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Guides to the Museum of the Boston Society of Natural History.

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# GUIDE TO THE INVERTEBRATES

OF THE

## SYNOPTIC COLLECTION

IN THE MUSEUM OF THE  
BOSTON SOCIETY OF NATURAL HISTORY.

By J. M. ARMS SHELDON.

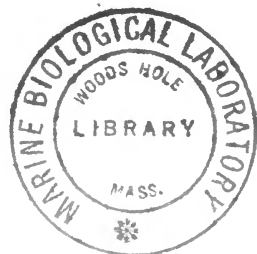
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## INTRODUCTION.

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IN many of our natural history museums one room is devoted to a Synoptic Collection of animals. The student who wishes to get a comprehensive view of the whole animal kingdom spends most of his time on such a collection, since it embraces representative forms of all the principal groups from the simplest protozoan to the most complex mammal; in other words, from the *Protamoeba* to man inclusive.

It may be truly said that mankind is seeking as never before for a rational explanation of the origin and the development of animal life upon our earth. The more strenuous this search, the more imperative is the demand made upon naturalists to present in their museums, so far as possible, the most advanced knowledge concerning these problems.

At the present time, therefore, it is not enough that a Synoptic Collection consist merely of specimens of animals effectively or artistically arranged. Neither is it sufficient that such a collection consist of species placed together by some arbitrary and artificial method.

The student of the New Zoology demands that relationship shall be the basis of classification, and that not only the descendants living to-day shall be represented, but also their primitive ancestors that existed in an early geologic age. Indeed, a genealogical classification of animals is the goal to be striven for constantly by the naturalist of the twentieth century. The recognition of the possibility of such a classification tends toward the unification of collections which have hitherto remained isolated. For instance, it has been customary to place

together all ancient animals existing in the form of fossils. These have been arranged stratigraphically, beginning with the fossils in the oldest strata and ending with those in the newest, or *vice versa*. For the purpose of historic geological study or for strictly palaeontological research, such collections are helpful. This arrangement has been, indeed, the only one possible up to within a very recent period. Even now there are naturalists who seriously question whether any other method of arrangement is possible. These maintain that our knowledge is not adequate to warrant an attempt at a natural classification of animals based upon genetic relationship.

It must be borne in mind, however, that a vast amount of material in the form of well proven facts has accumulated since 1859, when Darwin's *Origin of Species* gave a new directive impulse to biological research. This material is found largely, it is true, in an almost infinite number of papers in which isolated adult species are figured and described. But notwithstanding this fact, it is also true that of late years there has been a growing tendency toward considering the life history of the individual species described, and this study has led in turn to an investigation into the life history of the group to which the given species belonged. In this way the significant correlation existing between the development of the individual, known as ontogeny, and the development of its class, or phylogeny, have been discovered. When it is remembered that these correlations are proofs of relationship or of descent from a common ancestor, then one begins to realize how many trustworthy guides there are, all pointing toward the desired goal. Our artificial classifications of animals, therefore, are not due "so much to insufficient knowledge of their early stages as to insufficient attention to what is actually known and published regarding them," as Mr. Samuel H. Scudder<sup>1</sup>

<sup>1</sup> The Butterflies of New England, I, 1889, p. viii.

has already pointed out in the case of the arbitrary classifications of the Lepidoptera. When all this knowledge is brought together, assorted, and systematically used, then the sequence of life upon our planet will be demonstrated as never before. Then the isolation method of arrangement to which I have alluded will be relegated to the past and students will no longer receive the lasting impression that fossil forms are distinct creations having no connection with living organisms, but each museum will be in itself a revelation of the essential unity of all animal life.

It is true that many of our museums are so constructed that they are ill adapted for the demonstration of the evolution of inorganic and organic nature. But where this demonstration cannot be given with completeness, minor collections like a Synoptic Collection of geological or zoological specimens may point out the way to the desired end.

The following principles of classification Professor Alpheus Hyatt wished to have carried out in the Synoptic Collection of this Museum, of which he was Curator during the preparation of nearly all of this Guide.

First: In the arrangement of the material proceed always from the simple to the complex.

Second: So far as possible let each group be represented first by its primitive ancestors that lived in the pre-Cambrian, Cambrian, or early Palaeozoic times.

Third: From these primitive ancestors pass to the embryonic and larval stages of generalized members of the group existing to-day; and from these early stages to the adult stages which are invariably more specialized.

Fourth: From the generalized adult members in every group proceed to the specialized members which have reached their present condition through the law of specialization by addition.

Fifth: In some of the most impressive instances go still farther to those extremely specialized adults which have become so by the law of specialization by reduction.

We have attempted to carry out these principles in the different groups of invertebrates. With the increase of knowledge certain animals which are here described as primitive will doubtless be found to be reduced forms, while certain reduced forms may in reality be primitive. Notwithstanding these changes in the position of species, the principles of this genealogical classification will remain essentially the same.

In order to bring out these principles clearly and forcibly in the descriptive text of the Guide, it has been necessary to abandon altogether the use of certain terms, while the meaning of other terms has been restricted. Among those given up are the words "high," "low," "highest," "lowest." Textbooks and manuals have usually considered animals as either "high" or "low." Generally speaking, vertebrates have been studied first, as the "highest" representatives of animal life, and all other forms have been "low" in comparison. In other cases the study of a class has begun with the so called "lowest" forms; for instance, the Crustacea with the barnacles.

These classifications were the best that were possible at the time they were made, and they met the necessities of the period. But the time is now ripe, as we have already said, for a more natural system of classification which shall embody and set forth the history of animal life on our globe. In a genealogical classification that illustrates the broad natural relationships which bind animals together genetically there can be no "high" nor "low." There can be only simple, primary forms from which have been evolved in the process of the ages complex and secondary forms. This, in reality, is the fundamental principle of our classification. Granted that this is true, then the most profound knowledge is needed concerning the problems of heredity and of variation. Immense strides have been made the past quarter of a century, and epoch-making monographs on the development of certain animals have thrown strong light on these difficult problems.



We maintain that this new light should be reflected in our museums, especially in our Synoptic Collections; that here the workings of the law of heredity by which animals are bound together by blood relationship should be illustrated by specimens, drawings, models, by everything in brief, that can most strongly impress the student. This demonstration would be more effective had we a closer acquaintance with the ancestral fauna of pre-Cambrian and Cambrian times. The masterly researches of Walcott into the Cambrian and Lower Silurian rocks, and the invaluable investigations of Matthews in the Cambrian formations of New Brunswick prove how important are these sources for studies in evolution in a field hitherto almost unexplored.

Other terms which do not appear in this Guide are "degraded," "degenerate," "retrogressive," and "worm" as applied to the caterpillar stage of the Lepidoptera.

The first two, "degraded" and "degenerate," are not used for two reasons: first, because they are associated in the popular mind with moral considerations, and this association often leads to mental confusion; secondly, because we cannot see why an animal that has developed a part or an organ to the immense advantage of itself and its race should be called "degraded," even though many other organs have fallen into disuse or wholly disappeared in the process. In the case of parasites the use of these terms might be more allowable, were it not for the first reason stated.

The word "retrogressive" is not used because it is misleading, since animals do not in reality go back to a more primitive and generalized condition, however much they may appear to do so. This is proved by the position of the so called "retrogressive species" in a genealogical record which can never be among the ancestral trunk forms. It cannot be, because these species as a rule bear evidences of the evolutionary stages through which they have passed; and where such evidences are not apparent

to the eye, it is rational to infer that vestigial organs cannot be the same as rudimentary organs.

The use of the word "worm" is restricted to members of the subkingdom of Vermes. It is obviously misleading to apply it to such a specialized animal as a young butterfly or moth.

"Simple" and "rudimentary" are used only in describing primitive and generalized forms or organs.

"Direct development" applies, as we use it, to the mode of development of the more generalized members of a class. Some naturalists, on the contrary, use it in the sense in which we have used accelerated or abbreviated development; the latter we apply only to the mode of development of the forms specialized by addition or reduction.

Primitive forms are spoken of as primary, generalized, simple, fundamental; they have a primitive or a direct development, and some of their organs may exist as rudiments, hence the adjective rudimentary.

Specialized forms, on the other hand, are spoken of as secondary, differentiated, complex, adaptive; their development is either indirect (with a metamorphosis), accelerated (where the early stages are passed through quickly or skipped), or suppressed (where the advanced stages are omitted); some of their organs may exist as vestiges, hence the adjective vestigial.

The invertebrates or animals without a vertebral column are divided primarily into three divisions, the Protozoa, Mesozoa, and Metazoa. The Protozoa are represented in the collection by many forms, the Mesozoa by one species. The Metazoa are subdivided into nine large groups, the Porifera, Coelentera, Echinoderma, Mollusca, Vermes, Crustacea, Arachnozoa, Myriopoda, and Insecta. Some of these groups are again divided, as, for instance, the Insecta, where typical forms of sixteen orders are figured and described.

## THE SYNOPTIC COLLECTION.

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A Synoptic Collection of animals possesses one advantage over special collections, since it may illustrate on broad and general lines the principles of a natural classification. Our knowledge of the vast number of genera and species which make up many of the classes of the animal kingdom is not sufficient, as a rule, to enable us to group all the organisms of a given class according to their natural affinities, but in a Synoptic Collection, properly chosen specimens may be so arranged as to place before the student a more or less satisfactory demonstration of the principles that are based upon the genetic relationships of animals. A natural classification of all the species of the whole animal kingdom is, indeed, the goal of the natural philosopher, but this goal can be reached only through the tireless efforts of generations of devoted truth seekers.

It is a well known fact that certain animals are simpler in structure than others, and it is also most probable that the simplest forms living to-day are the nearest representatives of those primitive organisms which gave rise through countless ages and generations to animals of greater and greater complexity. For this reason these simplest forms are often spoken of as primitive or ancestral forms. Many of them are also called synthetic or generalized forms, since they combine, in essentially simple condition, certain structural characters that are found more developed in their descendants, and because this

further development was probably effected by a process of specialization.

This process of specialization may have followed along many lines of development in the successive generations of a species.

Thus, for example, not only the locomotive organs but also the mouth parts, sense organs, and skeletal structures may have become differentiated, while corresponding internal changes may have taken place, the resulting species possessing manifold organs and functions. Such animals are broadly differentiated species, becoming so by the law of specialization by addition. Secondly, the process of specialization may have followed along a few lines, resulting in the excessive development of a few organs and the partial or complete loss of others. These animals are specialists by the law of specialization by reduction acting under favorable conditions. Thirdly, the same process under the thwarting influence of an extremely unfavorable environment may have tended, not towards many sided development and the production of a broadly differentiated species; not towards the excessive development of a few organs with the loss of others and the consequent production of a more specialized species; but rather towards a gradual diminution in the size of the organisms, a loss of many organs and functions, and finally towards the gradual extinction of the species or group. Such a species we shall describe as reduced, since it is truly an extreme product of the law of specialization by reduction. In any one of these three cases mentioned above we have originally primitive forms giving rise to secondary forms, and in a collection based upon natural relationships the former should always precede the latter. We have adhered strictly to this principle in the Synoptic Collection of this Museum, so far as the present state of our knowledge would permit.

In the groups of the Metazoa or animals that follow after the Protozoa, and Mesozoa, the development of the

egg of any given species has been considered a more or less trustworthy guide for determining the phylogeny, or historic evolution, of the phylon or tribe to which the animal that produced the egg belonged. This egg, or ovum, as generally described, is a cell made of protoplasm and containing a nucleus within which is a nucleolus. It is, however, reasonable to suppose that this nucleated and therefore differentiated condition of protoplasm arose from an unnucleated and undifferentiated condition, and, therefore, we seek for what may be called the ancestral stages of the nucleated egg. If these stages have become obliterated in the eggs of the more specialized animals by the action of the law of acceleration in development, it would seem probable that they might be represented by the unnucleated adults of the Protozoa, and that a study of these simplest, one celled organisms, and of the specializations leading from an unnucleated to a nucleated condition of protoplasm, might throw light not only on the origin of the nucleated egg, but also upon the natural classification of the Protozoa. Thirty years ago it would not have been possible to attempt such a classification of this subkingdom. But the observations and experiments of many investigators during the past few years have thrown strong light upon the structure and development of many species and the possible phylogenetic history of several groups. The elaborate work of Bütschli, comprising three volumes of Bronn's *Thier-Reich*, and the great work of Haeckel,—the *Challenger Report on the Radiolaria*,—have both been published since 1880. Besides these, a large number of original papers and several special works on different groups have appeared since 1874; notable among these are the writings of Gruber, Hertwig and Lesser, Cienkowski, Schultze, Grenacher, Brandt, Verworn, Maupas, Mereschkowsky, Plate, Hofer, and of Leidy, W. Saville Kent, Brady, Dallinger and Drysdale, Lang, E. Ray Lankester, Hyatt, Ryder, Archer, Bessels, Calkins, Wilson, and others. Although we have

not followed any one author in the arrangement of the Protozoa of the Synoptic Collection, yet we are chiefly indebted to the above named investigators for the facts upon which the arrangement is based.

The Synoptic Collection of this Museum, is contained in Room E of the Main Hall. The two central floor cases (A and B) exhibit the classes of invertebrates, while the wall cases are reserved for the vertebrates. The Protozoa are in the horizontal part of section 1 of case A. These are represented by drawings, models, and fossils, since the animals living to-day are mostly microscopic. Beginning with the simplest Protozoan organisms, as represented by Plates 1-6, we pass to more and more differentiated forms until we reach the groups represented by Vorticella and Podophyra. Beyond these and under the Sponges are the Mesozoa, represented by Volvox. All the specimens and plates of drawings in each group are numbered in a continuous series. As a rule we begin at the lower right hand corner of each section, and pass to the left<sup>1</sup> and backward in the horizontal part, and upward in the erect part, ending at the upper left hand corner. Deviations from this rule are owing to the peculiar shape or the large size of the specimens. The figures on the plates are also numbered consecutively beginning with the lower left hand corner and ending with the upper right hand corner.

<sup>1</sup> This arrangement is necessary to accord with the arrangement adopted throughout the Museum.

## PROTOZOA.

## Section I (horizontal part).

## SARCODINA.—MONERA.

Scepticism prevails in regard to the existence of Haeckel's Monera. Nevertheless, as Calkins<sup>1</sup> remarks, the claim of Haeckel "that there are organisms without nuclei . . . although it rests upon negative evidence, cannot be rejected until all the forms considered have been shown to possess them."

It is readily conceivable that non-nucleated forms were the first to exist in a remote past, and that these antedated the nucleated forms seem a reasonable supposition. Some of these non-nucleated organisms have persisted, it would seem, since ancient times, although it is probable that all modern Protozoa differ in some respects from their primitive ancestors. Since these earliest ancestors were made of protoplasm only, being wholly without hard parts, no record of their structure has been preserved in the rocks. For this reason we must begin with the simplest Protozoa living to-day.

In Pl. 1, figs. 1-6a, is represented the salt and fresh water form, *Protamoeba primitiva* Hkl., and in Pl. 2, figs. 1-4a, a species of marine Protamoeba (*P. schultzeana* Hkl.). There are many and strong reasons for maintaining that the first animal life which existed was marine. The first Protamoeba described and figured by Haeckel (Pl. 1, figs. 1-6a) was found in fresh water, but since then *Protamoeba primitiva* Hkl., has been discovered in salt water. With our present knowledge of the properties

<sup>1</sup> The Protozoa, 1901, p. 40. (Columbia University Biological Series, VI.)

of the elements of inorganic nature it is possible to conceive of the origin of a mass of protoplasm like the young *Protamoeba* (Pl. 1, fig. 1). This is seen to be nearly as large as the adult (fig. 2), owing probably to rapid growth; in *P. schultzeana* Hkl., however, the young form (Pl. 2, fig. 1) is smaller than the full grown organism (Pl. 2, fig. 2). The youthful form of *Protamoeba primitiva*, like the adult, is a homogeneous, structureless mass of protoplasm or sarcode, possessing no organs nor covering, and is known as a cytode. No nucleus<sup>1</sup> is present, and no non-contractile or contractile cavities called vacuoles.

*Protamoeba schultzeana* differs from *Protamoeba primitiva* by having the protoplasm differentiated into an outer layer or ectosarc and an inner layer or endosarc, both of which are extended to form irregular, knobbed, spherical continuations, as seen in the drawings (Pl. 2, figs. 1-4a).

Notwithstanding the extreme simplicity of structure of *Protamoeba primitiva*, the organism has the power of locomotion, as is well shown by Pl. 1, figs. 2, 3. A prolongation of the body, or pseudopodium, is extended and the streaming of the protoplasm into it causes the animal to creep over surfaces. This is probably one of the simplest physiological modes of motion, and results in producing a crawling type.

The power of taking food by means of the pseudopodia was not observed by Haeckel, who described this form, although he proved that small particles were absorbed into the protoplasm of the body. In other species of the same genus the pseudopodia and body have been seen to envelop the food and the function of digestion followed.

<sup>1</sup> Bütschli considers that *Protamoeba* (as well as all of its group of Monera) has a nucleus, but that it was not detected at the time this organism was studied, on account of the imperfect means of investigation which then existed. On the other hand, no nucleus has been found in *Protamoeba vorax* by Gruber (stated by Rolleston and Jackson, *Forms of Animal Life*, ed. 2, 1888, p. 916), or in *Archerina* by E. Ray Lankester (*Quart. Journ. Micr. Sci.*, XXV, 1885, p. 61), and these investigators have carried on their researches with modern appliances and according to modern histological methods.



It may be that, in the earliest condition of living protoplasm, nourishment was simply taken into the mass by a process analogous to absorption, and that the additional strength acquired in this way, together with a subsequent deficiency in the food supply, gave rise to a desire to go in search of food and therefore originated the function of locomotion. In the development of the more specialized animals the passive, absorbent stage is not represented, so that the function of locomotion precedes the function of taking and digesting food.

The function of reproduction is shown in Pl. 1, figs. 4-6a, also in Pl. 2, figs. 3-4a. The body becomes constricted (Pl. 1, fig. 4), and this constriction continues unaffected by the change in form which each of the halves undergoes until only a mere thread connects the two parts (Pl. 1, fig. 5; Pl. 2, fig. 3); this finally separates and each half rounds itself off immediately and creeps away as an independent organism (Pl. 1, figs. 6, 6a; Pl. 2, figs. 4, 4a). This process of reproduction is known as division or fission. It will be noticed that the two youthful forms resemble the parent before constriction of its body has taken place.

We cannot fail to recognize in *Protamoeba* an organism performing the important vital functions of the more specialized animals. We shall presently see how this knowledge of its life history is a natural introduction to the more differentiated *Amoeba* (Pl. 9), which is regarded by all biologists as an animal; and for this reason we prefer to place the *Protamoeba* among animals rather than among plants or neutral organisms.

Portions of the sea bottom at great depths are covered by a vast gelatinous mass known as the *Bathybius* slime. This slime is, in part, made up of an infinite number of protoplasmic cytodes of various sizes, and imbedded in these are calcareous bodies called coccoliths, which are now considered to be vegetable in origin and therefore foreign to the true *Bathybius*.

Pl. 3, fig. 1, represents one of the smaller cytodes, showing the blunt pseudopodia, and Pl. 3, fig. 2, one of the larger cytodes in the form of an irregular network with the imbedded coccoliths, greatly magnified. The indefinite form of the cytodes, the absence of organs and outer covering, and the possession of blunt pseudopodia, together with the fact that movements have been observed in the protoplasm, suggest the possibility that we have here a vast number of marine Protamoeba-like organisms; but more investigations on the Bathybius are needed before its exact nature and relations can be determined with certainty. It was called a mineral deposit by Wyville Thomson, its discoverer, but was considered an organic form by Huxley and Haeckel.

If now the crawling marine Protamoeba should adapt itself to the life of a free swimmer in the open sea, we might expect to have as a result a form not unlike *Protogenes primordialis* Hkl. (Pl. 4, fig. 1). The flattened body of the creeping Protamoeba would tend to become more or less spherical when suspended in the water and the simple, blunt, ever-changing pseudopodia might develop into the long, branching, and more constant propelling organs which enable the animal to swim rapidly through the sea. Be this as it may, we certainly recognize in this unnuclated Protozoan specialization of structure and function, and we find a correlation existing between habit and structure. If we could find a young form (Pl. 4, fig. 2)<sup>1</sup> similar to Protogenes, which after growing to adult size divided by fission, and if these zoons,<sup>2</sup> instead of separating, remained together for a time at least, connected by their branching and anastomosing pseudopodia, then we should have a colonial form like *Myxodictyum sociale* Hkl. (Pl. 4, fig. 3). Here we

<sup>1</sup> It is probable, although not proved, that *Myxodictyum sociale* Hkl. arises by the detachment of single animals like Pl. 4, fig. 2.

<sup>2</sup> Zoon is substituted for individual. For reasons, see Hyatt, "Larval Theory of the Origin of Cellular Tissues," Proc. Boston Soc. Nat. Hist., XXIII, 1884, p. 46.

have a Protozoan that is probably single when young and colonial when adult, which illustrates an extremely interesting phase of development in animal life.

The *Protamoeba*, *Bathybius*, *Protogenes*, and *Myxodictyum* belong to the simplest Monera; other genera of this group illustrate further specialization in structure. *Archerina boltoni* Lankester is represented in Pl. 5, figs. 1, 2. Fig. 1 may be the form that issues from the hardened case or cyst. It consists of a spherical body with long, motionless pseudopodia radiating outward from the surface. A large vacuole is seen in the interior. This organism is especially interesting because it contains chlorophyl. The latter is confined to a single or bifid corpuscle. No nucleus exists, but the chlorophyl corpuscle appears to take the place of the nucleus, performing a similar function in the process of reproduction. The corpuscle usually divides into four parts followed by the division of the surrounding protoplasm, until a colony is formed (Pl. 5, fig. 2, a small bit taken from a large colony). This colony was decolorized, and the small chlorophyl corpuscles appeared as in Pl. 5, fig. 3, while the large ones were undergoing division (see Pl. 5, fig. 4). The *Haeckelina borealis* (Pl. 6), discovered by Mereschkowsky, shows a fixed or stationary Moner. The long, solid stem by which it is attached is secreted by the protoplasm, this secretion taking place constantly on one part of the body which, when the stem is formed, becomes the lower surface. This organism is without nucleus or vacuoles, but several round, strongly refracting balls are present in the protoplasm which are probably drops of oil. The pseudopodia are short and delicate, and are scattered over the whole surface.<sup>1</sup>

<sup>1</sup> Bütschli places this form among the Heliozoa, although he says vacuoles are wanting and presumably a nucleus, while there is no differentiation of the protoplasm into an outer part, or ectosarc, and inner part, or endosarc. Its striking resemblance to the Heliozoan, *Clathrulina*, will be seen by comparing Pl. 6 with Pl. 43, fig. 7, but if the observations already made are accurate, the two forms are not closely related genetically.

An unfilled gap exists between these forms, which are among the more undifferentiated members of the Monera and the Protomyxa, which Haeckel considers a Moner and Bütschli a Rhizopod. No nucleus has been discovered in Protomyxa, and for this reason we do not feel justified in placing it with the Rhizopods. On the other hand, the habit of fusing or blending with other zoons of its own kind, of covering itself with a hardened case or cyst and passing into a resting state, and especially of producing flagellate young, makes it seem not improbable that flagellate un-nucleated adults which have arisen through adaptation of structure to habit may have existed as the ancestors of Protomyxa. This may be the case or else a nucleus may be found, when the Protomyxa can be placed among the Rhizopods as Bütschli has already done.

The experiments of Gruber on *Dimorpha mutans* (Pl. 50, figs. 1-9) suggest still another view, namely, that the flagellate condition may be assumed quickly in response to the need for rapid motion. Therefore, the flagellum in many cases of these simpler Protozoans may often be an adaptive and not an inherited character.

Pl. 7, fig. 1, represents the younger stage of Protomyxa as it issues from the cyst. After the exit it adopts the more usual crawling motion, thereby assuming the Protamoeba-like form (Pl. 7, fig. 2) and showing an intermediate stage between the flagellate and the Protamoeboid condition. In Pl. 7, figs. 3, 4, the Protamoeboid state is more pronounced. Pl. 7, fig. 5, is a single zoon showing the function of nutrition, a Navicula being assimilated by the plasma of the body. After nourishment is taken, vacuoles or cavities filled with fluid and without distinct walls begin to appear which are not found in the young (Pl. 7, figs. 1-3). A form like Pl. 7, fig. 5, was seen to fuse with a similar zoon. Pl. 7, fig. 6, represents three or four zoons that have fused together. Pl. 7, fig. 7, is an adult formed by the fusion of several zoons, and Pl. 7, fig. 8, an adult after being well fed. The vacuoles are

present in considerable numbers; these, however, are non-contractile and inconstant in position. The pseudopodia branch and anastomose. Food material — diatoms and the like — is found in the protoplasm of the body. The adult draws in the pseudopodia and covers itself with a cyst (Pl. 7, fig. 9). A structureless, glassy membrane surrounds the orange-red contents. Pl. 7, fig. 10, represents another stage more advanced in which the interior mass has become divided into many orange-red balls. In Pl. 7, fig. 11, the cyst has opened and the flagellate young are issuing. This completes the cycle of the life of the *Protomyxa*.

Pl. 7, fig. 12, is an under-fed adult. We describe it here as an illustration of the fact that unfavorable conditions produce changes in structure which may tend towards the reduction of the zoon. The vacuoles have decreased in number and the pseudopodia only slightly branch and anastomose. The structural changes induced by the small quantity of food taken may be transient, as in the case figured above where the under-fed zoon might become like the over-fed specimen (Pl. 7, fig. 8) by giving it a larger supply of food. If, however, the cause of structural change, be it an insufficient diet or any other cause unfavorable for the development of the zoon, were continued through successive generations, the result probably would be the production of a smaller, weaker, perhaps distorted form, and finally the total extinction of the species. Such a species may be called a reduced or a suppressed species, since it has suffered diminution in organs and efficiency. It is also often called simple, but in order to avoid the mental confusion which arises when this word *simple* is applied both to primitive and to reduced forms, we prefer to restrict its use to the former which have comparatively few organs and these oftentimes in rudimentary or developing condition. There are other reasons for doing this. While it may be true that there are reduced animals which cannot be distinguished from the primitively simple forms, yet in the great majority of

cases they bear, at some time of life and especially when young, indubitable proofs of their evolutionary history. These proofs or revelations of their past condition make the reduced forms more complicated in reality than at first appears, and it is these structural characters which should receive a clear descriptive term free from ambiguity, since it is these characters which are of very great importance in tracing the phylogenetic history of animals.

The habit of fusion which has been observed in *Protomyxa* is probably one important cause of the origin and differentiation of the organ known as the nucleus. We cannot suppose, however, that this process of differentiation was rapid, so that a well developed nucleus was made at once, but there were doubtless transitional organisms in which the nucleus was in the process of forming. We had arrived at this conclusion before having seen the work of Gruber<sup>1</sup> on *Pachymyxa hystrix*.

In this form, *Pachymyxa hystrix* (Pl. 8, figs. 3-7; fig. 3, a living specimen containing brown food material, and fig. 6, the same probably in the process of division), Gruber was never able to observe a nucleus, but he saw scattered in the protoplasm a large number of dark colored granules which became red when treated with a reagent (Pl. 8, fig. 5). Specimens were also seen where the colored granules were surrounded by a colored zone of protoplasm so that they looked like little swarm buds (Pl. 8, fig. 4), but the exit of these small bodies was not observed. This form of *Pachymyxa* has an outer layer differentiated into thickly set rods, between which the pseudopodia are thrust out. This is seen in Pl. 8, figs. 3-5 and 7; in the last figure, fig. 7, a small portion is magnified, showing the rods and one pseudopodium drawn while in the coloring fluid.

<sup>1</sup> Zeitschr. f. wiss. Zool., XL, 1884, p. 122. On this subject Gruber says we may suppose that a stage preceded the formation of the typical *Rhizopod* nucleus, when little grains of nuclear substance lay scattered through the whole protoplasm, and that these only came together later to form the real nucleus.

In the naked and more simple form (Pl. 8, figs. 1, 2—probably a variety of the same species) there is, however, no such differentiation of the outer part; fig. 1 shows the brown food material in the interior and the pseudopodia, and fig. 2 is a specimen colored and showing probably one stage of division in which the organism is separating into two parts. The nuclear grains are seen in this figure, as also in fig. 5.

It is reasonable to suppose that a transitional organism exists, or has existed, in which the young stage has nuclear grains and the adult a well formed nucleus, but we have seen no such species described or figured.

#### SARCODINA.—RHIZOPODA.

The probable intermediate forms just mentioned lead naturally to the group, Amoebina, represented by the *Amoeba proteus* Leidy (Pl. 9, figs. 1-11). Here we have a typical Rhizopod with the organs and functions peculiar to such an animal. Pl. 9, fig. 1, is probably the young of this species and fig. 2 presumably an older stage. In both the young and the adult (fig. 3) the protoplasm has become more or less differentiated into a clear outer layer, the ectosarc, and an inner granular portion, the endosarc. When, however, one observes by the aid of a microscope the granular endosarc flowing into the clear ectosarc and, as it were, taking possession of it, one becomes convinced that there is no constant line of demarcation between the two.<sup>1</sup>

<sup>1</sup> According to Leidy (Fresh-water Rhizopods of North America, U. S. Geol. Surv. Terr., XII, 1879, p. 24), Dr. Wallich states that the ectosarc is due to a temporary and partial coagulation of the endosarc coming in contact with the water in which the animal lives, and it again reverts to the mass of the endosarc within the body. The process reminds one of the cooling of a molten mass of metal at the sides of a crucible, and the melting away again of the crust as it is stirred from the sides into the remainder of the molten mass within.

From this point of view the Amoeba is interesting as offering an intermediate position between organisms that are absolutely unprotected, like *Protamoeba* and others, and those that are permanently covered with hardened protoplasm or with a chitinous or a calcareous shell.

Within the endosarc is a nucleus (fig. 3, white; fig. 4, the same colored) which consists of a nuclear membrane, nuclear fluid, often called sap, and suspended in the latter a large number of grains which allow themselves to be colored and are therefore called chromatin grains. The non-contractile vacuoles are present, and also a contractile or pulsating vacuole, or vesicle, as it is often called (fig. 3, pink in color) which is more or less constant in position, and which may have arisen phylogenetically from the former, as suggested by Haeckel.<sup>1</sup>

Besides the vacuoles, nucleus, and minute crystals that are often found in the protoplasm, there are grains of sand which the animal has taken up in crawling over surfaces, but which it has not formed into an outer covering or shell. The pseudopodia are blunt, like those of *Protamoeba*, and are extended in the act of performing the function of locomotion (fig. 5). This figure shows also the transient tendency to an anterior and posterior region of the body which is sometimes observable. The Amoeba is a crawling type, although now and then it floats and swims. At such times its body becomes rounded and its pseudopodia radiate in different directions, as seen in fig. 6, which illustrates clearly the correlation of structure and habit. The power of taking food is finely shown in figs. 3 and 7. In fig. 7 a pair of pseudopodia, acting like the finger and thumb of the human hand, have come together at their ends, entirely encircling an active Infusorian, *Urocentrum*. Another recently captured *Urocentrum* is seen within the body of the Amoeba. In fig. 3, a diatom

<sup>1</sup> Jena. Zeitschr., IV, 1868. Engl. transl., Quart. Journ. Micr. Sci., IX, 1869, p. 114.



has been caught, and is probably taken into the body through the extension or flowing of the ectosarc over it.

After the food is digested the excrement is sometimes ejected simply by the unfolding of the protoplasmic body, and at other times is discharged from the posterior part of the body, as seen in fig. 5b.

As already stated, the contractile vacuole is a cavity which is filled with fluid and which contracts and dilates quite regularly. According to the experiments of Griffiths,<sup>1</sup> it performs at times an excretory function similar to that of the kidneys in the more specialized animals, but it is interesting to note that at other times no waste nitrogenous matter is found in the vacuole, and it is most likely, as stated by Griffiths, that the organ in its primitive condition performs more than one kind of work, combining, it may be, a respiratory with an excretory function. Experiments on the more differentiated Protozoa, such as *Paramoecium* and *Vorticella*, proved that the contractile vacuole in these forms performed the function of a true kidney, the product excreted being the same as in the most specialized animals.

Circulatory movements of the endosarc have already been spoken of under the head of structure, and are mentioned here again since they belong with the physiological activities of the *Amoeba*. Pl. 9, fig. 8, represents the granular endosarc flowing into the hyaline ectosarc, the direction of the current being indicated by arrows. The susceptibility of the organism to external forces is shown in different ways; whenever the glass slide on which the *Amoeba* is crawling is touched or jarred, its pseudopodia are partially or wholly drawn in and a more or less spherical form is assumed, as seen in fig. 9.<sup>2</sup> This irritability

<sup>1</sup> Proc. Roy. Soc. Edinburgh, XVI, 1888-'89, p. 131.

<sup>2</sup> *Amoeba radiosa*. According to C. Scheel, *Amoeba radiosa* is the young of *A. proteus*. See his Beiträge zur Fortpflanzung der Amöben, in C. von Kupffer's Festschrift zum siebenzigsten Geburtstag, 1899, pp. 569-580.

of protoplasm may give rise in time to nerve force which ultimately in the more specialized animals becomes localized in a nervous system, and which manifests itself in consciousness and will power.

The *Amoeba proteus* usually has but one nucleus (fig. 3), but sometimes a specimen is found with two nuclei (fig. 5). Reproduction in this species probably takes place by fission. Pl. 9, fig. 10, is a supposed *Amoeba proteus* in the act of dividing. The separation of the thread connecting the two parts occurred in ten minutes after the stage represented in the figure.

Gruber's important experiments on *Amoeba proteus* and other Protozoa, in order to determine the part played by the nucleus in reproduction, prove that by artificial division only the portion possessing the nucleus is capable of reproducing itself. The Amoeba was divided as shown in Pl. 9, fig. 11, and the portion marked *a* lived, while *b* drew in its pseudopodia and died. After many experiments Gruber concludes that it is an incontrovertible fact that the nucleus is the species-preservative constituent of the cell, and that to it is justly ascribed the highest importance in the processes of fecundation and inheritance.<sup>1</sup> If it is true that the continuance of the life of the species depends upon the nucleus, then it follows that in passing from the Protamoeba to the Amoeba a change has taken place in the protoplasmic organism. The generative power manifested by the cytode is certainly an indication of the existence of a generative substance making up a part at least of the cytode, and it would seem as if this substance had become localized in the nucleus of the Amoeba to form a distinct and species-preservative organ. The remarkable differentiations of the nucleus which are found in succeeding and more

<sup>1</sup> Ann. and Mag. Nat. Hist., (5), XVII, 1886, p. 473. Translated from the Berichte der naturforschenden Gesellschaft zu Freiburg i. B., 1, 1886. See also Hofer, Jena. Zeitschr., XXIV (Neue Folge, XVII), Heft 1, 1889, p. 105; and Morgan, Regeneration, 1901, p. 65 (Columbia University Biological Series, VII).

specialized genera of Protozoa tend to strengthen this hypothesis.

It is probable, although it is not yet proved, that *Amoeba proteus* forms swarm-buds in the shape of little Amoebae.

Pl. 9 is instructive since it places before the student a simple organism capable of performing in a simple way the vital functions of the most specialized animals.

Many interesting differentiations of structure are shown in other species of Amoeba. The marine Amoeba (*A. obtecta*) crawls with extreme slowness. According to Gruber these Rhizopods do not exhibit any tendency to undertake migrations, and therefore when the conditions are favorable they lie together in great numbers and thus form regular societies.<sup>1</sup>

In *Amoeba polypodia* M. Schultze (Pl. 10, figs. 1-8a), which may have one or several nuclei, the pseudopodia are numerous, and are more equal throughout their length, approaching the thread-like organs of many Foraminifera. The process of fission is shown in figs. 1-8a, which illustrate more clearly the different stages of development than preceding figures. The specimen observed had one nucleus. The division of this organ took place in one minute and a half, and that of the body in eight and a half minutes, so that ten minutes were required for the whole process. Figs. 2-8a are drawn in outline, showing the division of the nucleus and protoplasmic body and also the increase in the number of vacuoles.

There are organisms closely related to these Amoebae which seem to throw light on the origin of the flagellum, and to point to the probability that certain Rhizopods have given rise to the Mastigophora (= Flagellata.) According to Calkins,<sup>2</sup> however, there is no conclusive

<sup>1</sup> Zeitschr. f. wiss. Zool., XXXVIII, 1883, p. 56. Engl. transl., Ann. and Mag. Nat. Hist., (5), XI, 1883, p. 276.

<sup>2</sup> The Protozoa, 1901, p. 105. (Columbia University Biological Series, VI.)

evidence to support the view that Rhizopods are more primitive than Flagellata, or *vice versa*. He says: "Their mutual affinities are very close, and together they stand as the most primitive forms of modern Protozoa."

While this may be true, a much more consistent arrangement can be made if one begins with the Sarcodina, as Calkins has done, and passes to the Mastigophora (= Flagellata) and then to the most specialized Infusoria (see p. 53).

The whip-bearing Rhizopod (Pl. 11, figs. 1, 2) represents an adult which combines the flagellum with the Amoeboid pseudopodia. This flagellum is eight or ten times the length of the body. When the motion changes from creeping to swimming, the body lengthens as seen in fig. 2.

*Amoeba quinta*<sup>1</sup> shows a marked specialization of the nucleus. Pl. 12, fig. 1, is a young form with eight nuclei. Whether the youngest stage has one nucleus cannot be stated.<sup>2</sup> Pl. 12, fig. 2, represents an adult with twenty-four nuclei (more existed but were omitted for the sake of clearness), and the species may have hundreds, this increase taking place, as the figures show, with the growth of the animal. Pl. 12, fig. 2a, represents the nucleus as it appears before staining, which shows a differentiation in structure from the nucleus of *Amoeba proteus* (Pl. 9, fig. 3). The outer membrane lies over a peripheral layer of granules, and the central portion is filled with a mass which appears granular. When colored, the nucleus has the appearance seen in Pl. 12, fig. 2, which is much more

<sup>1</sup> This species was described by Gruber as *Amoeba proteus* (Zeitschr. f. wiss. Zool., XXXVIII, 1883, p. 382), but afterward was found by him to be *Amoeba quinta* (*ibid.*, XLI, 1885, p. 205). See his description of *Amoeba proteus* (*ibid.*, XLI, 1885, p. 216, pl. XV, figs. 43-45.)

<sup>2</sup> Gruber, Zeitschr. f. wiss. Zool., XLI, 1885. This author says that what Bütschli has shown as such appears to belong to another species of Amoeba.

specialized than the colored nucleus of *A. proteus* (Pl. 9, fig. 4). Inside of the dark colored outer layer is a zone of nuclear sap, while the central mass we may probably indicate as a nucleolus.<sup>1</sup> In Pl. 12, fig. 2, four of the twenty-four nuclei are in the process of division, and the figure is very instructive as showing the origin of the many-nucleated forms. The process is probably rapid, and this may account for the fact that few naturalists have been fortunate enough to observe and draw it.

In *Pelomyxa palustris* Greef we have an Amoeba-like form when young<sup>2</sup> (Pl. 13, figs. 1-4). Many of these Amoebae came from a dead *Pelomyxa*. After moving about, they became more quiet (Pl. 14, fig. 5), some contracted themselves into a spherical or pear-shaped body (Pl. 13, figs. 6, 7), after which a long vibrating thread was stretched out (Pl. 13, fig. 8), and the Amoeba became transformed into a flagellate animal. After rapid rotating movements this young flagellate organism passed out of sight, "rowing with the front, quickly swinging whip," so that unfortunately its further development was not observed. Whether the flagellate young remained a flagellate organism, or whether it passed into the unflagellate adult (Pl. 13, fig. 9) cannot be stated. In the adult, the tendency towards an anterior and a posterior region of the body is marked. The animal stretches itself out and moves in curves, turning the forward end, now to the right, now to the left (Pl. 13, fig. 9). At the posterior end there is a glassy disc-like expansion. Pl. 13, fig. 10, is a magnified portion of the body. Many nuclei are present which may be converted into the "shining bod-

<sup>1</sup> Gruber, Zeitschr. f. wiss. Zool., XXXVIII, 1883. According to Calkins, the Protozoan cell, with possibly one exception, has no true nucleolus comparable with the nucleolus of the Metazoan cell. What has been so called is, according to this author, either functional chromatin that has aggregated into a mass, or an intranuclear sphere or division center (see *The Protozoa*, 1901, p. 253).

<sup>2</sup> Greef, Arch. f. mikr. Anat., X, Supplement, 1874, p. 51.

ies"<sup>1</sup> that give rise to the Amoeba-like young (Pl. 13, figs. 1-4). The little rods (Pl. 13, fig. 10) are thought to be parasitic plants. The streaming of the endosarc with its vacuoles, rods, etc., into the hyaline ectosarc is well shown in the drawing.

If the flagellate condition is a normal stage in the development of *Pelomyxa* and not a parasitic organism as maintained by some naturalists, the species is an exceedingly interesting one. Observations on such forms as the whip-bearing *Rhizopods*, *Pelomyxa*, and also those of Gruber on *Dimorpha mutans* show that the amoeboid and flagellate conditions are marked in these less specialized organisms by extreme variability, depending, it may be, upon the need for slow or rapid motion. The flagellum arising in this way as an adaptive character may become fixed in the organization and finally inherited as a permanent organ, which would seem to be the case in the *Mastigophora* (= *Flagellata*).

The group of Amoebina represented by *Diffugia* (Pl. 14, fig. 1) not only possesses many nuclei, but these have become differentiated so that each contains one or more nucleoli (fig. 1a). In addition to this specialization in structure the protoplasm is not only capable of taking up sand grains, like that of the *Amoeba proteus*, but it is able to lay a part of these on the surface for a protective covering or shell.

Pl. 14, fig. 1, is a vertical section through the shell and body of *Diffugia urceolata* Carter. The hyaline ectosarc extends out into the pseudopodia which are stretched from the opening. In the protoplasm of the interior are seen the nuclei colored red (Pl. 14, fig. 1a, nucleus, uncolored and magnified), besides sand and bits of nourishment. Figs. 2-5 illustrate the division and shell formation of the same species. In order to determine how the shell was

<sup>1</sup>For views on this subject see Greef, Arch. f. mikr Anat., X, Supplement; also Gruber, Zeitschr. f. wiss. Zool., XLI, 1885.

formed, Verworn<sup>1</sup> isolated a specimen and gave it splinters of blue glass. He observed repeatedly that the *Diffugia* crept by the splinters, its pseudopodia pushing them away instead of taking them up. After a time a Cypris passed and irritated the pseudopodia, which caused a sticky secretion to form on their surface, so that pieces of glass were caught in it and were then taken into the body with the pseudopodia.

Afterward Verworn irritated the pseudopodia with a needle; the surface became rough and took up glass which before it did not do. The splinters were really drawn into the protoplasm so that the interior contained a little heap of them. These observations tend to prove that the origin of the shell of *Diffugia urceolata* is mechanical and largely a matter of accident.

Later experiments upon *Diffugia lobostoma* Verworn,<sup>2</sup> tend to prove that the animal does not exhibit a conscious choice in the taking up of material for its shell, nor does there seem to be any calculation in regard to the quantity of sand grains or glass splinters needed. Sometimes a mass was taken and then thrown out in order apparently to take up more—a desire to get, it would seem, rather than to use.

Verworn saw two, three, and even five zoons of this species of *Diffugia* in conjugation. He proved by experiment that two zoons might touch each other for a long time without blending, while other zoons united with the fusion of the protoplasm. Experiments were made to cause zoons to blend by keeping two close together, but were unsuccessful, and the author considers that it is proved indubitably that every zoon cannot blend with every other. On the other hand, two zoons which were in conjugation were separated but these came together again, showing that one must exert a directive influence upon the other or the two upon each other. The cause may be of a chemical nature, as maintained by Verworn.

<sup>1</sup> Zeitschr. f. wiss. Zool., XLVI, 1888, Heft IV, p. 455.

<sup>2</sup> Zeitschr. f. wiss. Zool., L, Heft 3, 1890, p. 449.

The process of division is illustrated by Pl. 14, figs. 2-5. First a swelling (fig. 2) is seen at the mouth of the shell which approaches the spherical form (fig. 3). The protoplasmic swelling reached in time the size of the parent form and a mass of glass splinters was seen entering the newly formed half (fig. 4) where the protoplasm with the splinters showed a slowly flowing movement. In the most advanced stage of division the protoplasm which had curved forward had taken the form of a Diffugia shell, and the glass splinters were placed in a layer upon its surface (fig. 5). The new half did not seem to have a firm shell, as the splinters of glass were still quite loosely joined to one another. The next day the zoon separated from the parent, its shell assumed the characteristic form, while the pieces of blue glass were united by means of a binding material which was still quite colorless, and which, after some days, began to assume a darker brownish shade. Verworn succeeded in taking off the shell and obtained the naked Diffugia. Several of these shell-less specimens he kept for three weeks, and no attempt was made on the part of the animal to make a new shell. He therefore concludes, after many experiments, that the species of Diffugia do not reconstruct an injured shell nor make another when one has been removed.

The Foraminifera are Rhizopods in which the protoplasm is differentiated into ectosarc and endosarc, and the nucleus has a membrane, a distinct chromatin network with one or more nucleoli (Bütschli). In certain forms, like *Trochammina* (= *Rotalina*<sup>1</sup>) *inflata*, and in *Ovulina*, one half of the nucleus has been found to consist of chromatin, the other of a non-staining substance. The less differentiated Foraminifera possess a one chambered shell, and are single forms, while the most differentiated have a complex, many chambered shell; each chamber, it may be, representing a zoon, and if so the

<sup>1</sup> Throughout this Guide synonyms are placed in parenthesis.



many chambered shell represents a colony. Many naturalists, however, hold that this is not a colony, but is one zoon with a polythalamous shell. In the case of *Diffugia* just described, the bud represented another zoon that in this species separates from the parent form, but which in the complex Foraminifera remains attached and makes its own covering. In the arrangement of the Foraminifera the single forms are given first when this is possible, and afterward the colonial forms which may have arisen from them phylogenetically.

