body changes form (Fig. 84 *A*-*D*) and becomes known as the bipinnaria with a number of ciliated lobes. In later development, the bipinnaria becomes further modified in form and is known as a brachiolarian larva (Fig. 84 *E*). Each of these larval forms is distinctly bilaterally symmetrical, yet by an intricate metamorphosis the radial symmetry of the adult starfish is superimposed. In some asteroids, development has become modified, resulting in the elimination or reduction of the free larval stages. In some instances (*Leptasterias hexactis*), the female carries the eggs and embryos in a brood pouch until the fully formed young are able to shift for themselves. Powers of regeneration are developed in an extreme degree among the Asteroidea.

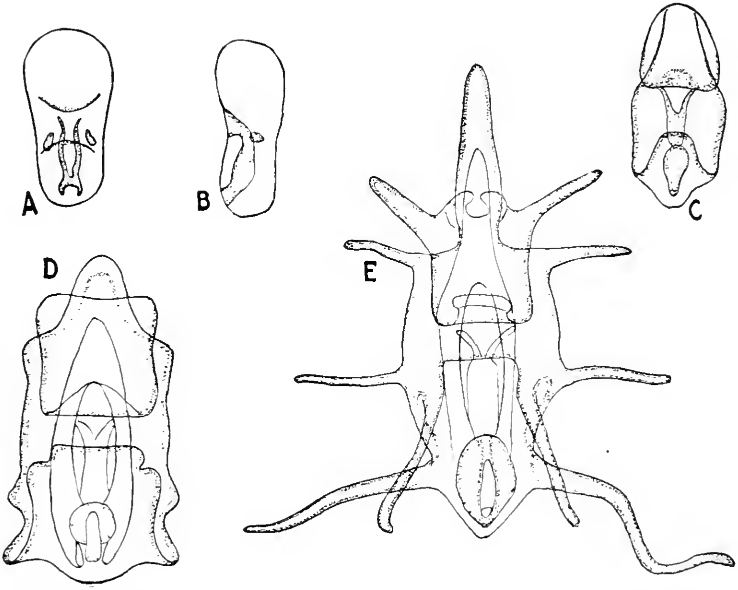

Fig. 84.—Development of starfish larvae. *A*, early larva, oral view; *B*, the same, lateral view; *C*, more advanced larva, oral view showing extent of ciliated bands; *D*, bipinnaria larva; *E*, larva in brachiolarian stage. (*Redrawn from A. Agassiz*).

The nervous system consists of a circumoral nerve ring with a radial nerve extending along each ambulacral area. The system is peculiar in that it retains a superficial location in the ectoderm. Minute branches are given off to the various organs. There are no centralized ganglia in this system but experiments indicate that the nerve ring serves as a coordination center.

Musculature.—Though there are no conspicuous muscle bundles encountered in the dissection of a starfish, muscle tissues play exceedingly important roles in the structure of this animal. The walls of the tube-feet are largely composed of muscle. Minute muscles manipulate the pedicellariae. Spines are moved, and the skeletal plates are articulated, by muscles. The stomach is everted by muscular action, and special bundles of muscles retract it. Movements of the arms are produced by delicate sheets of muscles just beneath the dorsal wall of each ray.

The common starfishes belong to the genus Asterias. Ctenodiscus has a pentagonal body without conspicuous arms. Solaster and Pycnopodia have numerous arms. Henricia is a northern genus with only two rows of feet on each ray.

Class Ophiuroidea

The brittle stars or serpent stars have highly flexible arms radiating from a central circular or pentagonal disc. Though superficially resembling the asteroids, they differ radically from them in details of organization. The ambulacral system is much reduced and fails to function in locomotion but serves rather as a series of tactile organs. Writhing movements of the arms produce locomotion. The ambulacral plates are withdrawn into the interior of each ray where they are fused together to form a jointed rodlike structure the units of which are called the vertebrae. Both internally and externally, each arm is composed of a large number of similar segments. In the basket stars, the arms become finely branched. The digestive system is confined to the disc and lacks an anus. Bursae are thin-walled sacs, leading inward from the ventral surface of the disc, which serve for respiration and into which the gonads open.

On the oral surface of the disc, five interradial groups of plates project in toward the mouth to form the jaws which are operated by muscles for masticating food or for selecting food particles. At the base of each jaw there are usually three plates, a large oral shield and two smaller adoral shields. One of the oral shields becomes modified to form the madreporite.

Development involves a bilaterally symmetrical larva (Fig. 85) known as the pluteus or, better, the ophiopluteus.

Ophiura, Ophiopholus, and Amphioplus are typical genera of brittle stars. Astrophyton is the basket star with its finely divided arms.

Class Echinoidea

The sea urchins and sand dollars are usually globular, hemispherical, or disc-shaped. The shape, which is unalterable in any given species, is determined by the arrangement of the skeletal plates. These are immovably united to form a firm shell or test.

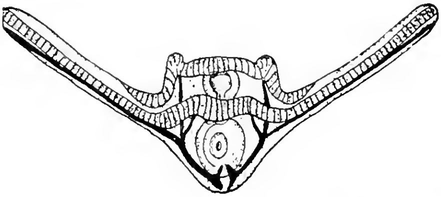

FIG. 85.—Ventral view of young ophiopluteus of *Ophiothrix fragilis*. (*Redrawn from MacBride, courtesy of Macmillan Co.*).

Spines usually cover most of the test except at the oral and aboral poles. Surrounding the mouth, there is a circular opening where the plates are replaced by a membrane termed the peristome. Normally, the anus occurs at the pole opposite the mouth in a region called the periproct, while in some instances it occurs on the margin of the disc. The skeletal plates are arranged in meridional bands part of which bear openings through which the ambulacral feet protrude and are therefore termed ambulacral areas. The non-perforated plates between two adjacent ambulacral areas are designated as an interambulacral area.

Each ambulacral area terminates at the periproct in a single ocular plate homologous to the ocular plate at the end of each arm in the Asteroidea. A series of genital plates alternate with the ocular plates around the periproct, and each marks the termination of an interambulacral area. One of the genital plates is modified to serve as a madreporite.

In its fundamental arrangement, the water-vascular system is essentially like that described for the asteroids. From the madreporite, the stone canal leads into the circumesophageal vessel. Interradially, five Polian vesicles communicate with the circular canal and a radial vessel passes along each ambulacral area on the inner surface of the test. In the ambulacral plates, there are two perforations for each tube-foot. Through one of these, the lateral branch of the radial canal passes to the tube-foot and through the other the foot is in communication with its ampulla. In many forms, the ambulacra are aided in the locomotor process by the highly developed mobile spines which are articulated with the surface of the test and are operated by special muscles.

One of the most characteristic structures of the echinoid is the Aristotle's lantern. From the oral surface of the animal, the five teeth with which this organ is supplied are visible in the center of the peristome. The main part of the lantern lies within the body cavity. The teeth are at the tips of a set of jaws which are operated by muscle bundles attached to a calcareous framework of intricate pattern surrounding the mouth cavity. From the aboral surface of the lantern is given off a short esophagus. This in turn leads into the stomach, a part of which is greatly dilated and flattened and extends almost around the body. The intestine bends backward in the opposite direction from that of the course of the stomach and in the case of the urchins passes to a median dorsal anus, while in the sand dollars it passes along the posterior interambulacrum to an anal opening on or near the margin of the disc. The siphon occurs as a branch from the esophagus which parallels the course of the stomach for some distance, then reunites with it. It seems probable that this heavily ciliated tubule may have a respiratory function and may also be of service in washing refuse from the intestine.

When a sea urchin is opened for dissection by removal of the aboral wall of the test, the gonads are usually the most conspicuous structures first encountered. These are five large masses, interambulacral in position, connected at the aboral pole by a band of tissue termed the genital rachis. From each gonad a gonoduct passes to the opening in the adjacent genital plate. The larva (Fig. 86 *A*) which results from the cleavage and later development of the fertilized egg is termed a pluteus. Since the term pluteus is also applied to the larva of Ophiuroidea, the name echinopluteus is frequently utilized.

Respiration is performed to a considerable extent by the water-vascular system. In some echinoids, only part of the tube-feet are ambulatory while the remaining ones lack the sucking disc and seem to have chiefly respiratory and tactile functions. A pair of branched, filamentous gills occurs on the margin of the peristome opposite each interambulacral area of the sea urchin. The siphon, as already mentioned, is also thought to aid in respiration.

The nervous system is fundamentally the same type as that described for the Asteroidea, comprising a nerve ring from which five primary branches are given off. In addition to pedicellariae, there are small organs known as sphaeridia scattered over the body surface of many species. These are thought to function as organs of equilibrium. Specially modified tube-feet on the peristome are associated with the sense of taste.

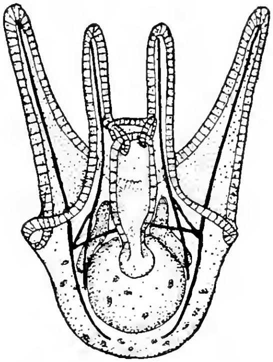

FIG. 86 A.—Dorsal view of young echinopluteus of *Echinus esculentus*. (*Redrawn from MacBride, courtesy of Macmillan Co.*).

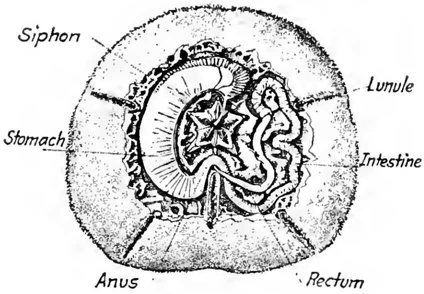

FIG. 86 B.—Anatomy of keyhole urchin, *Mellita pentapora*. (*After Coe*).

Arbacia, Strongylocentrotus, and Toxopneustes are genera of the common sea urchins. The tropical genus Clypeaster includes some of the largest urchins. This, with the sand dollar (Echinarachnius) and the keyhole urchin (Mellita, Fig. 86 *B*) represents the order Clypeastroidea. Members of the order Spatangoidea, of which Spatangus is an example, are usually more or less heart-shaped. There are several groups of echinoids which are known only from fossil remains.

Class Holothuroidea

The sea cucumbers are elongated echinoderns lacking a definite skeleton, with a mouth at one extremity surrounded by a circle of branched tentacles (Fig. 87) and an anus at the opposite extremity. Since the mouth end goes forward in locomotion, it is frequently called the anterior extremity in the holothurians. Typically, the body is five sided and on each side bears a double row of tube-feet. In some species, the three sides constituting the ventral surface have the tube-feet more highly developed than they are on the two dorsal ambulacral areas. Some few forms have feet irregularly scattered over the body surface, while some burrowing species lack feet. The body wall is highly muscular. The alternate use of longitudinal and circular muscles enables the cucumber to creep like a worm. Though there is no continuous skeleton, the body wall is rather firm. This is due in large measure to the presence of microscopic calcareous plates embedded in the tissues. The form of the plates is highly variable in different species and they serve as important features in classification. In some species, a calcareous ring of ten plates surrounds the esophagus and serves as a support for the tentacles. In a few forms, Psolus for example, the body is encased in hard scales or plates.

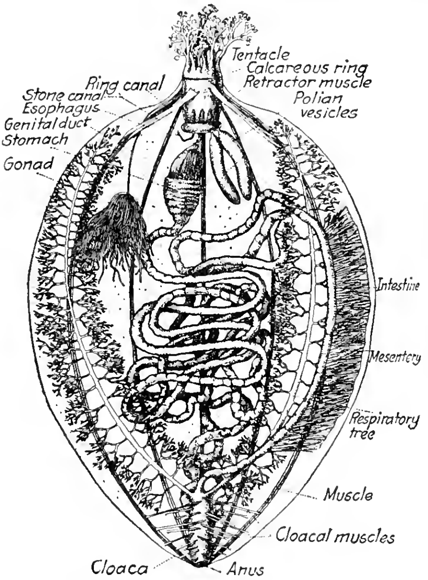

FIG. 87.—Anatomy of a holothurian, Thyone. (*After Coe*).

The ring canal of the ambulacral system is located around the esophagus just behind the tentacles. From the ring canal the radial canals pass to the posterior extremity of the body. In the first part of their course, they run anteriorly and give off branches to the oral tentacles which are in reality highly modified tube-feet. One or more Polian vesicles are frequently present. The stone canal, instead of opening to the exterior, bears one or more madreporites which open into the coelom. As in other echinoderms, the water-vascular system is rather closely paralleled by a blood-vascular system the vessels of which form extensive anastomoses on the alimentary canal. The nervous system is of the type previously described for other echinoderms, but the quick responses given by the holothurians seem to indicate that the nervous and sensory organs are more highly developed than in other members of the phylum.

The digestive canal is held in definite position by mesenteries. The esophagus passes into a stomach which is followed by a tubular intestine. The main course of this tube is, in most species, posterior in the median dorsal interradius, then anterior in the left ventral interradius, and finally posterior in the right dorsal interradius to the cloaca. From the walls of the cloaca, there are usually a pair of minutely branched respiratory trees which, by the muscular action of the cloaca, are filled with water and serve as respiratory organs.

A genital pore occurs in the anterior region of the body. This is the opening of the single, much-branched gonad. In development of the embryo, a larval form known as an auricularia is produced. Sea cucumbers have marked powers of regeneration. Individuals may automatically eject much of the internal organs and yet be able to regenerate them.

SUBPHYLUM PELMATOZOA

The Pelmatozoa are echinoderms which, during the whole or at least the early stages of their existence, are fixed by a jointed, flexible stalk or are attached by the dorsal or aboral surface of the body. The principle organs are enclosed in a cup-shaped or spherical test, called the calyx, the walls of which contain a system of calcareous plates and ambulacral or food grooves leading to the mouth. The crinoids are the only living examples of this group, which also includes the extinct Cystoidea and Blastoidea.

Class Crinoidea

The crinoids, or sea lilies, are usually provided with a long stalk or column at one end of which is attached the calyx with its movable arms. In numerous forms, lateral projections called cirri are borne along the stalk. In those instances where the stalk is lacking, the cirri are frequently attached directly to the base of the calyx. Occasionally, there are free-swimming crinoids, but in their development these pass through a fixed stage (Fig. 88), thus giving evidence that the free condition is not primitive in members of this class. Of present-day forms, most are restricted to the greater depths of the ocean. Though distinctly local in their distribution, they occur in great numbers, as must have also been the case in past geological times when they were abundant enough to form beds of rock of considerable thickness. The joints of the stems are very conspicuous in many limestone deposits.

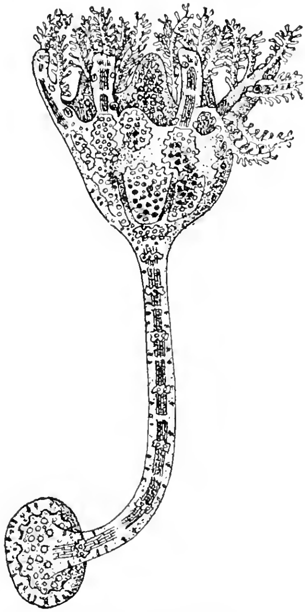

FIG. 88.—Fixed larva of a crinoid, *Antedon rosacea*. (*After Carpenter*).

The calyx is usually a globular or cup-shaped capsule which holds the more important internal organs. This cup is formed of two or more circles of plates. The ring of plates next to the point of attachment to the stalk or column and extending upward to the projections of the arms comprises the base of the calyx, within which there may be either a single circle of plates called the basals or two circles. In this last instance, the plates next to the stalk are termed the infrabasals, while the others are called the basals. A series of plates designated as the radials follows the cycle of basal plates. An arm has its origin with each radial plate. The arms are formed of a series of plates continuous with the radials and may be either simple or branched. In some of the more highly organized fossil forms, and in all of the recent crinoids, the arms are furnished with pinnules alternating on opposite sides. In these, the gonads are borne. Arms and pinnules are traversed on the ventral surface by an ambulacral groove at the bottom of which there is a tubular extension of the coelom.

That part of the calyx which lies between the bases of the arms may be either in the form of a membrane with thin calcareous ossicles embedded in it or in the form of a series of plates making a continuous disc. In or near the center of this area, the mouth opening (Fig. 89) is plainly discernible, while in an eccentric interradial position the anus usually occurs. The grooves mentioned in the description of the arms continue across the oral disc to the mouth opening. In the case of distinctly dichotomously branched arms, there may be but a single groove across the disc to represent each pair of arm branches. The grooves are ciliated and serve as channels along which food particles are borne to the mouth opening. Ambulacra line the margin of the groove along each arm but they function as tactile organs for they lack suckers and ampullae. The nervous and circulatory systems follow the course of the ambulacral system in muchthe same manner as already described for other echinoderms.

In its normal position, the crinoid directs the oral surface and tentacles upward. Its position is thus the reverse of that normally assumed by the echinoids, asteroids, and ophiuroids.

The full course of development is known for but a single species, *Antedon rosacea*. The germ cells are dehisced from the pinnules of the arms to the outside of which the eggs become attached. Fertilization of the heavily yolk-laden eggs is followed by cleavage resulting in the formation of a free-swimming ciliated larva, in which there is no communication between the mouth and the stomach. In this respect, the larva resembles that of some of the highly modified larvae of echinoderm groups rather than the typical free-living echinoderm pluteus, auricularian, or bipinnarian. Calcareous plates begin to make their appearance early in the development of the larva. After a few days of free-swimming existence, the larva becomes fixed (Fig. 88) and undergoes a complicated series of changes which lead to the differentiation of calyx and stalk. The larva in this condition is said to be in the Pentacrinus stage. In later development, there is considerable resorption of skeletal plates characteristic of the larva. Ultimately, the animal becomes detached from the stalk and capable of independent movement.

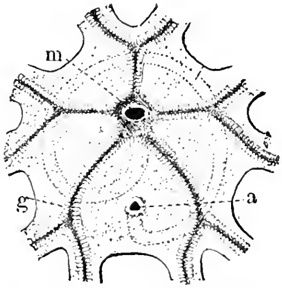

FIG. 89.—Oral area of crinoid (Antedon), showing by dotted lines the course of the intestine from mouth (*m*) to anus (*a*); *g*, ciliated grooves leading from arms to mouth. (*After Kingsley in Hertwig's Manual, courtesy of Henry Holt and Co.*).

Outline of Classification

Phylum Echinoderma.—Triploblastic; coelomate; radially symmetrical; calcareous plates in skin; water-vascular system; marine.

- *A*. **Subphylum Eleutherozoa.**—Echinoderms without stalk.
  - **I. Class Asteroidea.**—A disc with five radiating arms; arms not sharply set off from disc; ambulacral feet in grooves on oral surface.
    - **1. Order Forcipulata.**—Marginal plates inconspicuous; stalked pedicellariae; tube-feet with sucking discs. *Asterias, Pisaster, Evasterias, Leptasterias, Orthasterias, Astrometis, Pycnopodia.*
    - **2. Order Spinulosa.**—Marginal plates inconspicuous; pedicellariae wanting or at least not stalked; tube-feet with sucking discs. *Henricia, Solaster, Crossaster, Asterina.*
    - **3. Order Phanerozonia.**—Marginal plates large; pedicellariae usually sessile or in pits; tube-feet pointed or with discs. *Ceramaster, Mediaster, Dermasterias, Linckia, Astropecten, Luidia. Ctenodiscus.*
  - **II. Class Ophiuroidea.**—Arms slender, sharply set off from disc; no ambulacral grooves.
    - **1. Order Ophiurae.**—Arms unbranched. *Ophioderma, Ophiura, Ophionereis, Ophiothrix, Ophiopholis, Amphioplus.*
    - **2. Order Euryalae.**—Arms branched. *Astrophyton, Gorgonocephalus.*
  - **III. Class Echinoidea.**—No arms; rigid test; globe or disc-shaped.
    - **1. Order Regularia.**—Test nearly globular; mouth and anus in dorsoventral axis; large spines; Aristotle's lantern present. *Arbacia, Strongylocentrotus, Toxopneustes.*
    - **2. Order Clypeastroidea.**—Test more or less flattened; anus at margin of test; spines very small; Aristotle's lantern present. *Mellita; Clypeaster, Dendraster, Echinarachnius.*
    - **3. Order Spatangoidea.**—Test heart-shaped; mouth and anus eccentric; no Aristotle's lantern. *Spatangus, Lovenia.*
  - **IV. Class Holothuroidea.**—No continuous skeleton; plates small, scattered in skin; elongate; cylindrical; mouth surrounded by a circle of tentacles.
    - **1. Order Pedata.**—With tube-feet. *Thyone, Cucumaria, Psolus, Stychopus.*
    - **2. Order Apoda.**—Without tube-feet. *Synapta, Synaptula, Leptosynapta.*
- *B*. **Subphylum Pelmatozoa.**—Stalked at least during part of life.
  - **I. Class Crinoidea.**—Temporarily or permanently attached by a stalk; five feathery arms radiating from a cuplike disc. *Antedon, Pentacrinus, Rhizocrinus, Metacrinus.*
  - **II. Class Cystoidea.**—Fixed, stalked, or sessile; varying number of unbranched arms; wholly fossil. Lower Silurian to Carboniferous.
  - **III. Class Blastoidea.**—Stalked; arms lacking; wholly fossil. Upper Silurian to Carboniferous.
  - **IV. Class Edriasteroidea.**—Theca of irregular plates; arms unbranched and lying on theca; wholly fossil. Cambrian to Carboniferous.