*Saccamina* is a simple, hollow, spherical Rhizopod which usually occurs single (Pl. 15, fig. 1, *S. sphaerica* M. Sars). Sometimes several shells adhere by their external surfaces and the openings remain distinct, as shown in Pl. 15, fig. 2, a form which has received the name of *Saccamina socialis*. This association of zoons where there is no organic connection reminds one of the "societies" of the marine *Amoeba obtecta* (see p. 25) and of the association of the cytodes of *Bathybius*. In fig. 3 (*S. sphaerica*) we have such a rude attempt at a colony that it seems to be an initial effort. These zoons are connected by protoplasmic extensions, or stolons. The largest chamber was the primordial one, and was fastened between two stones; the succeeding zoons then arose as buds which formed their shells in an irregular manner, and the terminal chamber was merely a mass of sand grains with large interstitial openings through which passed the pseudopodia.

The specimen (No. 16) and Pl. 17, figs. 1-8, represent *Astrorhiza limicola* Sandahl,<sup>1</sup> described by Bessels under

<sup>1</sup> This name was given by Sandahl (Ofvers. Kongl. Vetenskaps-Akad. Forhandl., XIV, p. 299) in 1857, and is retained on account of priority. Brady places *Astrorhiza* among the Foraminifera. According to Sandahl there are many nuclei, but these are figured by him as occurring among the grains of the pseudopodia, an unusual position for nuclei. Bessels, whose observations are more extended, neither figures nor describes a nucleus. Until positive knowledge is obtained we place it provisionally among the Foraminifera.

the name of *Haeckelina gigantea*. Pl. 17, fig. 1, represents the young *Astrorhiza* which has arisen by a forcible separation of a piece of the arm, it being probable that new animals or zoons arise from the swollen ends of the arms. It is Amoeba-like, and is without a shell. The drawing represents it just after its separation; Pl. 17, fig. 2, is the same ten hours later; fig. 3, the same somewhat contracted; fig. 4, the same four days after separation (one projection sends out a number of delicate thread-like pseudopodia which branch slightly); fig. 5 is an older stage in which the dark brown protoplasm is not yet covered with a shell; fig. 6 represents one still further developed which appears to be on the point of making a shell. The process of specialization continues until the full grown organism (fig. 7) has the shell completed. The material of which it is made is usually sand or mud. It has a varying number of continuations from which extend the pseudopodia. Fig. 8 is the drawing of a colony of seven adult zoons united by their arms which in this case serve as stolons.

According to Neumayr<sup>1</sup> the irregular agglutinating Foraminifera, such as the *Astrorhizidae*, have given rise to the regular agglutinating forms, and these in turn to the imperforated and the perforated calcareous Foraminifera.

*Reophax bacillaris* Brady (No. 18), and *R. nodulosa* Brady (No. 19), are more regular than *Astrorhiza*, though they are rough on the surface and are usually made of sand with a silicious cement.

*Cornuspira involvens* Reuss. (Pl. 20, fig. 1), is one of the imperforate limy shells. It has a variable number of undivided convolutions making a circular flattened shell. Another species, *C. striolata* Brady (Pl. 20, fig. 2), broadens out and passes over into a form resembling *Peneroplis*, soon to be described.

<sup>1</sup>Die Stämme des Thierreiches, I, 1889, p. 198.

The Miliolidae are represented by the mounted specimens (No. 21). The term *Miliola* may be used very properly in a generic sense to comprehend a great variety of closely associated forms having the same general type of structure (Brady). It is reasonable to suppose that a single form, *Uniloculina* or *Loculina*, exists, or has existed in the past, although no such form has been described. The *Biloculina* (No. 21) has two chambers visible externally, and each successive segment encloses the younger ones on the same side.

The group of Foraminifera is a very remarkable one for studying gradational forms. Here, to the inexpressible delight of the student, all artificial systems break down. "It is only," says Brady, "as we learn to recognize the fact that among the Rhizopoda the so called 'species' represent no more than terms of a series of which very frequently every intermediate link can be supplied that we arrive at any just idea of their relationship."<sup>1</sup> Among the more specialized groups of animals many of the intermediate forms are unfortunately wanting, but these doubtless either exist at the present time or have existed in the past, and if the lesson taught by the Foraminifera could be impressed upon the student at the beginning of his studies, he would be less inclined to draw sharp lines of demarcation, since these are arbitrary and unauthorized by nature.

No. 22 and Pl. 23, figs. 1-7, represent *Peneroplis*, of which Brady says there is no genus of Foraminifera embracing so great a variety of external form in which the morphological sequence is at once so simple and so complete.<sup>2</sup>

Pl. 23, fig. 1, is a young specimen of *Peneroplis* showing the spiral mode of growth. Fig. 2 is an adult of the

<sup>1</sup> Challenger Report on the Foraminifera, IX, 1884, p. 49.

<sup>2</sup> For other figures showing the variety in external form of this genus, see Brady; Challenger Report on the Foraminifera, IX, 1884, Pl. XIII; also Carpenter, *Introd. to Study of Foraminifera*, Pl. VII.

Dendritine variety in which the last chamber is taking the rectilinear mode of growth. Fig. 3 is the Spiroline variety of the same genus in which a considerable portion of the shell is rectilinear. Fig. 4 (*Peneroplis arietinus* Batsch.), fig. 5 (longitudinal section of the same), and fig. 6 (*Peneroplis cylindraceus* Lamarck) show the gradual diminution of the spiral portion and the increase of the rectilinear part. These figures illustrate the changes from a spiral to a rectilinear mode of growth in different species of one genus, while the slides No. 24 (specimens obtained from the sand of the Bahamas) and Pl. 25, figs. 1-5, exhibit the changes from a spiral to an annular growth in one species, *Orbiculina adunca* F. u. M. Pl. 25, fig. 6, is a section giving the interior of the shell. It shows that the primordial chamber was globular and that subsequently spiral growth took place followed by annular growth.

Unusual interest attaches to the species *Orbitolites tenuissima* Carpenter (Pl. 26). Beginning as a globular shell it passes into the undivided Cornuspira condition which is clearly marked in the young; the later convolutions are sometimes constricted at opposite points, thus indicating the Milioline stage. Next the spiral stretches, after the fashion of a *Peneroplis*. The chambers extend themselves extraordinarily in breadth, until by the meeting of the lateral ends a ring is formed around the spiral part of the shell, as in *Orbiculina*. These annular rings or chambers are divided by cross walls into a great number of chamberlets. Finally the complex structure with many additional covering cells or chambers peculiar to *Orbitolites* is developed.<sup>1</sup>

Miliola, *Peneroplis*, *Orbiculina*, and *Orbitolites* belong to the calcareous group of Porcellanous Foraminifera. The calcareous group with a hyaline or glassy appear-

<sup>1</sup>For further information see Carpenter, Rep. Chall. Exped., Zool., VII, part XXI, 1883, pp. 1-49, pls. I-VIII.

ance is represented in the Collection both by fossils and by series of drawings. The simplest or most elementary structure in this latter group is to be found in the shell of *Lagena* (Pl. 27, figs. 1, 2). Fig. 1, *Lagena globosa* Montagu, shows the globular shell so common as the ground form of the Foraminifera, and fig. 2, *Lagena laevis* Montagu, represents a flask-shaped modification of the primitive form. The shell of *Lagena* is a single chamber with a terminal opening. The walls are calcareous and finely perforated for the exit of the pseudopodia. This genus like others exhibits great variation.

*Nodosaria* (Pl. 27, figs. 3-5, No. 28, *N. soluta* Reuss.) consists of chambers united in a straight or curved line, with the opening in the center of the terminal chamber. Pl. 27, fig. 3, is *Nodosaria simplex* Silvestri, consisting of two chambers in a straight line, and fig. 4 is another species of the same genus (*Nodosaria subtertenuata* Schwager) composed of several chambers. Fig. 5, *Nodosaria* (= *Dentalina*) *farcimien* Soldani, has more chambers and the shell shows a tendency to curve.

The group represented by *Globigerina* is one of great interest since the ooze of portions of the deep sea is largely made up of the shells of these Foraminifera. Although existing in such vast numbers to-day, both *Globigerina* and *Orbulina* (see p. 36) have been discovered recently in the ancient Cambrian formation of New Brunswick.<sup>1</sup> Here they occur well preserved in shales and in phosphate nodules. Sufficient investigations, however, have not been made to prove beyond doubt that this ancient *Orbulina* is the primitive ancestral form of *Globigerina*.

Cayeux's paper<sup>2</sup> is interesting in this connection. He

<sup>1</sup> Matthews, Trans. N. Y. Acad. Sci., XII, 1893; also XIV, March, 1895.

<sup>2</sup> Sur la présence de restes de Foraminifères dans les terrains pré-Cambriens de Bretagne. 1894. See also review of M. Cayeux's paper by G. F. Matthews, Amer. Geol., XV, 1895, p. 146.

has found one-chambered shells in the pre-Cambrian rocks of Brittany, but is unable to determine with certainty whether they are primitive Foraminifera or Radiolaria; he thinks they may be the latter and therefore does not figure them. They are doubtless older than those discovered in New Brunswick, as pointed out by Matthews, since they occur in an older series of rocks and are very much smaller in size. Associated with the unilocular forms are Foraminifera consisting of from two to seven chambers (Pl. 29, figs. 1-6) and belonging to the Perforata. Fig. 1 shows a two-chambered shell, figs. 2 and 3, three-chambered shells, figs. 4 and 5, two different forms of four-chambered shells; fig. 6 is the only shell possessing more than four chambers that M. Cayeux has found. The irregularity and imperfect attempts of these primitive Perforata to make a symmetrical shell remind one of the similar efforts and results among the Imperforata already figured and described.

The microscopic slide No. 30 represents the *Globigerina* ooze from the deep sea off Cape Hatteras obtained by the U. S. S. Albatross, in 1883. Although the *Globigerina* shells predominate in it, yet a number of other genera are also represented. Pl. 31 is a beautiful drawing taken from the Narrative of the Challenger Report (Vol. 1, part 2, Pl. N, fig. 10, p. 926) of *Globigerina* ooze seen by reflected light. This was dredged from a depth of 1900 fathoms in lat.  $21^{\circ} 38' N.$ , long.  $44^{\circ} 39' W.$  Slide No. 32 exhibits *Globigerina* shells dredged from the Atlantic. No. 33 is the rosy *Globigerina rubra* d'Orbigny. Pl. 34, fig. 1, is the young of a bottom specimen of *Globigerina bulliodes* d'Orbigny, which does not possess spines; Pl. 34, fig. 2, the adult, showing more chambers, and fig. 3, a view of the same, showing the large opening of the last chamber.

We have already pointed out that doubtless *Globigerina* arose from a single hollow sphere such as *Orbulina* (slide No. 35) appears to be when observed externally;

but the internal structure of many species of this genus shows it to be more specialized than *Globigerina*. In slide No. 36 a number of *Orbulina* shells are seen with *Globigerina*-like shells inside. (The broken yellow specimen on the slide is probably another genus.) Pl. 37, fig. 1, is *Orbulina universa* d'Orbigny, in which the *Globigerina*-like shell in the interior is not wholly covered by the exterior spherical shell. Fig. 2, a surface specimen, shows the covering entire but thin, so that the inner shell can be easily seen through it. Fig. 3 is the *Globigerina*-like shell from which the outer *Orbuline* sphere has been removed. The shell is provided with spines, like most surface specimens, and its chambers are partly or wholly filled with protoplasm. In fig. 4, a bottom specimen, the inner shell is not seen, owing to the thickness of the wall. Fig. 5 is an old bottom specimen in which the inner shell does not exist but the wall is laminated, giving the appearance when seen under the microscope of spheres within spheres. This laminated appearance is observable in some of the specimens in the microscopic preparation No. 36. According to the observations of Shacko,<sup>1</sup> which were made on bottom specimens, only the young *Orbulinae* have *Globigerina*-like shells, while in very large and old bottom specimens they do not occur.

From the observations made on *Globigerina* and *Orbulina* it may be possible that we have here only one genus. In such a case, the youngest or nepionic stage would be represented by a single thin-walled hollow sphere; the adolescent or neanic stage by several spheres fastened together; the mature or ephebic stage by several united spheres completely enclosed in the last globular chamber; and the old age or gerontic stage by a single hollow sphere, the thick wall of which is laminated. Either this is the case or else *Globigerina* is the more primitive, ancestral form, which in course of time was developed

<sup>1</sup>Arch. f. Naturgeschichte, XLIX, I, 1883.

into the *Orbulina* that possesses *Globigerina* characters in youth and loses them in age.

In Pl. 38, figs. 1, 2, *Hastigerina murrayi* Wy. T., which belongs to the *Globigerina* group, is represented. The shell is thin and possesses spines (fig. 1). The protoplasm of the living animal envelops the shell, taking the peculiar form of bubble-like extensions, and thrown outward beyond these are the extremely long pseudopodia (fig. 2).

The group of *Nummulitidae* is the most differentiated of the *Foraminifera*. The mounted specimen No. 39, *Fusilina*, is exclusively fossil. The shell is bilaterally symmetrical. The chambers extend from one end of the shell to the other, and each convolution encloses the previous whorl. The walls of the chambers are usually single, and there are no interseptal canals.

*Nummulites* is represented in the Collection by specimens (Nos. 40, 41). No. 40 shows two whole shells, and between these a horizontal and a vertical section; back of these single specimens are two pieces of *Nummulitic* limestone; one showing fresh surfaces, while the other has been weathered by the action of the carbon dioxide and moisture in the air so that the shells stand out more prominently. No. 41 is remarkable for its size, being a giant of its kind. The internal structure is shown in Pl. 42. The figure at the left is a horizontal section of *Nummulites granulosa* d'Arch., showing the double walls between the chambers and the canal system. The two central figures are *Nummulites laevigata* Lam.; one the whole shell and the other a vertical section showing chambers and walls. The figure at the right is *Nummulites mamillata* d'Arch., with a portion of the outer shell removed.



## SARCODINA.—HELIOZOA.

One of the most familiar examples of the Heliozoa is *Actinophrys sol* Ehr. (Pl. 43, figs. 1-3). Fig. 1 is the young stage observed by Kent, which possessed a flagellum. While swimming it projects blunt pseudopodia from all sides (fig. 2). Its motions then become slower, the flagellum is withdrawn, when suddenly thread-like organs are put out in every direction and the animal is transformed into the adult *Actinophrys* (fig. 3). If the naked spherical body of a typical Rhizopod should remain constant in form, and the pseudopodia should radiate as long thread-like organs and preserve this character essentially unchanged, then we should have the *Actinophrys* in outward appearance. In the Heliozoa there may be one or many nuclei. In *Actinosphaerium*, a Heliozoan closely related to *Actinophrys*, from one to two hundred nuclei are not uncommon, and this large number in the adult is reached from one nucleus or a few nuclei in the young (Bütschli). *Actinophrys* increases by fission, and this sometimes gives rise to a colony.<sup>1</sup>

Pl. 43, fig. 4, represents a young embryo of *Clathrulina elegans* Cienkowski<sup>2</sup> which soon develops into the form represented by fig. 5. Its striking resemblance at this stage to *Actinophrys* is at once apparent. Like that Heliozoan it is without a stem or a skeleton. In fig. 6 these have been developed, the stem being secreted first, but both are as yet nearly colorless. Fig. 7 is the stationary adult with its stem (only part of which is shown in the drawing) and skeleton. The pseudopodia extend in all directions from the openings of the shell. After a time these are drawn in and fission takes place, each prod-

<sup>1</sup> For views in regard to the process of conjugation of *Actinophrys* and the Heliozoa in general, see Bütschli, Bronn's Thier-Reich, I, 1881, p. 317.

<sup>2</sup> See Arch. f. mikr. Anat., III, 1867, p. 311.

uct of the fission becoming encysted within the shell. Fig. 8 shows four cysts, which in time are ruptured, allowing the embryos to slip out.

The process of development observed by Hertwig<sup>1</sup> differed somewhat from the above. He saw the division of the body with the formation of flagellate young (Pl. 44, fig. 1). Each swarmer possessed a nucleus and several contractile vacuoles, while in the forward end it was provided with two whips. About half an hour after leaving the parent, it settled perpendicularly upon an object, took on a spherical form and a naked *Clathrulina* resulted. The stem had its origin in a depression of the body which is visible on the surface as a sharply defined circle (seen in Pl. 44, fig. 2, in the center of the drawing). It grows long, as represented in fig. 3, which is a naked *Clathrulina* before the shell is formed.

#### SARCODINA. — RADIOLARIA.

We may turn with a feeling of assurance to the primitive forms of *Radiolaria* discovered by M. L. Cayeux<sup>2</sup> in pre-Cambrian rocks as the remote ancestral forms of *Radiolaria* living to-day. These minute, silicious shells remained practically unchanged during the metamorphism of the surrounding rock. The primitive *Radiolaria* were spherical, spineless, and some had an imperfectly trellised skeleton. Of those that were symmetrical *Cenosphoera* (Pl. 45, fig. 1,  $\times 1350$ ; fig. 2, section of the same) was one of the most generalized. The characteristic network is seen in these shells with perfect clearness. Though found in pre-Cambrian and Silurian rocks, this genus occurs at the present time both on the surface and at

<sup>1</sup> See Arch. f. mikr. Anat., X, Supplement, 1874, p. 2.

<sup>2</sup> Bull. Soc. Géol. de France, 3e Sér., XXII, 1894, p. 197. Comptes Rendu Soc. Géol. de France, May, 1894, p. lxxix. See also Amer. Geol., XV, 1895, p. 146.

great depths of the sea. The figures of Haeckel<sup>1</sup> show that this genus and several other genera of the Radiolaria have remained essentially unchanged since protozoic times. Some of the Radiolaria have spines, as seen in Pl. 45, figs. 3-5. Fig. 3, *Xiphosphoera*, has two equal spines; fig. 4, *Staurosphoera*, has four; while fig. 5, *Acanthosphoera*, has numerous spines at the nodes of the lattice work, though only three have been preserved. The basket form is seen in *Tripodiscium* (Pl. 45, fig. 6), while in fig. 7 (which belongs to the section of the Dicyrtida, though the family is not determined) the shell is divided into three parts with numerous spines.

It has been pointed out by Haeckel that the simple skeletonless Heliozoan, *Actinophrys*, might give rise to the simple shell-less Radiolarian, *Actissa princeps* Hkl. (Pl. 46, fig. 2), the stem-form from which probably the whole group of Radiolaria has descended. The young *Actissa* (fig. 1) possesses one nucleus and is a flagellate form. This passes probably into the *Actinophrys* stage which unfortunately has not been observed. Afterward a membrane, known as the central capsule, forms, which is wholly absent in the young. The possession of this organ separates the adult and more specialized *Actissa* from *Actinophrys*, and is the peculiar and marked characteristic of a Radiolarian. Pl. 46, fig. 2, is the adult. The large round nucleus is seen in the center with its nucleolus. Around the nucleus is finely granulated protoplasm containing many clear spherical vacuoles. These parts are contained in the porous central capsule; outside of the capsule is seen the jelly envelope or calymma which in the figure is yellow but colorless in the living Radiolarian. It is indeed seldom visible in the living, freshly taken animal when observed in sea water, but since it does not readily become colored, its size and form can be made out definitely by placing the specimen in

<sup>1</sup> Challenger Report, Zool., XVIII.

coloring matter. The calymma is pierced by the long radial pseudopodia, which arise outside of the central capsule. Late in the life of the adult the nucleus divides into a large number of nuclei, as seen in fig. 3a, which is a diagrammatic drawing of one half of a central capsule of an older specimen than fig. 2, the other half being like it, of course, at this stage of development. These nuclei together with a part of the surrounding protoplasm are transformed into the flagellate young (fig. 3b, a diagrammatic view of one half of a central capsule in a more advanced stage of development than fig. 3a).

Actissa is a single form like most of the Radiolaria. As has been stated, it never secretes a skeleton, but many Radiolaria make silicious shells of rare beauty and great complexity. The microscopic preparation (No. 47), when seen under a high power, shows delicate lattice-work forms known under the familiar name of Polycystina, which was given by Ehrenberg to that part of the Radiolaria described by Haeckel as the Spumellaria and Nasellaria. These shells were taken from the famous Polycystine marl of Barbadoes in the Antilles which belongs to the Miocene period, and which is the richest of all the Radiolarian deposits.

Living Radiolaria are represented, greatly magnified, in Pl. 48, figs. 1, 2. In fig. 1, *Thalassophysa pelagica*,<sup>1</sup> the delicate pseudopodia radiate in all directions from the shell. Fig. 2, *Theopilium cranoides*,<sup>2</sup> shows these and also the basket-like form and delicate lacework of the shell.

The colonial Radiolaria are represented by *Collozoum inerme* Hkl. (Pl. 49, figs. 1-10). Figs. 1-3 represent the young. Here we find for the first time different kinds of zoons and this differentiation in structure is suggestive of

<sup>1</sup> *Thalassicolla pelagica* in Haeckel's Monograph.

<sup>2</sup> *Eucyrtidium cranoides* in the Monograph.

a differentiation in the processes which have produced the zoons. Fig. 1 is known as an isospore; it is provided with a whip, a homogeneous nucleus of uniform constitution, and a little rod-like crystal. Figs. 2 and 3 represent the anisospores (fig. 2 the large macrospore and fig. 3 the smaller microspore) which are never produced by the less specialized *Actissa*. These are provided with a whip,<sup>1</sup> a heterogeneous nucleus of two-fold constitution, and fat granules, but the crystal is often wanting. Unfortunately all attempts have failed to follow the development of the flagellate young to the typical Radiolarian condition represented by *Actissa*. It is probable, however, that the phenomenon of accidental fusion of different zoons observable in the simpler Rhizopods has given rise in the colonial Radiolaria to the phenomenon of genetic union or conjugation, and that the macrospore and microspore unite; if this is true we may have here the simplest form of sexual reproduction. After this possible union it is probable that a single form arises like *Actissa* which becomes a colony by the division of the nucleus, the products of the division remaining united as seen in fig. 4, which is a young, unarticulated colony. Fig. 5 is a piece of a young colony showing how the many central capsules (represented by red dots in fig. 4) have arisen. There are eight of these capsules, two of which are in the act of dividing. The nucleus is seen in different stages of division. Around the central capsules extends the jelly-like calymma (blue in the figure) comparable with the jelly envelopes (yellow in the figure) of *Actissa*. Numerous vacuoles and yellow cells are seen in the calymma. The latter contain starch and are unicellular yellow algae which live with many Radiolaria. True to their plant nature, these yellow cells give out oxygen which is eagerly taken by the Radiolarian, while the latter, equally true to its ani-

<sup>1</sup> Brandt says they possess most probably two whips (see *Fauna und Flora des Golfes von Neapel*, XIII, p. 167).

mal nature, gives forth carbon dioxide. This supplementary relation where there is a mutual dependence of the one upon the other, is known as symbiosis and will be found to occur among other more specialized animals.

The division of the nucleus takes place early in life and this is a fact of great significance. The law of acceleration in development which has been demonstrated in many groups of the Metazoa, may have acted in this case, causing the characteristic late nuclear division peculiar to the single Radiolaria, like *Actissa*, to appear early in the life of the zoon. After the division the process of specialization is carried on in a most interesting manner, as shown in figs. 6-9, and results finally in the formation of the asexual isospores and the probably sexual anisospores. Fig. 6 is a zoon in the act of forming isospores. The original central nucleus has divided into many nuclei, and its place has been taken by a large oil globule. The nuclei lie close together but do not press upon each other sufficiently to be flattened into polyhedrons. The crystals first appear like lengthened granules and one is laid close to a nucleus. Gradually they grow into the form shown in fig. 6. In fig. 7, a, b (a diagrammatic representation of later stages in the process), the nuclei and crystals have arranged themselves near the periphery, while the large oil globule remains in the center. Finally disintegration takes place and the isospores appear. Fig. 8 is a diagrammatic representation of the process of forming anisospores drawn from balsam preparations. In early stages (fig. 8a, fig. 9) irregular groups of differentiated nuclei occur in spherical masses of plasma (fig. 9 shows a group of three nuclei in such a spherical mass), and in the inter-substance between these are found large, homogeneous nuclei, sometimes drawn out to a point at either end (fig. 9b). With the diminution of the central oil globule there appear the grape-like clusters of fat seen in figs. 8 a, b, c. In fig. 8b (a later stage than 8a) the groups of nuclei have increased in number and the homogeneous

nuclei with most of the intersubstance have disappeared. A difference in the size of the nuclei is apparent. This difference is still more plainly seen in the later stage (fig. 8c) in which scarcely a trace of the intersubstance remains. Finally the formation of anisospores takes place. The clusters of fat fall apart into granules and each spherical mass divides into as many wedge-shaped pieces as there are nuclei (fig. 8d). These ultimately fall apart when the large macrospores (fig. 2) and small microspores (fig. 3) appear. Fig. 10 is a mature (usually called "old vegetative") colony in which the flagellate young are ready to be set free by the disintegration of the colony. It is distinguished from the young colony (fig. 4) by its plain articulations.

According to Haeckel the same Polycyttaria or colonial Radiolaria which produce anisospores also produce, at other times, the asexual isospores, so that it would seem that these two forms of reproduction alternate with each other, and if so, we have here in the simplest subkingdom of animals the phenomenon of alternation of generations. This variability in function as well as variability in structure is just what one would expect to find among organisms which have not yet learned the ways of their more specialized and therefore more stable descendants.

#### MASTIGOPHORA.

We now come to a group whose peculiar and more or less constant characteristic is the possession of a whip or flagellum, and which for this reason is known by some as the Mastigophora and by others as the Flagellata. We have found the flagellum among the Rhizopoda, Heliozoa, and Radiolaria; wherever, in fact, there has been need for rapid motion it seems to have been developed as an adaptive character. In the typical Mastigophora it seems to have become fixed in the organization and therefore an

inherited character. The variability of this organ in the intermediate forms, and the close connection between the Heliozoa and Mastigophora are shown in the extremely interesting transitional organism, *Dimorpha mutans* Gruber,<sup>1</sup> to which we have already referred. When first observed the animal appeared to be an *Amoeba radiosa* or a Heliozoan, but suddenly it fell into a trembling motion and a long whip was thrown out. Pl. 50, figs. 1-8, show the changes undergone in about two hours. In fig. 1 the animal is leaving the Heliozoan stage, the body is still spherical, but the pseudopodia are short and one long whip begins to strike the water. The next moment the body is extended lengthwise and becomes egg-shaped. The pseudopodia shorten themselves still more, and the *Dimorpha* begins to swim propelled by two long whips. At times one of the whips beats the water while the other trails behind (fig. 2). Suddenly the animal stops swimming and turns the forward end of its body downward while the whips feel about on the bottom (fig. 3). All movements cease, the body becomes spherical and from every side fine ray-like pseudopodia are thrust out (fig. 4). But the *Dimorpha* seems not satisfied with the spot it has chosen, or it is disturbed in some other way, for the above described transformation occurs again (fig. 5), and the body becomes quite smooth during its rapid swimming (fig. 6). The little sun-animal has transformed itself into such a perfect whipped creature that it is difficult to keep track of it among the other flagellate organisms in the water. After swimming about it comes to rest again (fig. 7), thrusts out its pseudopodia, and transforms itself in a few moments into a Heliozoan (fig. 8). Fig. 9 represents the *Dimorpha* in its usual condition. The body is pointed at the posterior end where the food elements are crowded closely together. Gruber, to whom we are indebted for the above description, tried various experi-

<sup>1</sup> Zeitschr. f. wiss. Zool., XXXVI, 1882, p. 445.



ments and found he was able to force the animal from a Heliozoan to a flagellate condition by striking the sides of the dish when, as if disturbed, the Dimorpha would develop whips and swim quickly about.

The flagellate Mastigophora are well represented by the series of forms shown in Pl. 51. The body of *Monas termo* Ehr.? (fig. 1,  $\times 950$ ) is occasionally somewhat amoeboid, sending out short pseudopodia-like continuations. It is a free-swimming animal but may become fastened temporarily by a thread-like prolongation of the posterior end of the body (fig. 2,  $\times 1200$ ). At the forward end is the whip or flagellum, and on one side of its base is the beak-like prominence or lip. Between this lip and the base of the flagellum is the mouth, which, however, does not extend into an oesophagus. The flagellum catches the food and it is thrown with a sudden jerk directly against the mouth. "If acceptable for food the flagellum presses its base down upon the morsel, and at the same time the lip is thrown back so as to disclose the mouth, and then bent over the particle as it sinks into the latter. When the lip has obtained a fair hold upon the food, the flagellum withdraws from its incumbent position, and returns to its former rigid, watchful condition. The process of deglutition is then carried on by the help of the lip alone, which expands laterally until it completely overlies the particle. All this is done quite rapidly, in a few seconds; and then the food glides quickly into the depths of the body, and is enveloped in a digestive vacuole, whilst the lip assumes its usual conical shape and proportions." We have quoted the above from Prof. H. James-Clark<sup>1</sup> to show the specialization in structure which characterizes this animal. In none of the Protozoa already described have we found an apparatus for forcing food into the body at one particular place. If this process were long continued, it is not difficult to

<sup>1</sup> Mem. Boston Soc. Nat. Hist., I, 1866, p. 307.

understand how the mouth, oesophagus, and the other tubes and sacs of the digestive system originated. After the food has been retained in the body for a time the excrement is thrown out at a place near the mouth or through the mouth itself, instead of being ejected from any part of the body, as is the rule with the Amoeba.

Reproduction takes place in this genus by longitudinal fission and by the breaking up of the body into flagellate young. The researches of Messrs. Dallinger and Drysdale have shown that the phenomenon of fission in these minute forms "is not a mere division of undifferentiated sarcode into two parts." Before separation takes place there is always a germination of the anatomical elements which make the new monad complete, while in many instances the fission is preceded by a suddenly induced amoeboid condition.<sup>1</sup>

The young *Monosiga globulosa* S. K. (Pl. 51, fig. 3) is a free-swimming uniflagellate form which bears a resemblance to Monas (Pl. 51, fig. 1). In course of time it becomes stationary, as seen in fig. 4. Next, the stem and collar are developed (fig. 5 is the adult), the latter being the peculiar characteristic of many Flagellata but which is entirely wanting in the young *Monosiga* and in the adult Monas. It has been pointed out by Kent that this collar is a film of protoplasm which can be extended and withdrawn at will into the substance of the body in the same way as the pseudopodia of an Amoeba. Combined with the flagellum it serves as a most efficient trap for obtaining food. Fig. 6 is the adult of another species, *Monosiga gracilis* S. K., greatly magnified. The nucleus is seen near the central part of the body. The process of digestion is shown by the food particles colored blue which are circulating through the body. In this genus reproduction takes place both by longitudinal and by transverse fission and also by the breaking up of the body into flagellate young.

<sup>1</sup> Monthly Micr. Journ., XI, 1874, p.7.

We pass naturally from the solitary *Monosiga* to the colonial *Codosiga pulcherrimus* Jas.-Clk. Pl. 51, fig. 7, is the single, comparatively young zoon which has broken away from its colonial home and is a free-moving animal. During its young life it swims at times rapidly with its basal end extending forward, and the flagellum following behind "and vibrating in rapid undulatory and gyratory curves as if it were the screw propeller of some sub-aqueous vessel."<sup>1</sup> Finding a favorable spot whereon to settle, the *Codosiga* secretes a stem and becomes a fixed animal (fig. 8). The body is surmounted above by the high collar. The dotted lines in the drawing indicate the degree of the lateral vibratile expansion of the collar. From the middle of the cone of the body extends the flagellum. Figs. 9-16 of Pl. 51 illustrate the process of reproduction by fission, the stem not being drawn. At first the collar bulged as seen in fig. 9. Soon after this the flagellum grew shorter and finally disappeared, while a narrow furrow was seen in the anterior part of the body (fig. 10). This furrow extended downward, while the collar became more cone-like (fig. 11). Soon after this the collar began to expand and the body was divided about half way to its base. At each free rounded end a flagellum began to be developed which kept up a trembling motion (fig. 12). The body divided mostly to the base and the collar broadened (fig. 13). The process of division next extended into the collar (fig. 14) and continued, the collar growing broader and longer (fig. 15) until finally the self-division of the collar and body was complete and extended downward into the pedicel (fig. 16). A colony of two is often found; sometimes these increase to five (fig. 17), and occasionally as many as eight are produced. Fig. 18 is a free-swimming colony, *Desmarella moniliformis* S. K. The early stages of this species have not been observed, and therefore in the

<sup>1</sup>James-Clark, Mem. Boston Soc. Nat. Hist., I, 1866, p. 315.

absence of positive knowledge we can only reason from analogy in regard to the rightful position of the genus in a natural classification. In more specialized animals such as certain corals, Polyzoa, and others, the free-swimming colonies are derived from fixed colonial forms which have lost their organs of attachment. It is, therefore, probable that when the life history of *Desmarella* is known it will be found that the earliest stages of the genus bear structural evidences of its descent from a stationary form. If such evidences are not obtained by accurate microscopical research, it might still be possible that they have become wholly obliterated through the action of the law of acceleration in development. The colony of *Desmarella* is never large, numbering only from two to eight zoons.

In the light of the Flagellata already described, the development of *Proterospongia haeckeli* S. K. is extremely interesting. The animal begins its existence as a single attached uniflagellate organism without a collar (Pl. 51, fig. 19). Afterward the collar develops, and in this stage the *Proterospongia* resembles a *Monosiga*. Next a mucilaginous film is extended around the body below the collar (fig. 20). By binary fission two zoons are produced (fig. 21). Figs. 22 and 23 represent small colonies and fig. 24 a large one of between forty and fifty zoons. Cells migrate from the surface to the interior and become reproductive in function. Some of the zoons in figs. 23 and 24 have drawn in their flagella and the body has assumed an amoeboid appearance. This is in preparation for the encysted state (see fig. 24), after which the mass breaks up into a large number of flagellate young.

All the Mastigophora or Flagellata so far described belong to the subclass Flagellidia. The following Dinoflagellidia are represented by *Peridinium* and the Cystoflagellidia by *Noctiluca*.

The species *Peridinium tripos* Ehr. (Pl. 52, fig. 1) is provided with a transverse groove. According to the

observations of Klebs and Bütschli a second flagellum lies horizontally in this groove which has hitherto been mistaken for a girdle of cilia. The body is covered with a cellulose (Bergh) carapace formerly supposed to be silicious or chitinous, and its shape is unique, having three horns, two of which are in front and one behind. Kent<sup>1</sup> has pointed out the isomorphic resemblance existing between the bodies of the Peridinidae and the larvae of certain Echinoderms and Crustacea. The mechanical conditions for a floating existence have probably been the controlling cause of this peculiar shape of the body.

Pl. 52, fig. 2 (*P. arcticum* Ehr., dorsal view) has long arms and the serrations seen in fig. 1 have here become spines. According to Claparède and Lachmann these are two of a large number of varieties of the species of *Ceratium tripos*. Although these two forms may occur in the same locality, the *Peridinium arcticum* Ehr. is found most abundantly in the colder, denser waters of the arctic seas, where its broader and stouter arms probably assist in preserving the equilibrium of the body.

We come now to one of the members of the group of Mastigophora which has long been known on account of its remarkable property of brilliant phosphorescence. The *Noctiluca miliaris* Sur. is cosmopolitan, and to it are largely due the beautiful illuminations of the sea at night. The young Noctiluca (Pl. 53, figs. 1-6) shows specialization in structure by the possession of a whip and a tentacle-like organ near the mouth. The adult (Pl. 53, fig. 7) has a transparent body in the form of a peach surrounded by a distinct membrane. The protoplasm radiates from the center of the body, and spreads itself in a layer over the inner surface of the membrane (Kent). The mouth is at the bottom of a depression where the flagellum originates (which is not clearly seen in the drawing<sup>2</sup>) and

<sup>1</sup> Manual of the Infusoria, I, 1880, p. 452.

<sup>2</sup> See Huxley, Quart. Journ. Micr. Sci., III, 1855, Pl. 5, fig. 3.

near it is the "tooth" and the long tentacle-like organ which is transversely striated. The mouth leads into a tube and this to a digestive sac.<sup>1</sup>

The reproduction of the *Noctiluca* has been described in detail by Cienkowski.<sup>2</sup> This investigator maintains that we have here two identical histological cells blending and, therefore, that conjugation in the *Noctiluca* belongs in the rank of such phenomena of blending as aim at an accelerated assimilation, and that it stands in no relation with the more specialized sexual process of reproduction of the Metazoa. This view may certainly be questioned, since the act of conjugation, upon which, according to Cienkowski, the formation of swarmers seems to be in a high degree dependent, if not a sexual act, is most probably the initiative process leading towards the more specialized sexual process of the Metazoa.

While it is true that most of the Mastigophora have only one nucleus, yet this one is not probably identical in constitution with the simple nucleus of the *Amoeba* or with the nuclei of a many nucleated *Rhizopod*, since conjugation between the zoons of the Mastigophora is the rule rather than the exception, and this more constant differentiation in the process of reproduction is doubtless attended with a differentiation in the nature of the reproductive organ. Associated with this specialization of process and function there is also the structural differentiation of a primitive digestive system, and of a more or less stable body with its constant accompaniment, in youth as well as in adult life, of a locomotive and prehensile organ. For these reasons the Mastigophora (= Flagellata) may be considered as more specialized organisms than the *Rhizopods*. Although Bergh<sup>3</sup> has supported the opposite view considering that the *Rhizopods* have arisen from the Flagellata, nevertheless the burden of evidence

<sup>1</sup> Packard, Zoology, 1886, pp. 33, 34.

<sup>2</sup> Arch. f. mikr. Anat., IX, 1873.

<sup>3</sup> Morph. Jahrb., VII, 1882, pp. 272, 273.

seems to be against this view if we maintain that the more elementary organisms came into existence first and gave rise to the secondary or more complicated forms. Surely one of the simplest representatives of the Flagellata, the *Monas termo*, already described, is much more specialized than the structureless, organless, ever-changing mass of protoplasm, the Protamoeba.

### INFUSORIA.

The cilia or short hairs that clothe the cell of an Infusorian, either partly or wholly, constitute one of the important characters of this most specialized group of Protozoa. We have seen that pseudopodia and flagella can be converted the one into the other, but this is not the case with pseudopodia and cilia. The latter have become permanent and unchanging locomotive organs. They move in unison after the fashion of paddles, while the flagellum may be likened to a whip.

One of the commonest Infusorians to be found in stagnant water and vegetable infusions is *Paramoecium caudatum* Ehr. (Pl. 54). Although of comparatively large size, its rapid twisting motions make it difficult to observe its many interesting specializations of structure. The flagellum which we have seen so often in preceding forms has disappeared, and the body of the Paramoecium is provided with cilia which extend in longitudinal rows. Here is found greater differentiation in the digestive system, since the mouth which is at the bottom of the ciliated depression (near the lower of the two outer arrows in the left of the figure) leads into a tube that extends downward a short distance. Food was given the Paramoecium in the form of partly decomposed indigo obtained from maceration of the leaves of the indigo plant, also carmine from dried cochineal insects. The arrows on the left of the drawing indicate the course of the particles of indigo

as they were whirled along by the cilia of the disc. Many of the particles are seen passing downward into the tube at the end of which they have formed a pellet that becomes surrounded by a jelly-like substance. The arrows within the body show the definite course of the pellets in the body cavity. The nourishment having been separated from the food, the excrement is ejected at the swelling which rises temporarily on the ventral side of the posterior part of the body, as seen on the left of the drawing. The contractile vesicle according to Kent is normally spherical, as represented in the posterior part of the body, but under pressure it assumes the condition seen in the anterior portion of the body extending outward in the form of ray-like continuations. The nucleus, colored yellow in the drawing, is the long tubular organ with three enlargements just in front of the posterior spherical contractile vesicle. E. Ray Lankester<sup>1</sup> has shown in *Paramoecium aurelia* Müll.<sup>2</sup> a marked differentiation of the protoplasm into two well defined parts. The outer portion is bounded by a cuticle that is pierced by holes through which pass the cilia. Just under the cuticle are little sacs or tricocysts, each one containing a thread which can be thrown out, and which is helpful as a defensive and probably as an offensive organ. Attached to one side of the nucleus is the apparently small nucleus, the paranucleus,<sup>3</sup> which probably arises from the nucleus. The investigations of Balbiani and others have shown that the reproductive phenomena of *Paramoecium* and the Infusoria generally are more complicated than those of the Rhizopods or the Flagellata. Temporary conjugation takes place between the zoons of *Paramoecium* and

<sup>1</sup> Encycl. Brit., ed. 9, XIX, 1885.

<sup>2</sup> The *Paramoecium caudatum* of Ehrenberg is probably a variety of the *P. aurelia* of Müller.

<sup>3</sup> The paranuclei are sometimes called nucleoli, but objectionably, since the paranucleus has nothing to do with the nucleolus of a typical cell (E. Ray Lankester, Encycl. Brit., ed. 9, XIX, 1885).



may last five or six days or even longer. This union brings about important changes, the nucleus is broken up, the paranuclei divide, and protoplasm may be interchanged as well as paranuclei. The two zoons then separate and a reconstruction of the parts takes place with rejuvenescence of the organs followed by fission.<sup>1</sup>

While *Paramoecium* is a free-swimming single form in youth and adult life, *Stentor polymorphus* Müll. (Pl. 55, figs. 1-3) is sometimes a single swimmer when young and often a stationary and colonial form when full grown. The little embryo of *Stentor* (fig. 1) is nearly spherical in shape (the ground form of most Protozoa). Its cilia, even when within the body of the parent, are developed, but it possesses neither a mouth nor an esophageal tube. In time, however, these appear (fig. 2); the rounded body becomes trumpet-shaped and is often attached to some object. The *Stentor* then secretes a mucilaginous sheath about the posterior tubular portion of its graceful body (fig. 3). The upper anterior expansion of the trumpet has the delicate wreath of cilia and the large cilia near the mouth describe a spiral. The mouth extends into a spiral tube.

The protoplasm of *Stentor* has become differentiated to form a layer of thread-like fibrillae which extends from the anterior to the posterior end of the body and is extremely elastic. Another set of these fibrillae surrounds the ciliated disc and helps to close this region when the *Stentor* is contracted. This differentiated layer of elastic fibrillae is probably the initial form of the muscular system of the more specialized animals. The long beaded nucleus is seen at the right of Pl. 55, fig. 3. Unlike most

<sup>1</sup> According to Eigenmann (Bull. U. S. Fish Commission, XII, 1892), the ciliate Infusoria have two nuclei, the macronucleus and the micronucleus, the former of which is probably represented by the yolk nucleus of the Metazoa. This author gives a diagram showing the maturation, conjugation, and segmentation of Protozoa and Metazoa.

Protozoa the Stentor divides obliquely instead of transversely or longitudinally. This is in accordance with the spiral structure of the Infusoria. Just above the mucilaginous sheath the lateral line of cilia is seen to curve spirally; this marks the spot where a future zoon is to arise by fission. The newly formed zoon sometimes remains with the parent, producing a small colony.

Gruber<sup>1</sup> ascertained by experiment that division of Stentor took place in most cases at intervals of two days, that daughter zoons divided into granddaughters in the second day after their separation, and granddaughters in another two days into great granddaughters, and so on. In 42 out of 56 cases division took place on the second day after the preceding one. This mode of reproduction is not the only one peculiar to Stentor. A further differentiation in the process of fission is observable. The nucleus develops germs or embryos which, becoming detached from it, leave the body of the parent and swim freely about. Such embryos are represented by figs. 1 and 2 in Pl. 55.

We will now pass to a fixed colonial form of the Infusoria. The student of nature may find keen enjoyment in the study of the beautiful bell Vorticellidae. These Protozoa are characterized by marked specializations of structure. The protoplasm of which the bell-shaped body is made has become differentiated into three parts, the cuticle, ectosarc, and endosarc. Furthermore, the ectosarc has undergone a change whereby the outer portion has become converted into a muscular layer which, according to some authors, extends into the stem, forming the highly contractile spiral axis. The digestive system has become developed so that there is not only a mouth opening but a distinct tube-esophagus leading downward into the body. At the mouth opening this tube flares, and the enlargement is often called the vestibule, while the con-

<sup>1</sup> Ber. naturforsch. Gesellsch. Freiburg i. B., I, 1886, Heft 2. Engl. transl., Ann. and Mag. Nat. Hist., (5), XVII, 1886, p. 473.

tracted portion of the tube beyond is the esophagus proper. As yet the digestive system is not complete, there being no separate opening or anus on the surface for the exit of waste matter. If the Vorticella is given carmine or indigo, the way the food is caught by the cilia (which are borne on the thickened rim or peristome surrounding the disc of the bell) and its circulation through the ciliated vestibule and esophagus and through the endosarc of the body to its exit at the mouth, can all be observed with the microscope. With the differentiation of the muscular and digestive systems there is a greater specialization in the reproductive system and in the processes which lead to increase. Pl. 56, figs. 1-29, taken from Everts,<sup>1</sup> illustrate the process of reproduction through longitudinal fission, and figs. 30-34, after Greef,<sup>2</sup> the process through the conjugative act. Beginning with the little ball (fig. 1) which issues from the cyst, we find it a tiny mass of protoplasm showing no differentiation. It agrees structurally at this time with a cytode, since no cell wall is discovered, and it is not until the cilia are developed that it becomes a cell with a nucleus. A vacuole appears (fig. 2), next a swelling (fig. 3), and a wreath of cilia (fig. 4). The form changes and an organism appears which is likened by Everts to the *Trichodina grandinella* described by Ehrenberg.

This *Trichodina* (fig. 5) continues to grow (figs. 6-9) until transverse constriction takes place with a separation into two *Trichodinas* (fig. 10). Then the body lengthens (figs. 11, 12) with the formation of the peristome (fig. 13), after which the stem is secreted (figs. 14-17). Fig. 17a represents a stemmed Vorticella much enlarged. This form contracts (fig. 18), the body broadens (fig. 19), and the nucleus takes a position at right angles to the stem. A constriction takes place (fig. 20) which increases (fig. 21) until the division is complete (fig. 22). A wreath of

<sup>1</sup> Zeitschr. f. wiss. Zool., XXIII, 1873.

<sup>2</sup> Arch. f. Naturg., XXXVI, I, 1870.

cilia next appears at the posterior end of the body of one of the zoons (fig. 23), the forward end contracts, the disc and cilia are drawn in (fig. 24), and finally by strong efforts the zoon frees itself (fig. 25). The remaining zoon afterward becomes free in a similar manner. The movements of the free Vorticella are lively for a time, then it becomes quiet, takes on a spherical form (figs. 26, 27), the wreath disappears and the nucleus divides (fig. 28). The shrunken cyst covering is seen in fig. 29 with seven balls within. This completes the life cycle. This species also increases through conjugation, as has been stated. A smaller zoon, the microgonidium, approaches a larger stemmed zoon, the macrogonidium (fig. 30). The basal part becomes drawn in to form the sucker by means of which the small zoon attaches itself to the side of the larger one (fig. 31). When this is done, the conical base is stretched out again, whereby a boring organ is produced, and the body of the small Vorticella becomes a mere lump (fig. 32). Gradually the contents of the body pass wholly into the larger zoon, leaving only a sac-like skin (fig. 33). The bristles on this sac may be the wrinkles of the ring-like cuticle. Finally the sac-like skin is thrown off (fig. 34), and the two animals are fused together indistinguishably. It would seem that here the whole body of the zoon corresponds to the ovum and the spermatozoon, and if so, we have as the result of their union a fertilized egg. Much difference of opinion exists, however, in regard to the real significance of the act of conjugation. But whether this act is a sexual or an asexual one, it can be said with certainty that the process is far more specialized than the apparently accidental fusion of the Rhizopods. Furthermore, it is rational to suppose, as before stated, that this process is at least the initiatory leading to the complicated reproductive phenomena of the specialized Metazoa.<sup>1</sup>

<sup>1</sup>For a discussion of this subject, see Calkins, *The Protozoa*, 1901, chapter VII.

It is interesting to note that in one species of this genus, *Vorticella umbellaria* C. & L., there are nematocysts or thread cells which are more effective weapons than the tricocysts. Each of these cells contains a spirally wound thread, like the thread cells of the more specialized Coelentera soon to be described.

The compound colonial form, *Zoothamnium alternans* C. & L. (Pl. 57), is, according to Kent, one of the most remarkable instances of polymorphism among the Infusoria. In this genus there are three differentiated forms of zoons. Pl. 57 shows two of these forms. The large size of the macrogonidia in this species is unusual.

#### INFUSORIA.—TENTACULIFERA.

The Tentaculifera are represented in the Collection by the *Podophrya gemmipara* Hertwig (Pl. 58, figs. 1-4, a-e). By the possession of cilia, the young form (fig. 1) shows its probable relationship with the ciliate Infusoria. In the course of development the cilia disappear. Kent observed, however, in specimens obtained from North Wales in 1881, that the embryos were provided with short tentacles either in addition to or in place of a more or less conspicuously developed ciliary covering. Fig. 2 is a young form showing the origin of the stem. The adult (fig. 3) is much more differentiated. The food-catching organs or tentacles have increased in number. Nutting<sup>1</sup> has given figures of another species of *Podophrya* (probably *P. compressa*) showing how the young embryo after becoming attached, develops a few tentacles at first, which increase in number with the growth of the animal. Besides the tentacles there are sucking tubes which broaden out at the end after the fashion of a sucker (see fig. 3). The prey is caught by the tentacles

<sup>1</sup>Amer. Nat., XXII, 1888.

and afterward sucked into the body of the Podophrya by means of the sucking tube, though the process is not well understood.

Propagation takes place by the formation of buds or embryos from the oral surface. Eight of these buds are seen in Pl. 58, fig. 4. The nucleus in the young forms is comparatively simple, but in the large, old specimens it has an extraordinarily complicated structure. This increase in complexity is finely shown in figs. a-e. Fig. a is a young Podophrya with a simple horseshoe nucleus; in fig. b the nucleus has changed its form, and in fig. c it has become forked. Fig. d shows four embryos with the branches of the nucleus extending towards them, and in fig. e they have penetrated the embryos.

In this sketch of the Protozoa we have attempted to point out some of the many differentiations whereby a structureless mass of protoplasm, like Protamoeba, may become a specialized organism like an Infusorian.

## MESOOZOA.

The division of animals known as the Mesozoa holds middle ground between the Protozoa and the Metazoa, and is of great importance from a phylogenetic point of view, as will be seen hereafter when the development of the egg of a Metazoan is traced.

The Mesozoa are represented in the collection by *Volvox globator* L. No drawing can reproduce the beauty of the living Volvox. A tiny ball of vivid green, it revolves through the water with graceful and rapid motions, offering a puzzle to both the botanist and the zoologist. Although claimed as a plant by a number of botanists, its morphological relations to animal forms and the history of its development lead many zoologists to place it among animals.

It seems probable that Volvox has arisen from the

Protozoa Flagellata, among which it is placed by Bütschli, who, nevertheless, says that strictly speaking the genus does not belong here, since the so-called colonies are in reality many-celled individuals.<sup>1</sup>

We have in *Volvox* an organism of many cells which are arranged in one layer around a central cavity. This cavity is hollow in so far as it is destitute of cells, though it is filled with a gelatinous cellulose substance which is secreted by the cells and in the periphery of which they lie embedded, connected by delicate threads of protoplasm.

It has already been shown that many adult Protozoa represent the simple unfertilized egg, and that probably some of the most specialized members of this branch, such as *Vorticella*, reach in their development the condition of the fertilized egg. If, now, this egg were to divide and the products of division remain together and arrange themselves in a layer around a central cavity, then we should have the next stage of development of the fertilized egg, known as the blastula, which is well represented by the adult *Volvox*.

In *Volvox* the peripheral layer is made of flagellate motor and feeding cells called somatic cells (Pl. 59, fig. 1). There may be 12,000 of these cells in an adult and each one has two long whips which pierce the outer wall surrounding the cells. A few of these somatic cells which migrate from the surface and are just inside of this peripheral layer have the power of dividing or of asexual reproduction, and are known as parthenogonidia (Pl. 59, fig. 2 a-e, illustrating the process of division). These parthenogonidia give rise to asexual adults (fig. 3) that often contain eight smaller *Volvoce*s which revolve within the parent, and each of these in turn contains eight more, so that three generations are represented as seen in fig. 3. When the parent capsule is ruptured, the eight smaller

<sup>1</sup>Bronn's Thierreich, II, 1883, p. 775.

spheres leave the parent one by one, rotating swiftly through the water.

After asexual reproduction has continued for some time, cells which are apparently parthenogonidia at first become biflagellate male cells or microgonidia (fig. 4), and large, unflagellate female cells or macrogonidia; one of these macrogonidia (fig. 5) is being fertilized by the microgonidia. This process of fertilization is similar to that of specialized plants and animals; after fertilization, cleavage takes place and both somatic cells and parthenogonidia are formed before the embryo leaves the parent. After this, the young develops into a sexual adult (fig. 6). In this figure, a is a male cell seen from above; a<sup>2</sup> the same from the side; a<sup>3</sup> with the microgonidia separated; a<sup>4</sup> with only a few microgonidia; the others having escaped are moving about in the central cavity. Fig. 6 b, is a female cell; b<sup>2</sup> the same with vacuoles in the inside; in b<sup>3</sup> the microgonidia have fastened themselves on the gelatinous covering of the female cell; sometimes three penetrate the covering and bore into the interior, when a fertilized egg results, which is the sexual method of reproduction in *Volvox*.

The extremely interesting observation of Ryder<sup>1</sup> on *Volvox minor* shows that, in spite of its nearly spherical form, there is a polar differentiation of the body with the specialization of possible sense organs at the anterior pole. According to this investigator the anterior pole of the blastula is always directed forward when the animal is in motion, and therefore it is this pole which is brought into the most dangerous position. Now, it is instructive to note that the peculiar organs known as "eye-spots" are developed much more at this pole than elsewhere, being, in fact, so slightly developed at the posterior pole, where there is little use for them, as to be nearly absent. There-

<sup>1</sup> Amer. Nat., XXIII, 1889, p. 218-221; also Proc. Acad. Nat. Sci. Phila., May, 1889, p. 138-140.



fore it is plain, says Ryder, that if these organs are visual or sensitive to light or any other natural agent, they are best developed in just the position in which they are of the most service to the organism.

## METAZOA.

### PORIFERA.

#### Section 1 (erect part).

Great advances have been made in the direction of a natural classification of the Porifera since 1872, but nevertheless naturalists still differ not only in regard to the systematic position of these animals, but also in respect to their anatomical structure.<sup>1</sup>

They are considered as members of the next more specialized subkingdom, the Coelentera, by Haeckel, Leuckart, Marshall, Polejaeff, Schulze, R. von Lendenfeld,<sup>2</sup> and Ganin. Marshall<sup>3</sup> even goes so far as to regard them as reduced members of this group, finding evidences, as he thinks, of the former existence of tentacles, thread

<sup>1</sup> Dr. R. von Lendenfeld has given a clear and an extremely interesting history of our knowledge of sponges in the Introduction to his Monograph of the Australian Sponges, Proc. Linn. Soc. New South Wales, IX, part 1, 1884. For the most complete bibliography on the subject, see Rauff's great work on Palaeospongiologie, Palaeontographica, XI., 1893-'94.

<sup>2</sup> According to this author the Metazoa are naturally divided into two groups or grades; the Coelentera with a simple undivided body cavity, all the parts of which are in direct connection with one another; and the Coelomata, which have two distinct and entirely separated body cavities, — a gastral and a perigastric cavity. The sponges, according to this author, have a simple and continuous body cavity, so that they are regarded by him as Coelentera (Proc. Zool. Soc. London, 1886, p. 565).

<sup>3</sup> Zeitschr. f. wiss. Zool., XXXVII, 1882, p. 246. Jena. Zeitschr., XVIII, 1885. See Ann. and Mag. Nat. Hist., (5), XVI, 1885.

cells, and mesenteric pouches. This would place sponges *after* the Hydrozoa and Anthozoa in a natural classification, but the views of Marshall have not been established.<sup>1</sup> Bütschli and Sollas maintain that sponges belong to an independent phylum, and give it the name of Parazoa.<sup>2</sup>

Owing to certain marked structural characters we have considered the group as belonging to the Metazoa, but as an independent and primitive group of this phylum having more or less remote ancestral forms among the Protozoa. At the same time it must be borne in mind that the primitive characters are most plainly seen before the sponge becomes a sessile animal, and that after fixation takes place, certain adaptive characteristics and evidences of reduction appear. It would seem as if the Porifera and Coelentera, as descendants, speaking broadly, of the Protozoa and Mesozoa, traveled along similar roads for a short distance till the sedentary habits of the former and the free-swimming, active life of most of the latter caused a divergence of the roads.

The processes by which the Metazoa have arisen from the Protozoa through the Mesozoa have not been determined with certainty. The two leading views in regard to the subject are those of Haeckel and Metschnikoff. According to the gastraea theory of Haeckel the fertilized egg of a Metazoan, a sponge for example, arises from an unnucleated mass of protoplasm comparable with the Monera of the Protozoa. Becoming nucleated and fertilized, it may be compared with the adults of the most specialized Protozoa. This egg becomes segmented, thereby forming many similar but still united cells. These resemble remotely a mulberry, so that the egg at this stage is known as the morula. The cells arrange themselves about a central cavity filled with fluid, and this stage is the blastula. Next the cells at one pole of the

<sup>1</sup> See "The Relationships of the Porifera," Vosmaer, *Ann. and Mag. Nat. Hist.*, (5), XIX, 1887, p. 249.

<sup>2</sup> Reasons for this classification are given in the *Rep. Chall. Exp.*, Zool., XXV, 1888, p. xcii.

blastula become differentiated and turn inward or become invaginated, and the embryo possesses two layers (the outer layer or ectoderm and the inner layer or endoderm), a gastral cavity or archenteron, with an opening, the blastopore. As the process of digestion was supposed to go on in the gastral cavity, the embryo at this stage was called the gastrula.

It will be noticed, that, according to this theory, the invaginated gastrula represents a primitive stage in the development, arising directly from the blastula; also that the archenteron and blastopore are primitive and not secondarily acquired characters. Furthermore, the process of invagination, by which these conditions have been brought about, must of course, according to this theory, be a primitive process. Haeckel maintains that the process of delamination or the cross division of cells, to be spoken of hereafter, is a modification of invagination, but does not show how the one is derived from the other.

Extended observations on sponges and Coelentera proved that the occurrence of the invaginated gastrula was exceptional instead of normal, as would be expected in these, the simplest and most generalized groups. In *Ascetta primordialis*, one of the simplest calcareous sponges, and in the silicious and horny sponges, in the Hydrozoa and Anthozoa, the stage following the blastula is not, as a rule, an invaginated gastrula but something quite different. It is a solid, mouthless embryo, consisting of one layer of cells on the periphery and a mass of cells in the interior.

The parenchymella theory of Metschnikoff throws light on the origin of this stage of development. The blastula, according to this author, is converted into the solid embryo or parenchymella<sup>1</sup> by the process of immigration of cells from the surface (such as was seen in *Proterospongia*

<sup>1</sup> We use parenchymella (Metschnikoff) instead of planula (Lankester) because the theory of Metschnikoff is given the preference to that of Lankester. (See McMurrich, *Biol. Lect. Mar. Biol. Lab., Wood's Hole, 1891.*)

and Volvox) and also by the delamination of the inner ends of the ectoderm cells. The former process results from the longitudinal division of the cells, the latter from cross division. In Proterospongia and Volvox the migrating cells become reproductive, but with this differentiation in function it is not difficult to conceive that other cells might become digestive and pass to the interior, leaving the locomotor whipped cells on the surface.

The fact now demonstrated, that digestion in many of the more generalized Metazoa is intra-cellular, or carried on within the cells, and not in a stomach or archenteron, strengthens the theory of Metschnikoff. In time the cells within the solid embryo arrange themselves in a layer to form the endoderm. Later an opening breaks through the two layers, endoderm and ectoderm. The resultant form is similar in appearance to the invaginated gastrula, but in this case it is clear that the endoderm is not formed as a bag-shaped invagination with a terminal opening.

The parenchymella is in reality the primitive condition, arising from the blastula, and the gastrula-like stage is acquired later.

It is not difficult to see how the process of immigration might apparently give rise to invagination in certain cases, since if the cells migrated *en masse* from one pole of the blastula instead of individually from all points of the surface, a form would appear resembling an invaginated gastrula. The formation of the parenchymella and the resultant gastrula-like embryo is the normal development of most of the Porifera and Coelentera, the invaginated gastrula occurring rarely, as for example in *Sycandra*<sup>1</sup>

<sup>1</sup> Dr. Otto Maas (Zoologische Jahrbücher, Anat., VII, Heft 2, 1893) maintains that the invagination of the "ciliated" cells in *Sycandra* has nothing to do with the process of gastrulation, the two layered embryo being already formed, according to this author, before the occurrence of this invagination. A "fundamental similarity" Dr. Maas finds between the development of the calcareous and horny sponges, and he thinks that the apparent exceptions to the rule (*Sycandra*, *Oscarella*, etc.) will be found to conform to it on further study.

among the most specialized calcareous sponges and *Halisarca* (= *Oscarella*) among the silicious group. Up to the time of the formation of the gastrula-like embryo the development of the sponge is parallel and similar to that of the Coelentera. After the gastrula-like stage, however, the transformations that the young sponge goes through are peculiar to the Porifera. These stages end in the formation of an oval form with a girdle of larger cells and a circlet of cilia around what was the opening of the gastrula-like embryo, but which has been plugged up by the growth of cells in the interior. This larva is collared; it is the typical Poriferan form and when one finds it he knows that he is looking at the young of a sponge. This little active creature is not guided by its intelligence in the search for food nor by any particular instinct. The tides and currents carry it (since its own power of swimming is not very effective), and where they flow there is always food of the right sort in abundance. If the little larva floats out of the proper region it would fasten itself probably to any sufficiently smooth, hard substance, and either lead a half-starved abbreviated existence, or meet with an untimely death choked by muddy sediments or killed by some other equally effective agency. When about to settle, the collar spreads itself out by growth, forming the base, and by closely fitting itself to the surface excludes the water and air, thus fastening the body by the weight of these elements to its selected spot as a boy fastens a sucking disk of wet leather to a stone.

The cavity which appears in the body after this stage has no external opening; the latter breaks through at the end opposite the plugged up opening of the gastrula-like embryo. The cells of its walls have flagella and collars. These organs appear at different times, and on different parts of the body, but they become permanent in the interior of the ampullae or little sacs after this stage and are not found, as a rule, on the membranes of other parts or on the exterior.

The primitive and most generalized Porifera must be those sponges that in their adult form and characters most nearly approach the gastrula-like embryo. It will be seen that such sponges are the Calcarea or the group of calcareous sponges next to be described.

#### CALCAREA.

It cannot be doubted that a form existed in the past (if it is not living at the present time) which possessed the simple structure of the generalized Calcarea, but which was without a skeleton of any kind and also without the power of taking up foreign matter to make one. Such a sponge would be a primitive one, and its development would throw much light on the origin and classification of the Porifera. Until this gap is filled we must begin with *Prophysema primordiale* Hkl. (Pl. 60).<sup>1</sup> Although this sponge never develops a skeleton, yet it possesses the capacity, exhibited by a few other sponges and by some Protozoa, of taking up foreign substances (in this case both silicious and calcareous spicules) and of making a false skeleton sufficient for the support of its own body.

Prophysema is a simple attached tube with one opening, and with the body cavity lined with flagellate cells.

<sup>1</sup>This form was previously described by Haeckel as *Haliphysema primordiale* Hkl. (Jena. Zeitschr., XI, 1877). According to Kent, E. Ray Lankester, and Möbius, the type species of *Haliphysema* (*H. tumanowiczii*) is a Protozoan of the Rhizopod group. Haeckel now agrees with these authorities that the interior of this last named species is filled with protoplasm which extends from the single opening in the form of pseudopodia and that, therefore, this form is a Rhizopod, but he also maintains that in the species formerly called *Haliphysema primordiale* but now named *Prophysema primordiale* there is a distinct body cavity lined with flagellate epithelium, so that this species is a true sponge. For further information see Rep. Chall. Exp., Zool., XXXII, part 82, 1889, p. 26.

It may be that even pores do not exist, and if so the water may be taken in and thrown out at the large opening, but in the absence of any special apparatus for sifting the water it is more reasonable to suppose that if this body is really a sponge, as claimed by Haeckel, it would when living and feeding in its native element have temporary pores of minute size capable of opening through the walls between the cells. These could furnish the internal cavity with food of sufficiently minute size to be handled by the flagella and to be swallowed by the microscopic cells of the walls.

*Ascetta primordialis* Hkl., is the simplest form now known with certainty to be a sponge. If it were deprived of its skeleton it would represent the simplest sponge type, to which Haeckel<sup>1</sup> has given the name of Olynthus.

The fertilized egg (Pl. 61, figs. 1-3) of this species of *Ascetta* undergoes segmentation and a one layered blastula results. While still within the body of the parent cells migrate from the surface of the blastula to its interior central cavity and this process continues after the larva has passed into the water (Pl. 61, fig. 4) until the cavity is filled (fig. 5). The adult *Ascetta* (Pl. 62, fig. 1; fig. 2, the same with a portion of the external wall removed) is a simple bag which is capable of varying its form so that at times it resembles a vase, a cylinder, a pear, or even an egg. At one end it is attached, and at the other there is a large opening. The walls of the bag are thin and are pierced by numerous transient pores which are supposed to open anywhere through the walls of the body, not having any constant location. There are no persistent canals but the water passes through the shifting pores into the body cavity which is lined with flagellate and collared endodermal cells. The middle layer of cells known as the mesoderm is thin but gives rise to one, three, and four rayed spicules which are

<sup>1</sup>Rep. Chall. Exp., Zool., XXXII, part 82, 1889.

arranged in one layer. The ectoderm is colored blue in the figure, and is seen to invest the whole body and cover the projecting spicules.

Ascetta represents the group of sponges known as Ascones. The "canal system" of other sponges scarcely exists in this group, since the body cavity is a sac or ampulla without radiating canals. If we imagine a number of Ascetta-like forms budding from a common base and from each other's sides, so as to form a bushy colony, we have a sponge like *Leucosolenia* (No. 63), one of the commonest on our coast. This is a simple thin-walled, Calcareous sponge like Ascetta except that the young single tube gives rise to branches by budding, and these branches to others, until a colonial form is produced. Pl. 63, figs. 1-3, show the structure of the adult *Leucosolenia* (species probably *coriacea* Montague). A character of this genus is the sieve which extends over the cloacal opening seen in fig. 1, where a portion of the upper part of the tube has been cut away. Fig. 2 is a vertical section of one tube showing the flagellate cells of the endoderm, the large central cavity, the ectoderm, and at the top the sieve. Rising above the sieve, the ectoderm by doubling upon itself forms a two layered ectodermal collar. In fig. 3 the sieve is separated from the tube. Its cells have a central portion containing a nucleus which is more clearly seen in one of the upper and central cells, where it is indicated by a black circle. The cells extend out into a number of processes and unite with those of other cells, thus forming a network with large openings. In this case the body of the cell forms the node, but sometimes the node is produced by the union of three cell processes. Fig. 4 is a spicule of this genus. Fig. 5 is another species of *Leucosolenia* (*L. clathrus* O. S.) which has been described as without large openings. When seen in healthy living condition the cloaca is widely extended (fig. 6); when contracted the opening closes as in fig. 7. The sphincter by which the



work is accomplished is represented at the base of the collar by a black line.

Several authors describe the endoderm in this genus as many layered, but Minchin proved that this appearance is wholly due to contraction. When fully expanded the endoderm has only one layer, but when contracted it is as shown in fig. 8; fig. 9 is a portion of the endoderm from fig. 8 more highly magnified.

The genus *Sycandra* is one of the most differentiated of the calcareous sponges. Some of the species, like *Sycandra* (= *Sycon*) *raphanus* Hkl. (No. 65), are single, while other species, like *Sycandra arborea* Hkl., form colonies. The egg and spermatozoon in *Sycandra raphanus* Hkl., are transformed cells of the mesoderm. The fertilized egg (Pl. 64, fig. 1) possesses a nucleus and is capable of creeping amoeboid movements. In fig. 2 the nucleus has divided. Fig. 3 shows the first cleavage or furrowing stage from above, and fig. 3a the same from the side. Fig. 4 shows four cells, fig. 5 eight cells still lying in pairs; fig. 5a the same from the side; fig. 6 sixteen cells, fig. 6a the same from the side; in fig. 7 a large number are represented. This repeated division gives rise to a hollow sphere, the wall of which is formed by a single layer of cells. Pl. 64, fig. 8, is the blastula with its eight dark granular cells surrounding a basal opening, and fig. 9 is a further developed, entirely closed blastula. In fig. 10 the embryo has become differentiated into halves unlike each other, for which reason it is known as an amphiblastula. This is probably a modification of the primitive blastula already described, and if so it is a secondary and more specialized form. The granular cells have increased in number, and are at the broader end, while flagellated cells are at the smaller end. In this condition the embryo leaves the parent. Fig. 11 is a more advanced stage in which the flagellated layer has become flattened; in fig. 12, it is still more depressed, and in fig. 13 has disappeared within (see note p. 66). The larva settles mouth downward

(fig. 14), which is filled up with granular cells. Between the two layers of cells there is a narrow bright zone which Schultze considers the first indication of the gelatinous inter-layer, mesoderm, that reaches such a great development in most sponges.

The spicules appear in the mesoderm, first in the form of slender, straight little rods pointed at both ends (see fig. 15), which fact favors the view that the first formed spicules were one rayed and straight. They thicken as they grow and curve into a slightly S-shaped form. Afterwards three rayed and four rayed spicules are formed, one of the arms of which extends inward, while the other three are on the surface and probably serve for protection.

The larva lengthens, pores form in the wall, and the large opening at the top breaks through the ectoderm. It is now clear that this opening is not a mouth nor a primitive character, but a secondary feature, occurring in a past embryonic stage, and is in reality a cloacal opening for the ejection of the waste products of the body. The cells of the endoderm acquire collars and flagella. The body cavity of the young *Sycandra* is now a simple ampulla having as yet no branches. In this stage it is identical with an adult *Ascon*, like *Ascetta*, which it structurally represents. Later the mesoderm thickens, the pores grow into tubes, the ampullaceous sacs are formed near the food supply, the cells of the body cavity lose their flagella, the cells of the ampullaceous sacs acquire collars and flagella, and from that time the work of taking food and digesting it for the use of the other cells is done by them. Thus the single primitive digestive cavity becomes a cloacal trunk, pores become tubes branching from this trunk, and the function of the cavity is transferred to the little sacs or ampullae formed in the canals as they are stretched out by the thickening of the mesoderm. This is a process of reduction resulting in transforming a normally formed, symmetric, vase-shaped,

single individual with one central trunk into a creature with overgrown walls to the body, with a radiating or branching cavity, and with the digestive function of the central trunk transferred to expanded portions of the branches or canals near the exterior. The whole process evidently hinges on the rapid growth of the mesoderm, because when this is thin the food supply is close to the central cavity; when this is thickened the pores must become tubes; when it is still thicker, the tubes must lengthen. The food supply of the body is thus carried away from the central cavity, and it is but natural that the cells in the canals nearer the pores should get more, grow more and gradually make it unnecessary or impossible for the cells farther inward to get food. These last must then necessarily suffer reduction and lose first the use and then the habit of growing out collars and flagella, and sink into the form of epithelial membrane cells.

The function of the short canal leading into the ampulla from the exterior is obviously to bring food of microscopic size, and that of the continuation of the canal beyond the ampulla is to carry away the excrements of the ampullaceous cells. These cells are voracious feeders and throw out a large amount of waste matter which is carried into the great central cavity by the excurrent canals, and thence it is transported to be ejected at the cloacal opening above.

We shall presently see how in other orders of sponges the law of specialization by reduction has destroyed all tendency to grow into symmetrical shapes, so that the *Silicea* and *Keratosa* well deserve the designation of amorphous or formless, so often bestowed upon them.

This irregularity in form together with greater complexity of structure is found in *Leuconia aspera* (No. 66) which represents the group of Leucones, the most specialized of the calcareous sponges.

## SILICEA.

We cannot pass to the silicious sponges without considering briefly some of the embryological facts relating to their development. The egg of most silicious sponges in the earliest stages is solid<sup>1</sup> but becomes hollow subsequently. Later a granular mass accumulates in the interior so that the egg is again solid. The endoderm is formed not by an invagination of a portion of the ectoderm, but by delamination from the ectoderm, and it is this mass of cells cut off from the ectoderm which fills up the central portion of the young sponge. Both Hyatt and Barrois agree that no gastrula stage exists in either the silicious or the horny sponges. After the appearance of the ampullaceous sacs and the spicules, the larva becomes fixed by the collar at the oral end of its body. The canals and pores form and afterward, probably through the mechanical pressure of the water, the cloacal opening breaks through the ectoderm. It will be seen that here, as in the calcareous sponges, this opening is not comparable with the mouth of other animals, but is a secondary formation and in function a cloaca.

*Halisarca* (= *Oscarella*) *lobularis* O. Schmidt (*H. dujardini* Duj., Pl. 67, encrusting a stone), may be one of the simplest of the silicious sponges. Its cells are less differentiated than those of most sponges. The ectodermal cells retain their flagella throughout life, and the cells of the mesoderm are not modified, as in the more specialized forms.<sup>2</sup> There is no skeleton, and in the absence of positive information it is possible that *Halisarca* is one of the primitive forms. Authorities differ with regard to the origin of this genus, and it is at present impracticable to determine whether it is a reduced form, a descendant of

<sup>1</sup> Hyatt, Proc. Boston Soc. Nat. Hist., XIX, 1878, p. 12.

<sup>2</sup> Sollas, Quart. Journ. Micr. Sci., XXIV, 1884, p. 618.

genera with skeletal structures which has reached its present condition by reduction, or whether it is an existing representative of a primitive type which has never had any skeletal structures. Whatever way the result has been arrived at, the existing *Halisarca* is obviously a skeletonless kind of silicious sponge, and can be used to show what such forms are like. It is a fleshy animal with the typical characters of pores, canals, ampullaceous sacs, and cloacal opening. The genus is interesting because it increases not only by eggs but also by a process known as budding which is essentially the same as that of division so common among the Protozoa. In this case, however, there is not an equal division of the body, but a part separates from the rest and becomes a new animal.

#### SILICEA.—HEXACTINELLIDA.

This group is represented by fossils, and living members are mostly found in the deep seas. Although the oldest silicious sponges probably possessed separate spicules, yet on the death of the animal these would fall apart and be swept away and deposited along with other remains, so that no satisfactory inferences can be drawn in regard to the sponges possessing them.

The predominating six rayed spicules of the group have been shown to be simply a modification of the three rayed form which we have found among the *Calcarea*. It has also been proved that the anatomical structure and the development of these sponges are in some ways like those of the calcareous sponges. For these reasons, and because the group is found in the oldest geological formations, the *Hexactinellida* are considered as the more generalized of the silicious sponges.

*Ventriculites* (No. 68), often occurring in the chalk, is made up of six rayed spicules which are always fused together. It is more or less cup-shaped with a wide cen-

tral hollow. In *Hyalonema sieboldi* Gray (No. 69), the cup-shaped body is supported on a long tuft of silicious spicules, by means of which the animal is anchored in the mud. These rooting spicules are sometimes two feet long, while the spicules of the body are varied and beautiful in design.

The probable ancestor of *Euplectella speciosa* Q. & M., was one of the Dictyospongidae which were vase-shaped sponges composed of spicules that united to form a framework similar to that of *Euplectella*. This has disappeared from the fossils but the tracery of the fibers may be seen on their surfaces. In the living *Euplectella* (No. 70) the delicate skeleton is covered by a grayish brown fleshy matter and skin. It is interesting to note that the young *Euplectella* has the spicules separated, but with the growth of the animal fusion takes place to form the delicate framework. The sponge skeleton consists of longitudinal and circular silicious strands intersecting in such a way as to form meshes. Besides these there are ridges of fibers which run spirally around the skeleton. The upper end is closed by a sieve-like plate, while at the lower end long silicious spicules extend downward to anchor the animal in the mud. In dried specimens of the skeleton these long, fiber-like spicules are usually bent upward around the base of the sponge, and they are also thus represented in drawings. Such specimens and figures are misleading, since these spicules always extend downward and outward for the purpose of firmly anchoring the animal.

An interesting case of commensalism is offered by *Euplectella*, since it often harbors within the hollow of its vase-like structure a little shrimp, *Spongicola*.

In the Hexactinellida there is no drainage canal system, as the large ampullaceous sacs open directly into the great cloacal tube which is closed at the opening above by the sieve-like plate.

The members of this group resemble the *Calcarea* in

being more symmetrical and constant in form than the members of other orders of Silicea. They also stand correspondingly near to the Calcarea in their organization, as has already been stated. The mesoderm is not so thin, but it approximates to the condition of that of the more primitive calcareous sponges, and in accord with this the excurrent canals are not found, and the ampullae open directly into the cloacal trunk in some forms. Thus the organization is just a grade more specialized than in the Ascones with their digestive cells in the central trunk, and less specialized than Sycones with their ampullae in the canals of the lateral branches of the water system.

#### SILICEA.—LITHISTIDAE.

These forms have a thick stony wall and irregular spicules some of which are cleft into ragged branches. The fossil *Tragos* (No. 71) is a representative. It is shaped like a funnel and the exterior wall is often wrinkled concentrically.

#### SILICEA.—TETRACTINELLIDA.

*Tetilla sandalina* Sollas (Pl. 72, fig. 1) is a representative of the simple Tetractinellida. It has a single opening at one end with papillae at the other. The outer portion of the sponge is soft, not differing essentially from the inner. The mesoderm is slightly developed. The ampullaceous sacs (fig. 2) with their flagellate cells are large, and open by a wide mouth into the excurrent canals. The spicules vary from a straight rod to an S-shaped form (fig. 3). They are seen in fig. 2, where the straight ones overlap, forming "spicular fibers."

*Tethya* (No. 73; Pl. 74, figs. 1, 2) has a spherical form with one or more small openings. The outer sur-

face of the ectoderm is differentiated into a hardened wall or cortex with a distinct fibrous layer. The skeleton in *Tethya* has a radiate arrangement. The spicules when typical have a long straight axis with three curved horns. Besides these there are straight spicules with both ends alike, and also star-like silicious forms. Fig. 2 is a vertical section of *Tethya* showing its system of tubes, the cloacal opening to one side, and the silicious threads extending from the base. The power of adaptation possessed by most animals in a greater or less degree is strikingly seen in *Tethya*. With a rounded form and a yellowish color which have given it the name of "the orange of the sea" (see fig. 1), it has succeeded in securing a firmer hold by means of long, tough, silicious threads (Pl. 74) which act as anchors penetrating the mud and holding the growing sponge upright. The species shown has a peculiar adaptation of this habit, having a network of silicious threads like a mat of coarse wool on its base. These catch the fine gravel sifted out of the mud by the movements of the animal caused by the waves, and this gravel makes its lower side much the heavier. If now the animal is upset or swept away by the current or waves, the gravel acting as ballast will always serve to keep it right side up.

One of the most complex forms of this group is *Geodia* (No. 75). Here the outer part is differentiated to form a cortex and the mesoderm is thick. The spicules are unusually large and can be seen with the naked eye.

#### SILICEA.—MONAXONIA.

There is no sharp line of division between the *Tetractinellida* and the *Monaxonia*. *Suberites* (No. 76; No. 77, dried specimen) is instructive, since it has adapted itself to a free life on shifting sands. Its pores are so small and the structure so dense that the sand cannot pass



into the sponge, and its lightness keeps it from being buried (Hyatt, Stand. Nat. Hist., I, 1885, p. 66). The Suberitidae offer fine examples of spiral and radiate structure of the skeleton. This is seen in *Stylocordyla stipitata* var. *globosa* (Pl. 78, figs. 1-3). Fig. 1 shows spiral arrangement of the bands of spicules in one specimen; fig. 2 is a longitudinal section of another specimen, showing radiate structure; and fig. 3 is a cross section of the same, showing the longitudinal spicules of the stem by which the sponge is attached and the radiate arrangement of the spicules of the body part. The ends of the spicules of the stem which have been cut are seen near the center of the drawing. In most of the Monaxonia there is more or less horny cementing material called spongin. It is interesting to note that the chemical composition of this substance is similar to that of chitin, Krukenberg having given it the chemical formula  $C_{30}H_{46}N_9O_{13}$ , while that of chitin is  $C_{15}H_{26}N_2O_{10}$ .

Another member of the Suberitidae is *Raphiophora patera* Gray (No. 79), which is on the top of Section 1. This is one of the largest species of the Porifera and its size and shape have given it the name of Neptune's Cup.

*Cliona* (No. 80) is a borer into the living and dead shells of mollusks, especially the oyster, and into limestone, etc. Pl. 81, fig. 1, represents the openings of the young *Cliona* enlarged, and fig. 2 shows the work of the sponge in the interior of the shell. Just beneath the outer surface is a series of excavations, and narrow passages connect these with another series of cavities below. When the shell is completely mined, the sponge swells out in a bulbous mass on the outside (fig. 3). Having destroyed the shell, it will take sand into its body, as seen in fig. 4, which is a section of the sponge showing fine black sand in the tubes and cavities of the interior. It also surrounds stones and takes them in, as seen in fig. 5.

No. 82 is a specimen of Italian marble bored by

Cliona. This marble lay in water seven years, during which time the borings from one and a half to two inches in depth were made.

Dr. Leidy<sup>1</sup> states that the large and numerous shells of the dead oysters in an extensive bed planted by Beasley at Great Egg Harbor, were so completely riddled in two years by the Cliona that they were crushed with ease.

The process of boring is both mechanical and chemical, and the habit seems to be an acquired one which has been transmitted, Nassonow<sup>2</sup> stating that the young begin to bore before the formation of the spicular skeleton. The body puts forth fleshy outrunners and it is largely these that do the work. It is also probable that an acid is secreted which aids in the work. Unlike most sponges the Cliona discharges its eggs into the water before the formation of the embryo has begun, so that the whole development goes on outside the parent.

The skeleton is made up of one rayed spicules, many of which are pin-shaped. Ryder<sup>3</sup> has shown that the protoplasm in sponges executes delicate fluctuating movements, so that in Cliona as in Stylocordyla and many other genera, the needles are drawn into bundles or rows extending in particular directions.

In the fresh-water sponges (Spongilla, No. 83) the silicious spicules are numerous, while a small quantity of spongin is developed. These sponges, although probably derived from some marine form, yet develop a structure which is never found in the latter; namely, the statoblasts or winter buds. These are internal buds which are enclosed in horny cases with peculiar spicules. When the sponge dies the winter buds survive; these are so slightly affected by heat or cold that by them the perpetuation of the species is rendered more sure. In addition

<sup>1</sup>Proc. Acad. Nat. Sci. Phila., VIII, 1857, p. 162.

<sup>2</sup>Zeitschr. f. wiss. Zool., XXXIX, 1883, p. 300.

<sup>3</sup>Amer. Nat., XIII, May, 1879.

to the peculiar spicules just named there are two other kinds of spicules forming the skeleton and strengthening the dermis. An interesting specimen allied to *Spongilla lacustris* has been described by Edward Potts. This sponge is found incrusting marine organisms such as barnacles and the calcareous tubes of *Serpula*, in the fresh water of a creek in the southwestern part of Florida. The presence of the barnacles can only be accounted for by the action of the strong southeast winds which back up the salt water into the rivers and creeks. The young barnacles, having followed the influx of salt water and attached themselves to the rocks on the bottom, may have attained a portion of their growth while immersed in fresh water after the subsidence of the salt water. If this be true it is suggestive of the possibility of the conversion of the marine barnacle into a fresh-water species. The sponges already spoken of as occurring on these animals have the peculiar habit of hiding away the winter buds within the barnacles or in the tubes of the *Serpula*.

A sponge (*Reniera*), closely related to the *Chalinula* next to be described, is said to possess thread cells or nematocysts which were formerly supposed to be the exclusive possession of the next branch, the Coelentera, but which have already been found in the Protozoa. In this group the embryo has a pigmented spot on one end of its oval body which may perhaps be considered as an eye.<sup>1</sup>

*Chalinula oculata* Pallas is of especial interest to New Englanders since it grows abundantly along the eastern coast. In this sponge the spicules are straight and exist as vestiges, while the horny matter has increased in quantity.

Keller<sup>2</sup> has observed and figured the consecutive stages

<sup>1</sup> Lendenfeld, Mon. Australian Sponges, Proc. Linn. Soc. New South Wales, IX, part 2, 1884, p. 324.

<sup>2</sup> Zeitschr. f. wiss. Zool., XXXIII, 1880, p. 317.

of development of another species, *Chalinula fertilis* Keller, and by so doing has thrown strong light on many important points. Besides the asexual mode of increase through budding, there occurs a sexual propagation, the latter probably taking place only in the spring. In this sponge the sexes are distinct, the females being two or three times larger than the males. As soon as the formation of the egg begins the ordinary brown color of the female changes to red, becoming in very vigorous animals almost a cherry red. This color disappears after fertilization or at the beginning of the egg furrowing, and the female becomes ochre yellow at the time the larvae swarm out. The males do not change their color. Pl. 84, fig. 1, is a young, unfertilized egg which possesses amoeboid movements. Fig. 2 represents a spermatozoon which reminds one of a flagellate Protozoan. Fig. 3 is a mature egg which has become spherical in form and surrounded by a capsule. Nutritive mesoderm cells are seen near it. The capsule is formed early and it must be assumed, therefore, that the spermatozoon pierces it in order to reach the egg within. After impregnation, the furrowing takes place quickly, and normally covers from twenty to thirty hours. It is total, but the cells are unequal in size and there is no segmentation cavity. Fig. 4 shows the first two furrowing cells; fig. 5, the stage with four cells lying in a plane. In fig. 6 (figs. 6-9 drawn without capsule) these cells have arranged themselves in a pyramidal form, the large cell being the parent cell of the endoderm. Fig. 7 has seven cells and fig. 8 fourteen cells. Here the two large endoderm cells are partly surrounded by ectoderm cells. In fig. 9 the endoderm forms a central mass of cells and appears at the periphery as a plug. The other cells on the surface are ectodermic.<sup>1</sup>

<sup>1</sup>According to Wilson (see "Notes on the Development of some Sponges," Journ. of Morphology, V., no. 3, 1891, p. 516), it is probably not the endoderm that protrudes at this pole, but the ectoderm, which is greatly flattened over this region.

Pl. 84, fig. 10, is a later stage still enclosed in the capsule; the cylindrical ectoderm cells have already developed whips; the plug is strongly pigmented. In the mesoderm, flint needles (colored blue in the figure) have begun to form. They are at first irregular and scattered. It is a fact of great significance that the spicules appear *before* the formation of the cementing material, spongin. The latter is probably a secretion of the mesoderm, and is deposited according to need in layers around the spicules (see Pl. 84, fig. 20). This furnishes a strong argument in favor of the view that a part at least of the horny sponges are descendants of the silicious sponges. Pl. 84, fig. 11 is the free-swimming larva which has escaped from the capsule and the body of the parent. As it swims the pointed end is directed forward. No inner cavity yet exists. Figs. 12 and 13 represent the larva just before becoming attached. It is now much flattened (fig. 12, peripheral view; fig. 13, broadside). About thirty-six hours after settlement, it looks as shown in fig. 14. The isolated spicule in the larva is seen in fig. 15, still lying within its cell. No cavity had appeared two and a half days after settlement. Fig. 16 is a view of the young sponge (natural size) five days after becoming attached. The ampullaceous sacs with whipped cells are now numerous and open into a wide cavity. The cloacal opening arises on this day (the fifth) by the body cavity breaking through the outside wall, and on the same day and by a similar process the pores are formed (see fig. 17, a vertical section of the sponge at this stage). When the canals and pores appear the stream of water acts effectively upon the position of the needles and forms radial lines. Figs. 18 and 19 give us the external and internal structure of the adult. Fig. 20 shows the spicules of the adult bound together by spongin. Fig. 21 represents a small female colony. No. 85 is a larger adult.

The following is a summary of the time required for the six stages of development, as given by Keller.

First: Duration of the furrowing period, thirty hours. Second: Swarming out of the larvae, continuing to the end of the second day. Third: Free-living larva stage during third, fourth, and fifth days. Fourth: Settlement on fifth day. Fifth: Formation of the ampullaceous sacs and of the body cavity on the eighth day. Sixth: Breaking through of the cloacal opening and the formation of the skin pores.

According to Dendy<sup>1</sup> the West Indian Chalininae offer the strongest arguments in favor of the view that the Keratosa have descended polyphyletically from several distinct groups of silicious sponges. In different species of the same genus he has traced the gradual reduction and disappearance of the spicules until forms are reached like *Spinosella maxima* Dendy, and *Spinosella plicifera* D. & M., which sometimes still contain traces of the spicules imbedded in the horny fiber, and apparently on the verge of disappearance, while at other times they contain no spicules whatever, and yet the specimens with spicules and those without are specifically indistinguishable. No. 86 *Tuba* (= *Spinosella*<sup>2</sup>) *vaginalis* Lam. var. *sororia*, and No. 87, *Tuba scrobiculata* D. & M., show the variation in form peculiar to this genus of sponges.

#### KERATOSA.

The Keratosa are not found in a fossil condition. They are probably the specialized descendants of silicious forms, some of which have already been described. This view finds additional confirmation in the researches of Maas<sup>3</sup> who states that the embryological development

<sup>1</sup> Trans. Zool. Soc. London, XII, part 14, 1890.

<sup>2</sup> Vosmaer in 1885 substituted the generic name of *Spinosella* for the familiar one of *Tuba*.

<sup>3</sup> Zool. Jahrb., Anat., VII, Heft 2, 1893, p. 331.

of the horny sponges is so similar to that of the silicious sponges that a precise description would be mere repetition. According to this author the horny sponges are more nearly related to the silicious than are the silicious sponges among themselves; so that a separation of an independent order of fibrous sponges does not seem justified from a morphological point of view but only as a matter of convenience.

One of the simplest sponges belonging to this group is *Ammolynthus prototypus* Hkl. (Pl. 88, fig. 1). A cross section (partly diagrammatic) is seen in fig. 2 which exhibits the egg with its nucleus and nucleolus. The sponge that grows from this egg consists of a simple tube with one large opening (fig. 1). The body cavity is simple (fig. 2) and without branches, the canal system being similar to that of the Ascones among the Calcarea. The walls of the tubular body are pierced by many pores through which the water enters; this flows into the large central cavity which is lined with endodermal flagellate cells. No skeleton is developed, but the animal takes up Radiolarian shells (see figs. 1, 2) and in this way makes a false skeleton.

This sponge and the other species of the group to which it belongs are remarkable examples of symbiosis already seen among the Protozoa (see p. 44). In place of the horny fibers of other keratose sponges it has the tubes of a hydroid which serve the purpose of a supporting framework.

*Ammosolenia* (Pl. 88, fig. 3) is similar in structure to *Ammolynthus* but is a colonial sponge corresponding to the *Leucosolenia* in the calcareous group.

An extremely interesting form is represented by Pl. 89, fig. 1. Here in *Darwinella australiensis* Carter, we have a sponge with spicules made of spongin instead of carbonate of lime or silica. No spicules are wholly mineral, however, and this being the case, it is not difficult to understand, as pointed out by R. von Lendenfeld, how

the inorganic silica may have been replaced by the organic horny material. The spicules vary but are built on the triaxon plan. Besides the horny spicules there are horny fibers which do not unite to form a network.

We have here just those conditions which one might expect to find in a transitional form between the silicious and the horny sponges where the silica is replaced by spongin, and where the horny skeleton has not yet become the complex network seen in the more specialized genera.

The canal system of *Darwinella* is simple and unbranched and the ampullaceous sacs are of large size.

Another genus, *Aplysilla*, is placed near *Darwinella* which it resembles by having large ampullae, simple canals, and isolated erect horny fibers, but it differs from this genus by having no horny spicules. These have wholly disappeared and the skeleton, now entirely fibrous, is destined to develop in succeeding more specialized forms until a labyrinthian network of fibers is the result.