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(See general references at close of Chapter I)

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CHAPTER XII

PHYLUM MOLLUSCA

The phylum Mollusca includes essentially bilaterally symmetrical, unsegmented Metazoa in which the coelom has been reduced by invasion of connective tissue and of musculature until only the pericardial cavity and the lumen of the gonads represent its remains. The typical bilateral symmetry is frequently lost or obscured through secondary coiling or torsion of parts of the body. Head, visceral mass, foot, mantle, and shell are characteristic structures, but in many instances one or more of these are lacking and all are subject to great variability in the various groups. A rasplike organ known as the radula is associated with the mouth of most molluscs except the Acephala. This is a bandlike membrane bearing numerous cross rows of chitinous teeth for rasping off food material.

A modified trochophore, termed the veliger, is a larval form common to all of the major groups of molluscs, though in the modified development of some forms it has been suppressed. A larval organ, known as the shell gland, is typical though not always retained. Reproduction is exclusively sexual.

The usual means of locomotion is by crawling on an unpaired foot. Powers of locomotion are lost in some sessile forms and in still others swimming is made possible through modifications of various structures. The mantle, when present, secretes the shell and bounds a cavity which may either contain the gills or function directly as a lung. The central nervous system is typically composed of three pairs of ganglia of which each pair is associated with a special sensory organ. The cerebral ganglia communicate with the eyes, the pedal ganglia with the statocysts, and the visceral ganglia with the osphradia or olfactory organs.

In size, Mollusca range from minute individuals barely visible to the eye to some of the largest known invertebrates. One of the giant squids reaches a length of 18 feet.

The Mollusca have continued as important and conspicuous components through all the geological periods in which animal remains have been found.

In detail of structure, the members of the various classes differ so greatly that morphology will be discussed separately under the headings for the five classes.

Class Amphineura

The Amphineura seem to represent the most primitive group of the Mollusca. The chitons are the typical representatives. They are strictly marine, living at all depths but occurring in special abundance in shallow water where they move freely over the rocks by the action of the powerful foot. The head region is not sharply set off. There are no tentacles and usually no eyes. The eight transverse plates with which the dorsal surface is covered overlap like the tiles on a roof. The arrangement of the plates rather strongly suggests origin from segmented ancestors, though present-day molluscs lack metamerism. The plates are so articulated that the animal may roll into a ball. Sometimes, they are completely covered by the mantle, but more commonly the mantle only partially covers the plates and extends beyond them along the sides of the body where it is covered with spines. Mantle folds on the ventral surface produce a series of small gills or ctenidia. Nerves penetrate the skeletal plates and in the outer, less dense layer of each plate there are frequently small sense organs called aesthetes and in some instances eyes. The mouth and anus are located near the anterior and posterior extremities of the body on the ventral surface. The internal organs are disposed bilaterally along the median plane marked off by the oral-anal axis.

All representatives of this class are marine. The oval or flattened body, which is bilaterally symmetrical, may or may not have a differentiated head. The nervous system consists of a pair of cerebral ganglia connected by a circumesophageal ring and four longitudinal nerve cords which pass, two laterally and two ventrally, through the body. There is no centralization of the nerve cells in these cords to form ganglia. In many instances, the longitudinal cords are connected by numerous cross-commissures.

Some amphineurans are simpler in structure than the chitons. These wormlike forms without shells occur at fairly great depths of the ocean where they burrow in the mud or sand or are associated with various colonial coelenterates. The mantle covers the body completely and bears calcareous spicules instead of producing a definite shell. The foot is lacking and in its place there occurs a longitudinal, ventral, ciliated groove. The evidence seems to indicate that this is a degenerate rather than a primitive type of amphineuran. There are only a few genera of which Chaetoderma, Neomenia, and Dondersia are characteristic.

Class Acephala (Pelecypoda)

As is indicated by the name, the members of this class have no specialized head. Many writers on the Mollusca use the name Pelecypoda for the members of this class. This alternative name refers to the hatchet-shaped foot. The Acephala have a shell composed of two lateral valves. Typically the hinge of these valves is dorsal, though its position is modified in many instances. On the valves are usually found conspicuous concentric lines, known as the lines of growth. The umbo, a slight prominence on the dorsal surface around which the lines of growth are distributed, is the oldest part of the shell. An elastic hinge ligament tends to hold the margins opposite the hinge gaping open. The valves of the shell are closed only by the contraction of adductor muscles which extend from one valve to the other through the body. Immediately within the protective shell lie the right and left lobes of the mantle, secretions from which form the shell.

While the entire animal is usually capable of withdrawing completely into the shell, the development of the siphon in some of the burrowing clams is so great that the siphons cannot be pulled into the shell. In the peculiar wood-boring shipworm (Teredo) the shells are diminutive and are modified for boring wood, while protection of the body which is ordinarily afforded by the shell is given by the wooden tunnel within which the worm-shaped animal dwells permanently. Submerged timbers and wooden ships are frequently completely destroyed by the tunnels of shipworms. Another marine group of peculiar habits is that which comprises the rock borers. In these (pholads), the front edge of the shell is used as a rasp to bore into solid rocks.

The members of this class contain many forms of direct economic importance. The oysters, scallops, and clams are used as food. Shells of the fresh-water mussels and some marine forms are used in the manufacture of buttons. The members of this class play important roles in the food chains of organisms of both fresh water and seas.

Members of the class Acephala show extreme range of size. Many species of the finger-nail shells of the genus Pisidium are under 2 mm. in length, while the giant Tridacna from the Indian and Pacific oceans reaches a length of more than a meter.

Structure of the Shell.—The shell is covered externally by a thin, organic cuticula. The main bulk of the shell is composed of calcium carbonate. In some species, the innermost layer of the shell is composed of thin layers arranged parallel to the surface. These lamellae are minute enough to diffract the light and thereby produce an iridescence. The nacre, or mother-of-pearl, as this layer is termed, occurs in many fresh-water mussels and is especially conspicuous in the pearl oyster (Meleagrina). One type of pearls is formed by the deposition of nacre about foreign objects which have been introduced between the shell and the mantle. Many of the Acephala have a non-iridescent, porcelaneous lining of the shells. A short distance from the margin of the shell the mantle is joined to it by a line of muscle fibers called the mantle muscle. The line on the shell formed by the attachment of this muscle is termed the pallial line.

Adductor Muscles.—In many of the Acephala there are large adductor muscles, one attached near the anterior and the other near the posterior end of the shell. In the common sea mussels (Mytilus) the anterior adductor is greatly reduced so that closure of the shell depends chiefly upon an enlarged posterior adductor. In the oysters and pectens there are two adductors in the larva of which the anterior later entirely atrophies, leaving a single large posterior adductor near the middle of the shell.

The Siphons.—When the shell is nearly closed, the margins of the two mantle lobes are pressed together tightly except in the posterior region. Here the mantle lobes remain lightly separated to form two openings termed the siphons. Of these, the ventral or inhalant siphon is for the inflow of fresh water into the mantle chamber and over the gills, while the dorsal or exhalant siphon discharges water from the mantle cavity and carries the feces along with the water. The margins of the mantle adjacent to the siphons are, in some instances, fused together, thus leaving the siphons as permanent openings. The mantle in the region of the siphons frequently elongates and produces a siphon tube which projects beyond the shell. Both siphons may be united in a single tube or there may be two tubes entirely or only partially separated.

The Gills and Palpi.—The mantle lobes overlie the gills which are typically paired structures on each side of the body. In the most primitive Acephala the gills are featherlike structures similar to those found in the Gastropoda. Gills of all of the higher Acephala are derivable from this simple condition. As the flattened filaments elongate, the distal ends of the filaments become recurved and thus each filament becomes V-shaped. In the sea mussels the gill filaments may be either independent or united by interlocking cilia, while in the fresh-water bivalves and the marine clams the walls of adjoining filaments become grown together to form a continuous sheet.

Cilia covering these gills bring water currents through the siphon into the mantle chamber thereby making respiration possible and at the same time bringing into the mantle cavity microorganisms and other organic matter which finally enter the mouth and serve as food. A pair of small flaplike structures, the labial palpi, surround the mouth opening and aid in the selection of food.

The Foot.—The foot is highly characteristic in the Acephala, though in some instances, as in the oyster, it has become degenerate. In the adult stage the oyster loses all power of locomotion, for the left valve of the shell becomes permanently attached to a rock or some other object. Among the scallops (Pecten) the foot is degenerate, but locomotion is accomplished by a rapid snapping movement of the shells produced by the single, heavy adductor muscle. The foot is, typically, a hatchet-shaped muscular organ which, by protrusion through the gaping valves of the shell, becomes fixed in the sand or mud, then by contraction of the muscles the animal is drawn a slight distance forward. Posterior to the foot, there frequently occurs a byssus gland secretions from which form heavy silken threads by means of which permanent or temporary attachment is accomplished.

The visceral mass is a softer body, lying dorsal to the foot, within which various organs are located. As the name indicates, there is no head in the Acephala. The digestive system has its beginning in a mouth at the anterior extremity of the body, located between the small leaflike labial palpi. In the visceral mass, the digestive tube makes a number of coils and in most Acephala terminates in a rectum which passes through the pericardium and also through the ventricle. Gonads and liver occupy most of the visceral mass surrounding the alimentary canal. A gelatinous rod, called the crystalline style, frequently occurs in the stomach. Recent investigations seem to indicate that this organ aids in separating food from foreign particles and probably contains a store of enzymes for use in the digestive processes.

Circulatory System.—The heart, which lies in the dorsal part of the visceral mass, is surrounded by a pericardium and consists of a single ventricle and two auricles. A system of arteries carries the blood from the heart to the tissues, where they frequently terminate in sinuses. The veins which return the blood to the heart pass first through the excretory organ and then through the gills. Separate vessels supply the mantle with blood and return the blood directly to the heart without passing through the excretory organ or gills.

Excretory Organs.—The pair of nephridia characteristic of Acephala are frequently called the organs of Bojanus after their discoverer. They lie immediately below the pericardium. Each nephridium is a wide tube, bent upon itself, one end of which opens into the pericardial cavity and the other, non-glandular in structure, serves as a urinary bladder with its opening usually on a minute papilla into the inner cavity of the gill chamber. Another gland of excretory function, called Keber's organ, lies anterior to the pericardium into which it discharges.

Nervous System.—A pair of cerebropleural ganglia is located one on each side of the mouth near the base of the labial palpus. A transverse supraesophageal commissure connects this pair of ganglia. Two nerve cords originate in each cerebropleural ganglion and connect this ganglion with the two other nerve centers on each side of the body. One of these passes ventrally to communicate with the pedal ganglion, embedded in the muscles of the foot, and the other passes posteriorly to a region ventral to the posterior adductor where the parietal and viceral ganglia of the more primitive molluscs have become fused to form a single posterior ganglion.

Sense Organs.—There are but few highly specialized sensory organs. Statocysts are frequently found near the pedal ganglia, though they seem to have nerve connections with the cerebropleural ganglia. Patches of sensory epithelium called osphradia, and thought to have olfactory functions, are located near the base of the gills. The labial palpi and the edges of the mantle are highly sensory. The small projections from that part of the mantle which forms the siphons are especially sensitive to touch. Eyes (Fig. 90) are distributed over the margins of the mantle in some forms such as the scallops.

Reproduction.—Most of the Acephala are dioecious. In many of the marine forms the gonads discharge their germ cells directly into the water where they undergo fertilization and pass through cleavage and early larval development to form free-swimming larvae. In the fresh-water mussels, however, the eggs after discharge from the ovary are passed into brood pouches or marsupia located within the gills. Either in the marsupia, or en route to them, sperm cells, brought in with the water currents by way of the siphon, fertilize the eggs. Each egg undergoes cleavage to form a larva known as a glochidium (Fig. 91 *A-D*). This larval form is provided with a thin bivalve shell operated by a single adductor muscle. Other soft parts within the shell are not clearly organized except for the presence in some species of a "larval thread" of uncertain significance and of minute sensory hairs. The glochidia, when discharged from the

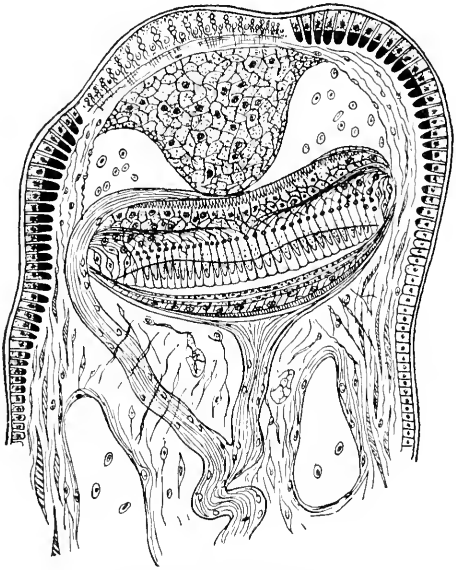

Fig. 90.—A section through an eye from the mantle margin of Pecten. (*Slightly modified from Patten*).

gills of the mother, are unable to continue development independently. Almost without exception the larval mussel must exist for some time as a parasite (Fig. 91 *E*) on the gills or fins of a fish. During this parasitic existence the glochidia undergo a metamorphosis and finally leave the host (Fig. 91 *F*) as juvenile mussels. Glochidia are frequently referred to as "hooked" or "hookless." In the hooked forms, the ventral margin of each shell bears a hinged hook. Glochidia of this type usually become attached to fins or scales of fishes (as in Lasmigona and Strophitus). Valves of the hookless glochidia are sometimes provided with small non-jointed spines (Fig. 91 *A*) as in the axe-head type or may be entirely devoid of spines (Fig. 91 *C* and *D*). Most of the hookless glochidia become attached to the gills of fish hosts. The fingernail shells are hermaphroditic and differ from the other fresh-water Eulamellibranchia in that the young are born alive and do not pass through a larval stage outside the body of the parent.

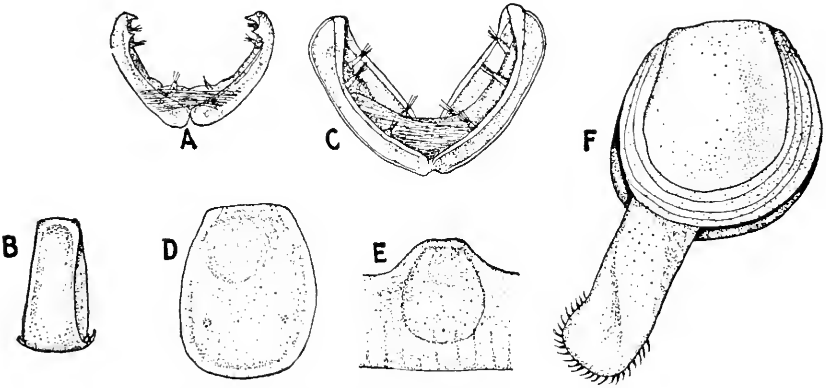

FIG. 91.—Development of fresh-water mussels. *A*, axe-head type of hookless glochidium of *Proptera alata*, anterior end view; *B*, lateral view of same; *C*, hookless glochidium (*Ligumia subrostrata*) posterior end view; *D*, lateral view of same; *E*, glochidium of *Actinonaias carinata* encysted in gill of rock-bass; *F*, young mussel, same species as *C*, one week after close of parasitic life, showing lines of growth beyond glochidial shell and protruded foot with its cilia. (*After Lefevre and Curtis*).

In the classification here adopted, the number and arrangement of the gills and of the adductor muscles serve as the chief characters for the recognition of orders. Some students of the Mollusca and paleontologists more frequently utilize a system of classification based largely upon hinge structure.

Class Scaphopoda

An external tubular shell, open at both ends and more or less curved, covers the body of the scaphopods. The shape of the shell is responsible for the common name tooth shell so frequently applied to members of this class. Jaws and radula are present but in the paired liver and general arrangement of the nervous system the Scaphopoda resemble the Acephala. Gills are wanting and the rudimentary heart possesses only a ventricle. The foot, which is rather long and conical, extends from the larger opening of the shell and bears two lateral lobes. Dentalium is a modern genus of this class all members of which are marine.

Class Gastropoda

The snails, limpets, slugs, and sea hares are examples of the Gastropoda. Representatives of this class usually have head, visceral mass, foot, and mantle, though in some instances one or more of these may be wanting. While most gastropods live in the oceans, many have become adapted to life in fresh water and some to terrestrial existence. A shell, when present, is composed of a single piece. In some snails, either a limy or a horny disc called the operculum serves for closing the opening when the animal is withdrawn into the shell but is not considered as comparable to a second valve. The foot is usually flattened so that it presents a large ventral surface upon which the animal crawls, but in many of the pteropods the foot is modified as a fin used for swimming. The head, which is located anterior to the foot, bears hollow tentacles, eyes either at the base or tips of the tentacles, and a mouth. The mantle covers the dorsal surface of the body and bounds a spacious mantle cavity which contains the gills in the water-breathing forms. A siphon, through which water enters and leaves the branchial chamber, is frequently formed by an outgrowth from the edge of the mantle. The shape of the shell is often greatly influenced by the presence of the siphon. In the pulmonate snails, the mantle cavity is largely replaced by a highly vascular sac or lung into which air is admitted through a single opening, the spiracle.

Gills occur in all marine snails and in some fresh-water forms. Lungs seem to have been developed in connection with the change to terrestrial habits, for land snails are the most characteristic pulmonates. Aquatic pulmonates such as the common genera

Physa, Planorbis, and Lymnaea probably were derived from terrestrial ancestors whose descendants have again returned to the aquatic habitat.

The visceral mass lies dorsal to the foot. With increase in its size, it frequently assumes a spiral form, and the mantle, which is carried with it, continues to secrete a shell at the free margin. As a result, the shell assumes a spiral form. The shell may be either simple cone-shaped or anything between this and a highly complex spiral. In the spiral type of shell, the coiled chamber usually surrounds a calcareous pillar which marks the axis of the shell and is termed the columella. In any given species, the coiling of the shell about the columella is normally in a fixed direction. Most coiled shells when held with the apex pointing upward and the aperture facing the observer have the aperture on the right side and are therefore said to be dextral. Some snails are characteristically sinistral (*e.g.*, Physa). Muscles from the body attached to the columella prevent the snail from being able to come clear out of the shell.

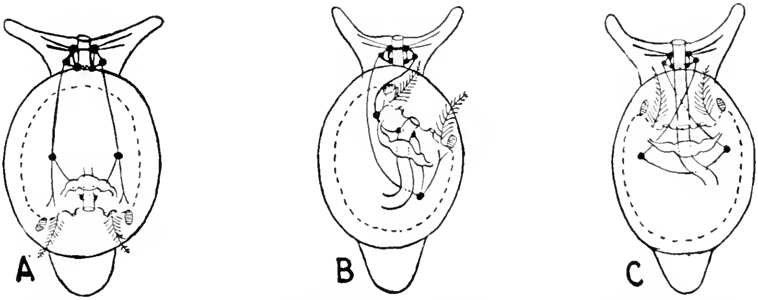

Fig. 92.—Diagrams to show shifting of organs in the development of the streptoneurous condition of gastropods. All diagrams as though viewed from dorsal surface. *A*, an orthoneurous gastropod with posterior anus, and gills, ganglia, and auricles arranged in perfect bilateral symmetry; *B*, hypothetical intermediate condition in torsion; *C*, streptoneurous condition with gill, auricle, and parietal ganglion of original left side now on right side of body. (*After Lang*).

Since growth takes place through the addition of new shell material by the mantle around the aperture, each whorl is successively larger than the preceding one. When a siphon is present, the aperture is drawn into an elongated process for containing it.

The nervous system consists of two cerebral ganglia, the pairs of pedal and visceral ganglia, and two or three additional pairs all of which are united by commissures. The cerebrovisceral commissures may be either parallel (Fig. 92 *A*, orthoneurous) or crossed (Fig. 92 *C*, streptoneurous) as a result of torsion within the body of the animal. Alimentary canal, nephridia, gills, circulatory and nervous systems are all affected in their arrangement by this torsion, which is usually toward the right side. The anus may open into the mantle cavity either on the right side or in extreme instances may occupy a location near the head. In this latter instance, gills, nephridia, and other organs which belong primitively on the left side of the body become shifted in position to the right, and *vice versa*.

Digestive System.—The mouth may be a mere opening on the ventral surface of the head or the opening at the end of a tubular introvert or proboscis. The buccal cavity is provided with an effective mechanism for breaking up food. This consists of a rasplike radula whose teeth tear off particles of food. In many instances, the radula is supplemented by a cutting or crushing jaw of chitinous nature. The form, number, and size of these radular teeth provide some of the most reliable criteria for separating genera and species. The esophagus leads from the mouth cavity to the stomach and this in turn into the intestine, though the divisions of the digestive tract are usually not sharply marked off in the convolutions within the visceral mass. The anal opening is rarely at the posterior end of the body. It is more commonly lateral or at the front end of the body as the consequence of shifting of position of organs due to torsion of the body. Various glands are associated with the digestive system. Of these the liver which extends into the smaller whorls of the shell and the salivary glands are the most important. In some of the carnivorous snails, the salivary glands secrete sulphuric acid. This acid aids the radula in perforating the shells of other molluscs.