*Hircinia campawa* Hyatt (No. 90), is normally vase-shaped, but is subject to great variation, sometimes becoming tubular, as proved by specimen No. 91. It has been shown<sup>1</sup> that although this variation is great as compared with the more specialized invertebrates, nevertheless a formula may be given which expresses the possible range of variation in every species. One of the simplest of the *Hircinia* (*H. cactus*) has a skeleton composed of simple main fibers which contain foreign substance and slightly branched connecting fibers which are free from foreign particles. The spongin of which the fibers are composed is stratified and a granular axial thread is present.

In *Verongia fistularis* Bon. (Nos. 92, 93), the fibers are so large that their tubular form can be seen with the eye. They are loosely put together, but the main and

<sup>1</sup>Hyatt, Mem. Boston Soc. Nat. Hist., II, pt. IV, no. 5, 1877, p. 483.



connecting fibers are not easily determined. The two specimens show variation in form.

*Carteriospongia radiata* Hyatt, var. *dulcina* (No. 94), is one of the most beautiful of horny sponges. It grows upward from a stem in the form of delicate fronds. The surface of the fronds is smooth and the fibers are so closely woven that they form a veil on the upper side, and sometimes on the lower, which bridges over the inequalities of the interior. Large specimens of *Carteriospongia* may have as many as sixty branches.

The most complex representatives of the group of horny sponges belong to the family Spongidae. Nos. 95-97 are *Spongia tubulifera* Lam., var. *rotunda* Hyatt. No. 95 is a vertical section through the body of the sponge, showing the flesh, the large central tubes with radiating tubes, and the openings of other tubes which run in all directions through the sponge body. No. 96 is a dried specimen of the flesh and skeleton, and No. 97 is the skeleton with the flesh removed. The fibers are fine and soft. No. 98 is another species of the same genus, *S. molissima* Schm., in which the fibers are dense and closely woven.

This collection of sponges with the supplementary drawings illustrates the following points.

The sponge animal arises from an egg which resembles many adult Protozoa.

The egg in its further development passes through a blastula stage, thereby representing the adult *Volvox* of the Mesozoa.

The blastula stage is succeeded in most sponges by a solid parenchymella stage. The endoderm arises by a process either of immigration or of delamination of cells, and a two layered organism is produced. Subsequently an internal cavity and an external mouth opening are formed. This stage is transient, since by the formation of a middle layer or mesoderm the adult always becomes a three layered organism.

The flagellate and collared cells of the endoderm are unique, and may indicate genetic relationship with the Flagellata of the Protozoa or parallelism of development in two different groups.

When fixation takes place, the sponge settles with its mouth downward, after which the cloaca breaks through the ectoderm, proving thereby that this opening is not a primitive but a secondary character.

The primitive, adult, ancestral form of the group of sponges was a simple, skeletonless, tubular organism with a water system consisting of transient pores, and a central cavity with no canals and no ampullaceous sacs.

This primitive form is inherited with certain modifications by many of the simpler members of the different orders of sponges. By a differentiation of this primitive form the most specialized sponges with canals and sacs have arisen.

The calcareous and silicious sponges are considered the most generalized and the keratose sponges the most specialized for the following reasons.

The calcareous sponges, as a group, are most rudimentary in structure. The Silicea are found in ancient geological formations and in the deep seas of to-day, while the Keratosa do not occur as fossils.

The history of the development of the transitional forms, the silica-and-keratose sponges, proves that the silica appears first and afterward the spongin is developed.

## COELENTERA.

## Section 2. — HYDROZOA.

## HYDROPHORA.

If we consider the Protozoa and Mesozoa as constituting the trunk of our genealogical tree and the Porifera as the first short branch sent off from this trunk, then the Coelentera through comparative simplicity of structure represent the second branch. Although an unbroken line of descent from the many-celled, one layered Mesozoan to the Hydrozoa (the most generalized class of the Coelentera) cannot be traced, yet it is not difficult to conceive of an animal like a primitive Hydroid arising from an ancestral form similar to that which produced in course of generations the simplest, tubular sponges.

The two theories held by naturalists in regard to the origin of the Metazoa have already been stated (see p. 64). Briefly summarized it may be said that, according to one view, the one layered blastula gives rise to a two layered invaginate gastrula, the ancestral form of which, the *Gastraea*, has not been discovered. The gastrula in turn produces a form that is two layered in youth and three layered in the adult, like the sponge.

According to the second theory, the blastula gives rise to a solid parenchymella which in time becomes two layered and hollow and afterward is provided with an opening. In this case no primitive invaginate gastrula exists. The Hydrophora or Hydromedusae, now to be described, illustrate almost universally the second mode of development, and some naturalists<sup>1</sup> even maintain that not a single invaginate hydroid gastrula has been observed.

<sup>1</sup> W. K. Brooks, Mem. Boston Soc. Nat. Hist., III, no. 12, 1886, p. 401.

It is probable that the ancestor of the class of Hydroids, like that of the Porifera, was a fleshy animal without either a horny or a stony skeleton, but under ordinary conditions such a form would not be preserved.

The skeleton of a primitive hydroid, *Corynoides calicularis* Nich. (No. 99; Pl. 100, drawing of the same enlarged), is found as a fossil in the ancient geological formations. It was tubular in form, chitinous in structure, and striated on the outside as shown in the figure. The body of the adult, one may infer from the skeleton, was tubular with an opening or mouth at one end raised, it may be, on an oral cone, the base of which may or may not have been surrounded by tentacles. This mouth probably led into a hollow body cavity. The basal portion of the tubular skeleton ended in two little spines, but there is no indication in the fossils that the animal was attached, and therefore the conclusion may be drawn that it was free-moving both in youth and in adult life.

Nothing is known of the development of this ancient hydroid, but the simplicity of its structure as shown by its skeleton leads to the natural supposition that the development was primitive; that is, without a metamorphosis of any kind.

The descendants of this single marine form may have budded, and if the new zoons remained together a free-moving colony would arise similar in some respects to Graptolites (Nos. 101-104).

According to Lapworth,<sup>1</sup> who has studied the development of the Graptolitidae, the colonies arise from a "small, pointed, triangular or rather dagger-like 'germ'," which he calls the sicula. It may be that this youthful stage is the representative of the single, ancestral *Corynoides*, although this is not proved. In time a solid axis or virgula develops in the outer wall of the sicula and often extends beyond it at either end. A small bud usually appears at

<sup>1</sup> Geol. Mag., London, X, 1873.

the larger end and this forms a protecting cup or theca. While this is the rule, there are genera in which the bud arises from the middle portion of the sicula and from the smaller end. As a general thing the sicula is retained unchanged in form by the mature animal, but in a few species it is absorbed or becomes obsolete in old age.

The group of Monograptidae is represented by *Monograptus* (No. 101), which has a single series of cups or thecae on one side and at their base a well developed virgula.

Wiman<sup>1</sup> has made a study of the Diplograptidae which are represented in the Collection by *Diplograptus* (No. 102). He finds that these forms arise in the same way as the Monograptidae, and it seems probable that they are the specialized descendants of the last named group. The sicula of *Diplograptus* (Pl. 103, fig. 1, young, dorsal view; fig. 2, adult, front view) consists of two parts: the proximal portion marked diagonally; the distal, longitudinally (seen in fig. 1). The sicula is open at its base, and at one side is the rod or virgula. This sicula gives forth one bud only, which does not develop into a canal as heretofore supposed, but into a cup or theca. Fig. 3 is a front view of the first theca budded from the sicula, and fig. 4 is a dorsal view of the same.

The circular perforation in fig. 3 marks its origin from the sicula. The theca grows downward, then outward. Fig. 5 is the first theca with three spines, two of which are united by a thin skin. The theca is seen to have grown outward and upward. In time this theca buds and the second theca grows around to the opposite side. This process is repeated, the second giving rise to the third, the third to the fourth, so that the statement can be made that each theca comes from the next more proximally situated theca of the opposite side and not from a canal. Fig. 6

<sup>1</sup> Journ. of Geol., II, no. 3, Apr.-May, 1894, p. 267. See also Holm, Geol. Mag., London, Decade IV, II, 1895.

is a front view showing especially the form and position of the second and third thecae, and fig. 7 shows four thecae and the partly imbedded sicula. In fig. 8 it is seen how the thecae extend more and more over the sicula until the latter becomes incorporated in the main mass or hydrozoma. At this time the distal end of the virgula begins to grow, and it becomes stouter the farther it gets from the point of the sicula. In fig. 9 the distal end only of a hydrozoma is drawn, the proximal end with its imbedded sicula not being represented.

It is interesting to note that Ruedemann<sup>1</sup> has shown that some species of *Diplograptus* occur in large compound colonies consisting of many branches or stipes united in the center as seen in Pl. 104. These hydroids probably consisted of nutritive zoons possessing tentacles for catching food and cavities for digesting it. Besides these there were doubtless other zoons which were reproductive in function. The latter in the more specialized forms may have freed themselves from the colony and swum away as independent organisms or medusae. That medusae lived as far back as the lower Cambrian has been proved by Walcott.<sup>2</sup> As we come down to the present time we find the probable representatives of the Graptolites in the Plumularian hydroids, *Aglaophenia* (No. 105) and *Sertularia* (No. 106; no. 107, dried specimen). The former has the thecae on one side of each branch, while *Sertularia* has them on both sides. These hydroids have reduced characters, since the reproductive buds or gonophores, which in a progressive form swim away as free medusae, here never become detached. These are finely shown in *Sertularia argentea* Ellis and Sol. (No. 106).

<sup>1</sup> Rep. State Geol. N. Y., 1894, p. 219.

<sup>2</sup> U. S. Geol. Surv., Monograph, XXX, 1898.

## HYDROPHORA. — HYDROCORALLINAE.

The position of the Hydrocorallinae in a natural classification has not been determined with certainty,<sup>1</sup> but they are placed here provisionally.

Millepora is a colonial form which secretes a calcareous skeleton (No. 108). The zoons occur in groups (Pl. 109, fig. 1), each group consisting of a short central zoon and six or eight long ones about it; in fig. 1 one of the latter is omitted for the sake of clearness. The central zoon, called the gastrozoid, possesses a mouth and four or more tentacles, while the surrounding dactylozooids are mouthless. The body cavities of these zoons are not divided by partitions, but are continuous into the canals which traverse the surrounding flesh or coenosarc in every direction.

The dactylozooids apparently catch the food and carry it to the gastrozoid, and are therefore tentacular in function while they bear numerous small tentacles on their sides. One of these is represented in fig. 2, much enlarged. Figs. 3 and 4 represent a nematocyst taken from the tentacles; these are like those of most hydroids. Fig. 3 represents the thread within the cell and fig. 4 shows it thrown out. Besides this kind of thread cell there is another in Millepora found near the bases of the zoons and shown in figs. 5 and 6. Fig. 7 is a cross section of a gastrozoid showing on the outside the ectoderm nematocysts in different stages of development. Inside are the large transparent cells which are called gastric because they occur only in the gastrozoid and therefore may be digestive in function. The muscles by which the zoons contract are shown in fig. 8 which is a diagram of the longitudinal

<sup>1</sup> For a discussion of the different views on the subject, see Moseley, *Chall. Rep.*, Zool., II, part 7, 1881, p. 98; also Hickson, *Quart. Journ. Micr. Sci.*, XXXII, 1891, p. 375; *Proc. Zool. Soc. London*, 1898, p. 246.

bundles of fibers that arise from the radiating vessels, the latter being the continuations of the body cavities of the zoons. Besides the longitudinal muscles the circular muscles are shown. Fig. 9 is a vertical section through the decalcified superficial fleshy lamina which was living before decalcification began; the ectoderm is distinctly seen, also the retracted gastrozooids on the right (one of the four tentacles is not drawn), and the retracted dactylozooid on the left. The network of fleshy tubes is finely seen and where these are cut the dark pigment cells of the endoderm are visible. The limy network of the skeleton is shown by the open spaces between the fleshy tubes. Figs. 10-15 represent the skeleton. Fig. 10 is a fragment magnified two diameters, showing the branching form and the pores scattered over the surface. Fig. 11 is a drawing of a thin section of the skeleton showing its fibro-crystalline structure. Fig. 12 is a complete group of pores consisting of one central gastrozooid pore and eight dactylozooid pores, greatly enlarged. The structure is brought out clearly by figs. 13-15. Fig. 13 is a vertical section of the skeleton. The large gastrozooid pore is seen in the middle and the floor that separated the last formed living chamber from those below which are dead. The branches of the canal system are plainly shown. Fig. 14 is a horizontal section cut parallel to the outer surface, showing part of a group and the system of canals. In fig. 15 the pores and canals have become filled with black foreign matter making a cast of the canal system of the flesh or coenosarc. Nothing was known of the generative organs of *Millepora* till 1884, when Quelch<sup>1</sup> found among the young branchlets of the hard skeleton large ampulla-like cavities similar to those that had previously been observed in a related group, the *Stylasteridae*. These cavities contained gonophores and in the specimen examined only the male elements, spermatozoa, were found.

<sup>1</sup> *Nature*, XXX, 1884, p. 539.



In 1886, Hickson<sup>1</sup> observed that the generative products of *Millepora* were formed in little capsules in the walls of the canals and that both male and female capsules were found in the same canals. This author has also described and figured<sup>2</sup> the medusae of *Millepora*. These are formed by a metamorphosis of an ordinary zoon, usually a dactylozoid but sometimes a gastrozoid. They occur in ampulla-like cavities of the coenosarc. When they leave the parent form they are without the radial or ring canals, veil (velum), and sensory organs common to the more specialized medusae. It may be that these develop later while the animal swims about in the water, or it may be the medusae remain in a primitive condition.

Pl. 110, fig. 1, is a section through a medusa of *Millepora murrayi*. It has a well developed manubrium (the part hanging down like a handle), containing a cavity continuous with a large canal of the parent stock; the rounded masses on either side of the manubrium represent the sperm, and the outer encircling portion the umbrella. The ectodermal parts are shaded pink and the endodermal blue. Fig. 2 is a section of an older medusa that is not organically connected with the colony at any point and is probably ready to escape.

*Distichopora* (No. 111) has a beautiful pink skeleton. The openings are not in groups as in *Millepora*, but are either in rows along the edges of the branches or arranged in wavy lines over the surface. The rows of pores consist of a middle row of gastrozooids with dactylozooids on either side. The ampulla-like cavities in this genus are on one or both faces of the branch. The gonophores are not metamorphosed dactylozooids, becoming free-swimming medusae, but are modifications of the ova and sperm cells in the canals of the coenosarc which never become detached.

<sup>1</sup> Proc. Roy. Soc. London, XL, 1886, p. 325.

<sup>2</sup> Quart. Journ. Micr. Sci., XXXII, 1891, p. 375.

## HYDROPHORA.—NARCOMEDUSAE.

The Narcomedusae are a group of living hydroids which throw considerable light on the evolutionary history of the Hydrozoa, as pointed out by Brooks.<sup>1</sup> Pl. 112, figs. 1-19, represents the development of *Aeginopsis* from the egg to the hydra stage. Fig. 1 is the fresh laid egg; fig. 2, the two celled stage; fig. 3, the beginning of the second furrowing stage; fig. 4, the four celled stage; fig. 5, the beginning of the third furrowing stage; fig. 6, the eight celled stage; and fig. 7, the beginning of the fourth furrowing stage; fig. 8 is the sixteen celled embryo in cross section; fig. 9, the embryo composed of about thirty-two cells. Figs. 10 and 11 show isolated cells of the same embryo; fig. 10 is the endoderm cell just formed, and fig. 11, the completed or finished endoderm cell. Fig. 12 is the embryo of fifty-nine cells; fig. 13 is the two layered larva; fig. 14, the larva lengthened; fig. 15, the further developed larva; figs. 16 and 17, cells of the same (16, cell of ectoderm; 17, of endoderm); fig. 18 is the larva with two tentacles and no mouth; fig. 19, the larva of the fourth day. It is now a hydra with a shortened body, a mouth at the end of a long oral cone, at the base of which are tentacles. Unfortunately Metschnikoff did not figure the further development of the hydra into the medusa. The tentacular zone, however, grows out into an umbrella which carries the tentacles with it; sense organs and a veil or velum are soon acquired, and the hydra becomes converted into a medusa. Its parts can be plainly traced in the medusa, and the difference in external appearance is due mainly to the great development of the middle layer or mesoderm which forms the umbrella. If now we could find a genus where the larva, while yet a hydra, should fasten itself to some object,

<sup>1</sup> Mem. Boston Soc. Nat. Hist., III, no. 12, 1886.

either an animal or a rock, and should bud, then a colony would arise. This is precisely the case with *Cunocantha* (= *Cunocantha*<sup>1</sup>) *octonaria* Hkl., or *Cunina octonaria* McGrady, the latter name being the more familiar one. Pl. 113 gives the development of this genus, and No. 114 is the medusa of *Cunina campanulata* Ed. Pl. 113, fig. 1, is the larva. (Figs. 1 and 3 are drawn in a position to show the *hydra-like* larva; fig. 5, to show the *medusa-like* adult.) The aboral end of the body is shortened; there are two opposite tentacles which have clusters of thread cells at their ends. The oral cone which extends above is very long and at its end is the small mouth. The internal cavity is lined with large endodermal cells seen in the figure. The ectoderm is thin excepting at the extremities of the tentacles and at the aboral end of the body. This larva now enters the bell cavity of *Turritopsis*, another Hydrozoan, and fastens itself by its tentacles, as seen in fig. 2. The oral cone becomes extremely long, is inserted in the mouth of *Turritopsis*, and two more tentacles grow. This stage is more clearly seen in fig. 3. Either before or after the secondary tentacles appear, the hydra puts forth buds from the aboral end of the body and a colony is formed as seen in figs. 4 and 5. A rim grows out from the body in the tentacular zone and this rim becomes divided into eight lobes, each one of which contains a branch from the central digestive cavity. The bud, thus changed, escapes into the water and is a medusa (Pl. 113, fig. 6) with a long oral cone. Later the umbrella enlarges while the oral cone remains about the same as seen in fig. 7, which is an aboral view of an adult medusa. Each member of the colony becomes converted into a medusa, so that here we have budding and a primitive kind of metamorphosis but no alternation of generations.

The *Cunina parasitica*, however, which attaches itself

<sup>1</sup> H. V. Wilson, Stud. Biol. Lab. Johns Hopkins Univ., IV, no. 2, 1887, p. 95.

to one of the Geryonids, remains a hydra, while its buds develop into medusae and swim away. Here, then, we have the metamorphosis of Aeginopsis converted into the alternation of generations so peculiar to this class of animals.

The objection may here be urged that the genus *Cunina* is parasitic or semi-parasitic in habit and that therefore it is a specialized and reduced genus. The stock form Aeginopsis, which is the key to our classification, is not a parasite at any period of life. *Cunina octonaria* does not seem to be much more of a parasite than an animal that happens to settle upon something, it may be another animal or a rock, for a short time. It is free at first, then attaches itself to an animal for a brief period, and afterward lives an independent life. The species *Cunina parasitica* is a parasite, as its name implies, but it illustrates so admirably what seems to us the next step in the evolutionary development of this class of animals that we use it provisionally, until at least a non-parasitic form can be found which will illustrate the same type of life history.

#### HYDROPHORA.—TRACHOMEDUSAE.

The Trachomedusae are represented in the Collection by *Carmarina* (= *Geryonia*) *hastata* Hkl. (No. 115), which corresponds to Aeginopsis among the Narcomedusae in passing through a metamorphosis without budding or alternation of generations. It is an interesting fact that the larval Geryonidae have solid tentacles, while in the adults these are replaced by hollow ones. The Trachomedusae include *Aglaura* whose complete development has been worked out by Metschnikoff. Pl. 116, fig. 1 is the fresh laid egg drawn from life; fig. 2, the same treated with osmic acid; fig. 3 shows the beginning of segmentation; fig. 4, the egg divided into two cells; fig. 5, the four celled stage; fig. 6 is the third furrowing stage from

above; fig. 7, the same in profile; fig. 8 is the beginning of the fourth furrowing stage; fig. 9, the same a half hour afterward; fig. 10, the same three quarters of an hour after fig. 8. The rotating movements of the embryo begin at this time. Figs. 11 and 12 are further developed stages; fig. 13 is the morula stage; fig. 14, the larva with two layers; figs. 15 and 16 are the free-swimming larvae; fig. 17 is the larva with nettle capsule; fig. 18, a further developed larva; fig. 19, a larva with projecting tentacles; fig. 20, larva with gastro-vascular cavity; fig. 21 shows the beginnings of the wider tentacles; fig. 22 is a larva forty-five hours old, and fig. 23, one fifty-two hours old; fig. 24 is a larva with eight tentacles, and fig. 25, one with twelve tentacles; fig. 26 is the same in profile, and fig. 27, the disc of same from above. Fig. 28 is the adult *Aglaura*.

In some of the most specialized genera of the Trachomedusae there are various secondary modifications, and the adult characteristic of a peculiar bell-shaped body appears in the young.

#### HYDROPHORA. — ANTHOMEDUSAE.

*Acaulis* (Pl. 117, figs. 1-3) may be one of the primitive forms of the Anthomedusae, although as yet it is not positively known that the medusae become free. Fig. 1 represents a portion of a young *Acaulis*. The blunt posterior end is shown with both the temporary tentacles, which are short and swollen at their ends, and the permanent ones which are long and slender throughout. Figs. 2 and 3 probably represent the adult, one much enlarged, the other natural size. The mouth is at the smaller end with numerous papillae about it; the temporary tentacles of the young have disappeared. Below the papillae are the clusters of gonophores which Stimpson observed "in an advanced stage of development, soon to become free-

swimming individuals." The adult *Acaulis* (figs. 2, 3) is attached by its base.

Among the Tubularians there are some species which develop free medusae, while others are more or less reduced. In this group the zoons are at the ends of long tubes, and those with the reproductive function are sometimes in the form of clusters of grapes.

*Corymorpha nutans* Sars (No. 118), is a solitary Tubularian. The natural size is represented at the left, while just back of it is the same greatly enlarged. At its base are many thread-like organs for anchoring the animal in the sand. A number of short tentacles are seen around the mouth, and farther down there is another circlet of much longer feelers. Between these two sets of tentacles are the medusae buds. These have only one tentacle when young and attached and also when mature and free (No. 118, at the right). This model clearly shows the four radiating canals and the manubrium.

In *Turritopsis* (No. 119) we have a greater complexity of the hydroid stage than that previously described. The free-swimming embryo does not grow into a hydra, but, spreading out more or less like a root, attaches itself and buds forth hydras. In this way a colony arises. The hydras in their turn bud medusae which swim away. Here we have a modification of the phenomenon of alternation of generations and a root-like form existing between the parenchymella and the hydroid stage.

The life history of *Podocoryne* is especially interesting. It begins its existence as a hydroid, then forms a colony by budding, and puts forth secondary buds in the form of medusae. These swim away, but after a time they take on reduced characters. The veil disappears, the bell is reversed, shrunken to a shapeless mass, and turned back with the tentacles (Pl. 120). The eggs are seen in the walls of the manubrium which hangs down below the shrunken bell.

This figure is instructive as showing the difference

between a reduced and a primitive form. While resembling each other in a general way, close examination reveals here, as in the great majority of cases, the evolutionary stages through which the hydroid has passed.

Cladonema (No. 121) is another Tubularian which illustrates suppressed development. The model represents the hydroid of natural size (a) and enlarged (b); c and d are the young and the adult medusae. When old, the medusa tends to lose its umbrella and takes on other reduced characters.

*Tubularia larynx* E. & S. (No. 122), is one of our common hydroids and is a good example of suppressed development. The zoons rise from basal stolons which form a network and grow to the height of four or five inches. The network and ascending tubes are protected by a chitinous sheath, but this does not cover the main body of the zoon, often called the hydranth. Each hydranth has a double row of tentacles. Below these on the reproductive zoons are the grape-like clusters of medusae which never become detached.

The scarlet colored masses of *Clava* (No. 123) are abundant on the New England coast. The larval hydra becomes attached and forms a colony like the parent. The model represents the nutritive zoons with many tentacles, and the reproductive zoons are in clusters beneath; as these are medusae which never become free, we have here another illustration of suppressed development.

#### HYDROPHORA.—HYDROIDEA.

The fresh-water *Microhydra ryderi* Potts,<sup>1</sup> is described here since it produces free-swimming medusae<sup>2</sup>, which,

<sup>1</sup> Amer. Nat., XIX, 1885, p. 1232. Quart. Journ. Micr. Sci. XXX, 1890, p. 507.

<sup>2</sup> Potts, Amer. Nat., XXXI, 1897, p. 1032.

so far as our knowledge goes, is not true of Protohydra or Hydra. In the hydroid state Microhydra is greatly reduced, since it possesses neither chitinous coat nor tentacles, and is also without a pedal disc. According to Potts this species was found living as a messmate among colonies of Bryozoa "where its own disabilities as a food collector . . . were supplemented by the life sustaining currents induced by its more active neighbors." This habit has doubtless brought about this reduced structural condition.

The marine and fresh-water Protohydra of Greef is represented by Pls. 124 and 125. It is less reduced than Microhydra, by possessing a chitinous coat and by living in both salt and fresh water, but, like this genus, it is without tentacles. Pl. 124, fig. 1 represents Protohydra contracted into a spherical form. Its color is a fox brown. Fig. 2 shows the little animal in the act of stretching out, and in figs. 3 and 4 it is still more extended. In the latter figure the mouth is seen at the top and the foot disc at the posterior end. Fig. 5 is a Protohydra that has swallowed a Copepod larger than its own body. The long bristles at the posterior end of the crustacean extend from the mouth. Inside the hydroid the outlines of the Copepod can be made out and also one of its red eyes. Fig. 6 is the forward end enlarged, showing the edges of the mouth without even the vestiges of tentacles. Fig. 7 is a portion of the body showing the network of cells. In these figures the nearly colorless ectoderm is seen and the underlying pigmented endoderm; no cuticle is represented excepting in fig. 8 (which is the posterior part of a specimen that has been paralyzed in fresh water) where it is visible outside of the cellular ectoderm. According to Greef<sup>1</sup> this is most constant at the end of the body where it has separated from the epithelium and surrounds the body like a tube. Towards the forward end it lies

<sup>1</sup> Zeitschr. f. wiss. Zool., XX, p. 1070.



so close to the surface that one may doubt its existence. Singularly enough Protohydra increases by cross division. Pl. 125, fig. 1 shows the beginning of the process. The constriction goes on until the two are nearly ready to separate (figs. 2, 3) when the two break away and live independent lives.

This process of reproduction may indicate affinities with the Protozoa, some of which, as we have seen, increase by transverse division, or it may be possible that Protohydra is a reduced form of the Discophora, a group which multiplies by cross division with alternation of generations, and one which will be described farther on.

We consider Hydra as a reduced form although most of the books place it as a primitive hydroid. Observations<sup>1</sup> have shown that the ectoderm of the embryo of Hydra excretes a chitinous coat. This is probably the vestige of the horny covering or exoskeleton of the Tubularian hydroids. Later this sheath is thrown off.

We have already seen that primitive forms are, as a rule, marine, and the Hydra has been found but once in brackish water,<sup>2</sup> being preeminently a fresh-water animal. The middle layer which exists under varying forms in the Coelentera consists in the Hydra of many delicate filaments extending from the cells of the ectoderm. These may represent either rudiments or vestiges of cells and in the present state of our knowledge it is impossible to say which they are with absolute certainty. It would seem, however, from observations already made, that they are vestiges and that we are not dealing here with a primitive adult two layered animal, whose proper taxonomic position would be before the sponges, but rather with a modified and reduced hydroid form.

<sup>1</sup> See Kleinenberg, *The Hydra*, 1872. Huxley, *Anatomy of Invertebrate Animals*, 1878, p. 121. Korotneff, *Embryology of the Hydra*, *Zeitschr. f. wiss. Zool.*, XXXVIII, 1883, pp. 314-321. Brauer, *Zeitschr. f. wiss. Zool.*, LII, 1891; abstract, *Journ. Roy. Micr. Soc.*, 1891, p. 609; also *Amer. Nat.*, XXV, 1891, p. 1027.

<sup>2</sup> *Stand. Nat. Hist.*, I, 1885, p. 77.

The adult Hydra (No. 126, natural size; Pl. 127, fig. 1) has a tubular body with a mouth at the end of an oral cone. At the base of the latter is a circle of tentacles. These never possess the primitive character of solidity but are from the first hollow prolongations of the body wall. This mature form buds into other hydras (No. 126); it also reproduces sexually. Pl. 127, fig. 2, represents the Hydra, enlarged, with a swelling which is an ovum or egg, and nearer the tentacles are two smaller swellings that are sacs containing the spermatozoa. This animal never buds a medusa; in fact, no medusoid characters have been observed in the embryo, and for this reason some naturalists maintain that the Hydra cannot be a reduced form. The difficulty of explaining the non-existence of medusoid characters in the young, however, is not so great as that which the advocates of the primitive character of Hydra find in explaining the existence of the chitinous sheath in the embryo. There are forms in other classes of the animal kingdom which have become so extremely reduced as to lose even in their embryological development the characters of their previously differentiated condition, and it seems probable that the Hydra can be numbered among these forms.

#### HYDROPHORA. — CAMPANULARIAE.

The Campanulariae are represented by *Obelia* (No. 128), *Tima* (No. 129), *Gonionemus* (No. 130), and *Gonothyraea* (No. 131; Pl. 132). In *Obelia* we have a complicated structure and life history. Its egg develops into a parenchymella which becomes attached. It now forms a "star-shaped root" or hydrorhiza from which the first zoon is budded; afterward other zoons bud out from it and a colony is produced. Here, as in *Turritopsis* of the Tubulariae, we have a precocious embryo and an alternation of generations between the parenchymella and hydra stages.

The hydras budded from the star-shaped root become differentiated into nutritive and reproductive zoons, the latter giving rise to medusa buds. These medusae are free in *Obelia*, *Tima*, and *Gonionemus* (No. 130, showing young stages), but in *Gonothyraea* (No. 131; Pl. 132, enlarged) they are reduced and always remain attached.

#### DISCOPHORA.

We have shown that the complex larval colonies and specialized adults of the *Hydrophora* may have arisen from the comparatively simple *Aeginopsis*. It may be possible also that this same form, or one similar to it, produced along another line of development the *Discophora*. The egg of most *Discophora*, like that of *Aeginopsis*, develops into a free-swimming, ciliated, solid embryo or parenchymella. This attaches itself and in time becomes a hydra. By a remarkable growth the height increases greatly. The body then begins to divide horizontally, and the saucer-like divisions free themselves as medusae. Thus it is seen that one hydra gives rise by the process of division to several medusae. The latter produce eggs which develop into the hydra form, so that we have an asexual hydroid generation alternating with a sexual medusa generation. The *Discophora* are represented in the Collection by *Cyanea capillata* Linn. (No. 133, greatly reduced), *Aurelia flavidula* Pér. & Less. (Pl. 134), and *Aurelia aurita* Linn. (No. 135, young medusa; No. 136, adult). It is interesting to note that the adult medusa of *Cyanea* sometimes attaches itself quite firmly to an object. One observed by Dr. Robert T. Jackson, at Eastport, Maine, in the summer of 1892, was settled so firmly that it required considerable force to separate it from the tub in which it was living. While attached, its resemblance to a hydra was striking.

The segmentation of the egg of *Cyanea* is regular and

results in the formation of a blastula. Cells then migrate into the interior and afterward arrange themselves as an incomplete layer on the inner side. Here, then, in *Cyanea* we have the stage following the blastula produced by the immigration of cells and not by the invagination of a layer. The parenchymella, after swimming about freely, settles down and forms a cyst. Soon after leaving the cyst a mouth opens and four tentacles are developed.<sup>1</sup>

The development of *Aurelia* illustrates that of most *Discophora*. Pl. 134, fig. 1, represents one of the early stages of the egg, and fig. 2, the fully grown egg. Segmentation takes place and when the embryo leaves the parent it swims about by means of cilia (fig. 3). Gradually the two layers are formed (fig. 4), then the digestive cavity (fig. 5). Afterward a depression in the outer surface of the inner wall marks the position of the future mouth (fig. 6); in time the outer wall is pierced and the mouth and passage leading to the digestive cavity appear. The embryo becomes elongated (fig. 7). It now gives up its free life. According to Prof. Louis Agassiz, "it settles down upon its narrow end; it wavers, and sways to and fro as if it were trying to force its way downward into the substance upon which it has fastened itself, and then, as if dissatisfied with the promise of a good basis for its foundation, it suddenly loosens its hold and swims away to another locality, there to repeat the same kind of examination until finally, after perhaps half a dozen attempts . . . it finds a suitable place to rest upon permanently." The changes which take place at this time are more clearly seen in figs. 8-11 which are taken from the development of *Cyanea* already briefly described. Fig. 8 represents the embryo with a chitinous base which serves to strengthen its attachment. In fig. 9 the two tentacles are just beginning to grow. Fig. 10 has four tentacles (well provided with thread cells) and a wide opened

<sup>1</sup> See Smith, Bull. Mus. Comp. Zool., XXII, 1891, p. 124.

mouth. Fig. 11 is a so called scyphostoma with four tentacles extended, surrounding a mouth at the end of an oral cone.

It is interesting to note that the scyphostoma of *Cyanea* has a horny sheath similar to that possessed by the Tubulariae. No such sheath has been observed in *Aurelia*. One feature of the anatomy of the scyphostoma is of importance. Four ridges extend from the inner wall into the central cavity and divide its outer portion into four chambers. These are probably the beginnings of the mesenteries of the Anthozoa.

The scyphostoma of *Aurelia* (fig. 12) normally develops sixteen tentacles. It is converted into the so called strobila in the following way. A horizontal constriction takes place just below the outer base of the tentacles (fig. 13); this is followed by another (fig. 14), and a third (fig. 15), and still others, until nearly the whole body is divided into saucer-like sections. At the base of these sections or discs (fig. 16) is developed a circle of tentacles similar to those at the top of the scyphostoma when it began to divide. Below this circle of secondary feelers is the remnant of the old scyphostoma. The strobila stage succeeding the scyphostoma is now completed. The uppermost and oldest disc which has become eight lobed, separates first, then the others follow in succession, fig. 17 representing the last disc about to drop off. This free stage of the Discophoran is known as the ephyra. After separation the ephyra turns over (fig. 18, enlarged ten diameters, with the lips of the mouth prominent) and is a well developed medusa (fig. 19, natural size). The parts are better seen in the larger species, *A. aurita* Linn. (Nos. 135, 136). The most important organ of the adult is the umbrella; this is usually divided into eight lobes (No. 136). Hanging from the center of the lower side are four long oral appendages. A system of tubes extends from the central digestive cavity to the circumference, and alternates with another system which connects with the large genital organs on the dorsal side of the *Aurelia*.

Aurelia generally develops with alternation of generations, as above described, but in isolated cases the development is accelerated, the hydroid stage being omitted, and the medusa develops at once from the egg.

In *Pelagia noctiluca* Pér. & Less. (No. 137), the sessile hydra stage is always omitted and the parenchymella develops without intermediate forms into the medusa. This process is not comparable with the simple, primitive development of ancestral forms, nor with the direct development of Aeginopsis; neither can it be compared with the indirect development peculiar to those forms which pass through an alternation of generations, nor with the suppressed development observed in Hydra. It is rather an illustration of accelerated development which characterizes not the primitive but the secondary and specialized members of a group.

A more complicated condition is found in *Rhizostoma pulmo* Linn. (Nos. 138, 139) in which the margins of the lips have become united so that the food is taken in through a large number of minute openings in the tentacles.

*Haliclystus auricula* Clark (No. 140), is our common Lucernarian. It is a beautiful green medusa about an inch in diameter and is fastened temporarily by a sucker on the smaller end of its body. The habit of creeping peculiar to the adult Haliclystus has become fixed in the young, so that the latter is not free-swimming but crawls over eel grass from an early age. This is also true of the young of Lucernaria, which is not provided with cilia but creeps over surfaces. The adult Lucernaria (No. 141) is divided into eight lobes. The cavity of the oral cone communicates with a central chamber whence four wide chambers pass into the lobes.

## SIPHONOPHORA.

There is a good reason for placing the Siphonophora as the most specialized group of the Hydrozoa, since the process of budding which we have found in the larval Hydra is carried back to a still earlier stage and exists in the embryo itself. This precocious germ develops into a complex colony of hydra-like and medusa-like zoons.

*Verella mutica* Bosc (No. 142) in addition to a float has a triangular sail. According to A. Agassiz, *Verella* has much in common with the Tubularians, the young medusa resembling in a marked degree the medusae of that group.

In the adult *Verella* a single feeding zoon extends downward from the lower side and around it are many small appendages in the form of delicate threads which bear tiny medusae buds; these separate and swim away. The float above is surmounted by the sail (finely seen in the alcoholic specimen, No. 142) which, according to Agassiz,<sup>1</sup> is left handed; that is, the sail runs northwest and southeast, the longitudinal axis of the float being placed north and south. In 2500 specimens thrown on the beaches at the Tortugas the position of the sail was the same, showing that this character has become so firmly fixed in the organization that it is not subject to variation.

*Porpita linnaeana* Less. (No. 143; No. 144, preserved specimen; No. 145, model of *P. umbrella* Esch.), probably possesses a sail in youth which is lost in maturity. It has a central disc, the upper side of which is corrugated. The internal structure is somewhat complex. Long and short tentacles extend from the edge of the disc (No. 145), and these are provided with knobs which can be seen flattened in the preserved specimen (No. 144). Near the disc and at the base of the tentacles are the

<sup>1</sup> Mem. Mus. Comp. Zool., VIII, 1883.

feeding and reproductive zoons. The latter give rise to medusae buds which may be seen in different stages of development in the living animals until finally they become detached and swim away.

Physalia, or the Portuguese Man-of-war (No. 146; No. 147, *P. arethusa* Till.; No. 148, model of *P. pelagica* Linn.), has a beautiful pear-shaped float surmounted by a crest or sail, well seen in No. 147. According to the observations of Huxley on young Physaliae it is probable that the float represents the primary Hydra. At the broader end of the lower side of the float are different kinds of zoons; these perform a different kind of work and are therefore unlike in structure. Prof. Agassiz observed that the largest zoons are on the windward side of the animal and are provided with tentacles which vary in length from 20 to 50 feet.

The feeding zoons are of two kinds, and besides these there are medusa buds which do not break away as free medusae but are modified into swimming or propelling bells.

*Agalma rigidum* Hkl. (No. 149), is a complex organism. It has a flexible hollow stem which is divided into two parts and which bears all the appendages. At one end the stem enlarges to form the air-bladder or float which is reduced and apparently too small to be functionally useful. The two parts of the stem are called the nectostem and polypstem. The nectostem carries bodies which resemble medusae but which are without a mouth or stomach. If originally medusae, they have become reduced into propelling organs or swimming bells. The polypstem has covering scales probably for protecting the bodies beneath them. These bodies are of three different kinds: nutritive zoons, small organs called tasters which, according to Haeckel,<sup>1</sup> have a sensory function acting as organs of taste or sight, and sexual bells or

<sup>1</sup> Chall. Rép., Zool., XXVIII, part 77, 1888, Siphonophora, p. 16.



zoons. The first have long tentacles and supply nourishing fluids to the whole colony, pouring them into the cavity of the stem, the common reservoir from which the swimming bells and other zoons draw. The sexual bells are male and female and each female bell contains one egg.

Apolemia (No. 150) is another float-bearing Siphonophore in which the polypstem has the covering scales arranged in clusters with the tasters, feeding and reproductive zoons.

*Abyla pentagona* Esch. (No. 151), undergoes an additional process in the course of its development. Each segment of the Siphonophore becomes detached and lives an independent life. It is a feeding zoon with two locomotive bells for swimming, in which are the reproductive organs. In this changed condition some of the parts may become greatly altered in form.

#### CTENOPHORA.

The Ctenophora are interesting since they possess characters in common with the Hydrozoa, the Worms, and the Echinoderms. It may be they have arisen from the Anthomedusan, *Ctenaria ctenophora*, and, if so, they are the most differentiated of Medusae. On the other hand, they have certain structures peculiar to the Turbellarian worms, while the possession of a digestive and water vascular system in communication with each other points to a relationship with the Echinoderms.<sup>1</sup> According to Chun,<sup>2</sup> the development of the egg of the Ctenophora is similar in the different genera, but the variations appear during the postembryonic development.

The group is represented in the Collection by *Pleuro-*

<sup>1</sup> A. Agassiz, Mem. Amer. Acad. Arts and Sci., X, no. 3, 1874, p. 379.

<sup>2</sup> Fauna und Flora des Golfes von Neapel, I, Leipzig, 1880.

*brachia rhododactyla* Ag. (No. 152), *Cestum veneris* Less. (No. 153), *Idyia roseola* Ag. (No. 154), and *Beroë ovata* Esch. (No. 155).

*Pleurobrachia rhododactyla* Ag. (No. 152), is frequently seen off the New England coast. Its transparent body is spherical, with eight rows of comb-like structures or plates extending from pole to pole. These are, in reality, cilia which have become united, as shown by the development of the animal. They constitute the peculiar characteristic of this group, giving it the name Ctenophora. The extremely long tentacles may extend from the body or else be tucked away out of sight in two lateral pockets. It has been found that another Ctenophoran, *Bolina*, is so similar to *Pleurobrachia* when it leaves the egg, that one cannot be distinguished from the other except that the compression of the body in *Bolina* is in a plane at right angles to that of *Pleurobrachia*. The postembryonic development, however, produces marked changes of form, complex windings of vessels, and the almost complete disappearance of tentacles which are at first developed like those of *Pleurobrachia*.

*Cestum veneris* Less. (No. 153), is instructive on account of its phylogenetic relations to other Ctenophora. There are few groups of the animal kingdom where the postembryonic metamorphosis so strikingly recapitulates, even in the details of organization, the adult forms of more simply organized groups, as do the larval stages of *Cestum* and the lobed Ctenophora recapitulate the adult stages of the generalized Ctenophora.<sup>1</sup>

The adult *Cestum* has distinct bilateral symmetry. Its long, belt-like appearance has won for it the name of Venus's girdle. Eight rows of plates or combs extend longitudinally down the body, and these aid in locomotion. The mouth is near the middle of the belt-like body and possesses two tentacles which extend from a pocket.

<sup>1</sup>Allman, On the Development of Ctenophora, Journ. Linn. Soc. London, Zool., XVI, 1882, p. 106.

*Idyia roseola* Ag. (No. 154) and *Beroë ovata* Esch. (No. 155) are elongated in form and both are without tentacles.

### Sections 3, 4.—ANTHOZOA.

#### ALCYONARIA.

It is reasonable to suppose from what is already known that the ancestral form of the Anthozoa possessed a simple, tubular, fleshy body with a mouth at the end of an oral cone, at the base of which was a limited number of solid tentacles. Such a form would resemble closely the scyphostoma of the Hydrozoa, and the majority of naturalists consider this as the ancestral form of the Anthozoa. If we imagine the oral cone of the scyphostoma turned inward, we have an internal bag hanging within the body cavity. Again, if we suppose that the fleshy walls or mesenteries which are indicated in *Cyanea* (see p. 107) grow longer and join the central bag, then we have the hydroid plan of structure converted into the Actinian plan. This is a crude but graphic way of illustrating the hydroid and the Actinian type of structure and the possible conversion of the one into the other, although it must be remembered that there are no embryological facts to prove that these changes actually took place.<sup>1</sup>

This early ancestral form probably followed essentially the same path of development as the hydroid, since the Actinian of to-day passes through the blastula, parenchymella, and secondary gastrula (not invaginated) stages. While, however, the parenchymella of the hydroid is usually produced by the immigration of cells from the surface to the interior, that of the Anthozoa is generally made by delamination of the inner ends of the ectoderm cells. This process is brought about through differentiation of

<sup>1</sup> E. B. Wilson, Phil. Trans., CLXXIV, 1883, p. 762.

these parts of the cells, owing to the accumulation in them of food material.

It is probable from the evidence now at hand that the ancestral form above described, developed four mesenteries. The Hexactiniae, to be described farther on, pass through a stage with four mesenteries, which antedates the Edwardsia stage of eight mesenteries. This form may have given rise to a branch which through continued specialization reached the condition now shown in the Alcyonaria. It is customary to consider the Alcyonaria as more specialized than the Hexactiniae, and for this reason they are generally placed *after* this group; but setting aside their variety of form and delicacy of structure, they seem in reality more simple, especially when the single, generalized Alcyonarians are considered.

There is also another good reason for placing the Alcyonaria as the more primitive group. Recent investigations<sup>1</sup> upon Alcyonaria and the ancient tabulate corals tend to prove that the latter group (with the exception of a few species) are ancestral forms of the Alcyonaria. For this reason some of the tabulate corals have been taken from the Zoantharia where hitherto they have been placed, and are here considered as the primitive forerunners of the Alcyonaria.

*Cladochonus* (= *Pyrgia*) *micelini* M.-Ed. & H., is a single, trumpet-shaped form when young (Pl. 156, fig. 1, natural size; fig. 2, enlarged), and though without pores, walls, or horizontal floors, called tabulae, it is probably related to *Aulopora* (No. 157) and the other tabulate corals. When mature it forms a simple colony and the zoons are attached by processes which extend from the lower surface. These are seen in Pl. 156, figs. 1, 2.

<sup>1</sup>Sardeson, Ueber die Beziehungen der fossilen Tabulaten zu den Alcyonarien. Neues Jahrb. f. Min., Geol. u. Pal., Beilage Band X, Heft 3, 1896; see also Moseley, Chall. Rep., Zool., II, part 7, 1881, p. 102.

*Aulopora serpens* Goldf. (No. 157) begins as a single form, then by budding, a creeping, irregular colony is produced. The origin and structure of a compound coral is illustrated by *Pleurodictyum lenticulare* Hall (Pl. 158, figs. 1-9). The first coral animal that started the colony was single. Its skeleton was shaped like an inverted cone smooth in the earliest and ribbed in the later stage (figs. 1, 2, 3). At first the interior is simply granulose, but above the middle portion the granules are arranged in rows which are probably the beginnings of walls. When limy walls exist in the Alcyonaria, they may be called pseudosepta, since the true septa of the Hexactiniae correspond in disposition and number to the fleshy mesenteries, which cannot be said of the walls of the Alcyonaria in general. These rudimentary walls are without pores and the whole skeleton is covered by an external limy layer, the epitheca.

Thus it is seen that the primitive ancestral form of corals, as proved by this first stage of the compound coral, is extremely simple, imperforate, and without tabulae or well developed walls. In the next stage a bud appears which is in direct communication with the parent form, giving rise to an opening or pore in the wall of the latter (fig. 4). This is the *Aulopora* stage which is seen more clearly in fig. 5. Some doubt exists in regard to this figure, but in all respects excepting the position and direction of the bud, this form agrees with *Pleurodictyum lenticulare* and may therefore be regarded as one of its early stages. The buds appear alternately (figs. 6, 7, 8) until a circle surrounds the original form (fig. 9). The second stage is now completed. The colony increases twice in diameter until the mature condition is reached.

The origin and growth of the colony of *Michelinia convexa* d'Orb., are shown diagrammatically in Pl. 159, figs. 1-7. In fig. 1 the first corallite is represented in the center with its circle of corallites which have arisen alternately, as in *Pleurodictyum lenticulare*. *Michelinia*, however, advances farther than the last named coral and

builds up a large colony by a process of intermural budding. Fig. 2 shows how the buds are given off between the walls of the corallites, truncating three angles of the parent form. Next, three more buds appear, truncating the other three angles and pushing the original circle farther away (fig. 3). Fig. 4 shows the circle of intermural buds larger in size, while the buds between the walls of the original circle (three of which are seen in fig. 3) have been formed. These have increased in size in fig. 5. In fig. 6 all these buds have grown and the corallites of the original circle are separated not only from the parent form but also from one another. Fig. 7 gives a vertical view of the same, the numbers 1-6 corresponding with the numbers of the views seen from above. These figures illustrate finely how the shape of the corallites is due to pressure.

Favosites (No. 160) is a compound colony like *Michelinia*. Its development follows the same general law that governs the intermural budding of *Michelinia*, but is more complicated, owing probably to acceleration in development. Girty<sup>1</sup> has shown that the colony springs from a single animal which is similar in general aspect to the original zoon of *Pleurodictyum*. This zoon is prostrate, slightly curved at first, and is attached by its dorsal side. When full grown the zoon is more erect and gives off four buds from its dorsal side. Each is connected with the parent form by means of a pore. Next, five buds appear in the peripheral spaces between those already existing. It is not until there are nineteen buds that the original one is surrounded. In this one-sided or unilateral budding *Favosites* differs from the last two colonies described.

The generalized members of the living *Alcyonaria*—the Proto-*Alcyonaria*—are the three genera *Monoxenia*, *Hartea*, and *Haimea*; of these, *Monoxenia* is represented in the Collection by a drawing. It is unfortunate that

<sup>1</sup> Amer. Geol., XV, Mar., 1895.

scarcely anything is known of the development of these primitive forms, since this knowledge would doubtless throw light on the phylogeny of the Anthozoa.

Monoxenia (Pl. 161, greatly enlarged) never secretes a skeleton or any hard parts. Its tubular fleshy body has only eight tentacles (Pl. 161) and these are hollow prolongations of the internal cavity (Pl. 162, fig. 1, longitudinal section of the body). The internal structure is simple, since there are only eight mesenteries (Pl. 162, fig. 2). These bear clusters of eggs which are also seen in fig. 1. The cross section is made near the central part of the body cavity which is marked by the dotted line. It cuts through a mesentery on one side and between two mesenteries on the other.

Hartea is another simple form with eight tentacles and mesenteries, but in this case the base of the body and the tentacles are provided with star-shaped spicules. Haimea has variously shaped spicules and this genus also possesses thread cells or nematocysts.\*

In these three genera no ciliated groove (siphonoglyph) at one end of the mouth opening has been described, and probably none exists. The last two genera have a skeleton consisting of spicules. They are found only on the base or in the body walls and are never secreted in the body cavity; there are therefore no false nor true septa. This can be said not only of these genera but also of all living Alcyonaria, and it is probable that this changed and reduced condition of the skeleton has been brought about since the tabulate ancestors of the Alcyonaria flourished in Palaeozoic times.

From single forms we pass to simple colonies. *Cornularia cornucopiae* Lam., is a simple colony without spicules but with more or less horny matter. It is interesting to note that in this species the ectoderm secretes a horny sheath (Pl. 163, fig. 1) which reminds one of the external skeleton of the hydroids.

A related genus, *Clavularia crassa* M. & K. (Pl. 163, fig. 2), is a simple colony with retractile zoons. It has spicules but no horny sheath. In *Clavularia viridis* Q. & G., the first zoons spring from the basal stolon, but higher up they are united by simple tubes from which other zoons are budded (see Pl. 164, fig. 1, showing the skeleton of a zoon that has budded from the connecting tube). The grooves on the surface of the skeleton mark the position of the eight mesenteries within. The skeleton consists of a coriaceous substance with a few scattered spicules, and is without openings, therefore imperforate.

*Clavularia glauca* Hickson<sup>1</sup> (= *Anthelia glauca* Savig.) (No. 165) puts out a fleshy membrane, the coenosarc, from the bases of the zoons; this fleshy floor is provided with nutritive canals and secretes the limy coenenchyma.

The organ-pipe coral, *Tubipora hemprichi* Ehr. (No. 166), when young has a long, tubular, fleshy body with the mouth in the middle of the oral disc surrounded by eight tentacles. The latter are fringed with small papillae, each one of which has a tiny opening at the end. The basal portion of the body sends out a fleshy layer which extends over the surface of the rock and from which other zoons are budded. As the colony increases in size this flat lamella ceases to grow and its work of giving origin to new zoons is at an end. Around the oral end of the body there spreads out a rim (No. 166). This may surround neighboring tubes or fuse with adjacent rims, thereby forming horizontal platforms from which other zoons arise.

The spicules first appear singly in the mesoderm of the base and walls of the tubes and of the cross platforms, but during the growth of the animals they become united by the serrations of their edges to form a solid skeleton (No. 167). The sutures between the spicules can be

<sup>1</sup> See Trans. Zool. Soc. London, XIII, 1892, p. 333.



plainly seen with the microscope; they extend crosswise, as do also the long axes of the spicules. Occasionally, according to Hickson, they project into the cavity of the coral animal and look like the so called "septa" of *Syringopora*. No true septa are developed in *Tubipora* but within the tubes are found variously shaped tabulae, some flat and others funnel-shaped. It is an interesting fact that at the free end of the zoon the spicules are separate as they were in the single form that started the colony.

The danger of multiplying species that really do not exist in nature has recently been pointed out by Hickson,<sup>1</sup> who states that the principal character which has been used for distinguishing species of *Tubipora* is the diameter of the zoon walls, "and this character in every specimen depends entirely upon the situation on the reef in which it happened to grow." "Our desire to make new species," says this author elsewhere, "seems to have blinded us to what is perhaps the most important feature of Zoophytes—the infinite variety of growth they may exhibit to meet the varying conditions of their existence."<sup>2</sup>

*Paralcyonium elegans* M.-Ed. & H., (No. 168) is a colonial form with a spicular skeleton. The lower, stem-like portion is more dense than the upper part and is without zoons, while the small branches which are given off from the upper portion are covered with zoons. Most of this part can be withdrawn to the stem. The zoons have very long tubes which can be seen in a vertical section extending from the stem to the surface. Surrounding these is a thick coenenchyma which reaches up to the retractile portion. The body cavities communicate with one another by a system of nutritive canals. *Alcyonium palmatum* Pallas (No. 169, the remaining Alcyonaria are placed, on

<sup>1</sup> A. Willey, Zoological Results, part 4, Apr., 1900, p. 493.

<sup>2</sup> Trans. and Ann. Rep. Manchester Micr. Soc., Address of President, 1899.

account of their shape, in the erect portion of Section 3) resembles *Paralcyonium*. The colony is supported by a short stem which is often without zoons and broadens out into several lobed masses which are thickly covered with coral animals. This genus is sometimes imbedded in sand while other species attach themselves to the stems of plants.

*Ammothea nitida* Verr. (No. 170), may have finger-like projections extending from a flat base. The zoons in this case are not retractile.

*Spongodes celosia* Less. (No. 171), is a colonial form in which the cortex of the stem and branches contains large spicules. The zoons are not retractile and their tops are protected by spindle-shaped spicules.

*Virgularia* (No. 172) bears the zoons nearly sessile on the central stem. This genus with the one that follows, is among the simpler forms of the Pennatulidae and they are both found in deep water. *Kophobelemnon* (No. 173, *K. stelliferum* O. F. Müll.) has the central stem thick and bears large retractile zoons.

The more complex Pennatulidae are represented by *Pennatula aculeata* Dan. & Rev. (No. 174), *Pennatula phosphorea* Linn. (No. 175), and *Pennatula rubra* Ellis (No. 176). In this genus there is a long central stem with well developed zoons on more than a half of its length. The stem is deeply grooved on the dorsal side and the lower portion is sunk in sand and mud. These zoons are dimorphic, some being sexual and others without reproductive organs.

In *Renilla*, (Pl. 177; Nos. 178, 179), the sexes are distinct and the eggs and spermatozoa are discharged at the same time, fertilization taking place in the water. It is interesting to note that the segmentation of the egg is so extremely variable "it is safe to say no two eggs ever develop in precisely the same way."

The following life history illustrates the good results which may be obtained when naturalists cooperate for a

common object. Three investigators<sup>1</sup> worked together on the eggs of *Renilla*, keeping them under continuous observation, and "were thus enabled to determine with all possible certainty the fact that at least five or six well-marked modes of yolk cleavage with many minor variations, may occur as normal phenomena of development, that the segmentation may be at first equal or unequal, complete or partial, regular or irregular, and that a great amount of variation exists in the duration of the various stages of activity and quiescence."

Pl. 177, figs. 1-14, illustrates the consecutive stages of development in one individual, the time required being 115 minutes. The egg first divided into eight spheres (one third of the specimens examined divided in this way, but usually this stage is skipped and the egg cleaves at once into sixteen spheres). When the sixteen-sphere stage is reached the process of delamination begins. This process does not go on simultaneously in all the spheres but occurs later in some cells than in others. Fig. 15 is a section of the embryo in which the inner ends of the cells are separating or have just separated from the outer portion. The cavities seen in the figure are caused by shrinkage. Fig. 16 shows the process of delamination completed. At this time the egg consists of a solid mass of cells in which there is no trace of the segmentation cavity. The cells of the outside and of the central mass grow smaller in size as they increase in number. Fig. 17 gives in outline the shape of a larva twelve hours old. When the embryo is about twenty hours old a change begins to take place, and a few hours later the endoderm appears by a differentiation of those cells of the central mass lying just under the outer layer. This is well seen in figs. 18 and 19.

Fig. 20 is a twenty-four hours old embryo. It is now covered with cilia which at first do not possess the power

<sup>1</sup> See E. B. Wilson, *Phil. Trans.*, London, 1883, p. 723.

of motion, but afterwards become active, propelling the larva through the water. When the larva is twenty-eight hours old the ends of the ectoderm cells are swollen and bulbous, as seen in fig. 21, and the ball-like portion separates off to form the supporting lamella or mesoderm (fig. 22, *m*). At the end of forty-eight hours all the central cells not used in the formation of the endoderm have been absorbed as food by the endoderm cells and the central region is an empty cavity. In this case, as pointed out by Wilson, digestion in the young *Renilla* is intra-cellular or amoeboid. This is the most primitive mode of digestion and is probably inherited by the Porifera and Coelentera from the Protozoa.

Usually between the fortieth and fiftieth hour the internal bag is formed and the central cavity is divided into chambers by mesenteries. The cells at the large end of the body increase rapidly and are pushed inward in a solid mass (fig. 23, *p*), forming a plug. In time a narrow cavity is seen in its center (fig. 24, *c*). This cavity has no communication with the exterior for twenty to twenty-five hours. At the end of this time the cavity breaks through and a mouth is formed; afterward an opening occurs at the lower end, placing the internal bag in communication with the central cavity. As already stated, the mesenteries appear at the same time that the bag is formed. They consist of eight thick plates of endoderm cells which extend down from the oral end of the body and are of different lengths. These are seen in fig. 25, which is a cross section of the anterior part of a forty-eight hours' larva, and in fig. 26, a cross section of the posterior portion of a four days' larva. In the living animal these mesenteries arise as bilateral organs; that is, they appear one on either side of the median plane of the body. (The figures 25 and 26 should be turned slightly to show the bilateral condition more plainly. The dotted line in fig. 26 indicates the median plane of the body.) For the reason that these partitions

are single and are arranged four on each side of the median line of the body they are called bilateral mesenteries. They can be distinguished from the biradial mesenteries of the Hexactiniae since these arise in pairs that radiate from the center to the circumference. When the animal is placed in accordance with this bilateral arrangement, there is a dorsal and a ventral side. The former differs from the latter by having the mesenteries much shorter, as shown in fig. 26. These walls may be seen on the outside in a three-and-a-half days' larva (fig. 27; fig. 28, the same contracted).

It is at this early time or even a little earlier (seventy-two hours) that buds appear, as will be described farther on.

Figures 29 and 30 show the larva when it has settled. The tentacles are at first quite simple but during growth become pinnate. The fact that, according to Wilson, the eight mesenteries and eight tentacles appear at one time and not in sequence, as is the case in the Hexactiniae, does not prove that the Alcyonaria are more specialized than the Hexactiniae. In order to demonstrate this view, evidences of the reduced character of the Hexactiniae, such as the reduction of biradial mesenteries, must be brought forward. The abbreviated record in the development of forms like *Renilla* tends to prove that these are more specialized members of the Alcyonaria, and we should predict that the primitive forms of the group would show a regular sequence in the appearance of the mesenteries.

The spicules of *Renilla* are formed, according to Wilson, in both the endoderm and the ectoderm. Those of the endoderm appear first; they are oval nodules and are not numerous. Fig. 31 represents a young stage; fig. 32, an old stage; and fig. 33, the spicule taken from the cell. The spicules of the ectoderm appear soon after the attachment of the larva. They are at first rod-like and colorless, and not until a colony is formed, do they

become purple. Figs. 34 and 35 are ectoderm cells containing young spicules; fig. 34 being not more than one eighth the length of a fully formed spicule. The calcareous matter first takes the form of elongated concretions and these like the endodermic spicules are formed by a process of crystallization, as shown by Prof. B. K. Emerson. It is an interesting fact that the development of the spicules in the Alcyonaria is similar to the formation of these hard parts in the mesoderm of sponges, as observed by Schultze and Metschnikoff, and seems not unlike the formation of crystals in vegetable cells, as suggested by Wilson.

It has already been stated that the larva begins to form a colony while it is free. It is probable, as pointed out by Wilson, that the necessity for motion is the cause for the early development of the buds. If the parent after becoming attached had no means of moving, it would doubtless be "smothered in the drifting sand." The position of the first two buds, as seen in fig. 27, is constant. The development differs from that of the parent zoon which has arisen from an egg, so that one ought not to compare egg development with bud development. The young colony takes in water and by means of strong internal currents is able to creep.

It is instructive to note that an allied genus, *Leptogorgia*, does not possess the power of creeping but fastens itself early in life to safe objects, and Dr. Wilson detected no buds at the end of two months. Fig. 36 is a young colony with five pairs of buds. In the adult (No. 178, with zoon expanded; No. 179, contracted) the young marginal zoons move the whole colony, and as they mature, become nutritive and reproductive. In time the zoons of this primary group become centers of multiplication and many secondary groups are formed, while complexity marks the whole organization.

The marked bilateral symmetry of *Renilla* is an evidence that the group to which it belongs is more primitive

than the Hexactiniae, since the latter are bilateral in early life and become radiate afterward, owing to attachment and the action of physical forces.

Another colonial form is Veretillum (No. 180) which is related to Renilla.

Briareum (No. 181, see upper shelf) of the Gorgonacea is an upright, irregularly lobed colony. The zoons are without protecting cups and can be entirely withdrawn into the coenenchyma which is abundantly supplied with spicules. The central mass, which can hardly be called an axis, is supplied with nutritive canals.

In Melitodes, (No. 182, *M. ochracea* Verr.), the axis is jointed and the sections consist of alternating portions of horny and calcareous matter. The horny sections are in reality made of a horny substance and loose spicules, while the calcareous parts are composed of consolidated spicules. All the joints are penetrated by canals.

The spicules in *Corallium rubrum* Linn. (No. 183), unite to form a dense calcareous axis (No. 184), which is a beautiful red color and used for ornaments. The young coral animal has a mouth surrounded by eight white, pinnate tentacles (No. 183). The internal bag leads into the body cavity which is divided by eight mesenteries into eight chambers. The outer flesh is a bright red color and is stiffened by spicules. This single zoon buds and a colony arises. The body cavities of all the zoons connect with a series of water tubes; these press upon the calcareous stem which is secreted by the bases of the zoons and while it is yet soft, indent its surface.

Isis (No. 185) has a jointed axis consisting of horny and silicious sections. The zoons can be withdrawn into the thick coenenchyma. The spicules are club-shaped and stellate in form.

An upright colony is formed by Xiphigorgia (No. 186). A related form, Plexaura (No. 187), has a horny axis, while the coenenchyma has variously shaped spicules.

Small canals radiate from the cavities of the zoons and open into the longitudinal canals around the axis.

The fan coral, *Rhipidogorgia*, (No. 188) is another upright coral, the branches of which unite to form a network. The zoons are arranged on either side of the intersecting branches. The yellow flesh is stiffened by spicules of different shapes and the axis (No. 189) is horny.

#### ANTHOZOA.

#### ZOANTHARIA.

Coming to the present day we find among living Zoantharia the fleshy Actiniae which never make a skeleton. The researches of Boveri,<sup>1</sup> McMurrich,<sup>2</sup> and others make it very probable that all the Actinian types have descended directly or indirectly from the Edwardsiae.

*Edwardsiae.* *Edwardsia claparèdi* Panc. (Pl. 190, figs. 1, 2) is a single form with eight simple tentacles. Its body cavity is divided into chambers by eight bilateral mesenteries (fig. 2). These Actiniae have the dorsal and ventral differentiation of the body well marked, so that a bilateral arrangement of the parts is the predominating characteristic (fig. 2). When young, *Edwardsia* is free-swimming, but later it becomes stationary by burying the posterior part of its body in sand. A related form, *Cerianthus membranaceus* (No. 191) has a similar habit.

*Antipathes subpinnata* (No. 192) represents the Antipathariae. Nothing has been done as yet with the embryological development of this group. The young *Antipathes* is a single, fleshy animal. At one end is the mouth with

<sup>1</sup> Zeitschr. f. wiss. Zool., XLIX, 1889, p. 492.

<sup>2</sup> Journ. of Morph., IV, V, 1890-'91; Proc. U. S. Nat. Mus., XVI, 1893.



six simple tentacles. The mouth leads into an internal bag<sup>1</sup> which communicates with the body cavity. The latter is divided by six bilateral mesenteries. So far no trace of biradial mesenteries has been discovered in the young *Antipathes*, and these mesenteries we should expect to find if the group were reduced descendants of the Hexactiniae as some naturalists maintain. The young *Antipathes* sends out fleshy prolongations from the basal portion of its body and these bud other zoons, thus giving rise to a colony (No. 192). The bases of all the zoons secrete a black horny stem or axis (No. 193, *A. dissecta* D. & M.), which gives rigidity to the stalk. This secretion is restricted to the "foot" of the zoons, the body walls never taking part. We have seen that this is also the case with some of the Alcyonaria, a group in which *Antipathes* is sometimes placed. The possession, however, of six bilateral mesenteries seems to show relationship with the Hexactiniae.

*Zoanthus solanderi* Less. (No. 194), is a simple colony, the members of which are connected by stolons. The arrangement of the mesenteries is still essentially bilateral.

In *Mammillifera*? (No. 195), the zoons arise from a basal membrane and are of about the same height.

*Hexactiniae*. The simple members of this group are illustrated by *Halcampa chrysanthellum* Gse. (No. 196), which is a free-swimming animal. In its development it passes through the *Edwardsia* stage of eight bilateral mesenteries, but when adult it possesses twelve biradial mesenteries.

The Actiniae next to be described are bilateral in the

<sup>1</sup> This organ is called in text books and manuals "oesophagus," "stomach," "stomodaeum." According to Prof. E. B. Wilson it is an ectodermic structure and has nothing to do with the stomach — structurally or functionally. It is homologous with a stomodaeum, or, what is more probable, with a fused stomodaeum and proctodaeum. We have called it simply a bag.

early stages of development, but afterward develop a radial symmetry.<sup>1</sup>

*Actiniae.* It is now pretty well established that the Actiniae are bisexual. The egg of our common sea anemone, *Metridium marginatum* Ag. (Pl. 197, figs. 1-10), leaves the parent form unfertilized. This is not the case with all Hexactiniae, the embryo of *Rhodactis* being so far developed when it passes into the water as to possess from two to four mesenteries, while that of *Aulactinia* possesses eight or twelve. Fig. 1 is an immature ovum taken from the ovary. The nucleus with its nucleolus and the process extending outward at one pole are clearly seen. Figs. 2-6 represent the segmentation of the egg; fig. 7 is the young blastula; fig. 8, an optical section of a free-swimming blastula. Some of the embryos at this stage are hollow and seem to be empty, while others (fig. 9) are filled with a liquid containing scattered cells. Fig. 10 illustrates the formation of the endoderm by delamination of the inner ends of the ectoderm cells. After this stage the mouth breaks through, making an opening to the internal cavity. The young Actinian (Pl. 198, figs. 1-3; the vertical line represents the height of the anemone when expanded) is a single, fleshy animal. The mouth is surrounded by a limited number of hollow tentacles. It leads into the internal bag which communicates with the body cavity. The latter is divided first by four, then by eight mesenteries which arise bilaterally. There is no indication of a skeleton in the young sea anemone, neither is there so great differentiation in the histological structure of the animal as in more specialized Anthozoa. For these reasons, and because the mesenteries arise on either side of the median plane of the body, producing bilateral symmetry, we regard the Actinia as a primitive rather than a reduced form. When the animal grows older the bilateral arrangement of parts gives way to a radial

<sup>1</sup>Moseley, Quart. Journ. Micr. Sci., XXII, 1882, p. 395.

arrangement. Thus the base of the anemone (Pl. 198, fig. 3) exhibits a small number of biradial partitions.

Young and adult stages of the anemone are seen in the alcoholic specimens (No. 199). The cylindrical body is usually attached by its base (No. 199), although it has the power of gliding over surfaces. The mouth is surrounded by tentacles (Nos. 199, 200) which can be drawn in and entirely concealed. The mouth is open and more or less circular in the alcoholic specimens (Nos. 199, 200), but in life it is slit-like. It is provided with two siphonoglyphs. In the living animal these are seen to be lined with long cilia. When the mouth is closed the central parts come together, while the siphonoglyph at either end is open so that a current of water can be kept circulating through the body. The mouth of the adult opens into the flattened internal bag, and the latter into the body cavity, which is divided into chambers by biradial mesenteries, seen in the preparation (No. 201). At each end of the flattened bag there is a pair of mesenteries called "directives." Four other pairs of long walls reach the central bag, making six pairs of primary mesenteries. Besides these there are cycles of shorter pairs, the number depending upon the age of the anemone. When mature the mesenteries bear the long convoluted reproductive organs.

The mesenteries are not arranged symmetrically and equally distant from one another, as might be inferred from figures often given in textbooks. In a collection of twenty-one anemones sent from Beverly bridge, not one showed a perfectly symmetrical arrangement. In nearly all, six or eight of the mesenteries which reached the central bag were bunched closely together, while the remaining ones were separated from these by a greater or less distance. One specimen had four biradial pairs and an odd one; two specimens had six pairs and an odd one; another was found with seven pairs and an odd one, while still another had eight pairs.

The shorter mesenteries bear long filaments which are provided with thread cells, and which can be thrown out of the mouth and through openings in the body wall.

Actiniae generally reproduce in the manner already described, but occasionally they increase by budding and by fission. No. 202 is a rare specimen of *Metridium* which has two mouths in the oral disc. When a constriction takes place between these two and the oral disc divides, the method of fission is illustrated, and two animals are produced which in No. 203 have not separated.

There are a number of different genera of Actiniae in the Collection illustrating interesting features.

*Anemonia sulcata* (No. 204), is remarkable for its short body and its numerous large, long tentacles which float in the water like hungry food catchers.

The slit-like mouth with thickened lips peculiar to anemones is well seen in *Adamsia rondeleti* (No. 205). This anemone has the habit of fastening itself to the inner part of the opening of a Gastropod shell, as shown in No. 205; the bases of the different animals often touch one another, but there is no organic connection. One species of this genus (*A. palliata*) is found as a messmate on the back of the crab, *Pagurus prideauxi*.

*Anthea cereus* Johnst. (No. 206), has little power of drawing in its tentacles, which are placed at the junction of the body wall and the oral disc. The exquisite coloring of Actiniae is illustrated by all the glass models of these animals but especially by this species of *Anthea*.

*Bunodes crista* Ehr. (No. 207), is a rare anemone. The surface of the upper part of the body has many warts which are used as suckers for mooring the animal or for the attachment of foreign particles.<sup>1</sup> There is an indefinite number of retractile tentacles, some small and others so large and long that they look like grasping organs. Suctorial warts similar to those of *Bunodes* are also found in *Tealia crassicornis* Müll. (No. 208).

<sup>1</sup>Proc. Roy. Dublin Soc., VI, 1889, p. 315.

The body of *Phymactis florida* Drayton (No. 209), is much shorter than that of *Metridium*; its mouth is elevated above the oral disc and surrounded by short tentacles.

*Phyllactis punctata* Couthouy (No. 210), is a large Actinian in which the inner tentacles are similar to those of our common sea anemone, while the outer ones are like fluted lobes edged with green. These lobes sometimes adhere together nearly their whole length. This Actinian is found buried up to its disc in sand. According to Dana this creature crawled on glass by means of its outer lobed tentacles.

*Bicidium parasiticum* Ag. (Pl. 211, figs. 1, 2, natural size), is interesting since, unlike most Actiniae, it possesses an anus at the posterior end of its body. It is found in the mouth-folds of the medusa, *Cyanea arctica* Pér. & Less. The body is long and ribbed from one end to the other. Besides the longitudinal markings there are many transverse wrinkles. Fig. 1 shows the body contracted and the anus open. The terminal opening in five tentacles is seen, two are closed, and one is turned from the observer. In fig. 2 the body is expanded and the anus closed; the twelve tentacles are visible. Fig. 3 is an enlarged drawing of the posterior portion of the body, showing the terminal anus and the rows of minute openings which radiate from it.

## ANTHOZOA.

### MADREPORARIA.

The Madreporaria may be grouped into the Aporosa or Imperforata, the Fungidae, and the Perforata. It must be borne in mind, however, that there are no sharp division lines between these groups. The time will doubtless come when the ancient imperforate Madreporaria will be distributed as ancestral forms among the different families

of corals living to-day, but at present so much uncertainty exists in regard to their true relationships that we consider them as ancestors of the whole group of Madreporaria.

The skeleton of the Madreporaria is not spicular, like that of the Alcyonaria, but it is a hard, solid secretion of carbonate of lime. The theca in the Imperforata is not pierced by openings or pores, so that there is no system of canals connecting different corallites. In the Madreporaria Fungidae the young are imperforate and the adult perforate, while in the Perforata there are numerous pores both in the young and the adult stages, and the corallites are in communication with one another.

The structure of these three groups is essentially similar to that of the sea anemones or Hexactiniae just described, with the exception that the Madreporaria possess a skeleton. The formation of the skeleton has been studied by many, notably by von Koch<sup>1</sup> and Ogilvie.<sup>2</sup> The larva begins to form a skeleton after it is attached. The first rudiment is a disc perforated in the center which afterward becomes entire. This disc is between the ectoderm of the larva and the rock to which the latter is attached, and is a secretion of the ectoderm. It cannot be formed by either the endoderm or the mesoderm, since it is separated from these layers by the ectoderm. In time there appear radial ridges or upward foldings of the basal disc. The ectoderm in these foldings secretes carbonate of lime and thus limy septa are formed. In one genus observed<sup>3</sup> there were twelve mesenteries and twelve septa, six in the chambers between each biradial pair of mesenteries (entosepta) and six others in the chambers between two adjoining biradial pairs (exosepta). In the younger zoons there were twelve mesenteries and only six septa, and

<sup>1</sup> Mitth. d. Zool. Stat. Neapel, III, 1882. Morph. Jahrb., V, VI, VIII. See also Fowler, Quart. Journ. Micr. Sci., XXV, 1885.

<sup>2</sup> Proc. Roy. Soc. London, LIX, 1895; Phil. Trans. Roy. Soc. London, B, CLXXXVII, 1896.

<sup>3</sup> *Madreporia variabilis*.

these were the entosepta. In time, according to von Koch, the septa fork at their ends and later these ends fuse to form the cups or thecae. According to Lacaze-Duthiers the theca arises as a ring-like thickening of the base entirely independent of the septa.<sup>1</sup> Sometimes the central ends of the septa fuse and form the columella.

While these changes are taking place, the ectoderm at the free margin of the young coral animal secretes lime whereby the epitheca is formed. This is a thin imperforate layer which is originally free from the theca but which secondarily fuses with it.

Many of the imperforate Madreporaria occur in the early geologic formations. The structure of the skeleton of these ancient corals—also called Rugosa and Tetracorralla—does not differ from that of recent corals. The tetrameral symmetry (or having the parts in multiples of four) peculiar to many of them is not a constant character, and a hexameral symmetry is not by any means characteristic of recent corals.<sup>2</sup>

The relationship between these ancient and modern forms causes them to be placed together under the head of the Madreporaria Aporosa.

It is probable that the earliest ancestors of our coral animals were disc-like in form, for the reason that this is the first condition of the skeleton of existing species. In time this disc-shaped coral probably became cup- or horn-shaped,—a very common form among ancient species.

The primitive disc-shaped ancestors are not known with certainty, so that we must pass to the cup-shaped forms; of these there are a number in the Collection.

*Cystiphyllum americanum* E. & H. (No. 212), has septa that are only slightly developed, being indicated by mere ridges. The coral is vesicular throughout but towards

<sup>1</sup> For a discussion of these views, see Fowler, Quart. Journ. Micr. Sci., XXV, 1885.

<sup>2</sup> Treatise on Zoology, ed. by E. Ray Lankester, Part 2, 1900, p. 70.

the base the vesicles are larger and there is a tendency towards forming tabulae. During periods of rest or comparative inactivity the vesicular mass becomes more or less dense and apparently a cup is formed. For this reason there is a succession of cups, representing not different zoons that have budded but different degrees of activity in forming the skeleton. If each were a bud, one ought to find the epitheca extending down into the cup, which is not the case. Still there are some specimens which appear to be made of the skeletons of two zoons, and as the epitheca is continued on the outside it is difficult to give an explanation. In most specimens the epitheca is worn off, but when preserved it shows distinct concentric ridges.

The operculated corals seem to be related to the Cystiphyllidae although they are more specialized in structure.

One of the forms whose affinities have so far baffled naturalists is the Cretaceous *Barrettia monilifera* Woodward (Pl. 213, fig. 1, greatly reduced). Its shape and general appearance would place it with *Calceola* and the other operculated corals, but in structure it is different from any fossil so far discovered. According to Woodward, who first described the specimen (1862), it belongs to the Rudistae, a group of molluscs to which also *Hippurites* and *Radiolites* (Pl. 428, figs. 1, 2) belong. This view was based upon the fact that in Woodward's specimens *Barrettia* possessed a bivalve shell. According to Whitfield (1897) *Barrettia* is more nearly related to corals than to molluscs.

The visceral cavity occupied the center (Pl. 213, fig. 2, longitudinal section; fig. 3, cross section). Below, it was divided by transverse partitions (fig. 4). Radiating from the central cavity were lines of vertical tubes or moniliform rays (figs. 3, 4), and close by it was a larger tube divided by transverse walls (fig. 4 a).

The spaces between the radiating rows of tubes were filled with four-walled tubes which were also divided



horizontally by walls (fig. 5, summit view; fig. 6, vertical section). The moniliform rays may be seen in fig. 5, in the ridges between the rows of four-walled cells.

The specimens described by Whitfield (figs. 4-6) showed no upper valve; in fact, there was nothing to indicate a molluscan character in the genus, such as is plainly seen among the Rudistae. At the same time the genus is different from any of the operculated corals, although it is placed in this group provisionally until more perfect specimens can be obtained.

The single form *Zaphrentis* (No. 214) of the family Zaphrentidae has a bilateral arrangement of the septa. The "pit" or fossula usually contains a shorter septum. Here were probably the mesenteries that bore the reproductive organs. The septa are contorted at the center and the tabulae are not clearly defined, while there is scarcely any vesicular structure.

*Cyathaxonia prolifera* McChes. (No. 215), is a single form with septa arranged radially and a central projecting columella. The young *Cyathaxonia* has an epitheca on the end, which is very delicate, so that it is usually worn off and is seldom seen in fossils.

*Heliophyllum halli* E. & H. (No. 216), is an illustration of a single *Cyathophylloid* coral. It has the form of a flaring shallow cup. The epitheca is seen on the outside, while the vertical septa are distinctly seen within the cup and are radially arranged. Between the septa on the outer side there is more or less vesicular structure; the tabulae cannot be made out in the specimens but the ridges on the septa are plainly seen and appear like cross bars between the septa.

*Acervularia ananas* Linn. (No. 217), is a colonial form consisting of many coral animals that lived closely together. Here there is an external epitheca. The septa extended to the central bag, and below this organ to the center. They are indicated on the surface of the coral by radiating lines. The vesicular structure has largely

disappeared. Budding takes place from the edge of the cup and a spreading form results.

*Lithostrotion canadense* Castelnau (No. 218), is another colonial form in which the vertical septa and columella are clearly shown; the tabulae are seen on a broken surface.

*Turbinolia sessilis* Blainv. (No. 219), of the family Turbinolidae is a single coral of more recent date. It has a columella projecting in the center (although not shown in the specimen) and the septa are arranged radially.

A single, deep-sea form is *Caryophyllia* (No. 220, *C. smithi* var. *castanea*). This is a most instructive specimen, for it exhibits the striking similarity between a sea anemone and a coral animal. The epitheca is formed around the lower part of the body. The septa of the skeleton are numerous and the larger ones predominate. In the center is a twisted columella.

*Oculina* (No. 221), is one of the irregular branching corals with rounded tips. The corallites are distinct, with the coenenchyma showing plainly near the base but almost wholly disappearing at the ends of the branches.

The colonial *Pocillopora*, represented by the large, handsome specimen on the lowest shelf of the erect portion of Section 4 (No. 222, *P. nobilis* Verr.), has stout obtuse branches. As in *Oculina*, the corallites on the sides of the branches are separated by the coenenchyma, but at the ends they are crowded closely together. The tabulae show finely in a side view. The columella is sometimes well developed but in other specimens poorly. This coral increases by budding and rarely by fission. The thecae in *Pocillopora* are divided by a long median septum; the other septa in this genus and in the beautiful *Seriatopora* (No. 223, see lowest shelf), are minute, and in the latter genus the tabulae are scarcely visible.

The family *Astraeidae* is a large one, including many genera. *Antillia explanata* Pourtales (= *Lithophyllia*

*cubensis*<sup>1</sup> M.-Ed. & H.) (Pl. 224), is one of the more generalized members of the family. It is disc-shaped (Pl. 224, fig. 1) like the original basal plate of the Madreporian skeleton. *Antillia* offers an illustration of the co-existence of the epitheca and theca in one zoon. The epitheca, which is well developed in this species, is shown in fig. 2, and also the central small area of attachment.

*Cladocora caespitosa* Lam. is seen in the glass model (No. 225). At the left is a single zoon much enlarged, and just back of it is the colony. The theca is present and the ridges on the outside correspond to the septa. Vesicular structure exists though in small quantities, and the epitheca is only slightly developed.

The little *Astrangia danae* Ag. (No. 226; No. 227, skeletons attached to a stone), is the only coral living in our New England waters. It is a colonial form and the corallites are connected by the coenenchyma. The septa unite at the center in a columella and there is no epitheca.

There are many corals, like *Mussa*, *Manicina*, and the like, that increase by a process of incomplete fission which results in winding furrows with such indistinct thecae that often the limits of the different skeletons cannot be made out with certainty.

The septa in *Mussa tenuidentata* M.-Ed. & H. (No. 228), are large and toothed and the columella is spongy. In some specimens the epitheca is slightly developed and in others it does not exist. According to Martin Duncan<sup>2</sup> the young of this genus cannot be distinguished from simple *Astraeidae* of the *Antillia* type. *Mussa* increases by fission, as we have said, and the process is often illustrated in one specimen where the original circular corallite may be found, and also more advanced corallites that are elongated, constricted, and nearly or wholly divided.

<sup>1</sup> Quart. Journ. Geol. Soc. London, LI, 1895, p. 259.

<sup>2</sup> Journ. Linn. Soc. London, Zool., XVIII, 1884, p. 83.

Manicina is interesting for the reason that it is a rapid swimmer when young, fixed by a pedicel when mature, and free again when old. In developing, the stage with eight mesenteries is followed in a day or two by the stage with twelve.<sup>1</sup> The skeletons (No. 229) show different stages of growth, the colony never becoming much larger than the largest specimen.

*Euphyllia gracilis* Dana (No. 230), forms small colonies. The thecae in this genus are circular, compressed, and sometimes meandering.

The same method of reproduction is illustrated by the massive brain coral, *Diploria cerebriformis* M.-Ed. & H. (No. 231), which grows to a great size and which represents the skeletons of a vast number of coral animals.

*Favia* (No. 232) is a hemispherical colonial form in which the corallites are united and the septa are toothed. The columella is spongy and an epitheca sometimes exists.

*Orbicella annularis* Dana (No. 233), is also hemispherical in shape and the new buds arise in the spaces between the corallites.

The corallites in *Galaxea fascicularis* Oken (No. 234), project from the surrounding coenenchyma. Each is marked by striae which indicate the septa. The latter are distinct and the longer ones reach to the columella which does not project upward. This genus increases by budding from the walls of the corallites and also from the basal coenosarc that extends between the corallites. The coral takes on a foliaceous shape in *Agaricia agaricites* E. & H. (No. 235). The columella is present but the septa are not numerous. *Pachyseris laevicollis* E. & H. (No. 236), is a related form.

<sup>1</sup>H. V. Wilson, Journ. of Morph., II, No. 2, 1888, p. 191.

## MADREPORAKIA FUNGIDAE.

Palaeocyclus (No. 237) and Cyclolites (No. 237) are mushroom-corals which antedate our present *Fungia*. From a study of the early stages of the latter, however, it is probable that all these coral animals arose from a cup-shaped rather than a mushroom-shaped ancestor. It may be that a still more remote ancestor was disc-shaped, as we have already said, and that the *Madreporaria Fungidae*, which possess a similar plate-like form, are its specialized and reduced descendants.

Nothing is known of the young stages of *Palaeocyclus* and *Cyclolites*. The adult is disc-shaped and the epitheca is confined to the base. The septa rise as so many walls of varying length from the basal plates.

Turning to the development of *Fungia* we find that the parent stock is attached (Pl. 239, fig. 1). It is cup-shaped with a distinct theca, while the cavity of the cup is divided into chambers by septa. In this stage it resembles *Caryophyllia*. In time the oral disc increases in size at the expense apparently of the thecal portion (fig. 2). The growth is lateral, until at last the young *Fungia* separates from the parent stock a short distance below the disc where the dark line is seen in fig. 3. When set free the *Fungia* has an opening beneath, where it was fastened, but this quickly fills up by a secretion of carbonate of lime. The scar is seen in young specimens (No. 240). The *Fungia* is henceforth free (Pl. 239, figs. 4, 5) with only slight evidences on the lower side of its attachment, and these finally disappear (fig. 6). The parent stock continues to bud forth other animals which likewise become detached. According to Semper<sup>1</sup> the parent stock is comparable to the strobila of the *Discophora* and exhibits a true alternation of generations.

<sup>1</sup> Zeitschr. f. wiss. Zool., XXII, 1872, p. 267.

Bourne<sup>1</sup> objects to the use of the word strobila which was originally applied to the dividing parent stock of Aurelia. This is essentially different from the bud-producing parent stock of Fungia, and since it is objectionable to use the same name for two very different phenomena Bourne uses nurse stock for the fixed parent of Fungia.

Rarely a specimen is found with the parent stock attached to it, as seen in No. 240. This stock was covered over with limy deposits by the growing animal, and these had to be removed by acid when the original stock form was exposed with its cup-like shape and internal walls.

The central or younger portions of the adult Fungia (No. 241) are imperforate but the older portions are perforated. The septa increase in number from the center outwards, as is well shown in No. 241.

#### MADREPORARIA PERFORATA.

The simpler members of the Madreporaria Perforata are Dendrophyllia (No. 242) and Coenopsammia (No. 243, *C. tenuilamillosa* Verr.). The former is a branching coral and the latter a low, spreading form. The corallites in both are large and the septa are distinct. Buds grow from the sides of the corallites but a massive colony never results.

*Astroides calycularis* Pallas (No. 244), is a simple colony in which the corallites are packed closely together and rise to about the same height. This was one of the species on which von Koch made his valuable investigations upon the formation of the coral skeleton.

The Madrepore coral (Nos. 245-248), is a typical example of the Perforata. The pores may be finely seen

<sup>1</sup> Quart. Journ. Micr. Sci., XXVII, 1887, p. 294.

when a specimen is held to the light. No. 247 is a vertical section of this coral that exhibits these characteristic openings by means of which the zoons communicate with one another. This coral assumes different shapes; it is branching (No. 245, in more natural condition than No. 248, which has been bleached), and it is flat and encrusting (No. 246, *Madrepora convexa* Dana). The long septa reach the center, where there is a more or less spongy columella. The walls of the corallites are not distinct from the coenenchyma, which is largely developed; and the epitheca is wanting.

Budding takes place from the central and parent form which has remarkable vitality, and also from the sides of other corallites which are larger and longer than most of their neighbors. The skeleton of the central parent zoon is seen cut in two in No. 247. In healthy condition the ends of the branches of Madrepore are always pointed, but in No. 248 there are a number of diseased tips with a puffed out, swollen appearance.

The corallites in *Porites* (No. 249, *P. claviaria* Lam., a branching form; No. 250, vertical section of *P. astraeoides* Lam., a rounded form) are crowded thickly together on a level, with no intervening coenenchyma. The septa are imperfect and spinous; there are no tabulae and the columella is small. The coral is more dense than in Madrepore (compare No. 247 with No. 250), and there is no large parent zoon.

We have attempted to show that the Coelentera as represented by the Hydrozoa and Anthozoa have a definite form and a body cavity all the parts of which are in communication with one another. Beginning with a primitive Palaeozoic ancestor we pass to living free-swimming hydroids that have a direct development, the hydroid growing into a medusa.

Again, free swimming hydroids become attached and colonies arise by budding. These produce free medusae

whose eggs develop into fixed or stationary hydroids, thereby illustrating the process of indirect development and the alternation of generations.

The eggs of other medusae develop into medusae, skipping altogether the hydroid stage and illustrating the process of accelerated development.

Lastly, certain hydroids whose ancestors, we have reason to believe, produced free medusae have taken on such reduced characters it seems probable that the medusa stage is omitted in their ontogeny, and, if so, they illustrate suppressed development.

Acceleration in development is shown by the Discophora, while specialization of structure and function, resulting in complex colonial life, is characteristic of the Siphonophora.

The Ctenophora constitute one of those interesting synthetic types whose relationships reach out beyond the limits of the Hydrozoa, beyond even the boundaries of the Coelentera, to the subkingdom of the Echinoderms.

The ancestors of the Alcyonarian branch of the Anthozoa are illustrated by a series of forms which show most admirably the gradual transition from the primitive and simple to the secondary and complex.

The living Alcyonaria have in addition to what the Hydrozoan possesses, an internal bag and a body cavity divided into chambers by eight bilateral mesenteries. Their skeleton is made of spicules and is chiefly a secretion of the ectoderm of the basal membrane of the zoons.

The Zoantharia likewise have an internal bag and in youth a body cavity divided by eight bilateral mesenteries, but in maturity this cavity is divided by numerous biradial mesenteries.

The skeleton of the Madreporaria is a solid secretion of the ectoderm and consists, speaking generally, of a basal disc and a theca with true septa.

The processes of reproduction — budding and fission — and the influence of physical forces have brought about



a great variety in form, but through this extreme diversity the fundamental type of structure remains the same.

The subkingdom of Vermes or Worms is placed next the Coelentera by many authorities, and the larvae of certain worms are considered as the nearest approach to the ancestral forms from which all the remaining invertebrates and also the vertebrates have descended.

There is a resemblance, speaking broadly, between the larvae of echinoderms, molluscs, and worms, but this similarity may be due to inheritance from some pre-Cambrian ancestor from which the three branches have developed along different lines. When one considers the varied and extreme specializations of worms; the articulate plan of structure differing so essentially from the radiate plan; the greatly developed muscular system and the complex excretory and reproductive organs; the large number of extremely reduced forms, one finds it easier to place the worms among the more specialized and the articulated animals than next to the comparatively simple Coelentera.

The Echinoderms, on the other hand, are pre-eminently radiate organisms, and in many ways they possess characters in common with the Coelentera.



## ECHINODERMA.

## Sections 5, 6.

## CYSTOIDEA.

Most palaeontologists consider the Cystoidea as the Palaeozoic ancestors of the Echinoderms, while embryologists hold that this view is not supported by facts. According to Bury<sup>1</sup> there is not the slightest embryological evidence that the Echinoderms have passed through a stage in which they are fixed by the aboral pole, like the Cystoids. He goes on to say, "Nevertheless, almost all embryologists, apparently out of deference to palaeontological conclusions, have thought it necessary to assume that ontogeny is misleading, and that a period of fixation really did take place of which all traces have since disappeared. Now this involves us in a question of fundamental importance. If palaeontologists have really proved beyond any reasonable doubt that the Echinozoa are derived from fixed ancestors, then ontogeny is misleading; but if it is misleading to such an extent as to obliterate all traces of a process of such immense importance, I for my part do not see how we can trust it in other particulars, and those who rely upon it for indications of phylogenetic history had better reconsider their position." Professor Bury then takes up the question at length from the embryological point of view and deduces reasons for considering that the ancestors of Echinoderms were unattached forms.