Respiratory Organs.—Typically there are two gills contained in the mantle cavity of the gastropods but this condition is subject to various modifications. Very commonly as an accompaniment of torsion the primitively right gill degenerates, leaving but one gill in most of the Streptoneura. In many instances, true gills become replaced by other modifications for respiration. Among the nudibranchs portions of the body surface may become modified as gills. The true gills are vestigial in the limpets and secondary branchiae are formed as a series of folds between the mantle and foot. The most pronounced modification of the respiratory system is found in the pulmonate snails. Here the walls of the mantle cavity become richly supplied with blood vessels and the cavity becomes recognizable as a lung. A small opening permits air to be taken directly into the lung. This is the usual method of respiration in most of the land snails. The aquatic pulmonates seem to be closely related to the land forms, and members of the genera Physa, Planorbis, and Lymnaea have a lung similar to that found in land snails.

Sense Organs.—The tentacles are the most conspicuous sensory organs. The eyes may be either at the bases of or at the tips of the tentacles but in some forms they are borne at the tips of a second pair of tentacles.

Torsion of Body.—Modifications of the body correlated with torsion (Fig. 92) have in some instances resulted in loss of gill, nephridium, and osphradium of the primitively left side. As in the other Mollusca, the number of auricles is directly correlated with the number of respiratory organs, consequently with the loss of one gill the heart comprises but a single auricle and a single ventricle. When the lungs or gills are located in the front of the heart (Prosobranchia and Pulmonata), the auricles are anterior to the ventricle, but when placed behind the heart (Opisthobranchia and Pteropoda), the auricle is posterior to the ventricle.

Reproduction.—The gonad is always single. In some instances, the sexes are separate but many genera are hermaphroditic. In the latter, though there is a single hermaphroditic gonad, each individual bears the accessory sexual organs of both sexes. There is great diversity in reproductive habits. In many species eggs are laid singly or in small groups, in others they are deposited in masses surrounded by a gelatinous substance, while in many of the marine snails complicated capsules are formed for containing the eggs and an albuminous fluid which serves to nourish the embryos. The course of development is fairly uniform throughout the group, involving the presence of a veliger larva. In terrestrial and fresh-water forms, the veliger stage is passed within the eggshell and not as a free larval stage. Some gastropods are viviparous.

Subclass PROSOBRANCHIA

In the Prosobranchia or Streptoneura are included those gastropods which have the cerebrovisceral commissures of the nervous system crossed or twisted into the form of a figure eight (Fig. 92 *C*). The sexes are separate. A shell is almost always present and is usually provided with an operculum.

I. ORDER ASPIDOBRANCHIA

The order Aspidobranchia includes prosobranchs with but little concentration of the nervous system. The limpets (suborder Docoglossa) include marine forms with a non-spiral shell and bearing either a single true ctenidium or a secondarily developed pallial gill beneath the mantle margin or with both true and secondary gills. Patella and Acmaea are representative genera. The abalones (Haliotis) and the genera Fissurella and Trochus exemplify the suborder Rhipidoglossa in which both limpetlike and spiral shells occur.

II. ORDER CTENOBRANCHIA

This order includes large numbers of marine, fresh-water, and terrestrial Streptoneura with the shell usually coiled in a more or less elevated spiral. The heart has but one auricle. Due to torsion, the primitively right gill is shifted to the left side of the body. Both shelled and naked forms are included within this order. The members of the suborder Heteropoda are free-swimming and pelagic marine molluscs in which the foot is modified to form a vertical fin. Carinaria, with its delicate, glassy shell, and Atlanta are examples. In the suborder Platypoda the foot is flattened ventrally. Littorina, Crepidula, Natica, Strombus, Pleurocera, Murex, and Terebra are examples of this highly diversified suborder.

Subclass EUTHYNEURA

The cerebrovisceral commissures are not crossed in the members of this subclass but form a single loop. The individuals are hermaphroditic. The shell, which is typically spiral or flattened, is frequently vestigial or wanting. In the order Opisthobranchia are included marine forms of which the tectibranchs (Aplysiidae or sea hares and pteropods) and nudibranchs are examples.

The order Pulmonata comprises chiefly terrestrial and fresh-water forms. The walls of the mantle cavity are modified to form a lung into which air is taken in respiration. Most of the aquatic forms depend upon periodic visits to the surface of the water for renewing the oxygen supply in the lung, though in some instances the lung has become adapted secondarily for water respiration. Physa, Lymnaea, Planorbis, and the limpet-shaped Ancylus are fresh-water pulmonates. The slugs (Limax, Arion, and Agriolimax) and many land snails (Polygra, Helix, Pupa, Bulimulus) are also pulmonate Euthyneura.

Class Cephalopoda

The cephalopods are the most highly organized molluscs. In habits, they are exclusively marine. Among present-day forms, they include the squids (Fig. 93 *A*), cuttlefishes, devilfishes (Fig. 93 *B*), and Nautilus. When a shell is present it is almost always internal, for only Nautilus of our recent cephalopods lives within a shell. In most instances (except in Nautilus), a head is well defined. A pair of strong jaws, each in shape resembling the beak of a parrot, are located within the mouth cavity. The eight or ten characteristic arms which surround the mouth and the funnel-shaped siphon are modifications of

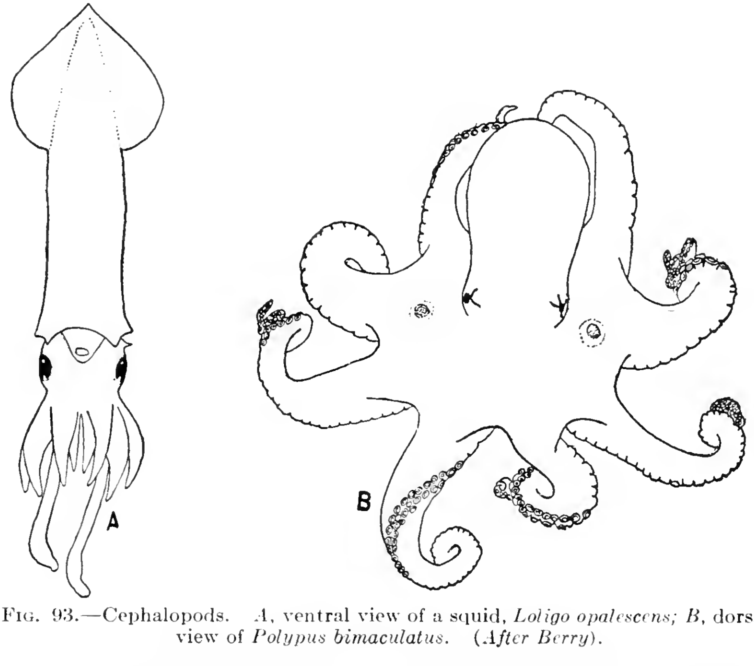

Fig. 93.—Cephalopods. *A*, ventral view of a squid, *Loligo opalescens; B*, dorsal view of *Polypus bimaculatus*. (*After Berry*).

the foot. The arms are provided with heavily rimmed sucking discs arranged in rows. In some forms the effectiveness of these grasping organs is increased by the presence of a strong clawlike hook within the cavity of each disc. The siphon is a highly muscular tube through which water is drawn into the mantle cavity for respiration and the body wastes are forcibly expelled. The jet of water issuing from the siphon drives the squid or devilfish backward with remarkable speed and constitutes one of the chief means of locomotion. The devilfish can move forward only by using the arms in crawling, but movement of the fins on the sides of the body of a squid enable it to swim either forward or backward. A fleshy mantle encloses a cavity which contains the gills and at the same time forms a protective covering for most of the other viscera. At will many cephalopods may eject a cloud of ink from an ink sac. The pigment sepia is derived from the cuttlefish, for the ink sac which is characteristic of the Decapoda stores quantities of this pigment. When the animal is disturbed, clouds of this ink are shot from the mantle cavity through the siphon and serve as an effective cover under which the cuttlefish moves off to safety.

Some cephalopods have unusual powers of changing color. Variously colored pigment cells in the skin may expand or contract, producing wonderful combinations. At one moment the entire body may be of a uniform color which may be changed instantaneously by a play of flashes of varied hues over the body. Some species of squid can produce almost every tint of the rainbow.

A pair of eyes, on the sides of the head beneath the bases of the tentacles, very closely resemble the eyes of vertebrates. In finer structure and origin, the cephalopod and vertebrate eyes are widely different, for despite their superficial resemblances the two seem to have had entirely independent origin. The cornea of the cephalopod eye is perforated and thereby allows water to enter the anterior chamber, while it is not perforated in the vertebrate eye. The arrangement of the sensory cells, the retina, is just the reverse in the two types of eye. The vertebrate retina is said to be inverted, for light passing through the eye strikes the sensory cells of the retina on the same end that bears attachment to the nerve endings. In contrast with this, the direct retina of the cephalopod eye is so organized that the light passing through the eye falls upon the free ends of the sensory cells. In Nautilus, much simpler eyes are found, for lens, vitreous body, cornea, and iris are wanting.

Two kinds of hearts are present. The systemic heart is of typical molluscan type with its single ventricle and two auricles corresponding to the number of gills and receiving blood from them, but in addition to this heart there is a branchial heart at the base of each ctenidium which forces the blood through the gills.

Cephalopods are of importance especially because of the part which they play in food chains. Squids and devilfish feed upon fishes and in turn serve as food for still larger fishes and for the sperm whale. They are used extensively for bait and in many regions as food for man.

The sexes are separate. The spermatophores of the male are frequently stored in arms which become more or less modified. In most instances, this modification involves only sufficient change to adapt the arms as accessory copulatory organs but in a few genera the entire arm bearing the spermatophores becomes severed from the body of the male and acquires independent powers of locomotion. When first observed, these wormlike castaway arms were thought to be entire organisms and were described under the name Hectocotylus before their relationship to the cephalopod body was understood. The term hectocotylization is used to indicate this type of spermatophore transfer through the agency of dissevered tentacles. The heavily yolk-laden telolecithal eggs undergo partial discoidal cleavage. The organs of the young cephalopod are formed from the blastoderm; first as flattened projections, but as these grow the young animal becomes recognizable, at first appended to the bulky yolk sac by the head end.

Largely on the basis of the number of gills, two subclasses of cephalopods are recognized, the Tetrabranchia with four gills and the Dibranchia with two.

Subclass TETRABRANCHIA

The genus Nautilus contains the only living representatives of the Tetrabranchia. A well-developed, chambered shell within which the animal lives, the presence of four gills, four auricles, and four nephridia, a divided siphon, and many tentacles without hooks or suckers characterize the living examples of this subclass. In past geological ages, numerous tetrabranchs flourished, the fossil shells of which show many interesting evolutionary tendencies in development. But little is known of the habits and development of Nautilus, for though the empty shells are cast ashore in quantities in the Pacific and Indian oceans the animal is rarely found alive.

Subclass DIBRANCHIA

In this subclass are included those cephalopods having two branched gills in the mantle cavity, two nephridia, two auricles, highly organized eyes, and eight or ten arms bearing suckers or hooks. On the basis of the number of arms, two orders are recognized, namely, Decapoda—with ten arms (devilfishes and Argonauta)—and Octopoda—with eight arms (squid, cuttlefish and Spirula).

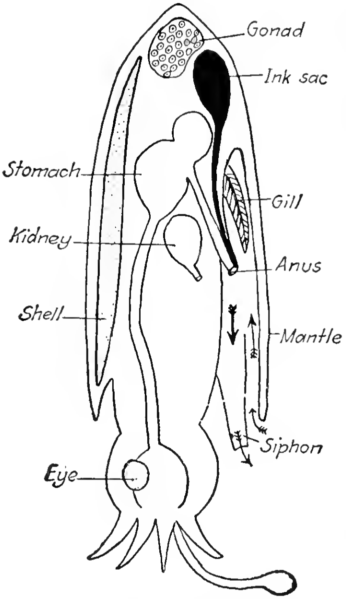

FIG. 94.—Diagram of median section of Sepia. (*From Lang*).

Some sort of shell is usually present, in the form of an internal, coiled, chambered shell as in Spirula; a long, horny pen of purely organic matter as in the squids (Loligo); or a highly calcareous plate known as the "cuttlebone" of the cuttlefish (Sepia, Fig. 94). In the argonauts, the female is provided with a thin, single-chambered shell, but the male argonauts and all other representatives of the order typically lack a shell.

An ink sac (Fig. 94) is usually present. The powerful, muscular arms are used both in swimming and in the capture of prey. A constriction separates the head from the body proper and marks the anterior boundary of the mantle. At this level, on the ventral surface occurs the respiratory opening.

OUTLINE OF CLASSIFICATION

Phylum Mollusca.—Triploblastic; unsegmented; coelom greatly reduced; shell or shell gland at least during larval development.

1. **Class Amphineura.**—Nervous system not concentrated; shell when present composed of eight transverse calcareous plates; marine.

1. Order Placophora.—Shell dorsal, of eight transverse plates; foot broad; gills lateral, simple, mantle folds. *Chiton, Cryptochiton, Trachydermon, Amicula, Chaetopleura, Lepidochitona, Ischnochiton.*

2. Order Aplacophora.—Elongate; covered by a mantle; spicules instead of shell; gills posterior. *Neomenia, Dondersia, Chaetoderma.*

II. Class Acephala.—No head; shell of two valves; aquatic.

1. Order Protobranchia.—One pair plumelike gills; *Yoldia, Nucula, Leda, Solenomya.*

2. Order Filibranchia.—Gills platelike, filaments V-shaped; anterior adductor reduced. *Mytilus, Modiola, Arca, Anomia, Trigonia.*

3. Order Pseudolamellibranchia.—Gills platelike, in vertical folds; but one adductor. *Pecten, Ostrea, Meleagrina.*

4. Order Eulamellibranchia.—Gill filaments grown together to form a continuous sheet; adductors approximately equal. *Mya, Venus, Cardium, Ensatella, Teredo, Unio, Anodonta, Lampsilis, Quadrula, Sphaerium, Pisidium, Pholas, Barnea.*

5. Order Septibranchia.—Gills a horizontal partition in mantle cavity. *Silenia, Cuspidaria.*

III. Class Scaphopoda.—Shell tubular; open at each end. *Dentalium, Cadulus.*

IV. Class Gastropoda.—Shell single, usually spiral; radula.

a. **Subclass Prosobranchia.**—Nervous system twisted in figure eight; sexes separate.

1. Order Aspidobranchia.—Nervous system little concentrated; one or two gills; two auricles. *Haliotus, Trochus, Fissurella, Patella, Acmaea.*

2. Order Ctenobranchia.—Usually one gill; one auricle. *Carinaria, Atlanta, Littorina, Crepidula, Natica, Strombus, Pleurocera, Campeloma, Murex, Terebra, Buccinum, Busycon.*

b. **Subclass Euthyneura.**—Nervous system not twisted; hermaphroditic.

1. Order Opisthobranchia.—Gills. *Bulla, Aeolis, Navanax, Tethys, Triopha.*

2. Order Pulmonata.—Lungs. *Physa, Planorbis, Lymnaea, Ferrissia, Limax, Arion, Agriolimax, Polygyra, Helix, Pupa, Gastrocopta.*

V. Class Cephalopoda.—Distinct head with arms bearing suckers; shell frequently reduced, internal.

a. **Subclass Tetrabranchia.**—Four gills; chambered shell. *Nautilus.*

b. **Subclass Dibranchia.**—Two gills; arms in circle around mouth; tubular funnel; shell internal.

1. Order Decapoda.—Ten arms, two of which are tentacular; suckers stalked. *Loligo, Sepia, Spirula, Rossia.*

2. Order Octopoda.—Eight arms; suckers sessile. *Argonauta, Polypus.*

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CHAPTER XIII

PHYLUM ARTHROPODA

INTRODUCTION AND CLASS CRUSTACEA

The arthropods are segmented animals distinguishable from all others in that they bear paired, jointed appendages and have a chitinous exoskeleton. This is by far the largest phylum in the animal kingdom, for it contains more than three times as many species as all the remaining phyla put together. In spite of the immense numbers, the group is clearly recognizable as a natural unit.

In many respects, the arthropods represent the highest development found in the non-chordate animals. In earlier chapters, it has been shown that the bodies of the higher segmented worms are composed of a linear repetition of similar rings or somites. The somites of these worms often bear appendages, called parapodia, but these in their highest development are mere flaplike folds of the body wall and are never jointed. The tendency toward specialization of appendages has been carried much further in the arthropods, for here they have become more highly organized and they are definitely articulated. Metamerism of the body also finds higher expression in the arthropods, for in most arthropods the segments of the body have undergone greater specialization and more distinct regional differentiation than is encountered in any annelids. Since the segments of the worms show so little differentiation, the metamerism of the worms is said to be homonomous, while that of the arthropods is very distinctly heteronomous. In most instances at least head and trunk regions are recognizable and in many cases three body divisions are distinctly set off as head, thorax, and abdomen.

The body covering or integument of arthropods is composed of a chitinous material overlying the hypodermis. To permit movement of the body, joints occur in this otherwise unwieldy exoskeleton. These joints are termed sutures, and skeletal areas bounded by sutures are designated as sclerites. Inorganic substances, especially lime, are frequently added to the chitin, thus giving the skeleton additional strength and thereby affording greater protection to the underlying parts. The skeletal plates are more or less telescoped at the more prominent joints, so the body surface presents an uninterrupted armor.

Ecdysis.—With age, the chitinous covering increases in thickness and becomes an effective barrier to further growth of the parts which it encases. Growth is then rendered possible only by periodic shedding of the cuticula in a process known as molting or ecdysis. Immediately following the ecdysis, the body covering is extremely soft and pliable and during this period there is rapid increase in size. Frequency of ecdysis varies greatly in different groups of the arthropods but it is of much more frequent occurrence in early stages of development. The Crustacea continue to shed the skin periodically throughout life. In the insects, attainment of the adult form marks the last ecdysis through which the individual passes, except in the mayflies which molt once after the wings become functional.

Number of Segments.—In the fundamental structural plan of an arthropod, each segment bears a pair of appendages. Fusion of segments and degeneration of appendages on some segments frequently obscure this plan, but even in such instances evidences of the primitive condition are often still observable in the embryo, for the vestiges of appendages occur here even though they may be entirely wanting in the adult.

Characteristic Organ Systems.—The chief organ of the circulatory system, a dorsal vessel or a heart, lies dorsal to the digestive canal. The circulatory system is of the open type, for the body fluid is not restricted to vessels throughout its course but is frequently spilled into sinuses or lacunae. These sinuses are so prominent that they are frequently mistaken for a coelom. These cavities are a development of a portion of the circulatory system, hence they are designated as a haemocoel, for they are not a true coelom.

The central nervous system consists of a ladderlike chain of ganglia (Fig. 123) and a brain or supraesophageal ganglion of which all but the brain is ventral to the digestive tract.

Various modifications for respiration and excretion are found, but these will be discussed under the several classes.

Development is always sexual but modified types of sexual development are found in the establishment of parthenogenetic and paedogenetic habits in some groups. Polyembryony has been demonstrated in some insects. Hermaphroditism is rare. The centrolecithal egg undergoes partial, superficial cleavage in most instances. So many different larval stages are involved in the various groups of arthropods that the developmental cycle will be considered separately for the individual classes of the phylum.

Classes.—There is much disagreement regarding the number of classes into which the Arthropoda should be divided. Until fairly recently, four or five classes were considered sufficient to express the extent to which differentiation has proceeded in this phylum. With the increase in our knowledge of the arthropods no less than eleven or twelve groups merit recognition as classes. Even a conservative judgment would demand that the Crustacea, the Acerata, the Onycophora, the Diplopoda, the Chilopoda, the Symphyla, the Myrientomata, and the Insecta be recognized as classes. Some writers maintain that in addition to these, several other groups such as the Pycnogonida, the Tardigrada, the Linguatulida, and the Pauropoda should be admitted to the rank of classes.

Class Crustacea

The cuticula of most crustaceans has become hardened through the addition of carbonate and phosphate of lime to the organic chitinous skeleton. Members of this class are typically aquatic, though some (the sow bugs and land crabs) have become modified for terrestrial existence. All modern representatives of this class have two pairs of antennae. A carapace is very frequently present. This has its origin as a fold at the head end and grows backward as a continuous shield protecting the underlying parts and obscuring the external evidences of segmentation of the parts covered. In some instances, the entire body is enclosed in this shell-like carapace (Fig. 99), which gives to these crustaceans a confusing external resemblance to molluscs. More frequently, the head and all or part of the thorax are covered by the carapace.

Appendages.—All of the present-day crustaceans have two pairs of antennae, though the trilobites (Fig. 96), all of which are extinct, have but a single pair. The appendages are typically Y-shaped and are said to be of the biramous or schizopodal type. The stem of the Y, which provides attachment with the body wall, is called the protopodite and is composed of two segments, namely, a proximal coxopodite and a distal basipodite. Distally, the basipodite characteristically bears two branches of which the one nearer the median line of the body is termed the endopodite and the other the exopodite. Many of the crustacean appendages have become modified so that the biramous condition is not observable, as, for example, the walking legs of the crayfish and lobster in which the protopodite bears but a single series of segments to form the leg. A study of the larvae of the lobsters (Fig. 95) gives proof that the distal part of the leg is the endopodite, for in larval lobsters the thoracic legs are distinctly biramous and it is only in later development that the exopodite of these appendages disappears. There are no free larval stages in the crayfishes, for the entire development is completed within the egg, but since other structures of the crayfish homologize so directly with those of the lobster, the leg of the crayfish is likewise considered as being composed of a protopodite and an endopodite.