It has been shown by Hyatt and other investigators that it may be possible for all traces of an ancestral structure to be lost, and still the ontogeny of the individual be abso-

<sup>1</sup> Metamorphosis of Echinoderms. Quart. Journ. Micr. Sci., n. s., XXXVIII, 1895, p. 93.

lutely luminous with the light it throws upon the phylogenetic history of its group. So far from being misleading, such an ontogeny is the normal and inevitable result of the operation of the law of acceleration in development by which adult characters are inherited earlier and earlier in the life of the individual, until it may be they appear in the embryo only, and finally disappear altogether.

According to A. Agassiz<sup>1</sup> the Cystoids and Blastoids represent among fossil Echinoderms the nearest approach we have yet discovered to the imaginary prototype of the subkingdom of spiny-skinned animals.

The characters possessed by the living Echinoderma are such that they can be explained satisfactorily only by supposing that these animals are the descendants of attached forms. It may be possible, as already suggested, that the ancestors of the attached forms, living in some remote pre-Cambrian age, were free-swimming, and that these free-swimming adults are represented, with few or many modifications, by the larvae of existing Echinoderms, molluscs, and worms. Be this as it may, the fact is pretty well established that our present free-moving Echinoderms are directly descended from fixed or stationary ancestors.

One of the simplest Cystoids is *Aristocystis* (Pl. 251, figs. 1, 2, *A. bohemicus* Hkl.). Here we have a body protected by many calcareous plates placed together irregularly. It was attached by its base (fig. 2), which was surrounded by more regular plates; as yet no stem had developed. The slit-like mouth was on the upper side (fig. 3, *m*), and at one side was the anus (fig. 3, *a*) closed by a pyramid of plates. Between these two openings there was a pore, now thought to be the genital pore (fig. 3, *g*). Near the mouth there was still another opening supposed to be for respiration and called a hydropore (fig. 3, *h*). In this genus there were no specialized areas

<sup>1</sup> Proc. Amer. Assoc. Adv. Sci., XXIX, 1880, p. 411.

of plates known as food grooves or ambulacra, and no arms extended from the body.

Another primitive form was *Lichenocrinus dyeri* Hall (Pl. 252, figs. 1-4). Little is positively known in regard to this genus, and it is only on account of the structure of the stem that a figure of it is placed on exhibition. The portion preserved (figs. 1, 2) was probably the basal part which was attached to shells, etc., as seen in fig. 1. It was covered by irregular and imperforate plates (fig. 2), which rested upon many radiating partitions, seen in fig. 3, where the outer plates have been weathered and have disappeared. They are also seen in fig. 4, which is the lower or attached side. There is no indication of arms or of areas of plates, the ambulacra, but in the center a stem is visible, which probably supported the body. The genus is chiefly valuable in showing the structure of a primitive stem. The five parts making up the column can be distinctly seen (fig. 2), whereas in the more specialized members of the group they are consolidated so that their boundaries cannot be made out.

In the Cystoid *Amygdalocystis* (Pl. 253, *A. florealis* Billings), the ambulacra consist of a double row of imperforate plates and are concealed by covering plates. This double row extended over the summit. The figure shows several joints of the ambulacrum, each one of which bears a pinnule; also the body with many plates indefinitely arranged, and the round stem. The mouth (*m*) and the anus (*a*) are seen on the upper side.

In *Mesocystis* (= *Mesites*) (Pl. 254, *M. pusirefski*), the five ambulacra are present and are built on top of the body plates. While the ambulacra are imperforate and there are no holes between the plates, the body plates are perforated. The position of the ambulacra in this genus suggests their possible origin (see p. 149). The mouth (Pl. 254, *m*) is at the summit and the anus (*a*) farther down; *h* is supposed to be a hydropore, though Lankester thinks it is due to a boring parasite.

We reach a condition in *Glyptosphaera* (Pl. 255, *G. leuchtenbergi*) in which the body plates are perforated, the pores being in pairs. The ambulacra are on top of the body plates, as in *Mesocystis*. They are long, narrow, and branching, and are apparently without pores. They lead to the mouth which is covered by plates.

The body of *Echinosphaerites* is globular, as shown by Pl. 257 (*E. aurantium* Hising); the specimen (No. 256) is somewhat distorted by pressure, though with this exception it shows the characteristic features well. The body is protected by irregular plates (No. 256; Pl. 257) and provided with two or three small imperfect arms which are broken off in most specimens. Just under a thin limy film covering the outer plates of the body there are ducts (No. 256), the openings to which are arranged in the form of rhombs, and they are therefore called "pore-rhombs" (see No. 256 and Pl. 257). These ducts pass horizontally from one plate to the other, but the pores of the rhombs communicate with short canals that pass vertically through the plates. Probably these canals and pores aided in respiration. The mouth in *Echinosphaerites* is at the apex, while the anus is on one side (No. 256) protected by a pyramid of plates, as shown in both specimen and figure. Between the mouth and anus, a little to the right of the former, is the genital pore (No. 256; Pl. 257).

One of the more specialized Cystoids is *Caryocrinus ornatus* Say (Nos. 258, 259). The stem by which it was fastened (not seen in the specimen) was composed of many discs. Above the stem was the body, protected by circles of regular plates, finely seen in No. 258. The basal plates compose the first circle and above these is the circle of radials (No. 259). In this genus the plates at the base of the arms, often called interradians, perform the work of true body plates. The arms were perhaps little appendages like pinnules, but are usually broken off, as in the specimens. The ambulacra in the middle

of the arms were covered and led to the mouth which was also covered over by a series of plates. The anus is in the body plates and outside of the arms. The possession of a complete digestive system ending in an anus and entirely separate from the body cavity is a distinctive feature of the Echinoderma, separating this subkingdom from the Coelentera. The body plates in *Caryocrinus* were pierced by holes which were the openings of the tubes that ran along the inner side of the plates, and which connected with the respiratory organs or hydrospires.

In the Cystoidea the ambulacra constitute the feeding and not the locomotive system, so that, were we considering function rather than homology, food grooves would be a good name for ambulacra and tentacles an appropriate name for the organs which came out of the openings of the food grooves. It is probable, as we have already said, that the first forms were without food grooves or ambulacra; these may have appeared later as hollows scooped out of the surface of the body, so that the ambulacral plates were set in between the body plates. The next step might be to set these on top of the body plates, as in *Mesocystis*. Finally, they might be pushed upward still more, until they were off of the body altogether, as in *Caryocrinus*, forming the ambulacra of the arms.

#### BLASTOIDEA.

The Blastoids probably sprang from the Cystoids. One of the most generalized Blastoids is *Codaster* (Pl. 260). Here the body is attached by a stem and it is made of regular plates consisting of basals, forked radials, and inter-radials. Its ventral side (Pl. 260) is wide and nearly flat, and on this flattened area the five imperforate ambulacra (Pl. 260, *am*) are spread out. The many slits (Pl. 260, *s*) of the hydrospires are exposed between the ambulacral areas. The anus (Pl. 260, *a*) is flush with the surface.

The central mouth was concealed by oral plates in the living animal, and the ambulacra were also covered. Co-daster like all Blastoids is without arms, but short pinnules are attached to the ambulacra.

In another genus, *Orophocrinus* (Pl. 261), the numerous hydrospiral slits are reduced to ten slits, two on each side of an ambulacrum (Pl. 261, s). In this figure the covering plates are seen over the ambulacra.

If we suppose the hydrospires crowded under the ambulacral areas and these slits shortened till only an opening is left at the top, we have the condition found in the following more specialized Blastoids.

*Pentremites godoni* Shum. (No. 262), is a stalked Blastoid, but the stem is so short and small that it is rarely preserved. The body in this genus, as in all Blastoids of its group (Pentremitidae), becomes constricted and the inner portion of the basal plates helps to form the uppermost disc of the stem. The basals and radials are well seen in No. 262, especially in the middle specimen (b) in the lower row, and the upper right hand specimen (e). Each of the five ambulacra consists of two parts, the lancet-shaped portion in the middle which is made of many small plates, and the side pieces or plates. Near the outer edge of the lancet plate there is a row of sockets where the long delicate pinnules were attached. The food was caught by these pinnules and carried by cilia in the transverse channels to the median channel and thence to the mouth which was in the center of the oral disc. The ambulacral groove is said to have been covered by plates, but these are not seen in any of the specimens in the Society's collection.

On the outer edges of each ambulacrum is a row of holes (No. 262, a, b, d, e) for admitting water to the tubes or hydrospires inside. The latter open at the top in the five holes or spiracles around the mouth (No. 262, c, d). In reality four of the spiracles are divided by a partition, while the largest one is divided twice. Of the eleven



openings thus formed ten are spiracles and one is the anus.

We have seen that the hydrospiral or respiratory system is not found in the primitive forms of Cystoids. Where it first occurs, it is independent of the feeding system and is on the surface, as in *Echinospaerites*. Later, among the Blastoids especially, it is sunk under and crowded closely against the feeding system.

Various interesting modifications take place in the structure of Blastoids. The body may become elongated and the ambulacra narrow, as seen in *Tricoelocrinus obliquatus* Worthen (No. 263), where the lancet plate is covered by the side plates.

In *Nucleocrinus vernueilli* Troost (No. 264), the basal plates are very small and sunken; the radials are also reduced in size, while the broad interradians and the narrow ambulacra make up most of the body. The latter extend from the top or ventral side downward to the lower side.

One genus of Blastoids, *Eleutherocrinus* (*E. casedayi* Shum., No. 265), shows a peculiar specialization of structure. One ambulacrum has become modified and is found at the top, leaving only four long ambulacra. It is interesting to note that this specialization of the ambulacra appears in a stemless and, therefore, a reduced blastoid.

#### CRINOIDEA.

The Crinoidea may be divided into two series, each one of which begins with stemmed species and ends in a stemless form.

The more generalized series is represented in the Collection by *Haplocrinus*, *Cupressocrinus*, *Cyathocrinus*, *Encrinus*, and *Marsupites*.

*Haplocrinus* (No. 266) has the body made up of two circles of plates; the circle at the base of the body and

just above the stem is composed of basals and the circle above of radials. The other genera have three circles of plates; the one at the base of the body and above the stem is the circle of underbasals and above this are the basals and radials.

Those forms which have basals and no underbasals are known as monocyclic Crinoids and those with both basals and underbasals as dicyclic forms.

According to some investigators the monocyclic Crinoids of recent geologic epochs and those living to-day have descended from the ancient dicyclic forms. If this is the case, they have become specialized by reduction. While this is probably true, it must be borne in mind that the ancient dicyclic forms may have arisen from primitive monocyclic Crinoids, which one would expect to find in pre-Cambrian formations.

According to Bather and Lankester,<sup>1</sup> there is evidence that the monocyclic forms have descended from Cambrian or pre-Cambrian monocyclic ancestors, and the dicyclic species from dicyclic ancestors, though it is not known in what forms these two independent lines converge. We will consider Haplocrinus as an example of the ancient monocyclic group. Its body (Pl. 266, figs. 1-3, *H. mespiliformis*) is small and attached by a round stem not seen in the drawings. It is composed of basals and radials, as we have already said, and these plates are fastened together by close sutures, so that they are immovable (fig. 1, side view). The radials are perforated. The ventral pyramid consists of oral plates only,<sup>2</sup> which rest upon the radials. Fig. 2 is the ventral surface with the pyramid of five oral plates; the posterior plate which contains the anus is seen to be larger and is carried forward between the lateral-anterior plates covering the mouth. Some-

<sup>1</sup> Treat. Zool., Part III, 1900, p. 138.

<sup>2</sup> Wachsmuth and Springer, Proc. Acad. Nat. Sci. Phila., 1888; also *ibid.*, 1890.

times this tongue-like projection has a node on top, as in fig. 3. The presence of the anus causes more or less irregularity in the plates of the body (see fig. 1). The ambulacra run out from the mouth across the ventral disc and under the oral plates to the arms.

The arms in Haplocrinus are only slightly developed, and are usually broken off in specimens, but their points of attachment are seen (figs. 1-3). They consist of one series of sections divided by joints, and they lie in grooves which run along the sides of the orals; in two of the grooves the first section of the arms is seen (fig. 3).

Haplocrinus retains its simplicity of structure throughout life, remaining "permanently in the condition of a very young larva."<sup>1</sup>

Certain peculiar specializations of structure are found in *Cupressocrinus abbreviatus* Goldf. (No. 267), which, though a primitive form, has developed, it would seem, along a different line from Haplocrinus.

This genus has a stout, round stem (Pl. 268, fig. 2), but according to Bather,<sup>2</sup> it "endeavours at times to break with old traditions, and appears with a triradiate or quinqueradiate stem" (see Pl. 268, figs. 3, 4). The body is composed of a centro-dorsal plate (fig. 1), made of a ring of united underbasal plates. Above this plate are five large basals and five radials (No. 267; also Pl. 268, figs. 1, 2). In this genus the regularity of the plates is slightly disturbed by the anal plates. The ventral disc is concealed in No. 267 by the five short, simple arms which are as broad at their point of attachment as the radial plates (Pl. 268, fig. 1). These arms bore pinnules which, according to Wachsmuth and Springer, were arranged like those of Blastoids, there being four or more to each arm joint.<sup>3</sup>

<sup>1</sup> Carpenter, Chall. Rep., Zool., XI, part 32, 1884, p. 157.

<sup>2</sup> Quart. Journ. Geol. Soc. London, Feb., 1889, p. 167.

<sup>3</sup> Proc. Acad. Nat. Sci. Phila., 1886, p. 180.

The most complex Cyathocrinoid must have passed through a stage in early life when it closely resembled Haplocrinus. Cyathocrinus (Pl. 269, figs. 1-10; No. 270), is attached by a round stem (No. 270, *C. multibrachiatus* L. & C.; Pl. 269, fig. 2) which never developed branches or cirri (see figs. 1, 4). Small underbasal plates, five in number, are found (not seen in No. 270, but figured in Pl. 269, fig. 1, young stage, and fig. 3, plates of body separated). The underbasals are characteristic of Palaeozoic Crinoids, as we have already said, but do not occur among recent adult forms.<sup>1</sup> Fig. 4 represents the adult in which the plates of the body are not so distinctly seen as in the young (fig. 1). Above the underbasals are five basals and five radials with a small anal plate. These are not seen in No. 270, but are shown in figs. 1, 3. The basals develop very early in the young and have nearly reached their full size when the radials are still small.<sup>2</sup> An anal tube (ventral sac, Wachsmuth and Springer) rose from the ventral surface, which was short and covered by plates (figs. 1, 4, 5).

The ambulacral grooves run out from the mouth, across the ventral surface, and are concealed by small, irregular covering plates (fig. 6; fig. 7, ventral surface with ambulacrals and covering plates removed). When the Crinoid was alive, these covering plates could open (fig. 8), and thus food could pass through the grooves (figs. 7, 9) to the mouth, after which the covering plates were again closed, as seen in fig. 10.

A few long, slender arms are sent off from the radials, which in some species fork many times forming armlets, but which are without pinnules (figs. 1, 4).

The interesting discovery was made by Wachsmuth and Springer<sup>3</sup> that what had been considered hitherto as

<sup>1</sup> Chall. Rep., Zool., XI, part 32, 1884, p. 152.

<sup>2</sup> Chall. Rep., *loc. cit.*, p. 169.

<sup>3</sup> Transition forms in Crinoids and description of five new species, Proc. Acad. Nat. Sci. Phila., 1878, p. 256.

four species<sup>1</sup> of this genus were in reality different stages of growth of one species, for which the older name of *Cyathocrinus iowensis* is retained. After an examination of a great number of specimens, it was found that the young was represented by the species *C. divaricatus* Hall which possessed good-sized basal plates. As the animal grew older, these plates became smaller, while at the same time the radials (subradials of Wachsmuth and Springer) increased in size. This is seen in *C. iowensis*, which these authorities have proved, is identical with *C. viminalis* Hall. The mature form, having the smallest basals and largest radials, is *C. malvaceus* Hall.

*Poteriocrinus zaeiformis* Schultze (No. 271; Pl. 272, figs. 1, 2, *P. circumtextus* M. & G.), has a long slender stem which is not seen in the figures. Its body is made up of underbasal, basal, and radial plates with the first arm sections or brachials fastened by suture to the radials.

The anal tube rises from the ventral disc, and is seen in both the specimens (No. 271) and figures (Pl. 272). The long, delicate arms are forked and their pinnules can be distinctly made out in the specimen (No. 271).

*Encrinurus liliiformis* Lam. (No. 273), is one of the best known Crinoids. The body is so large that it needs firmer support than the stem alone can furnish, and therefore root-like extensions or cirri are thrown out which help to fasten the animal securely in the mud. The plates of the body are regular, consisting normally of five underbasals, covered by the top stem joint, five basals, and five radials. The oral plates are present in the young but usually disappear in the adult, while the anal plates are found only in the young. The anus perforates the oral disc within the circle of arms instead of being outside the arms as in some Cystoids.

<sup>1</sup> *Cyathocrinus iowensis* O. & Sh., *C. divaricatus* Hall, *C. malvaceus* Hall, and *C. viminalis* Hall.

The mouth and five ambulacra are without covering plates. The arms of the very young *Encrinus* are at first made of single sections, that is, they are uniserial, but afterwards they become biserial<sup>1</sup> a proof that the uniserial condition is the more primitive.

In the Crinoids there were no tubes or hydrospires, but respiration took place through pores between the plates of the oral surface.

Marsupites (No. 274) is an instructive form. In youth it is attached by a stem, but later it breaks away, and the rounded posterior part of the body usually shows no scar. Underbasals, basals, and radials are all present; these are thin and flexible.<sup>2</sup> The ventral disc is not preserved in any of the specimens. The arms are uniserial, but are usually broken off.

The second series of Crinoids is more specialized, speaking generally, than the first.

Platycrinus (No. 275, *P. hemisphericus*; Pl. 276, *P. trigintidactylus* Aus.) has a body made of basals and radials, the former of which are unequal. From the ventral side rises a large anal tube (see Pl. 276). The arms are free, they fork a few times, and are well supplied with pinnules. The ambulacra are concealed by covering plates.

Actinocrinus (No. 277) has a small body without underbasals, and the arms are attached near its middle. The basals are reduced to three in this genus. The specimen (No. 277 a) has eight arms, and the pinnules of one are fairly well preserved. The food was caught by the pinnules and carried down to the base of the arms where it passed through the covered tunnels of the ambulacra to the mouth. The convergence of these ambulacral grooves a little to one side of the center is seen in the internal casts of *Actinocrinus* (No. 277 b-d). Here

<sup>1</sup> Wachsmuth and Springer, Proc. Acad. Nat. Sci. Phila., 1886, p. 230.

<sup>2</sup> Bather, Proc. Zool. Soc. London, 1895, p. 996.

the grooves have become filled with solid matter, but the position of the parts is well shown. The branching of the arms on leaving the body is seen in another cast, No. 277 e, where the aboral side is uppermost.

From the oral disc extended a long anal tube. This is seen in No. 277 a, while its position is indicated in the casts. Respiration was probably effected in *Actinocrinus* by tentacles on the edges of the ambulacra.

*Marsupiocrinus* (No. 278, *M. caelatus* Phil.) has a lower oral vault than *Actinocrinus*, and it is composed of a larger number of plates than usually is found. The arms are provided with pinnules (No. 278) but are unbranched. Similar in general structure to *Marsupiocrinus* is *Eucalyptocrinus caelatus* Hall (No. 279). This Crinoid when full grown had a large, plump, complex body, which was concave at the bottom, the basals and in some cases the radials extending upward and forming a cone. The arms are comparatively small, set in deep recesses (No. 279), and the ambulacra have the same structure as in *Actinocrinus*. Here the anal tube was very long and large.

*Apiocrinus* (No. 280) differs from the preceding in that the stem forms a portion of the body. These two parts can always be distinguished from each other, as the portion corresponding to the body of other Crinoids has vertical and oblique lines, while the stem portion has only circular lines, dividing it into horizontal discs. The ambulacra are uncovered, and there is no vault or anal tube.

*Millericrinus mespiliformis* d'Orb. (No. 281), is similar to *Apiocrinus* in some respects. As a general thing both have the stem enlarged, but that of *Millericrinus* widens more gradually, and the upper joint is not much larger than those below it. Recently, vestiges of underbasals have been found in two species of this genus, and in both cases these plates had separated from the basal and become attached to the top stem joint (No. 281).

Most of the forms of Crinoids already described have

had a body composed of five basals and five radials. This, however, is not the case with *Trigonocrinus*. Its peculiar structure tends to prove that it is a form specialized by reduction. Pl. 282, figs. 1-5, illustrate the probable evolution of this genus. Starting as a normal Crinoid with five basals and five radials (fig. 1) it loses in time one basal and one radial and is like fig. 2. Three basals then become larger at the expense of one, while two radials increase in size (fig. 3). *Trigonocrinus* has reached the stage represented by fig. 4, in which the three basals are fused into one ring with only a vestige of the fourth plate, while two of the radials are usually fused. If this process of specialization by reduction is carried still farther, the vestige of a fourth basal would disappear and the two radial plates would become united, leaving no suture, so that one could see only three basals and three radials (fig. 5).

An illustration of a Crinoid specialized by reduction is found in *Cheirocrinus* (No. 283, model of *C. clarus* Hall). For some reason the body with its drooping arms hung downward from the top of the stem (No. 283). This peculiar and unfavorable position has doubtless caused the irregularity in the body plates, and a reduction in the number of basals from five to three. The radials vary in form and bear only three arms.

The living Crinoids are represented in this Collection by *Metacrinus*, *Pentacrinus*, *Antedon*, and *Thaumatocrinus*.

The magnificent specimen of the living Crinoid, *Metacrinus interruptus* Carp. (No. 284), shows some of the parts on a large scale. The long stem is nearly round at its base, though it becomes pentagonal higher up. Many jointed cirri are given off in whorls along the whole length of the stem and the latter are closer together near the body. The body itself is surprisingly small. It consists of little basal and radial plates, while the lower plates of the five arms help to make up a portion of its upper part.



The large branching arms with their many pinnules are extremely graceful organs. The disc is small and the ambulacra extend from the mouth to the ends of the arms.

The body is also small in *Pentacrinus* (No. 285), consisting chiefly of five basals and five radials. There are vestiges of underbasals, but these are sometimes wholly resorbed in the adult. *Pentacrinus* is attached by a long pentagonal stem (No. 286), the joints of which bear cirri. The ventral surface is flexible and has many irregular plates. The mouth is exposed and from it extend the five uncovered ambulacra.

The uniserial arms are greatly developed, having a large number of branches which are well supplied with pinnules.

*Antedon* (= *Comatula*) *rosacea* Linck (Pl. 287; No. 288) is a living Crinoid of great interest, inasmuch as its development recapitulates in a marked degree the history of the group to which it belongs.

After escaping from the egg, the embryo is free and moves by means of bands of cilia (Pl. 287, fig. 1). Early on the eighth day (Bury) after development began, the larva became attached. On the tenth day the larva had developed a stem (fig. 2). In this stage the underbasals are found (fig. 2. *ub*) and above these the basals (fig. 2, *b*). Although the sutures indicate only three underbasal plates, one small and two large, nevertheless it is probable that each large plate is formed by the coalescence of two plates, so that originally there were five underbasals.<sup>1</sup>

The resemblance of *Antedon* to a Cystoid is now striking, and the existence of underbasals in the young is evidence of descent from the Palaeozoic Crinoids in which we have already seen underbasals well developed. As *Antedon* grows older, the underbasals and the top stem joint fuse into a single plate, the centro-dorsal, so that

<sup>1</sup> Phil. Trans. Roy. Soc. London, CLXXIX, 1888, p. 288.

Antedon passes through the condition already shown by *Millericrinus* (No. 281).

The armless Cystoid stage passes into the Penta-crinoid stage, in which uniserial arms grow out (fig. 3). These continue to increase in number. The centro-dorsal plate develops cirri, and by this time all trace of the underbasals is lost.<sup>1</sup>

When ten cirri are developed, a separation takes place between the centro-dorsal plate and the stem; the latter is left attached, while the animal breaks away and is henceforth free.

A tiny opening is left in the middle of the aboral side, but later this is filled, though traces of the scar may be seen internally.

After the animal liberates itself from its stem, it swims freely in the water. The cirri are used occasionally for crawling about on marine plants, or at other times for anchoring itself to rocks. According to Carpenter,<sup>2</sup> the adult *Antedon* has the habit of fixing itself to a rock and remaining for long periods. In this stage the body is extremely small and the basals have become metamorphosed into the so called rosette, which is wholly concealed in the cavity of the ring formed by the radials.

The mouth is in the middle of the oral disc and at one side of this opening is the anal tube. The five arms divide almost immediately to form ten organs which are disproportionately large for the size of the body and are well provided with pinnules.

The floor of each ambulacral groove is ciliated, and the five ciliated grooves extend from the mouth over the oral disc to the ends of the arms.

*Actinometra* (No. 289) is similar to *Antedon* but differs from it by having the mouth at one side of the oral disc and the anal tube near the center.

<sup>1</sup> Carpenter, stated by Wachsmuth and Springer, Proc. Acad. Nat. Sci. Phila., 1888, p. 352.

<sup>2</sup> Phil. Trans. Roy. Soc. London, CLVI, 1866, p. 698.

## ASTEROIDEA.

It is probable that *Agelacrinus*, belonging to the *Agelacrinidae*, was a descendant of an ancestral form from which the *Asteroidea* or starfishes of to-day arose. Using a simple but clear illustration we may say that if the hand should represent this trunk form, then the first finger would stand for the *Agelacrinidae*. Another finger would represent the *Asteroidea* which began with the same trunk but developed along another and quite independent line.

Since *Agelacrinus* comes nearer the probable ancestral form than any other fossil or any living species, we begin the study of the *Asteroidea* with this genus. *Agelacrinus* (No. 290, *A. rhenanus*) was without a stem, but it was attached by its dorsal or aboral side. The circular flattened body was covered by a great number of small irregular plates which were imbricated or arranged like shingles on a roof. These plates were perforated, and usually the pores were in pairs. The mouth was in the middle of the upper side and was covered by plates. Radiating from the mouth were five ambulacra (No. 290) also protected by covering plates. At the tip of each ambulacrum there was a hole for the admission of water. Each ambulacrum consisted of two rows of plates and between these plates there were holes.

The anus was situated in one of the areas outside of the oral disc, and between two of the ambulacra; it was also covered by plates which were set into the body plates.

The irregularity of the body plates, the absence of arms, and the fact that the mouth, ambulacra, and anus were concealed by plates, all remind one of both the *Cystoids* and the *Blastoids*. Zittel places this genus with the *Cystoidea*, though it seems to have more points of resemblance with the *Asteroidea*.

Since specialized Asteroidea occur with the Cystoidea in the Cambrian formations, it is impossible for the former to have descended from the latter. We must, therefore, look for the ancestors of both groups in the pre-Cambrian rocks, and it seems most likely that such a form will combine the characters of both Cystoidea and Asteroidea. Most of the Palaeozoic starfishes, like those of to-day, were free-moving and crawled with the oral or actinal side downward. If we suppose an ancient starfish to be attached by a stem extending downward from the middle of the aboral or abactinal surface, we have a striking resemblance to a stalked Crinoid. In such a case the mouth is in the middle of the upper side and the ambulacra run out from it into the arms. When, however, the starfish became free-moving, it turned upon the ventral side and the tentacles which had been useful in catching food became modified in time into locomotor organs.

It seems probable that the ancestral starfishes had a pentagonal body with spines slightly developed, and two rows of plates in each ambulacrum, the plates of one row alternating with those of the other. One of the descendants of such a form may be the living *Ctenodiscus* (No. 291, *C. crispatus* D. & Kor.). When young (No. 291 a), it has a dome-like body which becomes flatter with age (No. 291 b, c). The adult has a large disc and short arms, giving it a pentagonal outline. The plates of the aboral side (No. 291 b) are small and leathery, the spines being slightly developed. Near the center is the anal tubercle. Each ambulacrum on the ventral side (No. 291 c) consists of two rows of alternating plates which are broad and not crowded closely together. There are two rows of holes for the tentacles which are without sucking discs. Every ambulacrum is flanked on each side by a row of good-sized interambulacral plates, and outside of these are well developed marginal plates (No. 291 c).

Gradually the pentagonal form tended to give way in Palaeozoic time to the stellate form illustrated by the ancient starfish *Palaeaster* (No. 292, model). The plates of the aboral side of the central disc are small and indefinite, but those of the arms are more or less regular (No. 292, specimen on the left). The anus is found on the aboral side, though the model does not show its position. The mouth is uncovered, but is surrounded by five plates. The ambulacra are also uncovered and consist of two rows of alternating plates (No. 292, specimen on the right); on the outer edge of each plate there is an opening for a tentacle (No. 292). Thus there are two straight rows of holes extending through each ambulacral groove.

On either side of the ambulacral plates there is a row of prominent interambulacral (adambulacral, Zittel) plates (No. 292 b), and outside of these are large marginal plates.

Respiration was effected in these early forms as in modern species by means of a water system consisting of a sieve or madreporic body, which in ancient forms was on the ventral side (Zittel), and of radiating tubes.

The primitive forms are also represented by *Astropecten variabilis* Lütke. (No. 293), in which the marginal plates are conspicuous. Here the arms are more tapering than in *Ctenodiscus*, but the tentacles are still pointed and remain in two rows.

In *Hippasteria phrygiana* Ag. (No. 294), the ambulacral plates are opposite and not alternating; the tentacles are in two rows, but instead of being pointed they are provided with sucking discs and are, therefore, no longer true tentacles but rather locomotive organs or "tube feet." These organs are seen in the preparation (No. 295) which is a dissection to show the water-vascular system after injection with blue coloring fluid. This system will be described more at length under the common starfish, *Asterias* (see pp. 165-169). The ovaries

and their openings are also seen in this preparation. No. 296 shows the stomach and its coecal appendages.

The marginal plates in these forms are large, but those on the upper side have become small in *Pentaceros modestus* Gray (No. 297). The interambulacral plates are of good size and the tube feet have large suckers. The aboral disc and the sides of the arms are provided with stout conical spines.

This tendency for the large marginal plates of the primitive forms to become reduced in size is seen in *Paulia horrida* Gray (No. 298). The spines in this genus are large and strong, and are found on the most exposed points.

In the starfishes so far described the development of the ambulacral system and of the test or skeleton goes on together, but in the more specialized forms which follow, the development of the ambulacral system is accelerated.<sup>1</sup>

In *Linckia unifascialis* Gray (No. 299) the disc is small and the arms long and six in number. Like the earlier forms it is spineless. The marginal plates are reduced in size. The ambulacra are narrow and somewhat crowded, while they carry two rows of tube feet provided with suckers. The tendency to multiply the number of arms is seen in *Solaster endeca* Forbes (No. 300). Here there are nine rays radiating from a disc of considerable size. There are few spines, and the surface is granular. The two rows of ambulacral feet are provided with sucking discs.

The deep-sea species, *Zoroaster fulgens* Wyv. Thom. (Pl. 301, figs. 1-3), is of especial interest. The young (fig. 1) has a much higher disc than the adult. The plates of the aboral side are distinctly seen, and for this reason the genus is an admirable one for comparison with Crinoids. The central plate is surrounded by five

<sup>1</sup> Sladen, Chall. Rep., Zool., XXX, part 51, 1889, p. xxxv.

small underbasals (fig. 1) and five basals (shaded in fig. 1). Outside of these are five radials. Regular plates extend outward to the tip of the arms, where are found the terminal or ocular plates. This definite arrangement of plates so finely illustrated by both the larval and adult *Zoroaster*, occurs in some of the larvae of the more specialized Asteroidea, but is soon lost in the process of development.

While these characters are all of a primitive nature, *Zoroaster* possesses other peculiarities which place it near the more specialized genus *Asterias*. The disc is small and the arms long and tapering (fig. 2, showing spines but not plates). The tube feet have sucking discs, and, unlike the genera already described, there are four rows of these locomotive organs (fig. 3).

One of the commonest starfishes on the New England coast is *Asterias forbesi* Verr. (Nos. 302-308). This animal passes through an indirect development with a marked and peculiar metamorphosis.

Like most starfishes when young, the larva or brachiolaria, as it is called, is bilateral with four arms on either side, so that the marked radial symmetry which appears later is a secondary and not a primitive character.

The aboral side is raised and more or less dome-shaped. The spines are in regular rows, according to A. Agassiz, and the plates remind one of those of Crinoids. Underbasal plates have been found in two species of *Asterias* (*A. rubens* and *A. glacialis*<sup>1</sup>). The basals and radials appear in the very young larva and are homologous with the same plates in the Crinoid; but as development goes on, it becomes impossible to trace them. By many authors the terminals or ocular plates of starfishes, Ophiurans, and sea urchins have been considered as homologous with the radials of Crinoids; but it has been shown<sup>2</sup> that the radials in starfishes are developed be-

<sup>1</sup> Sladen, Quart. Journ. Micr. Sci., XXIV, 1884, p. 34.

<sup>2</sup> Sladen, *ibid.*, p. 29.

tween the basals and terminals, and that the latter are pushed outward with the growing arms. These are additional plates and are not homologous with any plates of the Crinoids. The anus in the young is near the edge of the oral or actinal side.

The arms at this time are broad, short, and unequal in length. The ambulacra running out from the mouth have two rows of organs which are like tentacles, being pointed at the end. The madreporic body is near the edge of the actinal side. As the starfish grows older, radial symmetry predominates, and the five equal arms radiate from the small central disc. The body becomes flattened, and the spines and plates more or less irregular. The monotony of the spiny upper surface is broken by the little radiately-grooved madreporic body (No. 302) which has moved from the actinal area and is at the junction of two arms on the abactinal side. The anus has also moved and is near the center of the abactinal side. The ambulacra carry four rows of organs which have developed suckers at the ends and become thereby efficient locomotive organs.

In the center of the ventral side is the mouth surrounded by a membrane and guarded by five sets of spines.

Although the normal number of arms is five, it sometimes happens that only four are developed. On the other hand in a collection of about eight hundred starfishes from Salem Harbor, there were, according to Mr. N. L. Wilson, two six-rayed specimens and one seven-rayed specimen.

The power of the animal to reproduce lost arms is shown in No. 303 where four arms have been lost, but one has grown out to half the size of the fully grown arms. No. 304 is probably a starfish that has been wounded in some way. In trying to repair the injury it produced the semblance of an arm. A specimen of this kind is met with occasionally on our coast.



The skeleton of the adult is composed of an irregular network of beams and spines which are covered by a thin layer often called the epidermis. This layer can be scraped off with a knife, proving that the skeleton is internal. The majority of the spines are immovably fastened to the beams of the skeleton, but on the lower side along each ambulacrum there are spines of quite a different character from those above. These are more slender and tapering, and are connected with the skeleton either by cushions or by ball-and-socket joints, allowing of considerable freedom of motion. Among the spines of the starfish are little characteristic forked organs called pedicellariae, which are spines modified for a special purpose not yet known with certainty, though it is evident that they are used for taking hold of objects. They are found at the bases of the spines, on the soft membrane between the spines, and also on the movable spines of the lower side. In those Asteroidea that have four rows of tube feet there are two kinds of pedicellariae; in one the blades are opposite and in the other they cross like scissors.

The plates of the skeleton are finely seen in the preparation. No: 305 (specimen on the left) shows the irregular network of plates in the upper side or back, and the specimen on the right the two rows of ambulacral and interambulacral plates in the lower side. The ambulacral plates are movably articulated at the inner end. Between the ambulacral plates can be seen the four rows of holes through which pass the tube feet with sucking discs at their ends. On each side of the groove formed by the ambulacral plates is the row of rounded, imperforate interambulacral plates which bear the movable spines already described. Nos. 306-308 are preparations of the starfish, showing the internal structure. The mouth leads into a stomach which can be thrown over a mussel or other animal. By the power of suction the food is taken in and the hard parts thrown out of the mouth. A coecal prolongation is con-

tinued from the stomach into each arm (No. 306). The stomach is extended above into a short, indefinite intestine which opens near the center of the aboral area. It does not seem to be functionally useful and may be the remaining vestige of the well defined anus of the Crinoids (Packard). Opening into the intestine is the liver which consists of two long branches that extend into each arm (see No. 306). According to Griffith and Johnstone<sup>1</sup> the "saccular diverticula" of the starfish are not hepatic but pancreatic in function. On chemical analysis they find the secretion is similar to that of the vertebrate pancreas.

The reproductive organs — ovaries or testes — are on either side of each arm (No. 308) and open by slits at the base of the arms near their junction with the central disc.

No. 306 and also No. 307 are specimens injected with blue colored fluid to show the water-vascular system, which arises as an outgrowth from the digestive system as is the case with the Ctenophora. It consists of the madreporic body, a short canal called the stone canal which extends to a circular ring around the mouth (circumoral ring) from which five radial vessels are given off, one into each arm; these in turn connect with the water sacs or ampullae of the tube feet which are seen in No. 307 extending in rows to the tip of each arm. The true vascular blood system is difficult to observe. The heart or pulsating vessel runs parallel with the stone canal. The body cavity is filled with a watery fluid containing corpuscles evidently representing the blood of more specialized animals. There are also delicate, tubular organs, described as dermal branchiae, extending from the dorsal surface, which probably have a respiratory function; sometimes these may be seen swollen with water. On the dorsal side there are many minute pores through which water may enter or leave the body cavity.

<sup>1</sup> Proc. Roy. Soc. Edinburgh, XV, 1888; quoted in Amer. Nat., XXIII, 1889, p. 1101.

The preparation (No. 308) shows the nervous system in part. This consists of a ring encircling the esophagus, and radial nerves which are the white cords seen in No. 308 running to the end of the arms.

#### OPHIUROIDEA.

The evidence seems to point to the view that the Ophiurans have descended from some one of the more specialized Crinoids.<sup>1</sup> Notwithstanding that many genera retain throughout life the underbasals, basals, and radials of the abactinal area possessed by some Crinoids and by larval Asteroidea, nevertheless peculiar modifications have arisen which place the adult Ophiurans farther from the primitive, pentagonal, larval form than the adult Asteroids.

Generally speaking the radials are developed before the basals and underbasals, and are of large size. We have seen in the specialized Crinoids the tendency toward the increasing development of the radials and the reduction of the basals.

It has been shown by Fewkes<sup>2</sup> and others that the young Ophiuran, like *Asterias*, is at first bilaterally symmetrical and that later it takes on the pentagonal form which gradually, with the development of the arms, changes to the modified stellate condition of the adult. The bilateral larva possesses an intestine and anus, but later both disappear, so that the adult is more reduced in this particular than the starfish.

*Ophiopholis aculeata* Gray (No. 309), has a circular, sharply defined disc which bears minute spines. The long, rounded, unbranched arms run out directly from the disc and are of about the same size throughout. They are protected by hard plates,— dorsal, lateral, and ventral shields,

<sup>1</sup> Sladen, Quart. Journ. Micr. Sci., XXIV, 1884.

<sup>2</sup> Bull. Mus. Comp. Zool., XIII, no. 4, 1887, p. 107.

— the homologies of which are a subject of much discussion.

It is generally considered that the ambulacral plates are inside the arms in the form of an axis of jointed sections or arm-bones. If this is the case, then the ventral plates are additional ones and are not homologous with any other plates of the Asteroids.<sup>1</sup> They may be developed for the purpose of protecting the delicate water-tube, blood-tube, and nerves which run through the arms and which are exposed in Asterias. The lateral plates bear lateral spines which are probably helpful in locomotion. Each arm-bone is pierced by a water-tube or tube foot which is without ampulla or sucking disc, and therefore of no use as a locomotive organ. These tube feet come out between the ventral and lateral shields. Above, the base of each arm is protected on either side by the so called radial shields, while below near the mouth are the oral shields.

The internal organs are all concentrated within the disc. The genital organs open by slits on the lower side at the base of the arms. The madreporic body is also on the lower side in one of the mouth plates. Ophiopholis develops without a metamorphosis. The disc of Ophiura (No. 310, *O. panamteri* Lützk.) is granulated, and the arms are well protected by the numerous short flattened spines.

Ophioplocus (No. 311) resembles Ophiura in having a granulated disc. The radial shields are small. *Ophiocoma aethiops* Lützk. (No. 312) has wide upper arm-plates and large spines.

The young Astrophyton resembles the typical Ophiuran in having a flat disc covered by plates. In the process of growth, these become covered by a granulation and later both granulation and plates, except those at the margin, disappear.<sup>2</sup>

<sup>1</sup> Bull. Mus. Comp. Zool., *loc. cit.*, p. 144.

<sup>2</sup> Chall. Rep., Zool., V, part 14, 1882, p. 253.

The radial shields increase in size. The arms divide many times and the great number of flexible branches intertwine with one another, giving a basket-like appearance, and the name of Basket-fish, to the animal (No. 313). These arms are without the dorsal or ventral plates peculiar to most Ophiurans, though there are irregular plates which may be vestiges under a thick skin. The arms are without spines. In some species of *Astrophyton* there are no oral shields, while there may be one madreporic body or five.

#### ECHINOIDEA.

The primitive rocks of the Lower Silurian formation have yielded a primitive sea urchin whose marked simplicity of structure offers a sufficient reason for considering it as an ancestral form. This urchin, *Bothriocidaris pahleni* Schmidt, by name (Pl. 314, fig. 1, enlarged twice), has a globular corona (popularly called shell) with the mouth in the middle of the lower or abactinal side and the anus opposite. It has a small number of simple spines, a few of which are seen attached in the figure. The spines are only 4 mm. long and are therefore not of disproportionate length. The ambulacra are the first areas to be developed, around the oral disc or peristome (fig. 2); they are, therefore, of primary importance, while the interambulacra arise secondarily in the spaces between the ambulacra. Beginning at the center of the actinal area it is seen that there are two complete circles of ambulacral plates extending around the mouth, then comes a circle of ten ambulacral plates and five interambulacral plates not wholly seen in fig. 2, 1'. The ambulacral plates are pierced by two holes which are separated by a partition. It is seen that each ambulacrum originates in two plates, while each interambulacrum arises from one plate. This stage is permanent throughout the

life of *Bothriocidaris*. It is a primitive and an extremely important stage, illuminating the otherwise obscurely complex structure of the specialized Echinoidea. For this reason it is called by Dr. Robert T. Jackson the *protechinus* stage.<sup>1</sup>

As we have already said, the anus is opposite the mouth. It is surrounded by plates, outside of which are ten terminal plates of the ambulacral and interambulacral areas. Each ambulacrum and interambulacrum ends in one plate but none of these plates have pores. Thus it is seen that there is little differentiation of the abactinal area from the corona proper.

Summing up the distinguishing characters of this ancient Echinoid we have the following:—A small number of plates in the globular corona; slight differentiation of the actinal and abactinal areas from the corona proper; a small number of simple spines.

If now we come to the present time and examine *Goniocidaris canaliculata* A. Ag., we find in the young (Pl. 315, fig. 1; fig. 2, side view of same) some instructive structural features.

Around the mouth is a circle of ambulacral plates, while the circle next to this one has ten ambulacral plates (fig. 1) and five interambulacral plates (fig. 1, 1') as in *Bothriocidaris*. Therefore it is true that each ambulacrum in *Goniocidaris* arises from two plates, and each interambulacrum from one as in the ancient genus.

The individual plates of the ambulacra are hexagonal and nearly on a level with the hexagonal interambulacral plates as in *Bothriocidaris*, but unlike this genus each plate has only one pore.

The similarity in structure between the young *Goniocidaris* and the adult *Bothriocidaris* is striking and of value

<sup>1</sup> We are indebted to Dr. Jackson for many of our figures and facts concerning fossil Echinoidea. See Bull. Geol. Soc. Amer., VII, 1896, pp. 135-170; also pp. 171-254.

from a phylogenetic point of view. As *Goniocidaris* grows older, two rows of interambulacral plates arise from the single plate (fig. 1, 1, 2; also fig. 2) so that there are two rows of ambulacral plates alternating with two rows of interambulacral plates. The ambulacral plates become differentiated and are lower than the pentagonal interambulacral plates, while each plate has two pores.

The adult *Goniocidaris* never goes beyond the stage represented by the two rowed ambulacra and interambulacra.

Correlated with this simplicity of external structure we have a primitive mode of development. In other words, *Goniocidaris* develops from the egg without passing through a metamorphosis.

We have already seen that while a few starfishes develop in a primitive way, most of them pass through a complex metamorphosis. The early stages of Echinoids that undergo such a transformation are similar to those of starfishes. The embryo or pluteus has eight arms and is bilaterally symmetrical. The metamorphosis of the Echinoid, however, is accomplished very rapidly. "In less than an hour," according to Bury,<sup>1</sup> "a perfect Pluteus is transformed into a small, rounded Echinoid in which radiate symmetry entirely replaces the bilateral symmetry of the larva."

The internal structure of the young *Goniocidaris* is primitive. For a time the intestine is a closed tube, there being no mouth nor anus. During this period the animal takes no food, and moves about by five provisional tube feet. It is later that the eating apparatus is developed which causes a modification of the oral area and a resorption of some of the plates of the corona; finally the intestine breaks through the anal disc.

The genus *Cidaris* (No. 316, *C. thouarsi* Val., with spines; No. 317, without spines) when young possesses the circle of ventral plates entire, and also the primitive

<sup>1</sup>Quart. Journ. Micr. Soc., XXXVIII, 1895, p. 77.

condition of the two rowed ambulacra and the one rowed interambulacra. Later some of the ventral plates are resorbed causing more or less irregularity in the shape of those that are left, while the two rowed interambulacra arise and remain essentially unchanged.

The ambulacra of the adult are narrow with a single nearly vertical row of paired pores. The interambulacra on the other hand are broad and carry the primary spines which are large and few in number.

The anus is somewhat raised above the anal disc. Surrounding the latter is the ring of genital and ocular plates, the genitals pointing outward and the triangular ocular plates inward.

The spines of this species are cylindrical. Some are young and short with distinct vertical ridges on the surface, while the older ones are long and are entirely covered with a growth of algae, etc. Very different from these are the modified spines which are found on the abactinal surface of the corona and which also crowd the actinal area. These are like short, stout, flattened clubs.