While the schizopodal or biramous appendages are characteristic of most crustaceans, there are some in which a more primitive type of appendage is found. In the Phyllopoda, there are leaf-like feet on the thorax (Fig. 97) though the antennae are biramous. The phyllopod appendages bear a number of lateral processes called endites projecting from a central axis of podomeres or foot segments. This type of appendage seems to be more generalized than the biramous type and the latter may have originated as a modification of the foliaceous type.

The number of body segments is highly variable. The anterior five somites are fused with the prostomium to form the head. This may be united with some or all of the thorax to form a cephalothorax. The abdominal somites are highly variable in number.

Respiratory and Excretory Organs.—Respiration is usually by means of gills, though in some instances there are no modified structures for respiration, because the entire body surface functions in this capacity directly. The gills are very frequently borne within a gill chamber formed by the walls of the carapace and the body wall. Special organs of excretion are the green glands and the so-called shell glands which open on the bases of the second antennae and the second maxillae respectively. These two organs occur together in the larvae, but in adult crustaceans one or the other fails to develop. They agree in fundamental structure. Each consists of a terminal vesicle which communicates with an external pore by a slender, greatly coiled tubule.

The digestive canal is largely ectodermal and is consequently lined with chitin. The stomodaeum includes not only the pharynx but also a dilated portion, modified for grinding, which is called the stomach. Much of the intestine is proctodaeum. The mesenteron is a relatively short region into which a paired digestive gland, the hepatopancreas, empties.

Sensory Organs.—Both antennae and antennules are tactile organs, innervated from the brain, but in some instances the antennae are the chief locomotor organs. Otocysts are found only in the Malacostraca, where they occupy a position in the protopodite of the antennules (Decapoda) or on the last abdominal appendages (Schizopoda). Paired compound eyes are characteristic of many crustaceans but there are some blind forms. An unpaired X-shaped "nauplius eye" occurs in the larvae of most crustaceans and is retained as the optic organ in the adults of the lower Crustacea.

Development.—The Crustacea typically pass through one or more larval stages before reaching adult organization. When direct development occurs, it has either resulted from a suppression of larval stages, or these stages have been passed before the embryo leaves the egg. The nauplius is one of the most important as well as most characteristic of the larval stages of Crustacea, for it is almost universal among the lower orders. This larva is composed of three segments bearing three pairs of appendages. The foremost of these appendages are simple and later develop into the antennules, while the second and third are biramous and in later development form the antennae and mandibles respectively. There is a single unpaired eye.

In a characteristic instance, as in the development of Cyclops, the nauplius after its first molt becomes a metanauplius bearing the rudiments of three pairs of appendages in addition to those found in the nauplius. These additional rudiments represent the two pairs of maxillae and one pair of maxillipeds. A pair of very rudimentary thoracic appendages also make their appearance on the metanauplius. In each of three successive molts, the Cyclops larva acquires an additional pair of these stumplike rudiments of the thoracic legs, so with the close of the larval period there are four pairs of the thoracic rudiments, and following a final larval molt the larva has practically attained the adult form.

Among the parasitic copepods, the nauplius and metanauplius stages are passed within the egg membranes, and the larva at hatching is termed a copepodid because of its fairly close resemblance to the general organization of the free-living copepod.

The zoea (Fig. 103 *B*) is characteristic of the Malacostraca where it is usually the first larval stage but in a few instances it is preceded by a nauplius. It consists of a cephalothorax bearing biramous appendages and an abdomen without appendages. The head bears a pair of lateral compound eyes. Typically, the zoea by several molts transforms into a mysis stage (Fig. 95 *A*), in which even the posterior thoracic appendages are biramous and are of use in swimming. In later development, the exopodite of these biramous thoracic appendages disappears and leaves the unbranched walking legs of the adult.

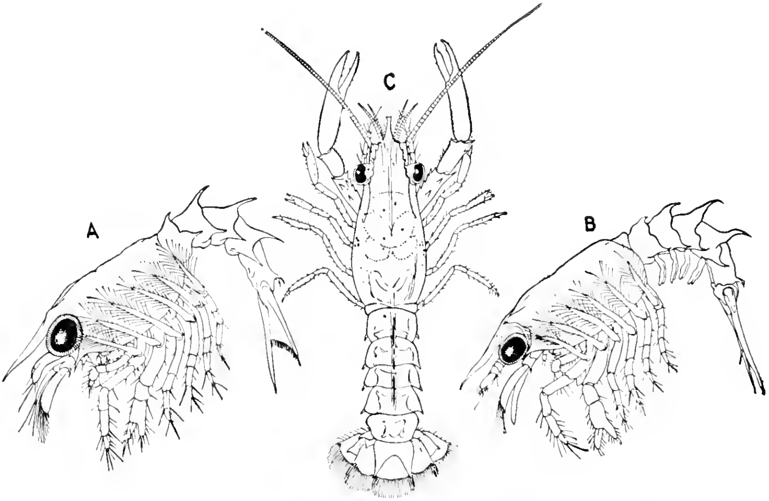

FIG. 95.—Typical stages in the development of the lobster. *A*, first swimming stage or mysis; *B*, second larval stage, with abdominal appendages; *C*, fourth larval stage showing loss of exopodites from walking legs. (*After Herrick*).

In the Brachyura (crabs), the thoracic appendages of the zoea, which are later destined to become the walking legs, develop in the free-swimming larva as only budlike rudiments and never acquire the biramous condition characteristic of the mysis larva. Thus in the crabs the mysis stage has been eliminated and the zoea in passing to the adult condition transforms through a more advanced type of larva (Fig. 103) which is termed the megalops.

Six subclasses of the Crustacea are here considered: the Trilobita, which are represented by fossil remains only, the Phyllopoda, the Copepoda, the Ostracoda, the Cirripedia which are exclusively marine, and the Malacostraca.

Subclass TRILOBITA

The trilobites are of importance because they represent a primitive type of crustacean which has not persisted to recent times but occurred in abundance during Cambrian times when the oldest fossil-bearing rocks were formed, reached an extreme development in the Silurian, and disappeared in the Permian. In habits, they were exclusively marine. Their remains are among the most popularly known fossils. The body contains a variable number of somites (Fig. 96) which are grouped into head, thorax, and abdomen. Each segment bears a pair of jointed appendages. The head bears five pairs all of which are biramous except the antennules and they are simple. A pair of compound eyes usually occurs on the head.

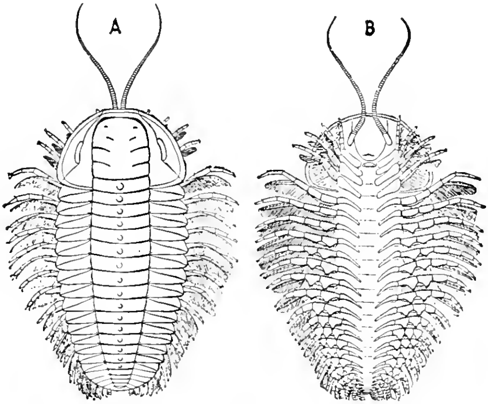

FIG. 96.—A trilobite, *Triarthrus Becki.* *A*, dorsal; *B*, ventral aspect. (*After Beecher, from Zittell*).

A pair of longitudinal grooves separates the body into a central axis and two lateral pleural lobes. This "trilobed" condition of the body suggests the origin of the group name.

About 2,000 species have been described. Proetus, Asaphus, Dalmanites, Triarthrus (Fig. 96), Harpes, Ctenocephalus, Paradoxides, and Homalonotus are examples of the 200 or more described genera.

Subclass PHYLLOPODA

Of the present-day Crustacea, the Phyllopoda are the most primitive. The name intimates one of the outstanding characters of the group, the presence of leaflike appendages, of which there are ten or more pairs located on the trunk. Here belong the fairy shrimps (Branchiopoda) and that host of minute, shelled crustaceans known as the water fleas (Cladocera). Fresh-water, marine, and brackish-water forms are included within the confines of this group the members of which have little more than the leaflike appendages as a common characteristic. In the two orders, Branchiopoda and Cladocera, members of the former have numerous segments, very distinctly marked, while members of the latter order have few somites and these are frequently not clearly defined. Even within each order, body form and structure are subject to great variation. There is usually a pair of conspicuous eyes and frequently in addition there is a small median eye. In some instances, the paired eyes, distinct in the young, fuse to form a single eye, but even then two optic nerves are retained, so the double nature of the eye is still observable. The sexes are distinct, though males are much less numerous than females.

Members of the two orders Branchiopoda and Cladocera are separable on the basis of the number of trunk appendages. In the former, there are ten or more pairs of trunk appendages, while in the Cladocera the appendages of this region do not exceed six pairs.

I. ORDER BRANCHIOPODA

With the exception of one genus, Artemia, the Branchiopoda are exclusively fresh-water phyllopods which occur in all parts of the world. Eubranchipus (the fairy shrimp, Fig. 97), Apus, and Estheria represent three distinctly different types of structure within this order. In habits, all of these are peculiar in that they are restricted to small pools and especially the temporary pools which are formed by spring rains and disappear during the summer. In these temporary pools, they appear in very great numbers in early spring, then after a few days or weeks they disappear entirely. An examination of the mud after the pool has dried up reveals large numbers of the eggs which are capable of withstanding desiccation. In fact, the eggs of some forms refuse to develop if they are returned to water immediately and develop normally only after being dried out. From the egg is derived a larva in the nauplius or metanauplius stage. Many phyllopods swim upon the back with the ventral surface uppermost. This is especially characteristic (Fig. 97) of Eubranchipus.

Eubranchipus and the brine shrimp Artemia are examples of the suborder Anostraca, the members of which have no carapace and bear stalked eyes. The members of suborder Notostraca, of which Apus and Lepidurus are examples, include branchiopods with a shield-shaped carapace covering part of the trunk and with sessile eyes. In the suborder Conchostraca are grouped forms which have a bivalve carapace enclosing the entire animal. Estheria, Limnadia, and Limnetus, with their strikingly molluscan appearances, are examples of this suborder.

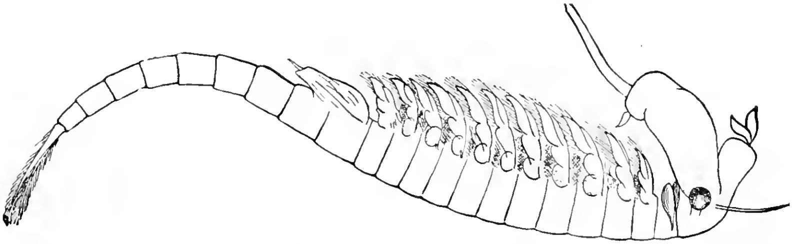

FIG. 97.—*Eubranchipus vernalis* in normal position for swimming. (*After Packard, from Kingsley's Hertwig, with permission of Henry Holt and Co.*).

II. ORDER CLADOCERA

The Cladocera are small phyllopods, rarely more than 3 mm. in length, with a distinct head and usually with a carapace covering the trunk and legs. They are commonly called water fleas. Daphnia is a characteristic genus. In a few instances (Leptodora and Polyphemus), the carapace is greatly reduced and serves only as a brood sac, leaving the trunk and legs entirely free.

The head holds a median compound eye which has usually resulted from the fusion of two lateral eyes and is capable of rotation within a capsule. The antennules are sensory but the second antennae are modified as swimming organs and constitute the chief organs for locomotion. In addition, the head bears a pair of mandibles and a pair of greatly reduced maxillae.

A dorsal heart, just back of the head, is the only circulatory organ, for vessels are wanting. An ostium on each side of the heart allows the blood to enter, and contraction of the heart forces the blood through a single anterior opening. There are no specialized organs for respiration. That portion of the body within the shell is divisible into two regions, one, the body proper which is not sharply segmented but bears six pairs of foliaceous appendages, and the other, an unsegmented postabdomen. The trunk appendages function chiefly in creating water currents through the space within the shell.

Most Cladocera react positively to weak light and negatively to strong light, but these reactions may be reversed by other stimuli acting as controlling factors in their behaviour. Thus, in cold water, Cladocera may respond positively to a light stimulus which would repel the same individuals living at a higher temperature.

Reproduction is largely parthenogenetic. The eggs are stored, frequently in considerable numbers, in a brood case formed within the dorsal portion of the carapace. Here they undergo full development without ever having a free larval stage. Under ordinary circumstances, all of the parthenogenetic eggs produce females. When unfavorable conditions arise, however, not all of the parthenogenetically developed individuals are females, but some males are hatched from parthenogenetic eggs. In the sexual cycle which follows, each female produces only one or two large thick-shelled eggs. These are true sexual eggs which require fertilization before development is initiated. The fertilized eggs pass into a brood sac the walls or portions of the walls of which become modified as an enclosing envelope (ephippium) within which the resting eggs lie until the return of conditions favorable for their development.

The Cladocera, along with some other crustaceans, have great value in that they are important as food for many aquatic animals, especially fish, while they in turn utilize the smaller algae which are abundant under conditions in which they are found. Daphnia and Bosmina are characteristic shelled forms, while Leptodora and Polyphemus have greatly reduced shells. Most cladocerans live in fresh water.

Subclass COPEPODA

Copepods inhabit both fresh and salt water. Some forms have become so highly modified through adaptation to the parasitic habit that they are recognizable only with difficulty as arthropods. In the free-living forms, the body is usually elongated and distinctly segmented. The appendages are characteristically biramous, though some have become so modified that they have lost their biramous nature. Six pairs of appendages are borne on the head and four or five on the anterior region of the trunk, while the posterior region of the trunk lacks appendages. The last abdominal segment is forked.

The unpaired nauplius eye is characteristic of copepods and prompted the application of the name Cyclops to one genus.

In many instances, the eggs when discharged from the female are surrounded by a gelatinous substance and remain attached to the body as prominent egg sacs. Conspicuous egg sacs are highly characteristic of the female Cyclops. Larvae hatching from the eggs are in the nauplius stage.

Copepods occur in such abundance and are important food items for such numbers of different animals that they have considerable economic importance. Many fishes feed almost exclusively upon small crustaceans of which the copepods are the most numerous. Even some whales subsist largely upon copepod diet.

There are a number of families displaying an extensive array of bizarre body forms. In many instances, all of the appendages excepting those modified for attachment to the host have degenerated.

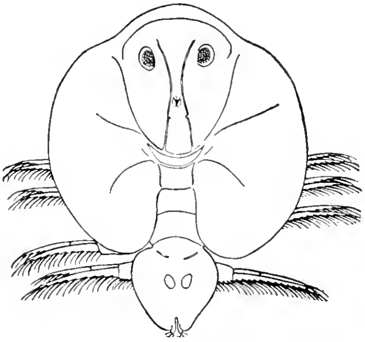

Fig. 98.—Dorsal view of a female parasitic copepod, *Argulus versicolor*. (*After Wilson*).

Parasitic Copepods.—In the foregoing, only the free-living copepods have been considered. There are immense numbers of copepods which dwell as parasites upon other animals. Fishes are especially prominent hosts of those parasites, which are popularly known as fish lice. Both the body and gills are subject to attack. Some of these parasitic copepods *e.g.*, the genus Argulus (Fig. 98) of the order Branchiura have a pair of compound eyes, fully developed swimming feet, and a modification of the first maxillipeds to form a pair of sucking discs for securing attachment to the host. These argulids are not permanent parasites, for especially at the breeding season they leave the body of the host and swim free in the water. In contrast with these stand some other parasitic copepods the bodies of which have become so greatly reduced as an adaptation to the parasitic habit that they are more like a simple worm in appearance than like an arthropod. It is only through the unaltered larval stages, the nauplius and the metanauplius, that the affinities of these degenerate adults are recognizable.

Subclass Ostracoda

Ostracoda are abundant in various fresh- and salt-water habitats. The entire animal is enclosed within a bivalve shell

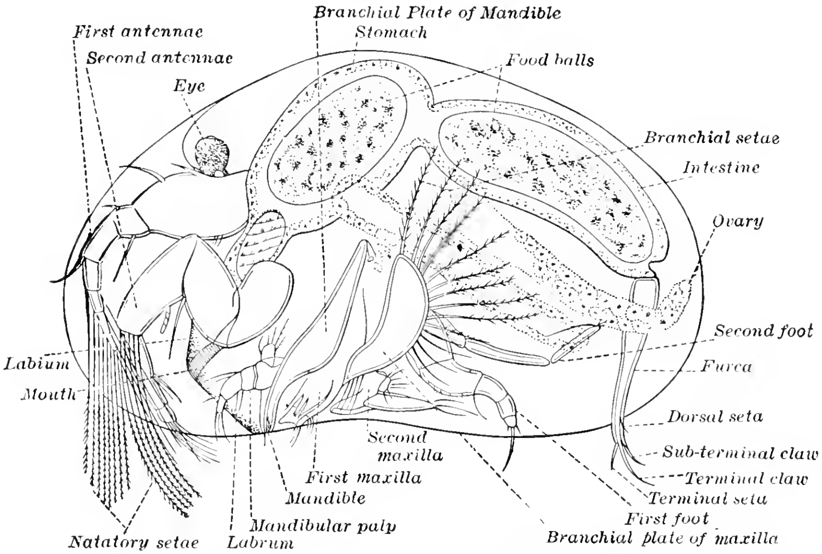

FIG. 99.—General anatomy of an ostracod, *Cypris virens* Jurine. (*After Vavra*). (*Reprinted by permission from Ward and Whipple's Fresh-water Biology, published by John Wiley and Sons, Inc.*).

(Fig. 99), but when the valves open the appendages protrude. Segmentation of the body is very indistinct or wanting. The head region bears two pairs of antennae, both used in swimming; the mandibles; and two pairs of maxillae. Ordinarily, the trunk region bears but two pairs of legs.

Most ostracods are omnivorous. Both parthenogenetic and true sexual reproduction occur. The eggs produce nauplii which undergo a number of molts before reaching the mature form.

Cypris is free-swimming, while Candona is of a burrowing habit. In the marine forms (Cypridinidae) a heart is present but in fresh-water ostracods there is no heart.

Subclass CIRRIPEDIA

Most Crustacea are free-moving animals except the parasitic forms and the members of the entire group known as the Cirripedia or barnacles. Not only are the barnacles sessile but as a consequence of this habit they show very marked degeneration of many structures. Adaptation to the sessile life also helps to explain the fact that hermaphroditism, which is so uncommon in Arthropods, is the usual condition among the Cirripedia. Though occasionally males are found, they are usually small, degenerate forms known as complemental males which very frequently live within the shell of the female, at times as parasites.

The body is enclosed in a membranous mantle which, in most instances, is encased in calcareous plates. It is not surprising that until less than a century ago barnacles were thought to be molluscs.

In development, the Cirripedia hatch from the egg as a nauplius. Because of its resemblance to the ostracod, Cypris, a second larval stage with a bivalve shell, is termed the cypris stage. The free-swimming larva comes into contact with some object to which it becomes attached. The first antennae, with their associated cement glands, aid in the fixation. Calcified plates usually make their appearance in the mantle folds and form a protective shell surrounding the animal. Within this shell, the body of the barnacle is peculiarly oriented, for, as is sometimes said, the barnacle stands on its head and kicks food into its mouth. Water currents bearing food to the mouth are set up by the beating of the usually six pairs of plumelike biramous appendages of the trunk. The mouth is surrounded by a pair of mandibles and two pairs of maxillae.

The goose barnacles (*Lepas anatifera*) have the region of attachment (Fig. 100) drawn out into a characteristically elongated stalk. A mediaeval myth maintains that the goose develops from these goose barnacles. The neckless barnacles (Balanus, for example), which encrust rocks and other submerged objects, have a flattened base of attachment from which the skeletal plates arise directly. Barnacles are exclusively marine and choose stones, wood, animals, plants—in short, any object—

as a place for attachment. When they become attached to the bodies of other animals, it is a very common thing for them to become dependent upon the animal which offers shelter, and as a consequence there is here shown in great detail the development of the parasitic habit. Various species become more or less dependent upon whales and sharks, while Sacculina becomes attached to the abdomen of decapod crabs and undergoes a parasitic degeneration rarely equaled. All traces of appendages and of digestive organs are lost, and, as the name implies, Sacculina becomes a mere saclike structure with a rootlike system penetrating the body of the host for absorbing food. The relationships of this degenerate form are shown only through the larval stages which are fully characteristic of the barnacles.

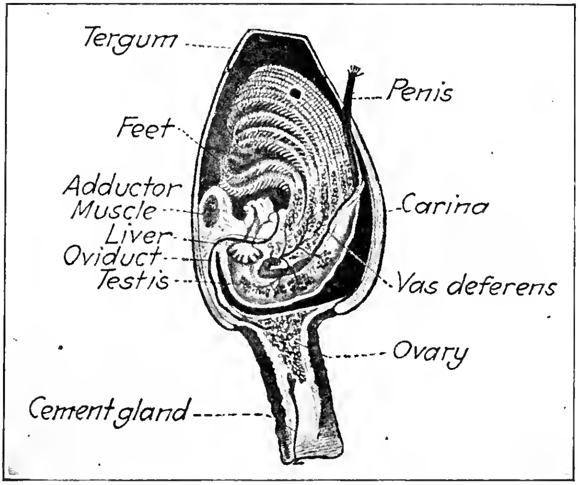

Fig. 100.—Barnacle.

Subclass MALACOSTRACA

The Malacostraca are frequently spoken of as the higher Crustacea. Lobsters, crayfishes, crabs, shrimps, prawns, sow bugs, scuds, and sand fleas are common names of some representatives of this subclass. The body segments, so highly variable in number in members of the foregoing groups, are in the Malacostraca almost rigidly limited to twenty or twenty-one. Usually the head consists of a prostomium and five additional somites, the thorax of eight, and the abdomen of seven of which the last (the telson) bears no appendages.