It has been seen that the Cidaridae of the present era retain in their youth many of the primitive characters of the ancestral *Bothriocidaris*. The changes that convert the young into the adult are an increase in the number of coronal plates, the differentiation of the actinal and abactinal areas from the rest of the corona and the modification of the spines.

While the Cidaridae represent one division of ancient Echinoids, another and more specialized division includes the Melonitidae. The generalized members of this family are *Rhoechinus* and *Palaeechinus*, and the specialized are *Oligoporus* and *Melonites*.

Although there is a slight overlapping of the ambulacral plates in *Rhoechinus*, as seen in Pl. 318, fig. 1, owing to the fact that these plates are not united along their edges, still they may be said to extend across one half of the ambulacral area as in the ancestral form so that only two rows of ambulacral plates exist.



The number of rows of plates in the interambulacral areas of the simplest species of this genus is four, and of the most specialized eight.

The adult *Palaeochinus gigas* McCoy, has the primitive ambulacral plates, *a*, *b*, on the margin of the ambulacral area (Pl. 318, fig. 2, shows a portion of one ambulacrum; *b*, primitive plate; *a* not drawn), while two other plates have arisen (*a'*, *b'*). The interambulacrum has from five to six or seven rows of plates; six are clearly shown by the red dotted lines in fig. 3. This drawing begins at the point of origination of the fifth row of plates, those below this point not being preserved in the specimen. The figure shows that the columns 5 and 6 originate in a single plate as we have already seen is the case with the interambulacral rows of *Bothriocidaris*. The initial plate is always near a seven-sided or heptagon plate (fig. 3, *H*). In *Palaeochinus* the anal disc is surrounded by the ring of alternating genital and ocular plates; the former are pierced by three holes while the latter have two.

When we pass to the genus *Oligoporus* we find in the young as represented at the ventral border two rows of ambulacral plates (Pl. 319, fig. 1, *a*, *b*), while farther up the corona the adult condition of four plates (fig. 1, *a*, *b*, *a'*, *b'*; fig. 2) is seen, and still farther up new plates arise (fig. 2).

The number of rows of interambulacral plates has increased to nine (fig. 3) in the most specialized species of this genus (*Oligoporus danae* M. & W.).

The forms we have already described lead the way to a better understanding of the complex structure of *Melonites* (No. 320, *a-d*, *M. multiporus* Norw. & Owen). These fossils are occasionally preserved with some of the spines attached. The latter are small (Pl. 321, fig. 1, magnified 6 + diameters) and when not fastened are sometimes found in the hollows of the corona.

The ventral border of the shell (see No. 320, *a*, *b*; Pl. 321, fig. 2) shows the ambulacra and interambulacra.

The ambulacra arise from four plates (Pl. 321, fig. 2, *a*, *b*, *a'*, *b'*; fig. 3, ambulacrum enlarged, *a*, *b*, *a'*, *b'*). This would indicate that in the development of *Melonites* the adult condition of *Bothriocidaris*, in which the ambulacra consist of two rows of plates, has been skipped by the law of acceleration in development, and that the four-plate stage is homologous with the adult of *Oligoporus*, as pointed out by Jackson, or it may be, as suggested by this investigator, that the ambulacrum of *Melonites* starts with two plates which might be seen in the young could such specimens be obtained. If this is the case these plates have been resorbed during the growth of the animal.

New rows of plates are added between those already formed (Pl. 321, fig. 3, *c*, *d*, and *e*, *f*), so that each ambulacrum becomes more complex than any so far described. A cross section of an ambulacrum (fig. 4, magnified 2 diameters) shows the relative thickness of the four ambulacral plates, and also proves the fact that the holes pass diagonally and not straight through the shell. The dotted portions of the pores are reconstructions, these parts not being clearly shown in the section.

The interambulacrum (No. 320; also Pl. 321, figs. 2, 5) apparently arises from two plates as seen in the specimens (No. 320, the dotted lines beginning in two plates; also seen in Pl. 321, figs. 2, 5). According to Jackson it is most probable that this area originates in one plate, which later was resorbed. With the growth of the animal the interambulacrum becomes complicated by the addition of a number of rows (fig. 5). This diagram represents the ideal arrangement of plates in one interambulacrum as determined by prolonged and critical observation of a large number of specimens. The theoretical plate *r'* is included in the figure to indicate all the possible plates the interambulacrum had at any period of growth. This plate is resorbed in the adult, as already stated. Eight rows are found most commonly. As these rows approach the anal area the mechanical necessity of the case com-

pels them to be drawn out and to diminish in number while at the same time the plates themselves become more or less rhombic in form.

The lines  $x$ ,  $y$ ,  $z$  in Pl. 321, fig. 5, bisect eight rows, and indicate by their narrowing angle the stringing-out arrangement of the plates in this area (Jackson). This reduction does not seem to be comparable to the dying out of parts or organs so characteristic of gerontic forms. As Dr. Jackson aptly says, it may be compared to a flock of sheep coming through a narrow pass. The small number in the pass does not mean that the flock is lessening, but that no more can get through at once. If this were a gerontic condition we should expect to find the middle or latest formed rows disappearing first and not the lateral or primary rows. This is the case in the few gerontic specimens observed (see below).

If now a graphic summary of our knowledge of the development of the ambulacra of the Palaeozoic Echini be given (Pl. 322, A-G) it will show at a glance that the primitive and fundamental simplicity of *Bothriocidaris* (A) has given rise through progressive steps represented by *Rhoechinus* (B), *Palaeechinus* (C), and *Oligoporus* (D at ventral border, E at ambitus) to the complexity of *Melonites* (F at ventral border, G at ambitus). Dotted lines are drawn through the primary plates  $a$ ,  $b$  in each, and also through the secondary plates  $a'$ ,  $b'$ . New plates begin to appear between these in *Oligoporus* (E) and probably constitute the rows  $c$ ,  $d$  in *Melonites* near the ventral border (Pl. 321, fig. 3), while at the ambitus ten rows are found. The remarkably large and fine specimen of *Melonites giganteus* Jackson (Pl. 323, photograph) shows still greater specialization than *Melonites multiporus*. There are twelve rows of ambulacral and eleven of interambulacral plates. The interambulacral area (Pl. 323, fig. 2, at the right) is especially interesting, since it shows a tendency toward specialization by reduction. The last formed row of plates (11) has died out

completely before reaching the anal area. Only a few specimens with this specialized character have been observed. In this species the new rows are introduced early in life, showing that the law of acceleration in development is in operation. The Melonite form is also much more pronounced than in *Melonites multiporus*.

The anal disc of *Melonites* is surrounded by the ring of alternating genital and ocular plates. The five genital plates can seldom be seen in specimens although well preserved in No. 320. These plates are pierced by holes, while the ocular plates, according to Jackson, are without perforations.<sup>1</sup>

It is seldom that the history of a group can be made out by the study of a portion of the adult of a single genus, but we have already seen that such is the case with *Melonites*. The primitive condition of *Bothriocidaris*, the successive progressive stages of *Rhoechinus*, *Palaeechinus*, and *Oligoporus* are all represented in the ventral border and in one ambulacral and one interambulacral area of *Melonites*. Nor is this all; the greater specialization by the process of reduction is illustrated by a few specimens of this genus.

We have seen that *Goniocidaris* and *Cidaris* are among the most primitive of living Echinoids. Alexander

<sup>1</sup> Meek and Worthen (Geological Survey of Illinois, II, 1866, p. 228) state that the ocular plates of *Melonites multiporus* M. & W., are without any traces of pores, and the figures are drawn without them. In a footnote, however, they add, since the above was written, we have examined "another fine specimen showing the disc. In this there are four ovarian pores in three plates, and three in each of the other two, while in two of the ocular pieces there is apparently a single pore near one side."

Roemer figures the oculars with two pores (see Arch. f. Naturg., I, 1855, pl. xii, fig. 4). In the text he says, p. 322, "The number and position of the pores in these [ocular plates] cannot be recognized with complete certainty, yet, there are apparently two of them in each plate and at the same height as those in the larger plates" [genital plates].

Agassiz<sup>1</sup> has shown that the young of all other Echini have the general characteristics of these primitive forms. They all agree in having a small number of plates in the corona, slight separation of the actinal and abactinal areas from the corona proper, nearly vertical rows of paired pores, and a few spines of disproportionate length. Having this common origin we shall see what variations arise in the adults of a number of species.

In *Arbacia pustulosa* Gray (No. 324), the actinal area is large and the ambulacra are broad at the starting point, growing narrower as they reach the edge or ambitus. The interambulacra, on the other hand, are narrow at the ventral border and broader towards the ambitus. The pores preserve their primitive character, being in simple vertical rows. The anal disc in this species consists of five plates; around these is the ring of five genital plates which are developed after the anal disc. The oculars are crowded outside of this ring and fit into the places left by the outer angles of the genitals. This genus is interesting for the fact that its spines never become articulated but remain in the more primitive condition of the unjointed spines of the starfish.

In *Diadema setosum* Gray (Nos. 325, 326), the nearly vertical row of pores in the narrow ambulacra becomes changed during the growth of the animal into nearly vertical arcs of three or four pairs of pores. The corona is thin with broad interambulacra. The actinal area is membranous with well developed teeth. The anal disc (No. 326) is also membranous and flexible, with the anus raised on a tube near the center. According to A. Agassiz<sup>2</sup> this anal tube is as prominent in the young as the anal tube of some species of Comatulæ. Three of

<sup>1</sup> Palaeontological and Embryological Development, Proc. Amer. Assoc. Adv. Sci., XXIX, 1880, p. 389; also consult review of the same by E. D. Cope, Amer. Nat., Oct., 1880, p. 725.

<sup>2</sup> Rev. of Echin., Mem. Mus. Comp. Zool., III, 1872, p. 276.

the ocular plates join the membranous disc, and separate the genital plates, while the other two which are each side of the madreporic plate are crowded outside of the ring so that they do not touch the anal membrane.

The slender spines of the adult (No. 325) are usually more or less solid though in youth they are hollow. They vary in size, the smaller ones being light colored and the large ones dark with longitudinal ridges. These ridges are provided with short pointed teeth, so that one cannot pass the finger downward from the tip end of the spine to its base without being pricked by the sharp points.

*Echinothrix turcarum* Ret. (No. 327), has the pores in arcs of three pairs similar to those of *Diadema*, but unlike this genus the arcs are independent of each other. The ambulacra broaden out slightly on the abactinal surface, suggesting the petaloid condition of the more specialized Clypeastroids.

The ambulacral areas are crowded with many small spines, while the longer and more delicate ones are on the interambulacra.

*Colobocentrotus atratus* Br. (No. 328), is peculiarly modified in the shape of its corona and spines. The ventral side of the former is very flat and the dorsal part rises like a low dome. The closely set, dark colored spines, like tiles in a pavement, cover this dome, completely concealing everything beneath. If these spines are removed the low rounded tubercles are seen (No. 328). The ventral surface is covered with short cylindrical spines crowded closely together. From the ambitus the long spines resembling clubs extend downward causing the sea urchin to look as though it were mounted on many stilts. It is these spines that mask the real shape of the corona, making the dome appear much higher than it really is.

In spite of the close pavement of spines there are many tube feet in the ambulacral areas; these are arranged in arcs of six or seven pairs.

The young *Heterocentrotus mammillatus* Br. (No. 329),

shows the dark pavement spines finely, especially on the dorsal side. Among these, on the ventral side, are spines similar to those on which *Colobocentrotus* stands. The longest club-shaped spines extend outward from the sides of the corona, while young ones are seen just growing from the upper surface. In the adult (Nos. 330, 331) the pavement spines have longer cylindrical stems by which they are attached, while the great club-shaped spines have become formidable organs of defence. The size of these organs is correlated with the increased thickness of the corona. The oral area is large, having encroached upon the corona. The ambulacra are broader on the lower side than the interambulacra, while above the ambitus they are narrow, and the pores are in narrow arcs of numerous pairs.

Our common sea urchin, *Strongylocentrotus dröbachiensis* A. Ag. (Pl. 332; No. 333, two spiny specimens and a preparation of the shell), has the corona made of two rowed ambulacra and interambulacra. Each ambulacrum begins in the young with two plates, as shown in Pl. 332, fig. 1, and each interambulacrum in one plate (fig. 1, 1'). As the urchin grows older a portion of the ventral border is resorbed, as shown in fig. 2, and the oral area is membranous and spineless. No new rows of plates are added in either the ambulacra or interambulacra, so that there are only twenty rows of plates in all. These are shown in the admirable preparation (No. 333), where each individual plate has been separated and mounted. The ambulacral plates show the arcs of pores which vary but usually consist of four or five pairs. These have arisen from the unbroken vertical rows of pores of the young.

The anal disc is seen to the right, made of tiny plates which are placed together with considerable irregularity; a little to one side of the center is the anus. The last plate terminating each interambulacrum is a genital, the largest of which is the madreporic body; an ocular plate is at the tip end of each ambulacral area. The five geni-

tals and the two oculars form the ring around the anal disc, the other three oculars being crowded outside the ring.

The globular form and melon-like aspect of *Echinus melo* Lam. (No. 334), are striking. These melon-like sections mark off distinctly the five ambulacral and five interambulacral areas.

The plates of the anal area are numerous, small, and irregular, while the five ocular plates are all crowded outside of the ring.

The spines of *Echinus acutus* Lam. (No. 335), are far removed from those of primitive and embryonic forms, being small, short, and similar on both ambulacra and interambulacra. In this specimen the tube feet are seen extending from the shell.

#### IRREGULAR SEA URCHINS.—CLYPEASTROIDS.

*Pygaster patelliformis* Ag. (No. 336), is one of the primitive Clypeastroids. The corona is dome-shaped above and flattened below, resembling the regular sea urchins. The mouth is placed near the center of the oral area, but the anus is not directly opposite as in the sea urchins so far examined. It extends from near the apical disc to the margin and is large in size. The ambulacral areas are narrow with simple vertical rows of paired pores, while the interambulacra are broad.

Young Clypeastroids in general possess a small number of plates in the globular corona, a few large spines and tubercles, simple vertical rows of pores with no petal-like pattern on the dorsal side. Internally there are no partitions. With age the corona becomes more flattened, the number of plates increases, the spines grow smaller, and the pores form into petals, proving that the petaloid condition is a specialized one; and that the sea urchins possessing it should be placed after those whose pores are in



vertical rows or in arcs. The internal partitions so characteristic of the irregular sea urchins are found in the adult, sometimes, however, in a rudimentary condition.

The typical characteristics of the first division of the irregular sea urchins are well shown in *Clypeaster subdepressus* Ag. (No. 337), and for this reason, it would seem, the name of Clypeastroids is given to the division. There is, however, no well defined line between this group and the next, the Spatangoids, so that it seems better to place both under the head of the irregular sea urchins.

The corona of *Clypeaster* is flattened and longer than it is broad. It can be so placed as to bring the odd ambulacral petal in the median line, and the remaining two pairs of petals on either side, thus dividing the test into two nearly equal parts.

The mouth is near the middle of the lower side and the simple ambulacral grooves extend outward from it. There are delicate spines in the grooves, and stronger ones on top of the conspicuous petals when these are formed.

The anal system has moved from the upper to the lower side, near the margin, and the anus is seen in No. 337, so that the Clypeastroid has an anterior and a posterior end.

The abactinal area is far more indefinite than in the regular urchins. It is made up partly of the madreporic body which is in the center. Four or five genital openings are seen, but the plates themselves do not appear.

If the upper portion of the test is removed (No. 337), the immense jaws with two teeth are exposed. These jaws consist of five strong parts which taken together constitute a powerful eating apparatus. The upper and lower parts of the shell are connected by slender pillars (No. 337) which are an important characteristic of the Clypeastroids, the regular sea urchins having nothing of the kind. Around the outer edge these pillars unite, forming more or less open walls, as seen in No. 337 where a portion of the edge has been removed.

Sometimes the ambulacral petals take up the greater part of the upper surface of the corona, as is the case with *Echinanthus rosaceus* Gray (Nos. 338-340). The central portion of each petal is raised while the furrows of the pore-bearing zones are sunken, making the rosette most conspicuous. Here, as in *Clypeaster*, the madreporic body is in the center. Joined to it are the ocular plates perforated for the ocular pores (not seen in No. 339), while beyond it are the genital plates with their openings (No. 339). The spines of this genus are small as are most of the *Clypeastroids*. When removed as in No. 339 the tubercles are seen to be much reduced in size from the regular urchins. The vertical section (No. 340) exhibits the powerful jaws and the massive pillars of the interior.

Not only are the upper and lower portions of the test united by pillars but in *Laganum depressum* Less. (No. 341), there are walls running parallel with the margin, as seen in the cross section (No. 342). In this genus the edge is much thickened, and the anus is on the lower side quite near the mouth.

The young *Echinarachnius parma* Gray, varies in form, but in No. 343 it is circular and somewhat dome-shaped, while in other specimens it is elliptical. No. 343, a-e, has light colored spines attached. There are two rows of these on both the ambulacra and interambulacra. They are short and delicate, very different from the long spines of the primitive and embryonic regular sea urchins. The youngest specimen (No. 343, a) is without a distinct ambulacral pattern, and the ambulacral grooves of the lower surface are scarcely visible. In an older specimen measuring 5.1 mm. these grooves have been seen, and according to A. Agassiz minute pores were formed in them.

The mouth is near the middle of the lower side protected by spines above (No. 343, c) and sunken within the corona are the five horizontal teeth. The anus at this stage is on the upper side a short distance from the

margin (No. 343, b), while the madreporic body occupies the usual central position of the anal area as seen in the regular sea urchins. No. 343, g, has been bleached by nature and through the microscope the openings of the madreporic body are clearly seen.

As the sand-dollar grows older it becomes flattened and more or less heart-shaped (No. 343, h-l). The petals become distinct, the outer ends are open, and the pores extend towards the ambitus, but do not reach the edge. At this time the internal partitions radiate in five pairs from the edge toward the center and there are few pillars.

The ambulacra and interambulacra are often distinctly seen in these younger stages, as in No. 343, m and n, where the limits of the individual plates can be easily traced; those on the lower surface are much more irregular than those above. The ambulacral furrows are simple but branch at their outer extremities. Sometimes, as in No. 343, p, there is no indication whatever of these furrows.

The ocular openings at the ends of the ambulacra are large, but the genital plates and pores cannot be detected.

The adult (No. 343, r, s) is more flattened than any of the Clypeastroids and is covered by tiny, dark colored spines (No. 343, r). It is usually difficult to make out the ambulacral and interambulacral plates, but if the specimen is bleached by nature, or treated with acid as is the case with No. 343, s, they come out more clearly. They are also finely seen from the inside when the dorsal side is removed. The ambulacral furrows are well defined and branch a few times. The petals above are large with furrows between the holes; they open at their outer ends in very flat sand-dollars while in more convex specimens they nearly converge. A few pairs of pores extend downward from the petals towards the edge (No. 343, s).

The anus has moved downward to the edge (No. 343,

r, s). Around the madreporic body are five ocular openings at the ends of the ambulacra, and four genital openings at the ends of the interambulacra. The interambulacrum opposite the odd petal is without a pore. The preparation (No. 344) shows the five pairs of partitions which radiate from the edge towards the center with space between each pair of partitions. There are other pairs that occupy the interambulacral areas while many pillars are crowded together on the ambulacra.

Greater specialization of structure marks the species *Echinarachnius excentricus* Val. (No. 345). Here the lower side is marked by radiating furrows that divide close to the mouth and afterward subdivide and send their branches over to the upper surface. Three of the petals are larger than the other two, and the mound bearing the rosette is not in the center but nearer the posterior end. The anus has moved from the edge to the lower side.

*Ecope grandis* Ag., when young is circular in outline and is without the rosette or lunules. The adult (No. 346) has five large openings into the margin besides the completed lunule in the median interambulacrum. The petals of the rosette differ in size and shape, the posterior pair being longer than the others and extending nearly to the lunules.

The madreporic body is star-shaped and four genital openings are at the tips of the rays, while the fifth opening is nearer the center. The five ocular pores are at the angles of the rays.

In conclusion it may be said that the young of all the Clypeastroids are much more like Echinometra and the regular sea urchins than they are like the adults of their own group. This is sufficient reason for placing the Clypeastroids next the regular sea urchins and before the Spatangoids.

## IRREGULAR SEA URCHINS. — SPATANGOIDS.

One of the ancestral forms of the more specialized division of the irregular sea urchins commonly called Spatangoids is *Pyrina subsphaeroidalis* d'Orb. (No. 347), in which the test is high and dome-shaped and the ambulacra are arranged in the primitive fashion of vertical rows from mouth to apex. The mouth is nearly central in this genus, while the anus is on the dorsal side of the posterior part.

The young forms of this group which are living to-day are similar to the young of the regular urchins and of the Clypeastroids. In fact the starting point of these groups is the same, as shown by A. Agassiz.<sup>1</sup>

The Spatangoids have at first the vertical row of pores running from mouth to apex, few tubercles of large size, spines of disproportionate length and size, and a simple lipless mouth. The adults, however, carry specialization much farther than any other members of the class.

Beginning with the more generalized forms we find *Echinoneus semilunaris* Lam. (No. 348), is dome-shaped with the ambulacra in vertical rows and no petals formed throughout life. The mouth is near the center and as in many Spatangoids is without teeth, while the anus in this genus is between the mouth and posterior end. Four genital and five ocular pores are seen in the abactinal area.

In addition to the ordinary tubercles *Echinoneus* has others that have the appearance of glass and carry no spines.

*Hyboclypus caudatus* Wright (No. 349), is a small somewhat flattened urchin with the three anterior ambulacra separated from the two posterior ones. Here the mouth has moved a little towards the anterior side while the anus is in a depression on the dorsal side.

<sup>1</sup> Proc. Amer. Assoc. Adv. Sci., XXIX, 1880, p. 397.

*Toxaster oblongus* Deluc. (No. 350), is longer than broad with a groove at the anterior end, the posterior end being high with the anus visible.

*Holaster striato-radiatus* d'Orb. (No. 351), is a high dome-shaped Spatangoid with simple narrow ambulacra and broad interambulacra. The mouth is at the anterior end of the ventral side and the anus at the posterior end. The abactinal area cannot be made out in the specimen but the boundary lines of some of the plates can be traced.

*Collyrites dorsalis* Ag. (No. 352), shows more plainly the specialization in the position of the ambulacra, three of which are in front while the other two are widely separated from them. This drawing out of the abactinal area in an antero-posterior direction has caused a separation in the genital and ocular plates.

No. 353 is an interesting specimen of *Micraster* from the Lower Greensand. It is a jasper cast in which the posterior end is preserved. The partition between the paired pores is clearly shown and three of the ambulacra, while the ornamentation is well preserved. This genus is usually distinctly heart-shaped with the bilabiate mouth placed far forward and the odd anterior ambulacrum in a groove.

*Hemiaster minimus* Desor (No. 354), when young has the anus nearly central and the test has much the appearance of that of the regular urchins. Marked changes take place, however, in the course of development. The outline of the urchin becomes more irregular and flattened, and some of the ambulacral plates become modified into four deep cups or pouches for the purpose of holding and protecting the eggs. Within these pouches the embryos develop; by the law of acceleration the metamorphosis is skipped, and the embryos are retained by the parent until the plates of the test are formed. The adult has a band of microscopic tubercles called fascioles encircling the petals.

A giant among its kindred is *Metalia pectoralis* A. Ag. (No. 355). Some of its spines are peculiarly modified, being so extremely long and delicate that they are rarely preserved. These are attached to small areas on each side of the dorsal median line and within the fasciole. They are capable of lying flat upon the corona, as seen in No. 355. On other parts of the body the spines vary in length and in some places they are distinctly curved. The mouth is near the forward end and the anus in the large blunt posterior extremity. The marked sexual difference in size is shown by No. 355; the female is much larger than the male, while the latter is rarely found. The corona denuded of spines is a beautiful object (No. 356).

Another large, robust urchin is *Meoma ventricosa* Lütke. (No. 357, ventral side). Here similar spines cover the whole surface. The mouth (No. 357) has a large lip and the anus is at the posterior end of the body. The sunken petaloid ambulacra above are conspicuous.

Among the most specialized of the irregular urchins is *Moira atropos* Ag. (No. 358). Here different parts of the test are made of variously shaped plates. The mouth is far forward, and the anus is at the upper side of the blunt posterior end. There appear to be deep slits on the upper side and on looking more closely the ambulacral pores are seen at the bottom of four slits. The fifth one, which is more like a groove than a slit, extends forward and turning downward reaches the mouth. The young are carried in these sunken ambulacra after much the same fashion as in *Hemiaster*. The variation in the shape and size of the interambulacral plates is great.

An extreme of specialization is reached when one examines *Amphidetus cordatus* Ag. (No. 359). The short silky spines (No. 359, c) conceal the ambulacra and interambulacra which are most curiously modified. Instead of simple vertical rows or the usual rosette of petals there is here a star-like arrangement of the ambulacra

(No. 359, b, d), the narrow points of the star radiating downward toward the ambitus when they become somewhat obscure only to reappear on the ventral side (No. 359, b) in the form of perforated bands which reach to the mouth. Between these bands the interambulacra are set in, the different areas and the individual plates composing them varying greatly in shape and size.

The mouth (No. 359, b) is at the anterior end with its lip, while the anal disc at the posterior end (No. 359, a, test of a younger specimen than the others) is perfectly preserved. Below this anal plate there is another with three openings on either side. In the sunken area at the top are four openings.

#### HOLOTHUROIDEA.

We know nothing of the ancient ancestral Holothuroids excepting by the minute hard parts, — spicules, wheels, anchors, etc., — which are preserved in the rocks. These occur no farther back than the Carbonic age (Zittel). They throw little light upon the phylogenetic history of the group, and therefore we must turn to the primitive forms living to-day.

Among the deep-sea Holothuroids are the Elaspoda which retain the characters of the larva in the adult stage more than any other members of the class. Accordingly in describing the adult we are giving the more essential larval characteristics.

Generally speaking, the body is distinctly bilateral (Pl. 360, figs. 1-4, *Elpidia verrucosa* Théel, and *Scotophanes murrayi* Théel), while its walls are provided with simple spicules of few rays. The dorsal part of the body extends in front, causing the mouth to turn towards the ventral side (see figs. 2, 4) instead of being terminal. The anus is dorsal in position (fig. 1) or terminal as in *Scotophanes* (fig. 4). The ventral surface is flattened,



consisting of two ambulacra (figs. 2, 4), and the ambulacral feet with sucking discs are restricted to this side and extend in pairs towards the posterior end of the body (figs. 1, 2, 4). On the dorsal side there are tubular organs which, as they perform a different function from the ambulacral feet, are without sucking discs (fig. 3; in fig. 1 these organs are broken off, but the four openings on the anterior part of the body show their position).

In many *Elasipoda* the water-vascular system communicates with the exterior by means of the madreporic body. Moreover, the circular ring around the mouth is made up of simple spicules which are separated from one another.

The internal respiratory organs lack the usual tree-like form, and the tentacles are few in number, usually not more than ten in the *Elpidiidae*, the most generalized family.

While the *Elasipoda* have retained the larval characters more than the other members of the class, still we cannot fail to see what Théel<sup>1</sup> has already pointed out, that these Echinoderms are more like the specialized forms of most invertebrates in several important particulars. They are bilaterally symmetrical. They have a distinct antero-posterior axis and a ventral side differentiated from the dorsal. They have a small number of locomotive organs and these have a definite position.

The remaining families of *Holothuroids* — the *Pedata* and *Apoda* — when young resemble the *Elasipoda*. Most of these forms belong to the shallow waters and they have become greatly modified to meet widely different conditions.

At first the madreporic body opens on the exterior, but later the connection is lost and the canal ends blindly in the interior.

<sup>1</sup>Chall. Rep., Zool., IV, part 13, 1882, p. 147.

*Pedata*. One of the more generalized members of the *Pedata* is *Holothuria tubulosa* Tied. (No. 361, model), in which the body exhibits a distinct antero-posterior axis. This genus has the feet scattered over the surface instead of being arranged in rows.

Another representative of this group is *Pentacta frondosa* Jaeger (No. 362), in which the division of the body into five distinct areas is finely shown. Two double rows of ambulacral feet extend down the dorsal side and three on the ventral side. There are also dorsal feet in the interambulacral areas. The terminal mouth is surrounded by numerous organs resembling tentacles but which serve as branchiae or external gills. The madreporic body is internal. The anus is at the posterior end, and the respiratory tree is given off from the cloaca near the vent. This is seen in No. 363 which is a dissection showing chiefly the digestive and reproductive systems.

A peculiar modification of structure is seen in *Psolus fabrici* Semper (= *Lophothuria fabrici* Verr.) (No. 364), where the lower surface is converted into a creeping-disc resembling the foot of a gastropod. It has three rows of ambulacral feet and there are none on the scaly dorsal side.

*Cucumaria crocea* Less., in its development skips altogether the larval stage and enters upon the adolescent or neanic period. The young of *Cucumaria crocea* Less. (Pl. 365, fig. 1, dorsal side; fig. 2, ventral side), were found by Sir Wyville Thomson<sup>1</sup> attached to the two rows of ambulacral feet on the back of the mother. They were all "miniatures of their parents," excepting that their dorsal ambulacral feet were in an undeveloped condition, while their ventral feet were early and well developed and used for clinging to the parent. The adult like the larva is elongated with distinct rows of feet

<sup>1</sup>Quoted by Théel in Chall. Rep., Zool., XIV, part 32, 1886, p. 60.

extending from one end to the other. The mouth and anus are both terminal.

*Apoda.* The reduction of parts is going on in the group to which *Caudina arenata* Stimp. (No. 366), belongs. The young and adult, both seen in No. 366, are similar in external appearance. The rows of feet have disappeared, and the water-vascular system is, therefore, much reduced. Ludwig has shown that an allied form, *Chirodota rotifera* Pourtalès, has a stage in which it loses its madreporic body and the stone canal detaches itself from the dorsal wall, becoming enclosed within the perisoma.

The most specialized of all the Holothuria is *Synapta* (No. 367, *S. glabra* Semper), found in the shallower waters of the shore region.

The body has become modified and is extremely elongated. It contains spicules in the shape of anchors and plates. The feet have disappeared and the radial ambulacral vessels are also wanting, so that the water-vascular system is reduced to a ring around the mouth. There is no respiratory tree and altogether the genus is a good illustration of specialization by reduction.

To recapitulate briefly: The pre-Cambrian ancestor of the Echinoderms was probably free swimming and may be represented by certain larvae of existing Echinoderms. The Palaeozoic ancestors, however, were with little doubt attached forms. Of these the Cystoids and Blastoids had a more or less globular body which was either sessile or fastened by a stem. The body was covered with plates which at first were placed together irregularly but in later forms were arranged in regular circles. The oral surface was above and the aboral below. By the differentiation of areas of plates, called ambulacra, and of feathery pinnules, the apparatus for catching food and carrying it to the mouth became more efficient. Pores through the body wall admitted water to the respiratory organs or hydrospires.

In the case of the Crinoids specialization not only brought about greater regularity in the body plates but arms were developed; the ambulacra still served as food grooves, through the holes of which numerous pointed tentacles were put out.

The digestive system in these ancient Echinoderms was distinct from the body cavity and its two openings—mouth and anus—were usually on the upper side.

The Asteroidea, living to-day, pass through a transient stage in their development when they are attached. In becoming free they turn over so that the oral side is below and the aboral above. In this favorable position for obtaining food from the sea bottom by means of the mouth, the pointed tentacles of the ambulacra develop suckers and become locomotive organs or tube feet. It is probable that further specialization causes the almost useless ambulacra of the Ophiuroidea to become internal, and the equally useless tube feet to take on reduced characters.

Besides the ambulacral plates of the typical Asteroidea there are rows of interambulacral plates on the ventral side, while the dorsal side is made of irregular plates. The digestive system is complete, but in most cases the anus opens opposite the mouth on the dorsal side.

Water is admitted to the body cavity of the Asteroidea through a sieve-like organ which connects with a series of tubes that serve the double function of respiration and locomotion. Greater concentration marked the organization of the Echinoidea. The ambulacral and interambulacral plates of the typical Asteroidea here reach an extreme development, while the irregular plates have almost wholly disappeared.

All trace of a fixed stage is lost in the ontogeny of the Echinoidea, so that the larvae are free from the start.

The digestive and water-vascular systems are similar to those of the typical Asteroidea, with the exception of certain specializations such as the eating apparatus or "teeth" and the reduced tube feet of many sea urchins.

The Holothuroidea like the Echinoidea have no fixed stage in their development. As has been said, they resemble the more specialized invertebrates in being bilaterally symmetrical and in having an antero-posterior axis of the body. They possess many reduced characters; the number of feet is limited, and the water-vascular system in some forms is a mere ring around the mouth. This reduction is indicative of specialization and it offers a reason for placing this group farthest from the primitive ancestral form of Echinoderms.

## MOLLUSCA.

## Section 7. — PELECYPODA.

The arrangement of the molluscs in the Synoptic Collection is governed by the same principle that controls the classification of the preceding subkingdoms. We consider first, primitive ancestral Pelecypods and the early stages of living forms; secondly, the specialization of adults. Since a fleshy animal antedates, as a rule, a skeleton-bearing animal, as we have seen in the Protozoa, Porifera, and Coelentera, and since, also, fleshy parts are not usually preserved in the geologic formations, we turn to the embryonic and larval stages of existing species to determine so far as possible the characters of the ancestral fleshy forms. On the other hand, since the skeleton or shell when made, is a comparatively sure guide to the structure of the soft parts, we regard with special interest the remains of the primitive Mollusca in the Protozoic and the Palaeozoic strata. An early stage of the present Pelecypod larva is the trochophore (Pl. 368). It is a little fleshy creature whose distinctive features are a ciliated locomotive ring (the velum) in front of the mouth, and a tiny sac or shell gland on the dorsal surface. This sac is simply a portion of the outer wall turned inward, but it plays an important part since it is soon everted and at once the shell begins to form on its surface. The latter is secreted extremely early in the life of the embryo, therefore it is inherited, and of value phylogenetically. At first it is shaped like a tiny plate or cap, and therefore the ancestor from which the Mollusca descended probably possessed such a shaped shell. In the case of the developing Pelecypod the tiny plate forms into two parts or valves, while in the Gastropod the cap becomes a cone and later a new shell is formed which in most cases becomes a spiral.

The name Pelecypoda is given to the most generalized class of molluscs in preference to Lamellibranchiata for three reasons, *viz.*, it has priority over the latter name; it is in uniformity with the names of the other classes of Mollusca (Gastropoda, Pteropoda, Cephalopoda); the word Lamellibranchiata refers to the gill which is one of the most variable organs of a mollusc, while Pelecypoda, Gastropoda, etc., refer to the foot, one of the most stable molluscan organs.<sup>1</sup>

The classification adopted in this guide is, with certain modifications, that of W. H. Dall<sup>2</sup> and of Dr. Robert T. Jackson. Dall considers the structure and development of the hinge first, and secondly, the sum total of organic characters. As a result of these studies he divides the class into three orders. The first possesses the simplest possible hinge, having the two toothless edges of the shell in contact and united by a ligament. The second has the hinge provided with transverse or cardinal teeth and the third has teeth parallel with the margin and known as lateral teeth.<sup>3</sup> There is no sharp line of division between the last two orders, as many shells have both the cardinal and the lateral teeth. In these cases the general characters usually enable one to decide to which order a shell belongs. There is here as in every class the difficulty of determining the primitive and the reduced forms. Some shells that do not possess teeth to-day are really the descendants of toothed shell-bearing Mollusca. On the other hand the most primitive Pelecypods were doubtless toothless. Whether these truly primitive forms exist at the present time is a question. Many of the members of Dall's first order have become extremely

<sup>1</sup> Dall, Amer. Journ. Sci., ser. 3, XXXVIII, 1889, p. 446.

<sup>2</sup> Rep. on Mollusca, Bull. Mus. Comp. Zool., XII, 1886; Amer. Journ. Sci., ser. 3, XXXVIII, 1889, p. 445; Trans. Wagner Free Inst. Sci., Phila., III, part 3, 1895.

<sup>3</sup> See Bernard, Bull. Soc. Géol. de France, ser. 3, XXIII, 1895; XXIV, 1896.

specialized through the habit of boring, etc., so that it would seem as if these were reduced rather than primitive forms of the class. It is probable, however, that they are simply reduced members of the order which has *Solenomya* and *Anatina* for its primitive representatives. The weak, toothless condition of the ancestors could hardly be preserved in the descendants, as pointed out by Dall, unless the animals became borers or burrowers.

If the shell-bearing ancestral form of the Mollusca is sought in the Cambrian formations, one finds that nearly four hundred species of molluscs then existed which include representatives of nearly all the great orders existing to-day, and which, according to Cooke,<sup>1</sup> are without the slightest sign of approximation to one another. If this is true, the point of convergence of these divergent lines lies far back in pre-Cambrian times. Until more investigations have been made on these ancient rocks, one can judge of the ancestral forms of Pelecypods succeeding the plate or cap-like condition by inference only. It seems probable, however, that such a form possessed a small, smooth, more or less circular shell; that the two valves were equal in size and were connected at the toothless hinge area by a flexible membrane, the ligament. This is the character of the young shell or prodissoconch (Jackson) of many larval bivalves existing to-day. Such a form may be represented by *Modioloides prisca* Walcott (No. 369, fig. 1, enlarged), found as an internal cast in the Cambrian formation. Another genus, *Cardiola* (No. 369, fig. 2, *C. cornucopiae* Goldf.), possesses most of the archetypal characters.

The descendants of such a form may be *Solenomya*, *Anatina*, and the like. *Solenomya velum* Say (No. 370; No. 371, shells), has a small, thin, delicate shell, having, contrary to rule, the posterior end shorter than the ante-

<sup>1</sup> Cambridge Natural History, III, 1895, p. 2.



rior.<sup>1</sup> A glossy horny layer covers the opening between the valves; when the animal is young (No. 371 a), this horny layer is entire or simply pinked at the anterior and posterior ends, but as the animal grows older it is slit into strips (No. 371). The hinge is without teeth. The internal portion of the ligament is back of the beaks in a triangular receptacle and is strengthened by limy, arched supports. Just in front of the latter are the distinct anterior muscle marks. The shell of most primitive forms is nacreous, that is, pearly, but *Solenomya* is only slightly so. The gills of this genus are in a primitive condition, similar to those of *Nucula* (see p. 202). The foot (No. 370) does much hard work enabling the animal to swim and to bore, so that it is large in proportion to the size of the animal. The mantle is not drawn out into tubes or siphons.

*Anatina truncata* Lam. (No. 372), is a delicate, translucent, and pearly shell with the posterior end truncated and the anterior rounded. The two valves are open nearly all the way round, so that, as compared with many bivalves, they afford slight protection to the soft body within. According to Smith<sup>2</sup> one species of this genus, *Anatina elliptica*, shows the two ends nearly alike, while others have the anterior portion longer than the posterior, the reverse being the case with the young.

The hinge has a socket for the internal ligament called a fossette, which is strengthened in its position by two limy supports that radiate downward towards the center of the shell (No. 372, specimen at right).

This genus has only two gills, one on each side of the so

<sup>1</sup> When we speak of the anterior and posterior end of a shell, the latter is mounted with the anterior end away from the observer — a favorable position for comparison with one's own body. In other cases the shells are mounted to show certain important features. In a few cases delicate shells have been left as first mounted, owing to the danger incurred in remounting.

<sup>2</sup> Chall. Rep., Zool., XIII, part 35, 1885, p. 77.

called body.<sup>1</sup> It has tubes or siphons which are separate throughout their whole extent, and a foot with a cleft.

A peculiar bivalve with a body larger than its shell is illustrated by *Cyrtodaria siliqua* Daudin (No. 373). One preparation shows the remarkably large muscular siphon extended at the posterior end and the comparatively small foot at the anterior end. The other preparation is the fleshy animal taken from its shell. The plump, rounded body contains most of the internal organs. There are two gills, one on either side of the body, and each gill consists of two leaves.

*Mya arenaria* Linn. (Pls. 374, 376; No. 375), is one of our commonest shells. Ryder<sup>2</sup> has shown that the young clam is attached by a mass of threads called a byssus, but probably only for a short time. The two valves in youth and maturity are equal, therefore the shell is equivalved (Pl. 374; No. 375), but the anterior end is broader than the posterior (Pl. 374). The light brown external horny layer is thin and usually worn off, showing the lines of growth which are the edges of the layers that make up the shell. The left valve (Pl. 374, valve on the left) is provided with one tooth (instead of three as is usually the case), and the right valve (Pl. 374, valve on the right) with a cavity which contains the internal ligament. The impressions of the two muscles, the mantle, and the siphon, are more distinctly seen in shells of *Mactra* (see Nos. 411-413).

The clam is a differentiated member of its order. Since the internal organs are also better seen in the larger genus, *Mactra*, we will speak briefly of them here. The mantle has become a sac-like organ with three openings, two at the end of the siphon and one at the anterior end through which the foot passes. The mantle is thickened on the edge and supplied with pigment cells which produce many of the colors of the shell.

<sup>1</sup> Bull. Mus. Comp. Zool., XII, 1886, p. 306.

<sup>2</sup> Amer. Nat., XXIII, 1889, p. 65.

The gills have become more complex, consisting of many longitudinal tubes connected by cross tubes.

The mouth is provided with two pairs of palpi and leads into the so called "body" containing the stomach, liver, most of the intestines, and the reproductive organs. The long, cartilaginous rod called the crystalline style may give rigidity to this part of the animal. The intestine leaves the body, passes dorsally under the beak and through the heart. It terminates a short distance from the upper tube of the siphon lying in the path of the outgoing current of water.

The more specialized members of the group are *Pholas*, *Aspergillum*, and *Teredo*.

*Pholas dactylus* (Nos. 377, 378) has a large opening in the anterior end filled by the foot. This genus has the habit of boring. The valves are united by an external ligament, and the hinge has two plates to strengthen the union but no teeth.

*Aspergillum* when young has a bivalve shell. As the animal grows older the siphon grows to a large size, and is covered by a limy tube in which the tiny reduced bivalve shell becomes imbedded, as seen in No. 379, specimen at the right. At the end of the tube is a sieve surrounded by a frill. At the other end are one or more frills which are broken off in the specimen. In *Aspergillum* the mantle is bag-like, having the two siphonal openings and one at the anterior end.

*Teredo* has a long body; at the larger end is a little bivalve shell which is without teeth or ligament. The mantle is drawn out into a long siphon near the end of which are organs probably used for boring into wood. It is a strange freak that causes the animal to live in wood, since it never uses it for food. Early in life, however, it begins to bore, and lines its tunnel with a calcareous secretion as seen in No. 380. It never leaves its tunnel and depends for food upon the microscopic plants and animals which are brought in the water. Many *Teredos*

may bore into the same piece of wood, but these tunnels do not, as a rule, come in contact.

The second group of Pelecypods, or those possessing transverse teeth on the hinge area, may have descended from forms like *Nucula* or even from some simpler species.<sup>1</sup> *Nucula* occurs in the ancient formations (No. 381, *N. ventricosa* Hall) and has continued slightly modified to the present day (No. 382, *N. tenuis*; No. 383, *N. margaritacea* Lam.). It is a smooth, symmetrical shell with equal valves. Contrary to the usual rule the umbos are directed towards the posterior end of the body which is short and rounded, while the forward end is longer and more pointed. The primitive hinge area is curved and bears a few teeth which are at right angles to the antero-posterior axis of the body. This primitive hinge area or cardo is better seen in the larger shell, *Arca occidentalis* Phil. (No. 384). Here it is long and straight, and the many transverse teeth are well developed. In this genus the umbos are widely separated and the ligament lies between them. In *Nucula* the hinge area has a triangular pit for the internal portion of the ligament, called by Dall the "resilium," which aids the external ligament in uniting and opening the valves. The whole shell is made of a pearly or nacreous substance, and in its young and adult stages no prismatic structure is ever developed. The fleshy animal is primitive in structure like its shell. The edges of the mantle are free, without tentacles, and are not drawn out to form a tube or siphon. Two adductor muscles are present, one at either end of the body. The gills are in two pairs in the form of simple, straight, and separate filaments. The young *Nucula* is active and throughout life it never becomes attached. The foot has a cleft and can be flattened into a disc and used in crawling.

<sup>1</sup> For a discussion of the subject see Verrill, Trans. Conn. Acad. Arts and Sci., X, part 1, 1899, p. 45.

Rhombopteria (Pl. 385) represents a branch from the primitive Nuculoid ancestral form, and is the probable ancestor of the Aviculidae to which Pecten belongs. Its shell was oblique, and it had a straight hinge line which extended on either side of the umbos.

The young of another genus, Pterinopecten, resembles the adult Rhombopteria, while the hinge line of the adult is long and the ears slightly developed. The young Aviculopecten resembles the adult Pterinopecten but the adult has a shortened hinge line and a much greater development of the ears.

The shell of the young Pecten (Pl. 386, fig. 1, viewed from the left side; fig. 2, the same from the right side;  $\times 50$  diameters) has the embryonic shell or prodissoconch which represents the ancestral Nucula while the succeeding stages resemble Rhombopteria, Pterinopecten, and Aviculopecten. At first there are no plications and the prodissoconch is without ears. According to Dall<sup>1</sup> the very young valves of many species of Pecten have the transverse groovings of the hinge, representing the teeth of Nucula and Arca. Fig. 3 is an older stage,  $\times 40$  diameters, and fig. 4 shows the fleshy animal at the same stage. The two mantle borders are free and each possesses a single row of eyes which alternate with single tentacles. In a later stage two tentacles alternate with one eye. The animal uses its long narrow foot actively so that it is finely developed. Fig. 5 is the same shell viewed from the right side, while fig. 6 is an older shell,  $\times 16$  diameters. The plications and ears are now well developed. The two borders of the mantle are extended to form a tube just under the dorsal ear. Here the effete matter is carried away in the outgoing current of water, the direction of the current being indicated by an arrow (fig. 6). The gills of the very young Pecten are probably four sets or two pairs of straight filaments, but when the

<sup>1</sup> Amer. Journ. Sci., ser. 3, XXXVIII, 1889, p. 459.

young animal has reached the stage represented by fig. 6 the ends of the inner pair are turned inward while those of the outer pair are reflected outward, as seen in fig. 7 which represents the gills of the adult. When young the Pecten attaches itself by a byssus and always lies on the right valve. After becoming attached it may detach itself but soon becomes fastened again. When it reaches adult life it is free, but keeps the same position with the right valve below, and swims by clapping its valves together. At this stage the hinge is toothless. No. 387 is a species of Pecten showing the mantle, large muscle, and gills. *Pecten varius* Linn. (No. 388), illustrates the unequal development of the ears and the variation in color in one species. No. 389 is a remarkably fine specimen of the adult *Pecten maximus*, and Pl. 390, figs. 1, 2, are drawings of the same. Here we have in one shell an epitome of a great part of the life history of the group to which Pecten belongs.