The antennal glands are the typical excretory organs of adults, though larvae and some Isopoda have a shell gland communicating with the second maxillae for excretion. The genital opening of the male is characteristically upon the coxopodite of the eighth thoracic appendage and of the female on the sixth.

Within the Malacostraca, a considerable number of orders are recognized, but for the purposes of this text attention is limited to but six of them.

I. ORDER PHYLLOCARIDA

A few marine species belonging to the genus Nebalia (Fig. 101) show unusual combinations of phyllopodan and malacostracan characters. In number of somites and in location of the genital openings, they agree with the higher crustacea, yet the thoracic appendages are leaflike.

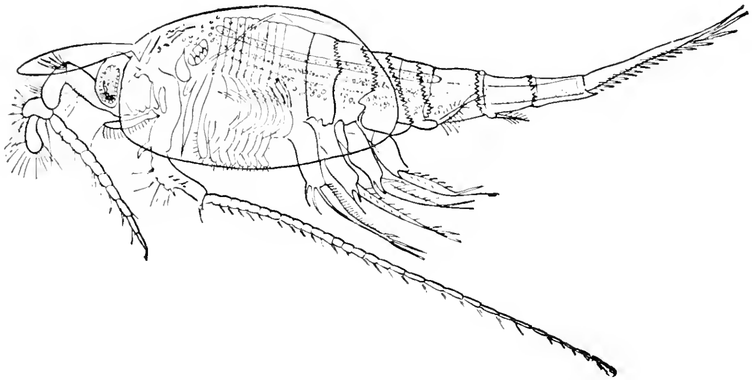

FIG. 101.—Male of the genus Nebalia. (*After Claus*).

II. ORDER SCHIZOPODA

These small, mostly marine, Malacostraca with compound eyes on movable stalks bear a delicate carapace covering the cephalothorax. The eight appendages of the thorax are biramous swimming organs with both exopodite and endopodite and in one family (Mysididae) bear gills projecting freely into the water. A postabdominal somite bears appendages which with the telson form a caudal fin. The use of this fin causes the animal to swim backward as do crayfishes and lobsters. This order includes a number of pelagic marine forms and the family Mysididae some species of which inhabit fresh water. *Mysis relicta* occurs in the

Great Lakes at considerable depths and is identical with specimens found in similar lakes of northern Europe.

III. Order Stomatopoda

In the Stomatopoda, the posterior three thoracic segments bear complete biramous appendages which are used in swimming, while of the five anterior to these all but the first bear appendages modified as prehensile maxillipeds. The terminal segment of these prehensile appendages folds into a groove of the preceding segment as a knife blade folds into its handle.

The carapace is short, for at least the posterior four segments of the thorax are not included within it. Antennules and stalked eyes are borne on two movable, independent somites at the anterior extremity of the head. Gills are borne on the abdominal appendages. These are chiefly burrowing forms living in mud. Squilla (Fig. 102), Gonodactylus, Chloridella are characteristic genera.

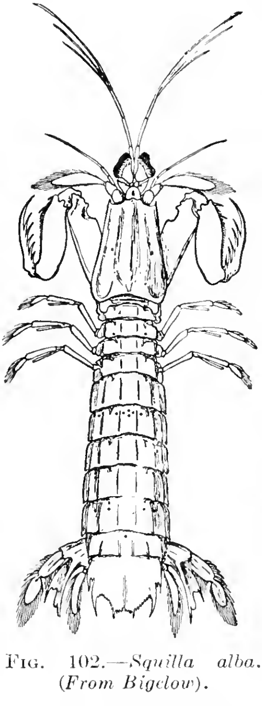

Fig. 102.—*Squilla alba.* (*From Bigelow*).

IV. Order Decapoda

The lobsters, crayfishes, shrimps, and crabs agree with the Schizopoda in having a carapace covering the entire cephalothorax. The head bears stalked eyes, antennules, antennae, mandibles, and two pairs of maxillae. Of the thoracic appendages, the anterior three pairs are modified as maxillipeds while the remaining five pairs are locomotor and lack an exopodite. All of the walking legs bear either pinchers or claws. The first pair of walking legs, which are known as the chelipeds, bear extremely strong pinchers termed the chelae. One jaw of the pinchers is the movable distal segment of the endopodite called the finger, while the other jaw is an immovable outgrowth from the next to the last segment forming the thumb.

The Decapoda have marked powers of regeneration. If an appendage is removed, a new one begins to develop beneath the old shell but does not become evident externally until the shell is shed at the next molt. Injury is frequent in nature, and consequently the claws are rarely of equal size. An injured claw is autotomously broken off by the animal at a special joint where there is but little exposed to heal over.

Abdominal Appendages.—Most of the abdominal segments bear small biramous appendages termed swimmerets, except in the crabs (Fig. 103) which have a rudimentary abdomen. The appendages of the sixth abdominal somite are enlarged and with the telson from a powerful tail fin. In the males, the first and second abdominal appendages are highly modified as a copulatory organ for the transfer of sperm. In the females, the swimmerets serve as a place for the attachment of the eggs during development.

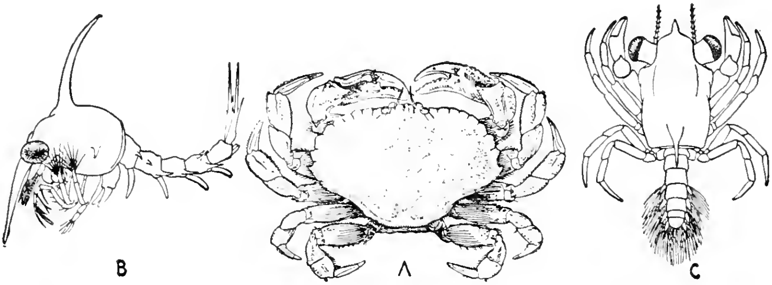

FIG. 103.—The rock crab, *Cancer irroratus*. *A*, adult male, about one-fourth size; *B*, larva in zoea stage; *C*, larva in megalops stage. (*After Rathbun*).

Respiration.—Gills are borne on the basal joints of certain of the maxillipeds and legs and on the body wall. These are usually contained within a branchial chamber formed by the overhanging lateral folds of the carapace. A process of the second maxilla becomes modified as a gill bailer the action of which pumps water through the gill chamber. The gill chamber retains water, thus keeping the gills moist and permitting decapods to remain out of water for some time without injury to the gills. In some crabs, the branchial chamber has become modified as a lung in correlation with terrestrial habits.

The circulatory system is of the open type. The heart lies within a pericardial sinus in the dorsal region of the thorax. Five arteries arise from the heart. Three of these pass anteriorly to the organs of the head and thorax, one passes along the median dorsal line of the abdomen, and the last is directed ventrally either from the posterior boundary of the heart or as a branch from the posterior vessel soon after the latter leaves the heart. Blood is received into the heart from the pericardial sinus through openings in the heart wall called ostia. The capillaries of the arteries allow the blood to pass into a large sternal sinus. In the thorax, offshoots from the sternal sinus pass into each gill as an afferent branchial vessel or vein. Within the branches of the gills, each afferent vein communicates with an efferent branchial vein from which the blood is returned to the pericardial sinus.

Digestive System.—From the mouth opening between the mandibles on the ventral surface of the head, the digestive system passes as a short tube, the esophagus, into a spacious chamber termed the stomach. The latter is divided into two regions: a large anterior sac, the cardiac chamber, which bears a chitinous organ for grinding food; and a smaller posterior pyloric chamber. The intestine, which proceeds from the pyloric chamber, receives the ducts from the two lateral hepatopancreases. On the wall of the cardiac chamber, there are frequently hard, rounded masses of lime, the gastroliths.

Excretory Organs.—Within the head, near the base of each antenna, lie the excretory organs, the green glands. Each discharges to the exterior by a pore located on the base of the antenna.

The central nervous system consists of a ventral chain of ganglia the number and disposition of which are correlated with the extent of the development of the abdomen. A brain, near the anterior extremity of the body, communicates with the ventral chain of ganglia by means of a pair of circumesophageal connectives. Six thoracic and six abdominal ganglia comprise the chain, except in the crabs, which have a rudimentary abdomen and here the entire ventral chain becomes fused to form a single ganglionic mass.

Reproduction.—The gonads frequently consist of two lateral and a single median lobe from which a pair of ducts lead to the genital openings on the ventral surface of certain walking legs. The eggs undergo superficial cleavage and give rise to either a larva or a young adult the larval stages of which are all passed through while in the egg. Considering the relative uniformity in structure of the adult decapods, there is a surprisingly great number of larval forms. Typically, the larva which leaves the egg is a zoea. From this develops a mysis stage (Fig. 95 *A*) with even the thoracic appendages biramous. In later development, the exopodites of these biramous thoracic appendages disappear (Fig. 95 *C*) leaving the unbranched walking legs of the adult. In the crabs, the thoracic appendages of the zoea, which are later destined to become the walking legs, develop in the free-swimming larva as rudimentary budlike appendages only (Fig. 103) and never acquire the biramous condition characteristic of the mysis. Thus in the crabs the mysis stage has been eliminated and the zoea in passing to the adult form involves a more advanced type of larva which has been called the megalops (*C*). Some of the prawns have the zoea preceded by a nauplius and metanauplius and thus show unique combinations of larvae of both the lower and the higher crustaceans.

V. ORDER AMPHIPODA

Almost all of the Amphipoda are aquatic. Characteristically, the body is compressed laterally. The common name of beach fleas or sand fleas is due to the leaping movements with which they spring into the air when out of the water. The head bears six pairs of appendages. There are seven segments in the thorax. The first of these bears a pair of small appendages which function as maxillipeds.

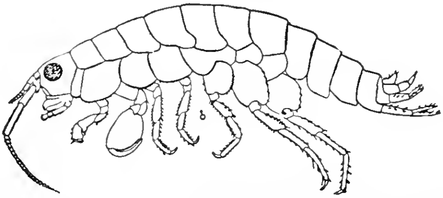

FIG. 104.—An amphipod, *Orchestia palustris*. (*After Kunkel*).

In the anterior region of the thorax, the sides of the body are frequently prolonged ventrally by epimeral plates which are borne upon the legs and serve to enclose the gills or gill sacs. In the same region, scales from the two sides of the body frequently enclose a brood pouch ventral to the ventral body wall. Within this pouch, eggs and the young are carried.

The abdominal appendages are of two types. On the anterior three somites of the abdomen are borne biramous feet with many joints and numerous hairs. Posterior to these the appendages are biramous but the branches are not segmented and form springing organs. Gammarus and Hyallela are common fresh-water genera, while Orchestia (Fig. 104) and Caprella are marine.

VI. ORDER ISOPODA

A dorsoventral flattening of the body is characteristic of most isopods. The first thoracic segment is coalesced with the head. Though the body superficially shows sharp marks of segmentation, there is a tendency for the abdominal somites to fuse. All of the abdominal appendages are similar and usually biramous. Gills are borne on the ventral side of the abdomen and in the terrestrial species are capable of utilizing moist air for respiration. A brood sac is borne ventral to the thorax as in the amphipods.

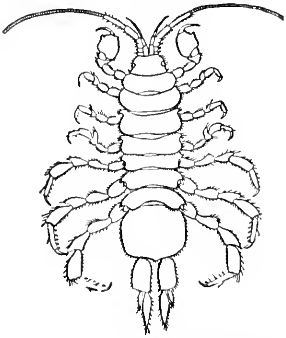

FIG. 105.—A fresh-water isopod, *Asellus communis*. (*After Kunkel*).

Isopods, or sow bugs or pill bugs as they are called popularly, are found in both fresh-water (Asellus, Fig. 105) and salt-water (Idotea) habitats, and a number of genera are terrestrial (Porcellio, Oniscus). In these last, the head bears but a single pair of antennae.

Very great degeneracy has accompanied the acquisition of the parasitic habit in a number of forms.

OUTLINE OF CLASSIFICATION

Phylum Arthropoda.—Segmented; with jointed, paired appendages; chitinous exoskeleton.

- I. **Class Crustacea.**—Skeleton limy; two pair antennae; chiefly aquatic.
  - *a.* **Subclass Trilobita.**—Exclusively marine; fossil only; two longitudinal grooves separate body into three lobes. *Triarthrus.*
  - *b.* **Subclass Phyllopoda.**—Most appendages leaflike.
    - 1. **Order Branchiopoda.**—Ten or more pairs trunk appendages; usually with carapace. *Apus, Lepidurus, Estheria, Limnadia, Limnetus, Artemia, Branchinecta, Eubranchipus.*
    - 2. **Order Cladocera.**—Not more than six pairs trunk appendages; usually a carapace including all but head. *Daphnia, Leptodora Polyphemus, Sida, Pleuroxus, Chydorus, Bosmina, Moina.*
  - *c.* **Subclass Copepoda.**—No carapace; trunk appendages biramous, four or five pairs; no appendages on abdomen.
    - 1. **Order Eucopepoda.**—No compound eyes. *Cyclops, Epischura, Diaptomus, Ergasilus, Lernaea.*
    - 2. **Order Branchiura.**—Two compound eyes. *Argulus.*

d. **Subclass Ostracoda.**—Carapace over whole body; two pairs trunk appendages. *Cypris, Candona.*

e. **Subclass Cirripedia.**—Marine; attached; usually enclosed by calcareous plates. *Lepas, Balanus.*

f. **Subclass Malacostraca.**—Twenty or twenty-one somites; all except last bear paired appendages.

1. **Order Phyllocarida.**—Marine; thoracic appendages leaflike. *Nebalia.*

2. **Order Schizopoda.**—Eyes stalked; gills thoracic; trunk appendages biramous. *Mysis.*

3. **Order Stomatopoda.**—Eyes stalked; gills abdominal. *Squilla, Gonodactylus, Chloridella.*

4. **Order Decapoda.**—Carapace covers cephalothorax; five pairs uniramous legs on thorax. *Cambarus, Astacus, Homarus, Crago, Peneus, Palaemon, Palaemonetes, Cancer, Callinectes, Carcinus, Gelasimus, Libinia, Macrocheira, Upogebia, Pagurus, Emerita, Hemigrapsus.*

5. **Order Amphipoda.**—Laterally compressed; gills thoracic; two types of abdominal appendages. *Gammarus, Hyallela, Orchestia, Caprella, Amphithoe.*

6. **Order Isopoda.**—Dorsoventrally depressed; gills abdominal; abdominal appendages (except uropods) similar. *Asellus, Mancasellus, Idothea, Porcellio, Oniscus.*

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CHAPTER XIV

PHYLUM ARTHROPODA (EXCLUSIVE OF CRUSTACEA AND INSECTA)

Class 2. Acerata

The horseshoe crabs, spiders, scorpions, mites, a number of degenerate forms, and some important extinct animals which are known only from fossil remains are grouped as a class to which the name Acerata is applied. This name signifies the lack of antennae common to all of the members of the class. The body usually consists of a cephalothorax and abdomen, though in the mites these two divisions are not separated. Six pairs of appendages upon the cephalothorax are arranged about the mouth. The bases of one or more pairs of these appendages are modified to serve as mandibles. The abdomen is composed of a variable number of somites which, in the embryo, bear appendages, but these are lost or highly modified in the adult, except in the Xiphosura.

Many modifications of the respiratory organs are found in this group. Gills occur on the abdomen of some but correlated with the air-dwelling habit the gills become drawn into the body where they are found as lung books which open to the exterior through narrow slits. In some instances, the lung books are replaced by tracheae which penetrate to all parts of the body as in the insects.

The basal segment of the abdomen bears the genital opening. In development, there is no metamorphosis.

Subclass GIGANTOSTRACA

The extinct eurypterids and the horseshoe crabs appear strikingly like Crustacea. In details of organization and in development, however, they show an intimate relationship with scorpions and other Acerata and are consequently recognized as constituting a subclass to which the name Gigantostraca has been applied.

Of the six pairs of cephalothoracic appendages, the first are preoral, and the remaining five pairs, which are for walking, have their bases modified as masticating organs. In addition to a pair of lateral compound eyes, the cephalothorax bears a pair of median ocelli.

Members of the order Eurypterida have a small cephalothorax and a large twelve-jointed abdomen. These forms flourished during past geological ages and in structure seem to be intermediate between the scorpions and the members of the order Xiphosura, of which Limulus, the horseshoe crab, is the only living example. In Limulus, the telson is long and spikelike. The abdomen bears six pairs of appendages of which the first forms a broad, flat operculum which overlaps the following five pairs of platelike appendages, each of which bears a gill. Upon hatching from the egg, the young Limulus is said to be in the trilobite stage (Fig. 106) because of its resemblance to the organisms of that group.

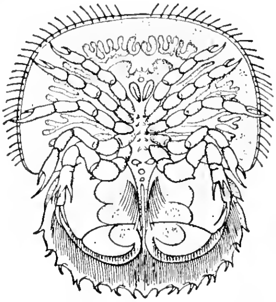

FIG. 106.—Ventral view of trilobite larva of *Limulus polyphemus*. (*After Kingsley*).

Subclass ARACHNIDA

Scorpions, spiders, mites, harvest men, and some less commonly known Acerata are grouped under a common subclass Arachnida. Most of these are air-breathing forms in which the cephalothorax bears one pair of pedipalps lateral or immediately posterior to the mouth and a pair of preoral appendages termed the chelicerae. In addition to these appendages, four pairs of walking legs are just as characteristic of the arachnids as three pairs are for the insects. As an exception to the foregoing, it should be noted that as a rule young mites have but three pairs of legs (Fig. 108 *C*), and in some gall mites only two pairs of legs are found.

True jaws are entirely lacking. Few arachnids swallow solid objects. The chelicerae and pedipalps are frequently modified for crushing the prey, and in some instances the bases of some of the walking legs serve the same function. Usually, only the body juices of the victim are taken into the stomach and this is accomplished by action of a muscular sucking stomach.

Some species of arachnids are eyeless, but more commonly there are from two to twelve simple eyes. Body form and structure are so highly variable in the members of this subclass that they will be discussed under the more important orders individually.

I. Order Scorpionida

Scorpions are tropical and subtropical in their distribution, occurring in the United States only in the southern part. Some look much like crustaceans, for in addition to the four pairs of walking legs there are a pair of large chelate pedipalps which are easily mistaken for legs. The chelicerae also bear chelae. Posterior to the cephalothorax, which bears the appendages, is the abdomen. This is conspicuously divided into two regions. Seven broad somites continue backward from the cephalothorax as the preabdomen and these are followed by a series of six somites of smaller size which constitute the postabdomen. The terminal somite of the postabdomen bears a sharp spine known as the sting with which a pair of poison glands are associated. This serves as an effective organ for killing insects upon which the scorpions feed and produces wounds painful even to man. Lung books occur in the last four somites of the preabdomen on the ventral wall of which they open as paired spiracles. From three to six pairs of eyes are commonly borne on the cephalothorax. A pair of comblike organs of undetermined function (Fig. 107), referred to as the pectines, occur on the ventral wall of the second preabdominal somite.

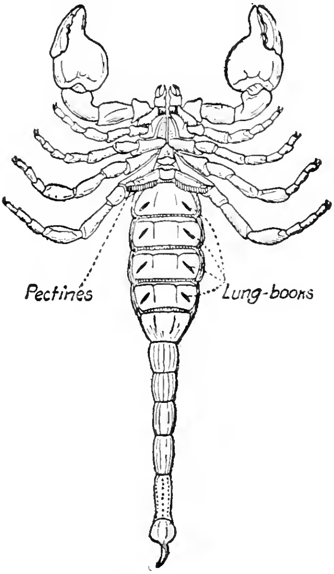

Fig. 107.—A scorpion (Pandinus) from ventral surface. (*From Versluys and Demoll*).

II. Order Araneina

Spiders are the most popularly known representatives of the arachnids and comprise the order Araneina. The body is divided by a deep constriction between the cephalothorax and abdomen.

The four prominent pairs of legs not only serve for walking and jumping but the posterior pair also aid in the formation of the characteristic silken webs. Except in members of one family, the abdomen is saclike, unsegmented, and joined to the cephalothorax by a narrow stalk. At the caudal end, the abdomen bears a small conical portion which represents a greatly reduced postabdomen.

Spinning organs are located on the ventral surface near the caudal extremity of the abdomen and consist, usually, of three pairs of spinnerets. These are fingerlike in form and are thought to represent rudiments of two pairs of abdominal appendages. Spinning tubes are distributed over the terminal portion of each spinneret and through these the fluid is expelled, which, upon contact with the air, hardens to form silk. An additional spinning organ known as the cribellum occurs in some spiders. This consists of a median, ventral, sievelike plate anterior to the spinnerets bearing very numerous spinning tubes.

The tarantulas (Eurypelma) and the orb weavers (many genera in the subfamily Araneinae) are among the extremely numerous representatives of this order.

III. ORDER ACARINA

The mites and ticks have a broad, unsegmented abdomen which is not constricted at its union with the cephalothorax. As a consequence the entire body appears saclike, though in some instances cephalothorax and abdomen are distinguishable. The part usually termed the abdomen includes two somites which in reality belong to the thorax. Frequently, the segments bearing the chelicerae and pedipalps are more or less distinct from the rest

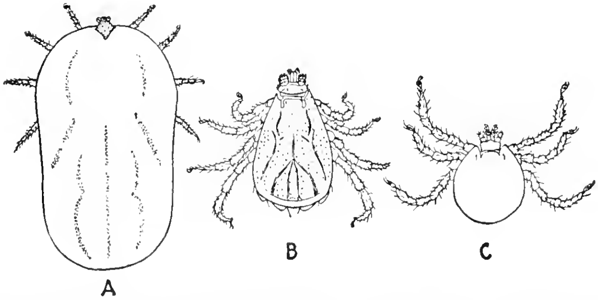

FIG. 108.—Acarina. *Boophilus annulatus*, the tick which carries Texas fever; *A*, female; *B*, male; *C*, young with only three pairs of legs. (*After Banks*).

of the body and are then designated as a beak or rostrum. Though the typical number of legs is four pairs, the newly hatched young usually have but three pairs (Fig. 108 *C*), and in one family (Eriophyidae) only two pairs are present in the adults.

The Acarina are of great biological importance. As parasites of man and of other animals they have great economic significance, and particularly the ticks, as carriers of disease-producing organisms, have received considerable attention. The southern cattle tick (*Boophilus annulatus*, Fig. 108) is the carrier of the organism (a protozoan, Babesia) which causes Texas fever or tick fever in cattle. The cattle industry in the South is greatly hampered by outbreaks of this disease. Through misunderstanding of the status of the generic name Boophilus, this tick has been referred to frequently in literature under the name Magaropus. The itch mites (*Sarcoptes scabei*, Fig. 109) burrow within the skin of man and produce a disease known as the itch. Mites of poultry and of other birds and of mammals also belong to the Acarina. The water mites (Hydrachnida) usually live as free adults in water, though the larvae are frequently encountered as parasites on molluscs, insects, and other animals.

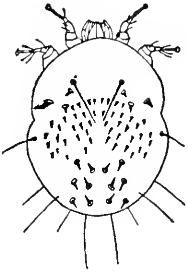

FIG. 109.—An itch mite, *Sarcoptes humanis*. (*After Banks*).

IV. OTHER ORDERS OF ARACHNIDA

There are a considerable number of small, though very sharply marked, groups of arachnids members of which fail to come within the foregoing descriptions of the larger groups. These are frequently recognized as comprising several independent orders. Chief of these are the Pseudoscorpionida. the Solpugida, the Phalangida, and the Linguatulida.

The **pseudoscorpions** resemble the scorpions except that there is no differentiation of pre- and postabdomen and no sting. The chelicerae function as spinning organs. Chelifer is a common genus.

The **Solpugida** are comparatively rare. The head bears a pair of extremely large chelicerae which serve for crushing the prey and long, leglike pedipalps which seem to function chiefly as feelers. The first thoracic segment is fused with the head, but the remaining three are free. The genus Eremobates is represented by several species in the southern United States.

The **Phalangida** are commonly called the harvest men or daddy-long-legs. As the latter name implies, the legs are inordinately long. Respiration is by means of tracheae. They feed largely on mites.

The **Linguatulida** or Pentastomida are arachnids the bodies of which have been so much modified in adaptation to the parasitic habit that the adults are distinctly wormlike. It is only through the larval stages that arachnidan relationships are evident, for the larva bears two pairs of legs. All but the hooks of these legs become lost in metamorphosis, and these are retained near the anterior extremity as organs of fixation. Numerous genera have been differentiated among these highly modified arachnids. Lungs, respiratory passages, and digestive system are usual seats of infestation. Pentastoma, Porocephalus. Armillifer, and Linguatula are characteristic genera.

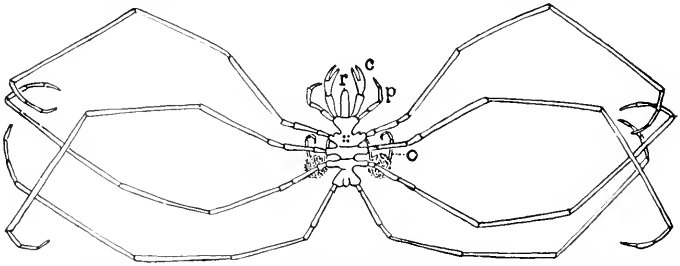

FIG. 110.—A male pycnogonid, *Nymphon stroemii*, *c*, chelicerae; *o*, ovigerous legs; *p*, pedipalpi; *r*, rostrum. (*After Kingsley, from Hertwig's Manual of Zoology, by Kingsley, courtesy Henry Holt and Co.*).

Class 3. Pycnogonida

The pycnogonids are small, exclusively marine arthropods which cling to seaweeds and hydroids and at times are dredged in great numbers from deep waters. The body consists of a cephalothorax and vestigial abdomen. The cephalothorax usually bears a terminal suctorial proboscis and seven pairs of jointed appendages. The appendages next to the proboscis bear chelae. Four pairs of appendages are usually used in walking. The third pair of appendages are in some species modified in the male for holding the eggs and are termed the ovigerous appendages. Reproductive organs open on the second segment of certain of the legs.

Though the abdomen is reduced to a mere vestige, without appendages and unsegmented, it contains two pairs of ganglia.

The pycnogonids rather closely resemble the spiders, but the presence of seven pairs of appendages is a character not encountered in the Arachnida. There is considerable question as to the proper place to include the members of this aberrant group. Nymphon (Fig. 110) is a characteristic genus.

Class 4. Tardigrada

The water-bears or tardigrades are microscopic organisms living in both fresh and salt water. The body is provided with four pairs of unsegmented appendages each of which bears terminal claws. The number and form of these claws differ in the various genera. Neither antennae nor mouth parts are found on the head. Thus far neither respiratory nor circulatory organs have been demonstrated.

A single gonad opens into the cloaca. The nervous system consists of a brain, a subesophageal ganglion, and a ventral chain of four ganglia.

There is a possibility that the tardigrades may belong to the annelid group, though the internal organization seems to indicate degenerate arthropod relationships. Macrobiotus is the name of one genus.

Class 5. Onycophora

The genus Peripatus and several other genera closely allied to it present such a mixture of annelidan and arthropodan characters that much significance is usually attached to these forms as a possible connecting link between the worms and the arthropods. The various species, which have been encountered in Africa, Australia, New Zealand, Central and South America, and the West Indies, comprise several genera which together seem to warrant their being grouped as an independent class.

The body is wormlike or caterpillar-like in form, without external marks of segmentation but with numerous paired legs the number of which varies in different species. Though these legs have a ringed appearance, they are not distinctly jointed, and in this respect they seem to be intermediate between the parapodia of worms and the jointed legs of arthropods. The metameric arrangement of the legs is paralleled by some features of the internal organization. Near each pair of legs, the ventral nerve cords bear a slight enlargement, though ganglia are not differentiated. The base of each leg carries a nephridial opening. Thus the nephridia are also metameric in their arrangement. The head bears three pairs of appendages. At the anterior extremity, it bears a pair of ringed antennae and behind these a pair of oral papillae. Two pairs of hooked plates within the mouth cavity have been regarded as mandibles. Spiracles in longitudinal rows, or scattered, communicate internally with respiratory tubes which are in the form of tracheae. The genital ducts, which are modified nephridia, opens just anterior to the anus. The Onycophora are viviparous. In habits, they are nocturnal, living during the day under bark and in decaying wood.

Class 6. Myrientomata

The minute arthropods included within the single order Protura are recognized by some as comprising an independent class to which the name Myrientomata has been applied. The representatives of this class are somewhat similar to the Thysanura in body form, but antennae and cerci are both lacking. The thorax bears three pairs of legs and on the abdomen there are the vestiges of three pairs of appendages.

Most of the described species live in humus. The group has been so recently established and the species have been so little studied that relationships to other arthropods have not been well established.

THE MYRIAPODS

In the older literature, a number of tracheate arthropods with numerous legs were considered as a single class under the name Myriapoda. These forms present so many differences in structure that at least four distinct classes are now recognized under the names Diplopoda (Class 7), Chilopoda (Class 8), Symphyla (Class 9), and Pauropoda (Class 10).

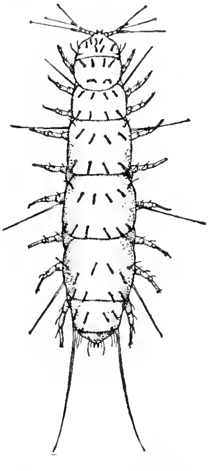
FIG. 111.—*Pauropus huxleyi.* (*After Kenyon*).

The Chilopoda show many evidences of close relationship with the insects, while members of the genus Scolopendrella, which represent the Symphyla, show remarkable combinations of diplopodan and insectan characters. Except for the eleven or twelve pairs of legs, Scolopendrella very closely resembles the insects belonging to the order Thysanura. The pauropods are minute forms usually under one millimeter in length (Fig. 111) bearing nine pairs of functional legs.

Class 7. Diplopoda

The thousand-legs, or millipeds, are terrestrial arthropods with the body consisting of two regions, head and trunk. The cylindrical body is composed of numerous segments each of which seems to bear two pairs of short legs inserted near the median line of the body. The apparent doubling in number of appendages on each somite, which is so uncommon in arthropods, seems to be explained on the grounds that each seeming segment is, in reality, a double somite, for on the ventral surface the double nature of the skeletal plates is evident. Some few of the segments, especially near the anterior extremity, remain simple and bear but a single pair of legs each. The distinct head bears a pair of short antennae, usually lateral groups of ocelli, and the mouth parts. The latter comprise an unpaired upper lip, a pair of mandibles, and one or two additional pairs of jaws.

Most millipeds are harmless and of little importance, for they feed largely upon decaying vegetable matter. Julus, Glomeris, Polyxenus, and Spirobolus are commonly encountered genera.

Class 8. Chilopoda

The centipeds are terrestrial tracheate arthropods with only two body regions in which each of the flattened trunk somites bears but a single pair of legs. On the first trunk somite these are modified as poison jaws bearing ducts of poison glands. The legs are lateral in position and are not borne near the median ventral line as in the diplopods.

The antennae are long and many jointed. The head also bears a pair of mandibles and two pairs of maxillae. The common house centiped, *Scutigera forceps*, is a representative of this class. Lithobius, Geophilus, and Scolopendra are other genera.

OUTLINE OF CLASSIFICATION

Phylum Arthropoda, continued.

II. Class Acerata.—No antennae; body usually cephalothorax and abdomen; usually six pairs cephalothoracic appendages; abdomen almost always lacking appendages in adult; respiration by abdominal gills, lung books or tracheae.

a. **Subclass Gigantostraca.**—Marine; gills on abdominal appendages two to six; a pair compound eyes and one pair median ocelli.

1. Order Xiphosura.—Cepthalothorax large; abdominal somites fused, terminating in a long spine. *Limulus.*

2. Order Eurypterida.—Extinct; cephalothorax small; abdomen twelve jointed; *Eurypterus, Pterygotus.*

b. **Subclass Arachnida.**—Chiefly air breathers; usually four pairs walking legs, one pair pedipalps, and one pair chelicerae on cephalothorax.

1. Order Scorpionida.—Abdomen segmented, posterior region slender, flexible, frequently ending in sting; pedipalps and chelicerae chelate. *Buthus, Uroplectus, Pandinus, Centrurus.*

2. Order Araneina.—Deep constriction between cephalothorax and abdomen; abdomen unsegmented; spinning organs near caudal extremity. *Epeira, Agalena, Eruypelma, Lycosa.*

3. Order Acarina.—Broad, unsegmented abdomen, not constricted at union with cephalothorax; frequently with piercing beak. *Boophilus, Sarcoptes, Dermacentor, Hydrachna.*

4. Order Pseudoscorpionida.—Resembling scorpions but abdomen not divided into two regions; no sting; chelicerae spinning organs. *Chelifer.*

5. Order Solpugida.—Extremely large chelicerae on head. *Emerobates, Galeodes, Datames.*

6. Order Phalangida.—Four pairs exceedingly long legs. *Liobonum, Phalangium.*

7. Order Linguatulida.—Wormlike; two pairs degenerate legs of which only claws remain. *Pentastoma, Linguatula, Armillifer, Porocephalus.*

III. Class Pycnogonida.—Marine; abdomen vestigial; cephalothorax bearing terminal suctorial proboscis and seven pairs very long legs. *Nymphon, Pycnogonum.*

IV. Class Tardigrada.—Microscopic; aquatic; four pairs unsegmented appendages, each with terminal claws. *Marcobiotus.*

V. Class Onycophora.—Wormlike; numerous, short, paired legs, ringed but not jointed; tracheae. *Peripatus.*

VI. Class Myrientomata.—Minute; antennae and cerci lacking.

1. Order Protura.—Three pairs legs on thorax; three pairs vestigial legs on abdomen. *Accrentomon.*

VII. Class Diplopoda.—Terrestrial; body cylindrical; numerous segments, mostly bearing two pairs of short legs inserted near midline. *Julus, Glomeris, Spirobolus, Polyxenus, Parajulus.*

VIII. Class Chilopoda.—Terrestrial; tracheate; numerous segments; body flattened; single pair legs to a somite, lateroventral. *Lithobius, Geophilus, Scutigera.*

IX. Class Symphyla.—Eleven or twelve pair legs. *Scolopendrella.*

X. Class Pauropoda.—Minute; nine pairs legs. *Pauropus.*

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CHAPTER XV

PHYLUM ARTHROPODA *(Concluded)*

Class 11. Insecta

The members of this class are air-breathing arthropods with distinct head, thorax, and abdomen, except in some larvae and in some modified adults. They have a single pair of antennae, three pairs of thoracic legs, and usually one or two pairs of wings in the adult stage. The opening of the reproductive organs is near the caudal extremity of the body. As chiefly terrestrial animals, insects have become adapted to the greatest variety of conditions and have been so successful that they outnumber all other animals both in species and in individuals. Practically every possible relationship of organic beings is found in a list of the habits of insects. Both as predators and as parasites upon plants and upon other animals and in their relations to the spread of disease, they occupy a position of economic importance not excelled by any other animal group.

Types of Metamorphosis.—Most insects in their development pass through conspicuous changes in form between the time that the individual leaves the egg and the time it reaches full maturity. In these changes, which are collectively known as metamorphosis, the young lacks some structures or organs characteristic of the adult. These are attained only in later development, and frequently some structures or organs of the young are distinctive and become lost during later development. Numerous gradations occur between the condition in which the young is but slightly different from the adult and that in which it bears practically no resemblance to the adult to which it later transforms. As a consequence, several different types of metamorphosis are recognizable. Insects which undergo a complete metamorphosis, that is, those which involve profound changes in form (Fig. 112) and have a pupal stage which is usually inactive, are said to be holometabolous or are referred to as the Holometabola. Egg, larva, pupa, and imago are all distinguishable in the Holometabola. The organs of one stage in development are not necessarily carried over directly into the following stage. Many of the larval organs disappear as a result of phagocytic or chemical action, and through histogenesis new organs of the adult are formed. In the Holometabola, wings and legs of the adult do not develop externally on the larva but develop internally as imaginal buds (Fig. 126) which emerge and become free only later in development.

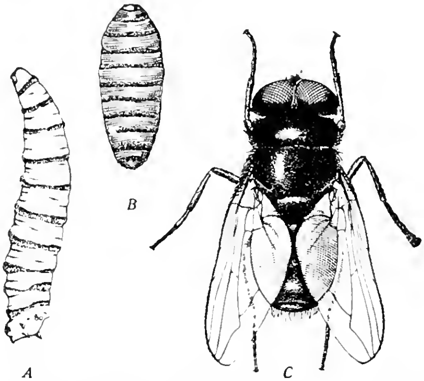

FIG. 112.—Development of a holometabolous insect. *A*, larva; *B*, puparium; *C*, imago of fly (*Phormia regina*). (*From Folsom's Entomology, courtesy of P. Blakiston's Son and Co.*).

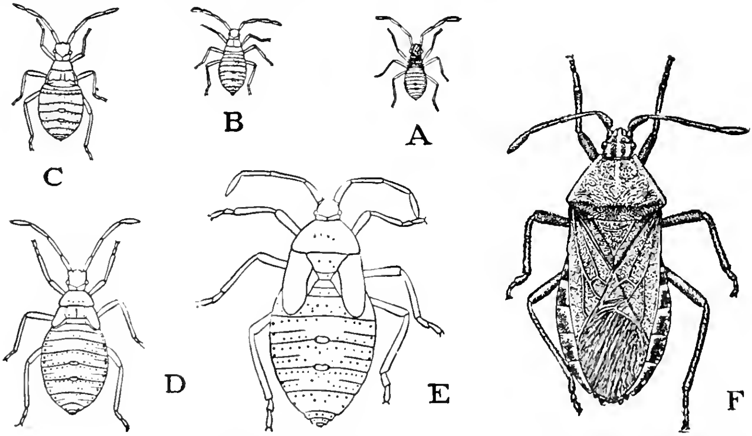

FIG. 113.—Development of a heterometabolous insect. Six successive instars of the squash bug, *Anasa tristis*. *A* to *E*, nymphs; *F*, adult or imago. (*From Folsom's Entomology, courtesy of P. Blakiston's Son and Co.*).

The Heterometabola include those insects which transform without a true pupal period. The stages between the egg and the imago fairly closely resemble the general bodily structure of the imago (Fig. 113) and are termed nymphs. The lack of functional wings usually differentiates the nymph from the adult, but external wing pads from which the wings later develop are characteristic of many nymphs.

The Thysanura and Collembola are wingless and throughout life retain essentially the forms they have at hatching. There are some changes, but these are so inconspicuous that many are inclined to refer to the insects of these two orders as the Ametabola.

Appendages of the Head.—The head of an insect bears a single pair of antennae, the eyes, and the mouth parts (Fig. 114). These last comprise an unpaired labrum or upper lip, a pair of mandibles, the hypopharynx, the maxillae, and the labium. The labium, or lower lip, is in reality a second pair of maxillae of which at least the basal portions are fused along the median line. Both the maxillae and the labium are composed of several distinct sclerites and bear palpi, designated respectively as maxillary and labial palpi. All of the appendages of the head are articulated with immovable parts, forming the head capsule.

Modifications of Mouth Parts.—The mouth parts are subject to numerous modifications of form and function. As described above, they are suited for holding and chewing food, but in many groups only liquid food is taken and in these groups some of the mouth parts are modified to form a sucking tube. The most significant of these suctorial modifications are found in the Hemiptera, the Lepidoptera, the Diptera, and the Hymenoptera.

The jointed beak of the Hemiptera consists of a troughlike labium partially covered above at its base by the labrum. Within this trough the elongated maxillae and mandibles are ensheathed.

The long, coiled proboscis of the Lepidoptera is formed of parts of the maxillae, while the labrum, mandibles, and labium are greatly reduced or wanting.

The female mosquito has a piercing type of mouth parts. The labrum and epipharynx are fused and with the hypopharynx form the food channel. The linear mandibles and maxillae are used in puncturing the skin of the victim, while the labium forms a sheath for the other mouth parts.

Suctorial and mandibulate functions are both performed by the mouth parts of the honeybee. The mandibles are used for cutting, crushing, and other purposes as in strictly mandibulate types. The maxillae and the labial palpi are folded to form a sheath within which an elongated portion of the labium serves as a lapping tongue.

Sclerites and Sutures of the Head.—A considerable number of sclerites are fused to form the head capsule. In many instances, the sutures separating the sclerites are visible, and both sutures and sclerites bear definite names. In the generalized insects, as, for example, in the Orthoptera, the epicranial suture (Fig. 114) is one of the best and most constant landmarks. This suture originates at the margin of the occipital opening (through which the vicera of the head and thorax are continuous) and extends as a median suture over the dorsal surface of the head. At its ventral extremity, the epicranial suture bifurcates, and thus its form is that of an inverted Y. Between the arms of the Y, there is an unpaired sclerite, called the front, which in most insects bears the median ocellus. An additional unpaired sclerite ventral to the front is the clypeus. On its ventral border the clypeus is articulated with the labrum or upper lip.

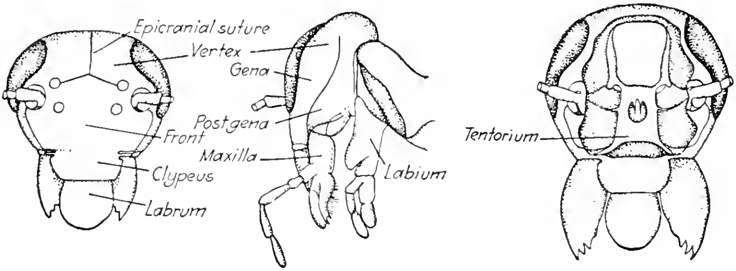

Fig. 114. Fig. 115. Fig. 116.

Figs. 114–116.—Morphology of an insect head. 114, frontal aspect of cockroach head; 115, lateral aspect; 116, dissected frontal aspect. (*Redrawn from Comstock with permission*).

The several paired sclerites of the head, including the lateral surfaces (Fig. 115) and the parts dorsal to the arms of the epicranial suture, constitute what is termed the epicranium. The vertex is just dorsal to the front. It is between the compound eyes and usually bears the paired ocelli. The occiput extends between the vertex and the occipital foramen mentioned above. The genae and the postgenae form the lateral portions or cheeks of the epicranium. A chitinous supporting structure called the tentorium (Fig. 116) is found within the head. This usually consists of a central plate from which two or three pairs of arms pass to the exoskeleton of the head.

Sensory Organs.—Both simple (Fig. 117) and compound eyes are found in the insects. Compound eyes occur on the sides of the head in most adult insects except some generalized and some parasitic forms. Practically all insects which have a complete metamorphosis (the Holometabola) have simple eyes in the larval stage.

Aside from the eyes, other sensory organs in insects show remarkable lack of uniformity in location upon the body and in localization and organization. Even the antennae, which are popularly thought of as tactile, have in some species of insects no less than seven different types of microscopic sensory organs. Most of these are probably tactile, auditory, and olfactory, though frequently it has been necessary to assume functions upon the basis of structure and position and by interpretation of the reactions of the insect rather than to determine them by actual demonstration. Hairs of graduated lengths upon the feathery antennae of mosquitoes and moths vibrate in response to sound waves through a range which in the mosquito coincides with the pitch of the mosquito hum. Another type of auditory organ, of widely different structure and location, is the tympanal organ, which consists of a drumlike membrane for the reception of sound waves. In the common grasshoppers, this tympanal organ is located on each side of the first abdominal somite, while in katydids a similarly constructed organ is found on the second joint of each front leg.

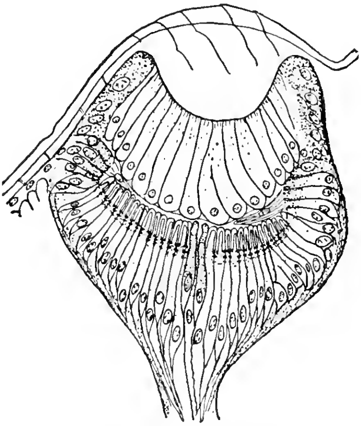

Fig. 117.—Median ocellus of a beetle, Acilius. (*After Patten*).

End organs of taste and smell are usually located on the maxillary palpi, the epipharynx, the hypopharynx, and the labial palpi, but they are not restricted to any given organ or appendage.

Tactile organs and sensory structures of undetermined functions occur as modifications of the body covering over most of the surface of an insect.

Somites of the Head.—As in the other arthropods, paired appendages are considered as a criterion for the determination of the number of somites in the head. There are evidences that the eyes, antennae, mandibles, maxillae, and labium are borne on distinct segments. Beyond this, study of early embryological stages furnishes evidence that an additional pair of appendages starts to form in the embryo but never becomes functional or is at most rudimentary in the adult. Traces of this embryonic appendage are between the fundaments of the antennae and mandibles. Thus in position these correspond to the second antennae of the crayfish and may be homologized with them. It thus seems probable that the head of an insect has resulted from the fusion of six original somites only five of which have retained their appendages or their rudiments in the adult insect.

The Thorax.—The thorax is the region which bears the legs and wings when they are present in the nymphs and adult insects. It is composed of three more or less firmly united segments. In order, backward from the head, these are: prothorax, mesothorax, and metathorax. In many insects, the last two bear wings. Each somite is composed of several sclerite groups which, according to their location, are recognized as comprising the parts of the tergum (dorsal wall), sternum (ventral wall), and pleura (lateral walls).

The Legs.—Each leg is articulated to the wall of the thorax partly by means of small articular sclerites in the region of articulation of the sternum and pleuron. Five divisions or regions are recognizable in each leg. From articulation outward, these are: coxa, trochanter, femur, tibia, and tarsus. In most insects, each region is but a single segment except the tarsus which commonly has five segments. Correlated with highly variable modifications in function the legs display numerous modifications in form.

The Wings.—In many of the winged insects the mesothorax and the metathorax each bears a pair of wings, but in instances of only one pair of wings these are usually borne upon the mesothorax. Rudiments of the second pair of wings are frequently present as halteres or balancing organs upon the metathorax. Some striking modifications of the primitively membranous wings occur. In beetles, the mesothoracic wings are thickened, horny structures, the elytra, modified for the protection of the metathoracic wings and the dorsal surface of the body. In some of the bugs, the bases of the front wings (hemelytra) are horny while the tips are membranous. In Orthoptera, the entire front wings are somewhat thickened and are designated as tegmina.

Structure and Origin of the Wings.—Typically, the wings of insects are two pairs of membranous appendages which develop as saclike folds of the body wall. In fully developed wings, this saclike nature is obscured because the two walls of the sac become so closely applied that they appear as a single membrane, and a very delicate one at that. A framework upon which this membrane is supported is composed of hollow tubes or veins which originate as modified tracheae of the respiratory system. In the early stages of development, the tracheae are accompanied by nerves and blood-filled outgrowths of the body cavity. The pattern which this framework assumes is spoken of as the "wing venation." In most groups, this pattern shows remarkable constancy among the members of the same species. Between genera and the larger groups there is usually considerable variation in the details of arrangement of the veins. It seems, however, that the wings of all insects are directly homologous and that their principal individual veins are likewise homologous. Comparisons of numerous wings and the study of the arrangement of the tracheae

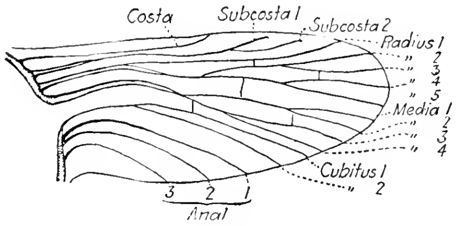

FIG. 118.

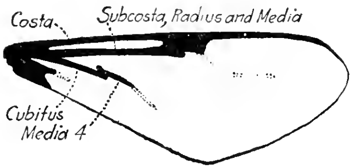

FIG. 119.

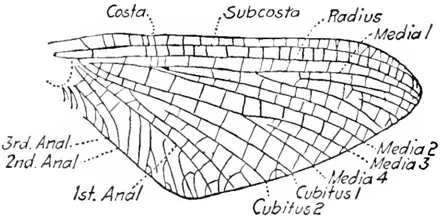

FIG. 120.

FIGS. 118–120.—Insect wing venation. 118, hypothetical primitive type of wing venation with cross-veins added; 119, forewing of Hyptia showing great reduction in number of veins; 120, forewing of a May fly showing great increase in number of veins. (*Redrawn from Comstock with permission*).

before the wings reach their functional form have led to the formulation of a hypothetical plan of primitive venation (Fig. 118) from which all wing patterns are derivable, though all of the homologies are not readily observable by the beginner in this study.

Plan of Wing Venation.—In the plan of primitive venation (Fig. 118), eight principal veins are present and most of these may be branched. Beginning with the anterior margin when the wings are at right angles to the body, these veins are: costa, subcosta, radius, media, cubitus, first anal, second anal, and third anal. Changes from the hypothetical type occur either by the addition of new veins or branches (Fig. 120) or through the reduction in the number of veins (Fig. 119) through atrophy or through coalescence of two or more veins. Cross-veins frequently connect two of the longitudinal veins.

The Abdomen and Its Appendages.—The abdomen bears a highly variable number of segments in the various groups of insects. A study of insect embryology shows that the abdomen consists normally of eleven segments, but in later development adjacent segments may coalesce and in some adults they are telescoped one with another. The wall of each segment is composed of a tergum and a sternum united by a pair of pleural membranes. The segments are typically without appendages and are approximately similar except near the caudal extremity where certain segments are more or less modified. In the Thysanura, rudimentary abdominal limbs occur and in the embryos of some other insects each segment may bear a pair of rudimentary appendages. Those of the first seven abdominal segments are usually lost during early embryonic life, while the last two or three pairs frequently persist to form the genitalia—the genital claspers of the males and the ovipositors of the females (Fig. 121).

A true ovipositor consists of three pairs of valves, called gonopophyses, arranged as a dorsal and a ventral pair surrounding an inner pair. The inner valves form a channel through which the eggs are conveyed. There is strong evidence that these three pairs of gonopophyses represent the paired appendages of the eighth, ninth, and tenth abdominal somites and are serially homologous with the thoracic legs. In the Hymenoptera, the ovipositor is modified as a stinging organ and has poison glands associated with it.

The inner pair of gonopophyses of the males are modified as an intromittent organ or cirrus, while the other two pairs of gonopophyses are frequently modified as clasping organs which function in copulation. Through many groups the external genitalia show remarkable constancy of form within each species. In many instances, the forms grouped together as single species by early writers are at present being separated into several clearly distinct species chiefly on the basis of characters furnished by a study of the male genitalia. The last (eleventh) abdominal somite in many insects bears a pair of caudal appendages known as cerci. Both in form and in function these are highly variable.

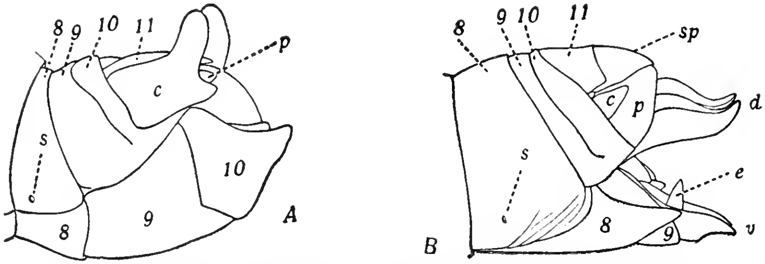

FIG. 121.—Extremity of abdomen of a grasshopper, *Melanoplus differentialis*; *A*, male; *B*, female. The terga and sterna are numbered. *c*, cercus; *d*, dorsal valves of ovipositor; *e*, egg guide; *p*, podical plate; *s*, spiracle, *s.p.*, suranal plate; *v*, ventral valves of ovipositor. (*From Folsom's Entomology*).

The Respiratory System.—The internal organization of insects is essentially like that of the other arthropods already described. The respiratory system offers one of the most conspicuous points of difference from most other arthropodan groups. This is a system of air tubes, called tracheae and tracheoles, which carries air to all parts of the body (Fig. 122). This system is in communication with the outside air through openings in the body wall, termed spiracles, of which there are normally ten pairs, arranged, as a rule, two pairs on the thorax and eight on the abdomen. Opening and closing of the spiracles for the admission or expulsion of air is under control of the insect. From each spiracle a short trachea commonly leads to a main tracheal trunk of which there is one on each side of the body. Branches from these two main trunks penetrate into even the minutest parts of the body.

Tracheae arise as invaginations of the body wall, and consequently the infolded chitinous covering of the body continues within the tracheae as a chitinous internal lining of the tubes. Within the tracheae the chitin is not disposed in a uniform layer but assumes the form of a coiled spiral thread lining the inner wall of the tracheal vessel. Small tubes lacking the spiral chitinous threads form the most minute subdivisions of the tracheal system and are designated as tracheoles. Tracheae in some insects may become modified as enlarged sacs which serve as air reservoirs.

Modifications of the Respiratory System.—Of the typical respiratory system with spiracles communicating directly between the tracheae and the outside air, there are many modifications. In the Collembola, and in many aquatic larvae, there are no specialized organs for respiration, for that function is performed directly through the skin. Gills occur in many aquatic nymphs and larvae. These are of two distinct types, tracheal and blood gills. In the former, lateral or caudal evaginations of the body wall are furnished with numerous tracheae which are continuous with the vessels of the tracheal system within the body and conditions suitable for a respiratory exchange are thus provided. Even a portion of the digestive tract may be appropriated as a respiratory organ, as in the rectal tracheal gills of the dragonfly nymphs. Blood gills are usually threadlike evaginations from the body wall of aquatic insects. The spaces within these gills are in direct communication with the fluid-filled body cavity, and through the delicate walls of the gills a respiratory exchange is made possible without requiring the presence of tracheal tubes.

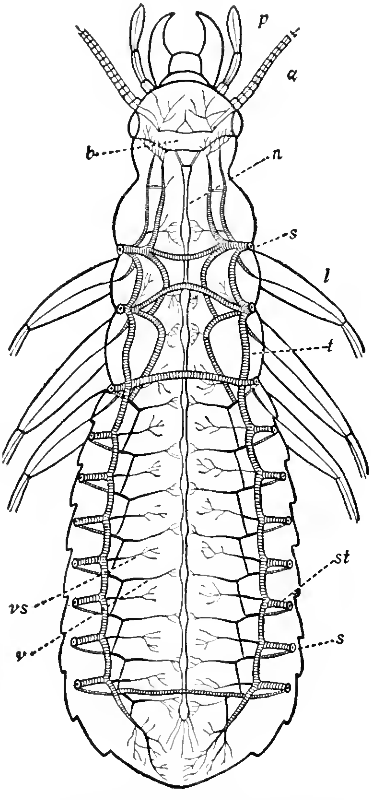

Fig. 122.—Tracheal system of an insect. *a*, antenna; *b*, brain; *l*, leg; *n*, nerve cord; *p*, palpus; *s*, spiracle; *st*, spiracular branch; *t*, main tracheal trunk; *v*, ventral branch; *v.s.*, visceral branch. *(From Folsom's Entomology, after Kolbe)*.

A few insects, especially larvae, live under conditions which exclude the presence of oxygen. This is especially true of some larvae living in very deep water. Under these conditions, anaerobic respiration is carried on.

The central nervous system consists of a brain or supraesophageal ganglion and a longitudinal nerve chain ventral to the digestive tract as in all of the Arthropoda. Typically each thoracic and abdominal somite is supplied with a ganglion (Fig. 123 *A*). It is, however, a very common thing for the nerve chain to undergo concentration as a result of which the ganglia in adjoining somites fuse (*B* and *C*). The extent of such longitudinal condensation of the nervous system varies greatly in different arthropods and even shows remarkable changes during the life of a single individual. Thus, in the honeybee, the larva has a distinctly metameric nerve chain through the thorax and abdomen but when the adult stage is reached the thoracic ganglia has been reduced to two and the abdominal to five.

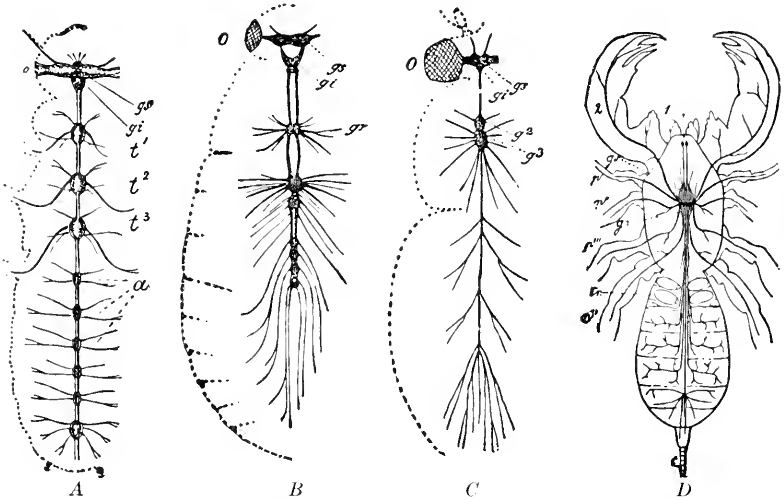

FIG. 123.—Different degrees of concentration of the ventral cord of arthropods (*from Gegenbauer*). *A*, termite (*after Lespès*); *B*, water beetle (*after Blanchard*); *C*, fly (*after Blanchard*); *D*, scorpion spider (*after Blanchard*). *a*, abdomen; g^2, g^3, ganglia of ventral cord; *gi*, infraesophageal ganglion; *gs*, supraesophageal ganglion; *o*, eye; *p'p''*, walking feet; *tr*, lung books; 1, chelicerae; 2, pedipalpi. (*From Hertwig's Manual of Zoology by Kingsley, courtesy Henry Holt and Co.*).

A sympathetic nervous system may include a ventral trunk associated with the central nervous system and some very delicate branches near the dorsal part of the body. Branches from this sympathetic system pass chiefly to the dorsal vessel and the tracheal system.

Embryology.—The fertilized egg nucleus of insects undergoes several divisions and many of the resulting nuclei migrate from the yolk mass to the superficial layer of the cytoplasm. The layer of cytoplasm containing these nuclei undergoes cleavage and there is thus formed a layer of cells surrounging a central yolk mass (Fig. 8). This is essentially a blastula stage in development, and the cell layer is frequently termed the blastoderm. Those nuclei which remain within the yolk become surrounded by cytoplasm and are designated as the yolk cells. The blastoderm becomes thickened in one region and forms the germ band from which the ventral surface of the embryo later develops. The course of this development follows two different paths in different insect groups. These are known as the overgrown and the invaginated types of development.

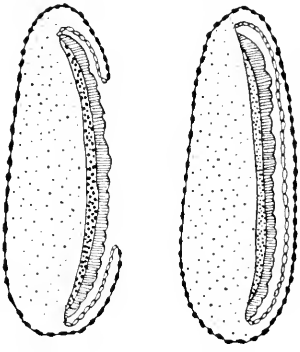

FIG. 124.—Two diagrammatic sagittal sections to show overgrown type of insect development. A, amniotic folds starting to cover the germ band (cross-lined); B, amniotic folds completed. (*From Korschelt and Heider*).

The former of these involves much the less complicated narration. The germ band (Fig. 124) sinks below the surface of the surrounding blastoderm to form a groove. As this groove deepens, the walls of the blastoderm fold up over the germ band. When the folds of the blastoderm meet, they fuse and the double wall thus formed encloses a cavity known as the amniotic cavity, which lies between the germ band and the before-mentioned double wall. The outer layer of cells, which comprises the outer margin of the double wall, is termed the serosa and is directly continuous with the blastoderm surrounding the yolk. The inner cell layer, which lines the amniotic cavity, is termed the amnion. The cells of the germ band comprise a layer of ectoderm adjacent to the amniotic cavity, and underlying this ectoderm is a mass of cells which represent both the entoderm and the mesoderm of the embryo. The surface of this germ band, which represents the ventral surface of the developing insect, becomes traversed by a series of transverse grooves to form the primitive segments of the embryo. Upon these primitive segments, paired outgrowths occur. These are the fundaments of the legs and other appendages. At first these appendages are all similar in appearance, but as development proceeds some of them become suppressed while the remaining ones begin to take on different forms depending upon the kind of appendage each is to form in the adult animal. Lateral and dorsal parts of the insect body result from the growth and extension of the germ band after the ventral structures have been laid down.

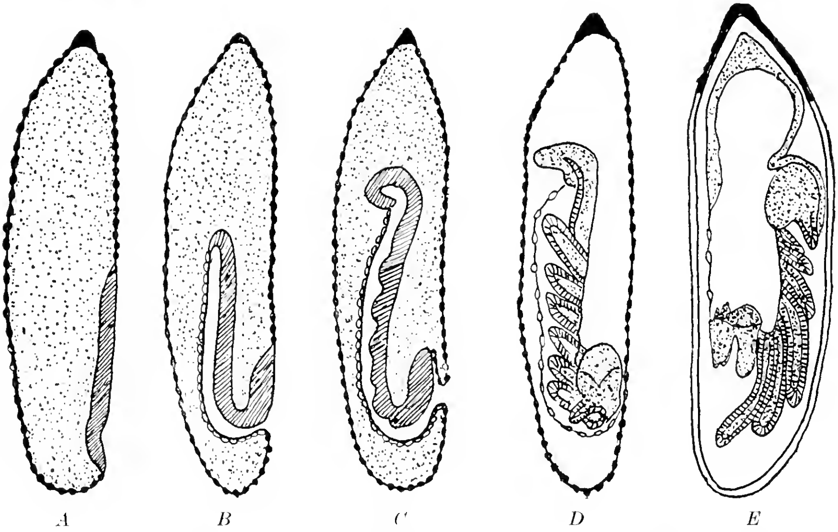

Fig. 125.—Diagrammatic median sections to illustrate development of a Libellulid egg. *A*, development of germ band; *B*, invagination of germ band; *C*, development of amniotic fold; *D*, closure of opening into amniotic cavity and development of rudiments of appendages; *E*, migration of embryo from amniotic cavity back to surface of egg. (*From Korschelt and Heider after Brandt*).

A much more complicated condition exists when the germ band undergoes invagination. In such an instance, the germ band makes its appearance (Fig. 125 *A*) on the posterior ventral surface of the egg. One end of the germ band sinks into the underlying portion of the egg and, submerged within the egg, begins to grow forward (*B*) toward the anterior pole of the egg, carrying with it the blastoderm which was attached to the posterior margin of the band. Practically all of the germ band thus invaginates. The cavity formed within the egg by this invagination is the amniotic cavity, one wall of which is composed of the cells of the germ band and the other of the blastoderm cells. The amniotic cavity is then cut off from the exterior. The invagination which has brought the germ band to lie within the amniotic cavity has seriously altered the orientation of the germ band with reference to other parts of the egg. The ventral surface of the embryo, which originated on the ventral external surface of the egg, has by invagination come to be directed toward the dorsal side of the egg. While in this position (*C* and *D*), the embryonic appendages make their appearance. Soon afterward the embryo is everted from the amniotic cavity and again comes to lie (*E*) on the surface of the egg with its parts coinciding with the original orientation of the egg.

In the embryological development of most of the Orthoptera, Trichoptera, Diptera, Lepidoptera, and Hymenoptera the overgrown or superficial type of germ band occurs. The invaginated or immersed type of germ band is found in some of the Odonata, Coleoptera, Thysanoptera, and Hemiptera. Transitional conditions, which seem to be intermediate between these two types, are found in some of the Coleoptera and the Orthoptera.

Internal Metamorphosis and the Imaginal Discs.—In both types of metamorphosis, an insect undergoes radical changes in its internal organization before reaching the adult stage. Even organs which are found alike in the larval and adult stages do not pass over directly from one stage to the next, but through the processes of histolysis the tissues of one stage disappear and entirely new tissues are formed through the processes known as histogenesis. In the Holometabola, where entirely new structures such as wings and legs become functional for the first time with attainment of the adult form, still more profound internal changes accompany metamorphosis. During the larval and pupal stages, rudiments of the legs, wings, and head appendages make their appearance as internal buds. These imaginal discs, as they are called, are, throughout their early development, enclosed within internal sacs (Fig. 126 *A*). The hypoderm of the body wall invaginates to form these sacs, and the rudiment of the appendage which each of these sacs contains lies thus within a cavity entirely surrounded by hypoderm. Only in later development (Fig. 126 *C* and *D*) do the sacs open and allow the developing appendages to extend freely beyond the body surface. The development and transformation of the imaginal discs of the head and thorax of a fly are shown in Fig. 126.

In the classification of Linnaeus, there were but seven order of insects recognized. These have, in recent times, been subdivided and new orders have been added until today there are more than twenty well-defined orders of the Insecta. In the accompanying table, these orders are listed and some of the characters which are usually considered of importance are furnished for each.

The Importance of Insects.—Insects have such significance in their relations to human welfare that it is difficult to give even a faint idea of their importance without going into extensive details, for volumes have been written upon this phase of the subject. The honeybees, the silk worms, and the various insects which pollinate flowers are so widely and so popularly known that their importance need not be discussed here. As pests, the Hemiptera occupy a place of extreme significance, with the chinch bug (*Blissus leucopterus*) as a menace to grain farming and the hundreds of species of scale insects which attack trees and shrubs as outstanding examples. Among the Diptera, numerous disease-carrying flies and mosquitoes, the Hessian fly which destroys growing grain, and warbles and bots which attack domestic animals demand attention. The gipsy moth in its ravages upon shade trees, the coddling moth in its molestation of the apple industry, and the numerous cutworms are examples of important Lepidoptera. Extensive damage to cotton crops through the boll weevil and much of the injury by wood-boring and leaf-eating insects are attributable to species of the Coleoptera.

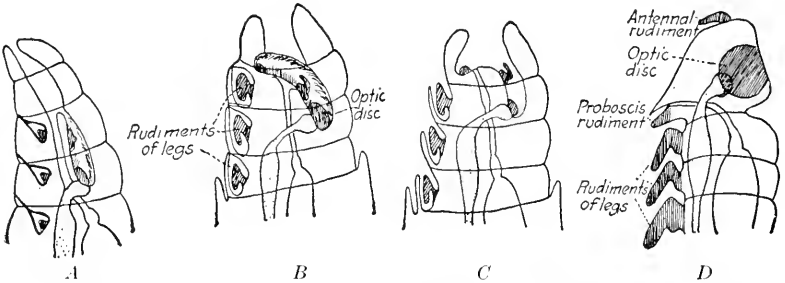

FIG. 126.—Development and transformation of imaginal discs in head and thorax of *A*, larva; and *B–D*, pupa of a fly (Musca). Wing rudiments are omitted. (*From Korschelt and Heider after VanRees, in part after Kowalevsky*).

Predaceous insects such as the coccinelid beetles, the dragon flies, and the Neuroptera aid materially in checking the damage

THE ORDERS OF INSECTS

A Table Showing Some of the More Important Characters

Order	Examples		Metamorphosis	Mouthparts	Wings	
	Genera	Common names			Mesothoracic	Metathoracic
Thysanura	Lepisma	Silverfish	Ametabolous	Mandibulate	Wanting	Wanting
Collembola	Sminthurus	Snowfleas	Ametabolous	Mandibulate	Wanting	Wanting
Orthoptera	Blatta Melanoplus	Cockroaches, grasshoppers	Heterometabolous	Mandibulate	Tegmina (leathery)	Membranous folded
Dermaptera	Forficula	Earwig	Heterometabolous	Mandibulate	Elytra or wanting	Membranous
Plecoptera	Pteronarcys	Stonefly	Heterometabolous	Mandibulate	Membranous	Membranous (larger)
Isoptera	Termes	White ants	Heterometabolous	Mandibulate	Membranous	Membranous
Embioptera	Embia	Embiids	Heterometabolous	Mandibulate	Membranous or wanting	Membranous
Corrodentia	Psocus	Book lice	Heterometabolous	Mandibulate	Membranous or wanting	Membranous
Mallophaga	Menopon	Bird lice	Heterometabolous	Mandibulate	Wanting	Wanting
Odonata	Anax, Lestes	Dragon flies	Heterometabolous	Mandibulate	Membranous	Membranous
Ephemerida	Hexagenia	Mayflies	Heterometabolous	Atrophied in adult	Membranous narrow, fringed with hair or wanting	Membranous (smaller)
Thysanoptera	Thrips	Thrips	Heterometabolous	Suctorial		Similar
Hemiptera	Anasa, Aphis	Squash bug, plant lice	Heterometabolous	Suctorial	Hemelytra or membranous or wanting	Membranous or wanting
Anoplura	Pediculus	Sucking lice	Heterometabolous	Suctorial	Wanting	Wanting
Coleoptera	Phyllophaga	Beetles	Holometabolous	Mandibulate	Elytra	Membranous
Neuroptera	Corydalus	Dobson fly	Holometabolous	Mandibulate	Membranous	Membranous
Trichoptera	Molanna	Caddice flies	Holometabolous	Suctorial or rudimentary in adult	Membranous	Membranous
Hymenoptera	Apis, Lasius	Bees, ants	Holometabolous	Mandibulate and suctorial	Membranous	Membranous
Strepsiptera	Xenos	Twisted-wings	Holometabolous	Mandibulate	Rudimentary or wanting	Membranous
Mecoptera	Panorpa	Scorpion flies	Holometabolous	Mandibulate, usually at end of beak	Membranous or wanting	Membranous
Lepidoptera	Cecropia, Pieris	Moths and butterflies	Holometabolous	Suctorial	Membranous	Membranous
Siphonaptera	Ctenocephalus	Fleas	Holometabolous	Suctorial	Wanting	Wanting
Diptera	Musca, Anopheles	Flies and mosquitoes	Holometabolous	Suctorial	Membranous	Wanting (halteres)

wrought by other insects. Likewise, the Hymenoptera and the Diptera include many useful species in that they are frequently parasitic upon and cause the death of destructive insects. The illustrations cited here are only a start in the enumeration of the economically significant representatives of the class Insecta.

OUTLINE OF CLASSIFICATION

Phylum Arthropoda, concluded.

XI. Class Insecta.—Three pairs legs; typically two pairs wings; head, thorax, and abdomen distinct; air breathers.

See table giving The Orders of Insects (page 251).

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(See general references at close of Chapter I)

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CHAPTER XVI

PHYLOGENY

The phylogenetic relationships of organisms and the origin of species have long been topics of more than ordinary interest to the scientists. In one of the most generally maintained of the early conceptions, all relationship was denied because it was thought that each species represents an independent, supernatural creation. Such was the belief of even so recent a scientist as Linnaeus whose systematic arrangement and classification of plant and animal forms furnish one of the best clues to an interpretation of the relationships of many groups. The natural origin of species from preexisting forms of life was first given strong support through the careful observations and generalizations of Charles Darwin, whose book "The Origin of Species" (1859) has probably been more discussed than any other scientific work. With the establishing of a belief in blood relationship between the various animals a new interest in the tracing out of that relationship became awakened.

At the present time there is much ground for lack of agreement concerning how species have come into existence, but among scientists there is no longer any doubt that species, genera, and even phyla have moved in a continuous procession since the inception of life upon this planet. Even a cursory survey of the evidences from paleontology reminds one of the facts that there are no indications of vertebrates existing upon the earth prior to the Lower Cambrian period of the earth's history and that in general the faunas of successive periods and eras show advancement beyond, yet undeniable relationships with, the preexisting life. It is not the purpose of this chapter to prove the ideas of continuity, development, and differentiation of living organisms, for this is now accepted by those who take the trouble to examine the evidences as little less than axiomatic. Nor yet is it the intention to speculate upon the methods or processes whereby these changes in the fauna and the creation of different types have come about. Even among the best informed scientists there is yet lack of unanimity of opinion upon these subjects.

Any attempt at classification in some measure endeavors to convey a concept of relationships. Groupings or separations are based upon an evaluation of the presence or the lack of common characteristics. In most instances, the possession of fundamental characters of like nature is considered as indicative of common origin. As pointed out in Chapter I, the student is apt to consider phylogenetic relationships from an erroneous point of view, assuming that such kinship is traced between the respresentatives of present-day groups when as a matter of fact all of our existing organisms have undergone some degree of differentiation since their origin. It is only through common ancestry that these lines of kinship are traced.

Sources of Evidences of Relationships.—Obviously, then, relationships are not observable directly but frequently may be deduced from evidences gathered from one or more of the fields of paleontology, embryology, and comparative anatomy. Even these available sources in many instances give incomplete and inconclusive evidence of an organism's past history. Present-day organisms are but points in the lines of evolutionary progress. The source and the termination of any such line are but rarely discovered. Through the study of paleontology and embryology we gain a glimpse here and there of portions of the path which various organisms have followed in reaching their present position in the lines of evolutionary progression.

Paleontology.—In determining a broad outline of the course of phylogeny among the invertebrates, the science of paleontology offers but fragmentary and woefully incomplete data concerning the ancestral forms. The Cambrian period has disclosed representatives of most of the important invertebrate phyla, yet, as Schuchert has said, more fundamental evolution had taken place up to this time than subsequently. Studies of the rocks of the preceding periods have revealed rare and imperfect and almost indecipherable evidences of a marine fauna including Protozoa and marine worms. Careful studies by Walcott and others have furnished evidences that practically all of the important invertebrate phyla were represented in the fauna of pre-Cambrian times. However, the pre-Cambrian rocks, have undergone metamorphosis under the action of heat and pressure until their contained fossil remains have become concealed or even destroyed.

Because of the incompleteness of our knowledge of pre-Cambrian life, the evidences of phylogeny of the lower forms must be sought elsewhere than in the fossil remains. In individual development, there is furnished a clue to racial history.

Law of Biogenesis or Recapitulation Theory.—Since the days of von Baer, it has been commonly observed that individuals which are markedly different in appearance as adults have stages in their development when the embryos have much the same appearance. Structures common in the embryos may have entirely different fates in the adults. The works of Haeckel did much to popularize this observation. So generally did the principle seem possible of application that it became expressed as a law—the law of biogenesis—which states that ontogeny is a brief recapitulation of phylogeny.

Thus, since the course of individual development more or less faithfully repeats racial history, those characters which make their appearance early in the course of embryology represent a heritage from distant ancestors of the race. The more distant the ancester the more numerous the offspring and consequently the more kinds of animals which would display these ancestral characters in the course of their development. Such ancestral characters, appearing early in development, have been designated as palingenetic. In contrast with them, the coenogenetic characters which appear relatively late in development are more nearly specific and are found in much smaller groups of individuals.

There are many instances in which individual development has become so highly modified that the operation of the biogenetic law seems to be invalidated. In some instances, the processes of ontogeny become so much shortened that whole chapters in the racial history are deleted in the course of individual genesis. These and other facts have led some investigators to discredit the law entirely. It seems probable, however, that in many instances valuable light is thrown upon racial history through the study of embryology.

Gastraea Theory.—Since a gastrula stage occurs in the ontogeny of practically all of the Metazoa, Haeckel propounded a theory which endeavored to establish a blood relationship among all Metazoa through an ancestral form to which he applied the name of the Gastraea. The Gastraea he considered as a hypothetical form which in its adult organization displayed the characters of the embryonic gastrula. Though our present-day Coelenterata are said to stand on a level of the gastrula in fundamental structure, the Gastraea must not be confused with the members of this phylum which have undergone great differentiation and progressive evolution.

Without discrediting the Gastraea theory in the least, it represents but a step in the right direction, for do not the various gastrulae in turn originate from a single-celled condition—the fertilized egg? Thus all animal forms may be traced along their phylogenetic paths to a common ancestry in the one-celled organisms. Even Haeckel recognized this fact at the time when he propounded his Gastraea theory. The highways between the single-celled condition and our highly diversified Metazoa have not all been surveyed. Only here and there are there indications of the routes which have been taken. Some forms seems to have gone on an independent track early in the course of evolution. Others seem to have traveled long distances together before the ancestral stock became diversified to form various ones of our present-day animals. Some groups, such as the Vertebrata, the Echinoderma, and the Nematoda, seem to have left no conclusive evidence regarding their relationships to any other animal groups. Speculation plays a large part in attempting to decipher the faint lines which are directed toward but never lead to any of the usual roads of descent.

In the following section attention will be directed to some of the probable ancestral lines of the various Metazoa.

Metazoan Tendencies in the Protozoa.—In Chapter II, it has been pointed out that within the Protozoa are found many indications of tendencies toward metazoan conditions. Chief among these are colony formation and isolation of germ plasm from the soma. Much has been made of the parallel between the blastula stage in the embryology of the Metazoa and the spherical arrangement of the cells in colonies such as Volvox. By one or several paths of descent, the ancestors of our present-day Protozoa have probably been the direct or indirect source of all the remaining phyla.

Porifera.—While the Porifera are usually accorded a position as the lowest phylum of the Metazoa, there are numerous reasons for assuming that the simplicity of sponges is attributable, in part, to degeneracy or to regressive evolution. The collared cells of the Porifera are the exact counterparts of the bodies of choanoflagellates. Proterospongia (Fig. 50 *B*) is a unique form which might resemble the ancestors of the Porifera and in an unusual manner stands intermediate between the choanoflagellates and the sponges. This is a colony of choanoflagellates the individual cells of which are embedded in a matrix containing some wandering amoeboid cells comparable to the mesoderm cells of the Porifera.

Coelenterata and Ctenophora.—It seems probable that a primitive gastrula of the nature of Haeckel's hypothetical Gastraea must have had its origin from a spherical protozoan colony by more rapid growth at one pole which resulted in an invagination to form the gastrula cavity. The planula, some modification of which occurs in the larval development of all coelenterates and of the ctenophores, is but a slightly modified gastrula. As MacBride has so well pointed out, a planula-like ancestor probably gave origin to the members of these two phyla.

Plathelminthes.—In an earlier chapter it has been stated that Coeloplana (Fig. 59) and Ctenoplana are modern genera which stand intermediate between the flatworms and the ctenophores and display an odd combination of characters some of which had come to be considered as diagnostic for one or the other of the two phyla. It is probable that through some form similar to these the flatworms have arisen from a ctenophore-like stock.

Nemathelminthes.—Regarding the origin and relationships of the Nemathelminthes practically nothing is known. They stand as peculiarly isolated forms whose history has never been deciphered. The method of mesoderm formation seems to preclude any close relationships with the annelid worms. There has been no well-founded theory advanced as to their origin or relationships. The numerous suggestions which have been offered are based upon very minor details.

The Trochophore.—In the Plathelminthes, Coelhelminthes, Molluscoidea, Trochelminthes, and Mollusca there occur larvae which represent only minor modifications of the trochophore (Fig. 76). Thus a direct relationship among these forms is traceable through the larvae. In fundamental structure the trochophore has been likened to the ctenophores. It has already been shown that the Plathelminthes are readily derivable from the ctenophore organization. The metamerism, so characteristic of the Annelida, has been explained on various grounds. Beginnings of metamerism are readily observable in the flatworms. Regular arrangement of the lateral diverticula from the digestive tract and orderly disposition of the gonads between these diverticula indicate preparations for a segmentation of the body before the septa make their appearance as in the annelids.

Echinoderma.—The echinoderms offer but few clews to an explanation of their origin. Their radial symmetry is not primitive, and, since the larvae are bilaterally symmetrical throughout, it seems probable that the members of this group have evolved from a bilaterally symmetrical coelomate ancestor. MacBride has emphasized the fact that echinoderm larvae represent a primitive type not directly related to the trochophore. Echinoderm larvae show more resemblance to the tornaria larva of Balanoglossus than to any of the lower Metazoa. In some instances this fact has been utilized in tracing a possibile ancestry of the vertebrates through a line which passes back through the Enteropneusta (Balanoglossus) to a primitive type from which the echinoderms and the Enteropneusta have arisen.

Arthropoda.—The arthropods have many points in their morphology which are likewise shared by the annelids. Even the parapodia of the annelids are not so markedly different from the foliaceous appendages of the lower Crustacea. The Onycophora (Peripatus) were for a long time considered as worms, but closer investigation revealed characters which have been looked upon as diagnostic of the Arthropoda. Standing as they do, midway between the arthropods and the annelids, the Onycophora show a transition from one group to the other which may well be taken as indicative of a wormlike ancestry for the arthropods.

In this phylum there arises an interesting conflict between the evidences presented by embryology and morphology. On the basis of morphological study the arthropods seem to have their closest affinities with the elongate annelidlike forms, but in development all of the lower Crustacea pass through a characteristic larval form known as the nauplius. This larval form is very short and bears but three pairs of appendages. There is no conclusive method of weighing the relative merits of the two lines of evidence. It seems, however, that the nauplius might be an adaptation to a free-swimming existence and thus may have undergone changes a full record of which has not been retained in the much shortened history of the race which is presented by ontogeny. Some who see in the nauplius a significant ancestral form have considered it as a modified trochophore not fundamentally different in structure from some of our present-day rotifers. The swimming appendages of rotifers like Pedalion are thought by some to represent incipient arthropod appendages.

Ancestry of the Vertebrates.—Some of the most widespread interest in the blood relationships of animals centers around the question of the origin of the Chordata. Even though the vertebrates seem to have made their appearance at a time when a fairly complete picture of the fauna is observable through the fossil remains, there is little light thrown upon the origin of the vertebrates through the study of paleontology. Fossils of some of the heavily armored fishes, the Ostracoderms, closely resemble the fossil arachnids known as the Merostomata and our modern Limulus which some one has called a "living fossil." The study of comparative anatomy, however, seems to indicate that the vertebrates must have had a simpler beginning than this would indicate.

The three subphyla of the Prochordata, represented by Amphioxus (or Branchiostoma), Balanoglossus, and the tunicates, have characters which permit them to be classified with the Chordata yet in most instances display a low type of general organization which seems to relate them to the non-chordate forms. Each of these groups has been considered as a possible ancestral stock from which the true vertebrates have had their origin. Since these forms lie outside the scope of this textbook, their relationships to the problem of vertebrate phylogeny will not be considered in detail, but attention will be directed to some of the invertebrate groups through which the ancestry of the vertebrates has been derived by various investigators.

As has been pointed out in an earlier discussion, the Metazoa in general, including the Vertebrata, develop from a single cell, the zygote. Thus a possible ancestral history of the vertebrates leads back to the single-celled organisms. This relationship is so distant, however, that many attempts have been made to find satisfactory evidences of vertebrate geneology through the higher groups of the invertebrates. Early metamerism of the vertebrate embryos indicates that some segmented organism gave rise to the vertebrate line, but further than this the evidences are capable of broadly divergent interpretations. In consequence, numerous theories have been advanced. Space does not permit a detailed account of all of these but some of the more important ones have been chosen for discussion. The coelenterates, the nemertines, the annelids, and various arthropods have been championed as the possible origin of the vertebrate series.

Annelid Theory.—The metameric condition of annelids, the relation of their nephridia to the coelom, and the fundamental relationships of vascular and nervous systems to the digestive tract closely resemble the conditions found in the lower vertebrates and in vertebrate embryos. Semper and other investigators have shown that by inverting the position of the body of an annelid the fundamental systems are brought into almost complete harmony with their arrangement in the vertebrates. Such a shift in the orientation of the body is not at all uncommon in various animal groups. Many of the crustaceans and molluscs move with their ventral surface in a dorsal position. Even the notochord, which is distinctive for the Chordata, has a counterpart in the bundles of supporting fibers which accompany the annelidan nerve chain. Recent publications of Delsman have awakened a new interest in the annelid theory of vertebrate origin.

Nemertine Theory.—Hubrecht has maintained that the nemertines stand in the direct line of ancestry of the vertebrates. One of the chief arguments in favor of this theory is the possible homology between the proboscis sheath of the nemertine and the notochord of the chordate. The lateral nerve cords of the nemertine could assume a dorsal position as in the chordates without a complete change in the orientation of the body such as is necessitated in the annelid theory.

Arachnid Theory.—Patten has seen in the arachnids, especially in forms like the scorpions and Limulus, many points of structure in direct harmony with vertebrate organization. Through comparisons of these arachnids with fishlike Ostracoderms he has built up an elaborate theory showing a possible origin of the vertebrates from arachnidan ancestry.

Conclusion.—Each of the numerous theories, of which the foregoing are characteristic examples, is based upon a group of facts derived from studies in comparative anatomy and embryology. Yet no one theory depicts a satisfying genealogy of the vertebrate group. At most, the various hypotheses furnish ground for a belief in kinship between the vertebrate and the invertebrate. Kinship or common origin would explain most of the facts which have been arrayed as a proof or demonstration of vertebrate origin from the invertebrates.

Similarity in structure and development and even homologies between the members of two animal groups do not prove that one has originated from the other. At most, they point to a common heritage. Our various theories demonstrate undisputed interrelationships between the chordate phylum and the non-chordates, but the key to the ancestry of the vertebrates lies hidden, possibly lost, in some form of past ages which has been an ancestor alike to the vertebrates and the higher invertebrates and through which both of these groups have inherited the characters which they hold in common. A search for this ancestral form among the highly differentiated animal forms of today is little short of hopeless.

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