The prodissoconch has disappeared, the peduncle having usurped its place, but the tiny cavity (No. 389; Pl. 390, fig. 2) at the beak remains, telling of the rounded outline and long hinge line of the embryonic shell. The larval or nepionic stage is convex at first and smooth with concentric markings. The hinge is long, while ears and ribs are not developed. In the later nepionic stage the beginnings of ribs are seen. At this time the shell is light yellow in color. In the adolescent or neanic stage the shell becomes concave and ribs are more developed. The mature or ephebic stage is convex at first and the ribs are prominent, while the color has changed to reddish. The later ephebic stage shows a tendency to return to the concave condition which increases in the gerontic stage. This is seen in the specimen and in fig. 2, but still better in fig. 1, which is a section through the middle of the two valves, the lower valve being on the right. The ribs tend to flatten out in the gerontic stage, while the concentric markings become prominent and are nearer together.

In passing through these stages the shell illustrates Minot's law of growth; *i. e.*, growth decreases as the size of the animal increases. In the younger stages growth was rapid, the hinge extended in length and the shell doubled its size in a brief time, but in the gerontic stage, growth is limited and the hinge area is narrow, as seen by tracing the edges of the layers from the broad, rounded, posterior part to the comparatively short hinge line.

Anomia (Pl. 391, *A. simplex*, No. 392), is related to Pecten though it is a much more specialized form. When young it is found free and crawls by means of its large foot which is seen extended in Pl. 391, fig. 2. The very young shell (fig. 1, left or upper valve) has the prodissoconch on the edge. Fig. 2 is a somewhat older stage seen from the left or upper side. The later dissoconch layers of shell are beginning to encircle the prodissoconch. Fig. 3 is the same shell as Fig. 2 viewed from the right or lower side. The byssal notch is indicated on the edge of the prodissoconch in which particular, Anomia differs from Pecten, the latter having an entire prodissoconch. The byssal notch was originally on the edge, but has extended nearly to the center and is partly encircled by the layers. The prodissoconch becomes entirely enclosed by layers. Fig. 4 is an older stage which shows how the encircling layers have pushed the prodissoconch inward some distance from its original position on the margin.

The byssal notch of the lower valve is finally completely enclosed by shell layers, as seen in fig. 5 (adult Anomia, lower side; fig. 6, side view of the same).

At first, when the byssus is surrounded, the opening or foramen is small, but it becomes larger by the resorption of the shell.

Specimens of the adult are seen in No. 392; (a) is the whole shell; (b) the upper valve showing the scaly appearance due to the irregular layers of shell; (c) is the lower valve.

The same trunk forms, *Nucula* and *Rhombopteria*,

probably gave rise to *Leptodesma* (Pl. 393) which has an oblique body with the posterior wing extended, while the anterior border is acute and there is a byssal sinus. These forms may in time have produced another series represented by *Aviculopinna* and *Pinna*.

*Aviculopinna* (Pl. 394) is wedge-shaped and without ears. The two valves are equal and marked by concentric lines. The beaks are a little behind the anterior end of the shell.

*Pinna* (No. 395, *P. rudis* Linn.), the probable descendant of *Aviculopinna*, has the same wedge-shaped, equal-valved, and earless shell. The concentric and longitudinal markings are about equally developed. The beaks in *Pinna* are placed at the anterior end of the shell. The hinge is in a reduced condition, having no teeth, and the substance of the shell is mostly prismatic, very little nacreous matter being found.

In this form the anterior muscle is four or five times smaller than the posterior, being on the way to a reduced condition.<sup>1</sup>

Other descendants of *Nucula*, *Rhombopteria*, and *Leptodesma* were probably *Melina*, *Avicula*, (= *Pteria*) *Malleus*, and *Ostrea*.

The shell of *Melina* (No. 396; Pl. 397, figs. 1, 2) is extremely flat, and the posterior part is prolonged to one side making the shell appear as if deformed. The hinge area (Pl. 397, fig. 2) has little pits for the ligament which holds the two valves together.

*Avicula* (Pl. 398, fig. 1, young), has the *Nucula*-like prodissoconch and the subsequent nepionic stage representing *Rhombopteria*. It has a straight hinge line, but its posterior wing is extended and there is a deep byssal sinus in the right valve (fig. 2). The triangular pit exists in all *Aviculas*. The later stage represented by fig. 3 is the *Leptodesma* stage. The adult has the shell oblique

<sup>1</sup> Sharp, Proc. Acad. Nat. Sci., Phila., 1888, pp. 122, 123.



and the right valve is smaller and flatter than the left. The hinge has one or two transverse or cardinal teeth.

Malleus when young (No. 399 a) somewhat resembles the adult *Avicula*. The hinge line is long with the beak at one end. Only one wing is developed. Later growth takes place on the other side of the beak (No. 399 b) and the result is a wing in masquerade. The adult (No. 400) for obvious reasons is familiarly known as the "hammer-oyster."

One of the ancestral forms of the oyster was *Gryphaea arcuata* Lam. (No. 401). The large deep lower valve and the small lid-like upper valve, the curved beak and the lines of growth are all well preserved in the fossil.

The development of the oyster from the embryo to the adult is given in Pl. 402, figs. 1-19; figs. 1-3, *Ostrea edulis* Linn.; figs. 4-19, our common species, *O. virginiana* Listner (= *O. virginica* Gmel.). The segmentation and earliest embryonic stages are omitted, although like the later stages, they illustrate accelerated development. In the embryonic stage (figs. 1-3) the shell is symmetrical with a straight hinge line (fig. 1) situated on the dorsal side. The valves are equal (fig. 2) with only slightly developed umbos. In this condition the shell bears a striking resemblance to the equivalved bivalves already described.

At this time both the mouth (fig. 3, *m*) and anus (fig. 3, *a*) are situated ventrally, while there is but a single muscle, the anterior adductor (fig. 3, *a, a*). A ciliated velum (fig. 3, *v*) still persists as the little oyster swims about freely in the sea.

The stages of development between the one represented by figs. 1-3 and that shown by figs. 4, 5, have never been figured or described. The latter (figs. 4, 5) represents our common species, when it has completed the embryonic or prodissoconch stage, and has fastened itself by the edge of the left valve (fig. 5), using the reflected margin of the mantle (fig. 5, *m*) to accomplish the work.

This early fixation of the oyster has doubtless caused the reduction of the foot, which exists as a mere vestige in an early embryonic stage and is lost altogether before the embryonic stages figured in Pl. 402.

The straight hinge line of the embryonic shell has given way to a curved line with high umbos (figs. 4, 5; also fig. 6, which shows the shell attached by the left valve in an almost vertical position). An important change has taken place in the structure of the oyster, for instead of having one muscle it now possesses two, a posterior adductor (figs. 4, 5, *pa*) having been developed.

The gills (figs. 4, 5, *g*) are still in a primitive condition, consisting of straight simple filaments (fig. 7). The situation of the mouth can be judged by the position of the palpi (figs. 4, 5, *pl*), but the anus has changed its place, having moved dorsally before the development of the posterior adductor muscle which took place on its ventral side.

The beginning of the nepionic stage is represented in fig. 8. Here the left valve is below and the right above, and on the edges of these valves the new growth of the nepionic shell is being added to the prodissoconch. The internal organs in the early nepionic stage are shown in fig. 9. The single adductor muscle (fig. 9, *ad*) is in a similar position to that of the adult. The gills have passed through the stage represented by fig. 10 and are now in the condition illustrated by fig. 11, in which the filaments are connected by cross bars.

The substages of the nepionic stage are so well shown in the shell of the oyster, that contrary to our usual rule, we illustrate them by figures. Fig. 12, *p*, represents the prodissoconch succeeded by the first nepionic growth. In figs. 13 and 14 two and a half of the third nepionic substages are figured. At this time the right or upper valve is convex (fig. 13) and the left or lower valve (fig. 14) is flat. The tip of the left valve (fig. 15,  $\times 87$  diameters, view of interior) shows the prodissoconch (fig. 15, *p*)

and the nepionic growth with the cartilage pit or furrow running through the middle. On either side of the true nepionic shell there is a flange-like extension (fig. 15, *J*) of the margin which passes over the object of support.

The shell, as it appears at the end of the four nepionic substages and the neanic stage, is represented in fig. 16, right valve, and fig. 17, left valve. The sinus (figs. 16, 17, *s*) is clearly indicated, and it marks the position of the outgoing current of water. Changes take place in the shape of the shell during the ephebic stage, the variations depending largely upon the surroundings. As a rule the lower or left valve becomes deep and cup-shaped, while the right valve flattens. This is seen in fig. 18, which represents two adults. The upper specimen is growing with the left, deep valve below, and the right, flat valve above. The right hand specimen, however, reverses this condition, so that the left, deep, attached valve is above and the flat valve below. In both cases the same relative form of the valves is maintained.

The adult oyster (No. 403, alcoholic specimen; 404, model; 405, shells, young and adult) has but one muscle, the anterior adductor having disappeared. The posterior adductor holds a more central position (Nos. 403, 404) and the dark purple scar is seen in No. 405. The palpi have moved dorsally and are nearer the hinge line. The model shows the two leaves of the mantle, one of which is thrown back exposing the gills. These organs have become more complicated in structure, as shown by Pl. 402, fig. 19.

*Unionidae.* It is very rare to find parasites at any period of life among molluscs. The fresh-water *Lampisilis* (= *Unio*) (No. 406, *L. nasutus* Say; Nos. 407, 408, *L. radiata* Gmel.) and *Anodonta* (No. 409) however, pass the young stage attached to fishes. Their development is, therefore, more complicated than that of most molluscs. The eggs are carried in little pouches in the gill cavities of the parents. No. 407 is the female of

*Lampsilis radiata* with the broad sacs of the outer gills filled with embryos.

The peculiar characters which separate the larvae of the Unionidae from those of other Pelecypods appear very early in the embryo and are found in both the internal and the external parts. A shell is formed with a straight hinge line. It is provided with hooks which later become a necessity to the larvae. The byssus and spiny beaks form, and peculiar sense organs are developed on the inner surface of the mantle. All this takes place before the animal leaves its parent. This stage is known as the glochidium. Becoming free, the glochidium attaches itself by the byssus, or if fish are near it, fastens itself to the gills, fins, or other parts of the fish by the hooks of its shell and lives the life of a parasite, its host providing the necessary nourishment. All this time the intestine is a closed internal sac and of little use. Later the sac elongates and an opening breaks through. A metamorphosis takes place, two adductors appear in place of one, gills develop, and the peculiar sense organs disappear. When fully developed, with the exception of the reproductive organs, it leaves the fish and becomes extremely lively while its further development goes on. The adult shell (No. 406, *Lampsilis nasutus* Say; No. 407, *L. radiata* Gmel.), has the transverse teeth which prove the origin of the Unionidae, while the peculiar marginal teeth of the third group are developed later. The hinge of Anodonta (No. 409), however, is so much reduced that it is toothless.

The third order, in which there are teeth parallel to the margin, is represented by a number of genera. It is important to bear in mind that transverse teeth also usually occur, so that in the differentiated forms the hinge is remarkable for its perfection of mechanism for efficient work.

Petricola is both a free and a boring mollusc. It is found in soft marshy earth as at Revere Beach and also

in limestone rocks (No. 410, *P. corditoides*). The teeth of the hinge are usually broken off, but when preserved there are two in each valve. The mantle lobes are united. The anterior end is short and the posterior gaping.

*Maetra* (= *Spisula*) *solidissima* Dillw. (No. 411), is one of our largest New England bivalves. The animal is free-moving and is therefore symmetrical. The horny layer is light brown in color (Nos. 411, 412). The umbos are directed anteriorly. The pit, with its internal ligament, and the external ligament are sometimes developed. The cardinal tooth is nearly vertical while the marginal teeth are long. The dissection (No. 413) and model (No. 412) show the principal internal organs and give their names. The mantle is seen extending along the edge of the shell (Nos. 412, 413); it has three openings; one at the anterior end through which the foot passes out, and two at the end of the siphon. This siphon is really a double tube; one, "the branchial siphon," is for the ingoing current of water, and the other, "the cloacal siphon," for the outgoing current. The anterior and posterior adductor muscles, the gills injected with red coloring fluid, the mouth organs called palpi, and the strong muscular foot are all shown in the preparation.

*Psammobia vespertina* Gmel. (No. 414), has two long delicate siphonal tubes separate throughout their whole length. The siphonal tubes are separate only a short distance in *Psammosolen strigillatus* Linn. (No. 415). The foot in this genus is of great size and strength.

*Ensis directus* Con. (*Ensis americana* Verr.) (Nos. 416-418), and the European species, *Ensis ensis* Linn. (No. 419) have a long razor-like shell covered when young (No. 416) with a glossy horny layer, but which is often partly worn off in the adult (No. 417). This animal travels rapidly through the sand as can be proved by any one who attempts to dig it up. Notwithstanding this fact, the horny layer is seldom found entirely worn off. The model (No. 418) shows the adult animal with the mantle

extended from the shell; at one end is the siphon and at the other the foot (Nos. 417, 418).

*Donax scortum* Linn. (No. 420), is triangular in shape. The hinge area has two cardinal teeth on one valve and one on the other that fits between the two. The two marginal teeth fit into depressions. A rounded ligament is external.

*Cardium edule* Linn. (No. 421), is represented by shells of different ages. At first the shell has shallow grooves or plications, but these grow deeper and cause the shell to be thicker and stronger. The hinge has both transverse and parallel teeth. The umbos are close together and the ligament is external. The muscle impressions are distinct, but the mantle mark is often obscure, while there is no siphon impression, although the animal has a short siphon. In *Cardium* the foot (No. 422, *C. aculeatum*) can be suddenly bent so that the animal leaps through the water.

The changes in color of the external horny layer are finely illustrated by *Cyprina islandica* Lam. The young (Nos. 423, 424) is light brown in color. This becomes a rich shade of brown in the adult, while in the old shell (No. 424, specimen at the right) it is nearly black, and so brittle that it can be easily scraped off (No. 424). The ligament is partly internal and the hinge has three cardinal teeth besides the marginal teeth. The two muscle impressions and the mantle impression in this shell are often distinct but the short siphon makes no mark.

*Cytherea* (= *Venus*) *verrucosa* Linn. (No. 425), is a large plump shell when full grown with prominent beaks, behind which is a large external ligament. The well developed hinge area has three cardinal teeth. The shell is porcellanous like most of the more specialized shells, with both muscle, mantle, and siphon marks well shown. Smith says<sup>1</sup> that one species of this genus (*C. torresiana*) has the posterior end broader in the early stages than

<sup>1</sup> Chall. Rep., Zool., XIII, part 35, 1885, p. 119.

the anterior end, while in the adult it is narrower. This indicates a development of the forward or head end of the body.

*Hysteroconcha lupanaria* Less. (No. 426), is instructive as showing how age affects the development and increase of spines, ridges, and projecting shelves. The young shell is smooth. In the nepionic stage the spines are short. They appear to be formed by the shell layers meeting along two ridges on the posterior end and being prolonged in such a way as to leave a groove on the upper side of the long tapering spine; in these grooves foreign particles are often caught.

A unique specialization of the Pelecypods is found in the Cretaceous Coralliochama (No. 427, *C. orcutti* White), and Radiolites (Pl. 428). In Coralliochama one valve is deep and more or less distorted, while the upper valve is convex (see No. 427). In Radiolites the upper valve is flat and serves as a lid or cover. These Pelecypods may be related to the Chamidae.

Specialization has gone on in *Tridacna crocea* Lam. (No. 429). As the circular young shell grows older, the wavy lines become ridges and the shell lengthens in an antero-posterior direction. This species in the adult stage is colossal in size and all traces of the young shell are lost. The same tendency is observed in *Chama lazarus* Linn. (No. 430) where the originally smooth shell quickly becomes ornamented, the edges of the layers of shell extending into short, broad, flat spines.

#### Section 8. — GASTROPODA.

The earliest larval stage of existing Gastropods is the trochophore which is so strikingly like the trochophore of Pelecypods already described that the two probably arose from a common ancestor. As a rule the tiny cap-like shell of the Gastropod becomes a cone, as seen in

Pl. 431. This stage succeeds the trochophore, and is known as the veliger—a characteristic stage in the development of Gastropods. The ciliated velum still exists and the foot is also formed.

In most Gastropods this cone-like shell becomes a spiral, but in Chitons (No. 432, *C. magnificus* Desh.), which may be primitive Gastropods,<sup>1</sup> the one-valved shell is made of eight pieces. In No. 433 these pieces are separated and are seen to be essentially alike.

Chiton existed in the Silurian age and has undergone comparatively little change since that time. The animal agrees with many Pelecypods in being bilaterally symmetrical. On the other hand, the head is indistinctly marked off from the rest of the body and there is a well developed lingual ribbon (an apparatus for eating) which is possessed by Gastropods.

The cone-like shell may be represented by Tryblidium (Pl. 434, *T. nycteis* Billings) from the Cambrian, which had a smooth cap-like shell when young with an entire margin, becoming in the adult like a shallow cone (Pl. 434, fig. 1) with the apex placed near the forward end (fig. 2).

As we have just said, the cone of most young Gastropods becomes a spiral and this youngest spiral shell or protoconch (Pl. 435)<sup>2</sup> is smooth, rounded, and light colored. It is formed at the apex of the shell but is usually broken off and lost.

In the Ordovician fauna, Pleurotomaria (No. 436, *P.*

<sup>1</sup> Conflicting views are held in regard to the position of the Chitons. Some naturalists place them before the Pelecypods, while others assign them a position between the Pelecypods and Gastropods. They are here placed provisionally among the more primitive Gastropods.

<sup>2</sup> Although this is the protoconch of Fulgur, (see p. 223 and Nos. 462-465), a more specialized species than those we are now describing, yet it is placed here for the purpose of showing the general characters of the Gastropod protoconch.



*sulcomarginata*) occurs, which was a coiled shell consisting of a few whorls with a slit in the margin of the aperture, that was either filled as the animal grew older, making a continuous band, or partly filled giving rise to openings.

In the Silurian and Devonian ages, *Platyceras* (No. 437, *P. erectum* Hall) existed, the apex of which was twisted so as to form a spiral while the later whorl was flaring, showing a tendency to uncoil,—an old age or gerontic character.

In the group of Gastropods represented by *Tryblidium*, *Pleurotomaria*, and their descendants *Patella*, *Haliotis*, etc., there seems not to be any primitive genus with a cap-like shell in the adult stage. Neither is there a genus with the loosely-coiled shell, the transitional form between the cap and the close spiral, such as is found in the class of Cephalopoda.

Both *Patella* and *Fissurella* were formerly supposed to be primitive members of the group to which they belong; but in reality they are found to be specialized forms. This is proved by their development, which in the case of *Fissurella* has been figured and described from the egg to the adult stage.<sup>1</sup>

Since the adult *Patella* is less modified than the adult *Fissurella*, it will be briefly described.

We pass over the development of the egg and the formation of the embryonic nautiloid shell figured by Patten,<sup>2</sup> and come to the patelliform stages of the shell. In one of the simplest Patellidae, *Acmaea*, the shell is without ribs, spines, or ornaments of any kind, and one species, *A. punctulata* Gmel., is conical when young though it is depressed like most of its group when full grown.

In *Helcioniscus exaratus* Nutt., often called *Patella* (No. 438), the perfect shell is smooth at the apex, but

<sup>1</sup> Boutan, Arch. de Zool. Expér. et Gén., ser. 2, III, suppl., 1885.

<sup>2</sup> Arbeit. zool. Inst. Univ. Wien, VI, 1886.

later becomes ribbed or crenulated. In all the shells the margin is entire. The adult of *Helcioniscus* has a circular foot, and the functional lamellar gills which are called pallial gills lie in a groove between the foot and the mantle. These are really secondary gills, as the original breathing organs exist as mere remnants on each side of the neck. The heart of *Helcioniscus* consists of a single auricle and ventricle.

The eggs of *Fissurella* (Pl. 439, figs. 1-12) are joined together by an albuminous substance which swells in water to a large size, like that in which frogs' eggs are embedded. These eggs (fig. 1) are not laid through the apical hole, as has been supposed, but through the anterior opening of the branchial chamber. The egg passes through the usual stages of segmentation until the embryo (fig. 2) with velum, beginning of foot, primitive mouth, and invaginated shell gland is attained.

While the embryo is still within the egg, the shell is formed (fig. 2). At first it is made of particles of lime separated from each other; afterwards these become consolidated, and the shell exhibits a lace-like pattern. Since the characteristic twisting of the embryo has already begun, the shell is asymmetrical, and the little embryo has the characters of a young *Gastropod*, *i. e.*, a coiled shell, a ciliated velum, and a foot (figs. 3, 4). When still older, the shell possesses an operculum (fig. 5).

When the embryo leaves the egg, the last vestiges of the velum remain and aid the foot in locomotion. The embryonic shell is not replaced by another but is persistent. Its margin begins to spread out, and the new layers take on markings very different from the plain embryonic shell (fig. 6, dorsal view; fig. 7, ventral side). At this time the foot is long and narrow, and the long tentacles have eyes at their bases. Up to this time the margin has been entire, like the margin of *Patella*, but soon a slit appears (fig. 8). Gradually this slit is surrounded by shell layers whereby it is converted into a

hole, while the coil portion of the shell becomes reduced in size and is carried towards the posterior end (fig. 9). This is seen on the edge of fig. 10, which is a ventral view showing the foot, eyes, radula, and mantle. With the growth of the shell the hole approaches the summit (fig. 11), until finally it occupies a nearly central position with the vestige of the coiled shell behind it (fig. 12). Thus it is seen that the symmetry of the adult (fig. 12; see also No. 440) is not primitive but is secondarily acquired.

A fold of the mantle lies in the slit, and later occupies the hole. It is thought to have an excretory function, and if so, it serves as an anal siphon. *Fissurella* has the original gills fully developed, one on each side of the neck. The nephridia are also present. The heart has two auricles and a ventricle.

Some specimens of the Stomatellidae are limpet-like, while others (No. 441, *Stomatella imbricata* Lam.), have a spiral shell without perforations and with a large aperture.

The young *Haliotis* has an imperforate shell, but in the course of development a slit occurs in the margin of the aperture through which the siphon is extended. With the growth of the shell this slit is not continuous but a series of holes is formed (see Nos. 442, 443) some of which, according to Cooke, admit water to the gills, while others are anal in function. With the growth of the animal the first formed holes tend to become filled with a limy deposit. The primitive gills and excretory organs or nephridia are in pairs although the beginning of the spiral has brought the anus from the posterior end of the body towards the anterior median line.

The specimen of *Crucibulum* (No. 444, *C. striatum* Say), exhibits the fleshy body in the shell with its mantle and muscular foot. The anterior part of the body has become differentiated to form a head (see No. 444) which bears sense organs. This specialization of the Gastropods in general shows a marked advance over all the classes of animals so far described.

The shell of *Crepidula* (No. 445, *C. nivea* C. B. Adams), is slightly coiled and the last whorl is large and flaring like that of *Haliotis*. In the inside a projecting horizontal wall covers the posterior half of the shell. No. 446 shows the peculiar habit these animals possess of growing on top of one another. Sometimes one species of *Crepidula* (*C. plana* Say) takes possession of the inner side of a univalve shell, often *Lunatia heros* (No. 446). Five or six different stages are seen in this specimen. The young shells are round and smooth, as compared with the adults, which are long, narrow, and extremely flat. Owing probably to the hidden situation in which they live, they are nearly colorless.

The gills in the family Calyptraeidae, to which *Crepidula* belongs, are much more like Pelecypod gills than are those of most Gastropods. The lamellae are long and much like filaments and are strengthened by chitinous rods.<sup>1</sup>

Since the primitive or embryonic shell is uncoiled and imperforate, and in shape like a cap or the beginning of a cone, we know that the spiral condition is a secondary one. It would seem most probable that before the perfect spiral form was attained the cone would be loosely coiled, and that only after many generations and a long period of time could we have the complete amalgamation of the inner wall of a whorl to the preceding whorl which marks the tightly coiled spirals of many existing species. Since, also, the primitive shell is usually both smooth and colorless or nearly so, it follows that the highly ornamented and brilliantly colored shells are far removed from the primitive form. The ontogeny of many Gastropods has not been worked out, so that it is impossible to give a classification which shall show the genetic relationships of all the different species. It is most probable that the ancestral form, represented by the embryonic shell of

<sup>1</sup> Dall, Bull. Mus. Comp. Zool., XVIII, 1889, p. 285.

many existing species, gave rise to different branches, each one of which has passed or is passing through a straight, a loosely coiled, and a tightly coiled stage. In such a case we should have many similar forms which are not closely related genetically but which are examples of parallelism. In a natural classification these hold their rightful position between the primitive and the more specialized members of their respective groups.

Such a classification is not based upon the structure of the shell exclusively, inasmuch as the shell is a tell-tale part of the organism; generally speaking, a straight shell has a straight body within it, and a coiled shell a coiled body. The straight body has the bilateral symmetry characteristic of early stages of animals, while the coiled body has succeeded in making such a twist in its organs as to bring the opening of the alimentary canal at the anterior instead of the posterior end. This twisting is indicative of complexity, and removes the form possessing it from its primitive ancestor. We shall illustrate the possible evolution of the Gastropod organism from straight through loosely to tightly coiled and involute forms. Future research will not probably change the principle of classification, though it will doubtless bring the special forms selected into genetic relations, so that each will hold its proper place in its own particular series. We can readily conceive of a straight tube becoming coiled so that the whorls would barely touch one another. In this case the resultant form would be a smooth unornamented spiral. In the loosely coiled shell of to-day the margin of the aperture has a reflected lip as in Scala (No. 447, *S. pretiosa* Linn.). This shell shows how a tube may be twisted so that the whorls scarcely come in contact. The first whorl (No. 447) is nearly smooth, but each successive whorl shows an increase in the size of the ridges till they look like projecting shelves extending entirely around the tube. By examining the opening, it is seen that a shelf is in reality the lip of the aperture which is made by the mantle during a period of rest.

*Solarium modestum* Phil. (No. 448), exhibits a much closer coiling of the tube. The youngest portion of the shell which is always at the apex is smooth and polished (No. 448). Each succeeding whorl becomes consolidated with the preceding one on the inner side, but in turning round, the tube leaves so large a space in the middle (called the umbilicus) that one can see nearly to the apex of the shell (No. 449, *S. perspectivum* Lam.).

*Surcula australis* Roissy (No. 450), looks like an ineffectual attempt to make a perfect spiral. The revolving bands and lines are often broken where additions have been put on at the margin. In this way the apertures of the younger shells can be easily traced and the length of the successive canals ascertained. This irregularity is chiefly due to the anal slit in the posterior end of the aperture which reminds one of the slit in *Pleurotomaria*, *Haliotis*, and the like. Most of the members of the family *Pleurotomidae* to which *Surcula* belongs, are without a horny or calcareous operculum for closing the aperture, and this is a characteristic of the deep-sea forms where the struggle for existence is reduced to a minimum and where therefore there is little need of protection from other animals.<sup>1</sup>

The shell of *Lunatia heros* Adams (No. 451; see the lowest shelf of the erect portion of Section 8) is a simple spiral of a few turns, and is open nearly to the apex. The shell is thin and covered by a yellowish brown layer which is usually more or less worn off. As the shell increases in size it becomes thicker. Those living on the outer beaches where the waves break with force are much larger and stronger than those in quiet waters. The specimen (No. 451) shows the large size of the foot and the mantle extending over the edge of the shell. This foot can be completely withdrawn into the shell and the aperture closed by a horny operculum.

<sup>1</sup> Dall, Bull. Mus. Comp. Zool., XVIII, 1889, p. 455.

One of the distinctive organs of the Gastropods is the lingual ribbon or odontophore (No. 452, odontophore of *Lunatia heros*). It is a band armed on the upper side with chitinous teeth and attached at the back of the mouth; the forward end is free. It is used as a rasping and scraping organ in obtaining food. One of the many classifications of the Gastropods is based on the structure and variations of the odontophore.

Like *Lunatia*, *Natica hebraea* Mart. (No. 453), is a simple spiral but the umbilicus contains a solid pillar or columella round which the whorls of the shell turn. No. 454 (*Neverita duplicata* Stimp., see lowest shelf of erect part of Section) shows still better than *Lunatia* the greatly distended muscular foot. It seems incredible that so large an organ can be contained in so small a shell.

An instructive series is furnished by *Polinices* (No. 455, *P. mamilla* Linn.): (a) is the young shell showing the open umbilicus; a wire thrust into this opening reaches upward nearly to the apex; (b) has the umbilicus still visible though the wire does not penetrate so near the apex, showing that the umbilicus is becoming filled by the columella which adheres to it and is spirally twisted; at this stage the inner lip has a sharp edge. In (c) the umbilicus is entirely concealed by the thickened inner lip; in this specimen the horny operculum is in place; the lines of growth near the margin are fine and close together while in (d) which likewise has the umbilicus concealed, the lines of growth are coarser. No. 455 e, is probably a reduced form; although about a third smaller than (d), its weight is essentially the same, and a thick heavy deposit is laid on over the umbilicus. This series shows that the open umbilicus is a primary condition and the concealed umbilicus is secondary. This furnishes a good phylogenetic reason for placing those shells with the open umbilicus as more generalized in a system of classification.

The next group of plain but tightly coiled shells with-

out umbilicus is represented in the Collection by a number of specimens which may belong, as we have already pointed out, to as many different series.

Ianthina has a spiral shell resembling Lunatia in shape. It is translucent with violet colored areas. This mollusc makes a swimming float of cartilaginous air sacs which serves to keep it at the surface. To the under surface of this float are attached the egg capsules (see No. 456).

The egg cases (No. 457; see erect part of Section) of *Buccinum undatum* Linn., are in masses. The shell is closely coiled and ribbed at right angles to the lines of growth (see No. 458).

*Turbo setosus* Gmel. (No. 459) begins as a smooth, colorless or yellow shell, then becomes ridged and is of a vivid green color, while the older whorls are dark green, marked by reddish brown spots. The aperture is entire. *Litorina littorea* Linn., has been imported from Europe, and in 1872 appeared in Massachusetts; since then it has spread with remarkable rapidity. The British form (No. 460, *L. obtusata* Linn.), is a smooth spiral without an umbilicus. The shape varies like that of most littoral species, some specimens having a spire of three or four whorls, while in others the spire is depressed so that all the whorls excepting the last or body whorl are on a horizontal plane. Our New England species generally has a sharp spire and revolving lines on the whorls, while the color is a dingy brown or red. The external horny layer when fresh is a chestnut brown.

*Cyclostoma elegans* Drap. (No. 461 model), is similar to *Litorina* in many structural points but it has become more specialized by losing gills and breathing air by means of lungs. In a classification based strictly upon the structure of the breathing organs the *Cyclostoma* would be placed with the Pulmonifera, but it is not probable that this would indicate its relationships. The model represents the animal with the foot expanded; at the anterior end is the head with two tentacles extended, at the base of which are the eyes.



*Fulgur* (Nos. 462-465, *F. canaliculatum* Say), places its eggs in horny sacs or capsules which it fastens together in a long string (No. 463; see lowest shelf). These may be opened and the young (No. 462) observed in different stages of development. The specimens possess a smooth rounded protoconch, so thin and translucent as to show the yellow body within. The succeeding whorl is ribbed, and extends into a long canal giving the shell a pear-like shape which remains essentially the same in older stages (Nos. 464, 465). The model (No. 465, placed on account of size at the back of the Section on the right) shows the large foot extended as in the act of crawling; the head with its tentacles; the mantle on the edge of the shell; and the siphon in the long canal.

Fasciolaria is nearly related to *Fulgur* and its exquisite egg cases are seen in No. 466 (see erect portion of Section). This species (*F. tulipa* Linn.) fastens these flower-like cases to some foreign object, — coral in this instance. Across the free end of the tube, stretches a membrane which opens when the young are ready to escape.

*Magilus antiquus* Mont. is a reduced form, the reduction being due most probably to the habit of living in coral. The young shell (Pl. 467) is a thin spiral of three or four whorls, proving that its more immediate ancestors had a spiral shell. The latter is similar to that of *Natica*, *Buccinum*, and the like, and for this reason it is placed near them. In order to keep on a level with the surface of the growing coral, *Magilus* ceases to revolve, and puts out a long, nearly straight tube (No. 468). As it advances with the new growth it fills up the spiral and tube behind it.

The veliger stage of *Astyris* (Pls. 469, 470,  $\times 100$  diameters; the colors are schematic), shows the large lobed, ciliated velum, so characteristic of this stage of Gastropods, and the spiral shell. The adult (No. 471) has a shell with few whorls. The model represents the animal as walking on the sand with extended foot, tentacles, and siphon.

In *Terebra* and *Turritella* we have illustrations of a perfect spiral of many whorls without projecting ornamentation in the form of spikes or flutings. In *Terebra subulata* Lam. (No. 472), the early whorls are nearly colorless but those succeeding are marked by deep red spots. Both the young and adult shells are smooth, not having even the revolving lines and ridges seen in *Turritella* (No. 473; in this shell the youngest specimen has nineteen whorls and the one with the largest body whorl only sixteen, showing that the youngest whorls are broken off). The margin is entire in both genera. *Cerithium tuberosum* Fabr. (No. 474), has the revolving lines of *Turritella* and in addition the vertical ridges. The margin has a short, slightly recurved canal.

*Vermicularia* begins its life with a tightly coiled shell (see No. 475, *V. spirata* Phil.) that is similar to *Turritella*. Living in the cavities of a sponge it needs to keep at the surface of the growing animal in order to obtain food. It succeeds in doing this by forming a loosely coiled shell (No. 475) or in growing straight. We have here and in *Magilus* similar conditions producing similar results, and both are good illustrations of adaptation of structure to habit.

On the west coast of Florida, *Vermetus lumbricalis*, var. *nigricans* Dall, forms rock-like masses, as shown in No. 476 (which, on account of its size, is placed at the back of Section 8). When in the water the tubes are erect. The greater part of each tube is straight though some of the tubes show a spiral structure at the smaller end.

*Gyrineum spinosum* Lam. (No. 477), has a colorless, smooth, snail-like spiral at the apex, the general appearance of which is distinctively unlike the succeeding whorls. The latter are somewhat flattened and have vertical ridges or varices with intervening short knobs and spikes. According to Adams the shells that are armed with these knobs are found in rocky places, while the smoother specimens come from deep waters.

Murex (No. 478, *M. tenuispina* Lam.), is an illustration of a specialized shell of this group. In this species the protoconch is preserved as a tiny white pearly shell. Extending below this are two or three whorls with ridges but without the long slender projections which ornament the succeeding whorls to an extreme degree.

*Conus bandanus* Brug. (No. 479), is like an inverted cone, the last whorl being large and making most of the cone. The number of whorls can be indistinctly traced, encircling the apex at the broad posterior end. The aperture is neither notched nor drawn into a long canal.

*Trochus* (= *Tectus*) *fenestratus* Gmel. (No. 480), is a tightly coiled tube, the whorls increasing in number and being uniform in ornamentation.

*Aulica deshayesi* Reeve (No. 481), is an instructive species since the protoconch is so large that its distinctive characters can be seen and thereby the ancestral form of the genus determined. This embryonic shell is a plump, globular spiral, light colored and smooth, and revolves in a different plane from the rest of the shell. One can distinctly make out where the nepionic stage begins by noting the origin of the revolving lines and vertical ridges. The ephebic stage lasts until the ridges begin to disappear, as seen in No. 481. The vertical markings become coarser, which are characters of the gerontic stage. *Oliva erythrostoma* Lam. (No. 482), is similar in the different stages, as shown in the specimens, but by examining the apex, a colorless translucent spiral is seen which represents the ancestral form. The last whorl constitutes most of the visible shell, but the number of whorls encircling the apex can be easily counted. The specimens show considerable variation in color.

The resemblance of *Oliva*, *Aulica*, and the like to the young *Cypraea* argues for a close relationship between these forms.

In *Cymbium cymbium* Linn. (No. 483), the apex is smooth and flattened, and only two whorls are visible.

The shell is notched and the animal has a short siphon. According to Adanson<sup>1</sup> many living *Cymbia* were found with living young in their bodies, thus proving them to be viviparous. The young (there are only four or five in each *Cymbium*) leave the mother when the shell is an inch long.

*Strombus costatus* Gmel. is a plain spiral in which the whorls can be readily counted. The aperture of the adult extends upward on the preceding whorl and becomes flaring with a recurved canal. No. 484 is an antero-posterior section through the middle of the shell, showing the internal structure, and No. 485 is a cross section of another species, *S. gigas*.

*Pteroceras lambis* Linn. carries this mode of development farther than *Strombus*. It is illustrated by a fine series (No. 486) showing marked changes between the young and adult stages: (a) is a plain spiral having a long, narrow, notched aperture with a thin, sharp, unornamented margin; (b) is the dorsal side, showing yellowish color banded with red; (c-f) all exhibit the plainness of slightly older shells. In (g) the margin of the aperture extends toward the apex as in *Strombus*, and in (h) and (i) it goes beyond it, changing essentially the shape of the shell and giving a wide, flaring aperture with a canal at either end. The margin becomes fluted at first and afterward extends outward in long, half open canals which finally become closed solid spines<sup>2</sup> (see j and k).

*Phalium inflata* Shaw (No. 487), has the first whorls light colored and plain; those succeeding may have the marks of the lip or not, one being without them and two having them. The canal is short and instead of being prolonged as in *Murex*, it is sharply recurved.

No. 488 is a section of a small specimen of *Cassis cameo* Stimp. *Cassis* grows to a large size and is much used in making cameos.

<sup>1</sup> See Adams, *Genera of Moll.*, I, 1858, p. 158.

<sup>2</sup> Adams, *loc. cit.*, I, p. 260.

The series of *Cypraea cervus* Linn. (No. 489 a-c) is extremely instructive. The young shell (a) is a spiral in which the number of whorls can be easily counted. A still earlier stage, of which there is no specimen, is a simple, thin, snail-like spiral (Adams). The shape of (a) is similar to *Oliva*, *Cymbium*, and the like. The aperture is also long with a thin, sharp, untoothed, and unornamented margin, and a slight notch at the anterior end. In (b) the shape has changed, the margin of the aperture has thickened and turned inward, while both sides of the opening are toothed and both ends notched. In (c) only vestiges of the spiral remain, which no one would recognize who had not seen the younger stages; thus the shell has taken on a character that separates it from those previously described and which places it with the more specialized forms. If a vertical section of the shell is made, the whorls are seen inside (No. 490, *C. exanthema* Linn.) concealed by the last body whorl. No. 489 c is of remarkable size and is lighter in weight than some of smaller size.

It is thus seen that the development of *Cypraea* is an epitome of the life history of those Gastropods which have a simple, snail-like spiral in adult life, and of those with the modified spiral of *Oliva* and *Cymbium*.

A still more specialized form is *Cypraea mauritiana* Linn. Its development is shown in the series No. 491. The first six specimens would hardly be called the young of the last six, so unlike are they in shape and coloring. In the youngest specimen in the series, the spire with its small whorls and large body whorl is seen. The shell is now strikingly like *Oliva*. The long aperture has a sharp margin which as yet has not turned inward. In the older stages the shape changes; the early spiral is concealed by the enamel which the mantle has laid on. There are two broad, thick, flat, toothed lips with a narrow aperture and a canal at either end. The two largest specimens have grown high vertically, and this peculiar

shape with the flattened lips makes the shell more specialized than those of the other species of *Cypraea* already described. *Cypraea* is a transitional form between those shells that have the external spiral represented by the young and those which have the spiral partly or wholly internal, being covered by the growth of the later whorls.

*Ultimus gibbosa* Linn. (No. 492), does not show even in youth any embryonic shell or spiral. The shell revolves so that each whorl covers the preceding. The margin of the aperture is thin and easily broken. In course of growth the margin thickens and turns inward, so that the adult has a strong incurving lip.

A related species, *Simnia acicularis* Lam. (No. 493), offers a striking example of mimicry. In the present instance it has taken on the uniform deep purple color of the coral on which it lives. When it chooses the yellow coral, *Rhipidogorgia*, for its home, it assumes the yellow color, and on white coral it is nearly white. Its foot is narrow and well adapted for clinging to the coral.

Transitional forms between marine Gastropods and fresh-water or land species are found in *Nerita*, *Neritina*, and the like. The transition from the one to the other is governed by natural causes which we have already found are not difficult to explain.

The youngest portion of the shell of *Nerita versicolor* Gmel. is yellow, smooth, and unmarked by color spots, as seen in the first whorl of No. 494. In the next whorl the surface is ridged, and the color is nearly white marked by dark irregular spots. The teeth on the left of the aperture are barely indicated and none are seen on the right side. In (b) the ridges are more pronounced and there are suggestions of teeth on the right side. In (c) the youngest portion is colorless, as is the case with a number of the older forms; (e) has a predominance of red color over the darker shade of the youngest shell, and the teeth on both sides are well developed; (g) and (h) illustrate the variation in color from a light to a dark

shell. This subject of color variation in a single species is shown still better by *Nerita peloronta* Linn. (No. 495). Here we have nineteen shells varying from a nearly white shell spotted here and there with pink to a dark purplish shell apparently banded and spotted with lighter shades. The youngest stage in all the specimens is either white or yellow, without spots or bands, and is smooth; (y) and (z) are in their natural state, while the others have been boiled in caustic potash for about ten minutes, so that these bright colors are not seen in the living animals; (z) is an adult which is mounted to show the bright red spot near the large tooth that has given the name of Bleeding Tooth to this species, and also the operculum which is in place and is deeply colored. (q) is an illustration of albinism, the spot that is usually blood red being nearly colorless.

*Neritina* (No. 496, *N. canalis* Sowb.), is a genus of especial interest since some of the species live in the saltiest of sea water, that of a lagoon, while most are either brackish or fresh-water or land animals. Certain marine species are practically land animals, since they live where they cannot be immersed in water excepting at extremely high tides, and even then they would not be covered unless the waves dash upon the rocks where they live. Adams<sup>1</sup> speaks of some species living in trees overhanging water.

The shell of *Neritina canalis* Sowb. (No. 496), is covered by a thick, dark brown horny layer which, when broken off, reveals a shell of peculiar whiteness.

*Pulmonifera*. Many Gastropods that were originally marine animals have doubtless become in the course of many generations, and a longer or shorter period of time, fresh-water or land animals. Most of these now bear the name of Pulmonifera, since they no longer breathe air dissolved in water, but are equipped with

<sup>1</sup> Genera of Moll., I, 1858, p. 381.

primitive lungs in the form of a pulmonary sac or cavity. As a proof that the Pulmonifera are more specialized than the groups already described, it may be stated that many Pulmonates fill their lung sac with fresh water in the younger stages and only later in life dispense with the water. There are objections to the use of the term Pulmonifera, since some of the air-breathing Gastropods (Cyclostoma, for instance; see No. 461) are so different in structure from the typical Pulmonifera that they cannot be placed in this group but are specialized air-breathing members of more generalized groups.

As a rule the shells of the Pulmonifera do not attain that brilliancy of coloring and that extreme ornamentation which may be observed in their marine ancestors.

Among the fresh-water and land Gastropods there are no forms possessing the straight cone-like shell, but the shallow cup of Patella and the spiral of Crepidula are represented by Ancylus and Gundlachia. These Gastropods have habits similar to those of their marine relatives and the structure is similar. We have not found a spiral so loosely coiled as Scala; the majority represent the group of tightly coiled plain spirals, the chief difference between the genera being in the plane of the coiling.

*Ampularia globosa* Swains. (No. 497), is a simple spiral with a small umbilicus, holding a similar place among fresh-water univalves that Lunatia holds among the marine. The glossy, horny layer of this genus is striking, reminding one of this finely developed layer on fresh-water bivalves. The operculum of the young and the adult shell is not spiral, but the additions are made concentrically (see No. 497).

In this genus the left gill is vestigial, the mantle cavity having a large pulmonary sac on each side. These molluscs are amphibious, being able to live a long time out of water.

Another fresh-water form is the pond snail, *Limnaeus stagnalis* O. F. Müll. (No. 498). It comes to the sur-



face for air, but whether this is a necessity for maintaining life is not yet settled. The model shows the long respiratory tube containing bubbles of air which the snail extends from the respiratory opening to the surface of the water. The tentacles are flattened, as seen in No. 498. When ponds dry up, these snails bury themselves in the mud and in this situation can live for a considerable time.

*Planorbis corneus* Linn. (No. 499), is a good example of a shell coiled on a horizontal plane. The whorls are few in number and the aperture is entire and flaring. *Polygyratia polygyrata* Bonn. (No. 500), is a still better example of a horizontal spiral consisting of eight closely coiled whorls with the ninth unfinished. The aperture like that of *Planorbis* is entire.

*Campeloma* (No. 501, *C. decisa* Say) and *Melania* (No. 502, *M. hastata* Lea), are exceptional Gastropods, inasmuch as both are viviparous. Vivipara (= *Paludina*) carries its young about with it for three or four weeks after birth.

The land Gastropods are represented by a number of species. *Helicostyla leai* Pfr. (No. 503), is a smooth beautiful white spiral of three or four whorls. The aperture is entire, and there is no umbilicus. The eggs of this genus are protected by a limy shell so that they resemble those of birds.

*Helix* (No. 504) is one of the commonest land snails. The youngest shells (see No. 504) are so thin and fragile that they can be easily crushed between the fingers. The margin is sharp and lipless. When older the shell is stouter with a thick white lip (No. 504). The last specimen in the upper right hand corner is reduced, being small in size but provided with the thickened lip. The adult animal (No. 505, *H. hortensis* O. F. Müll.; No. 506, *H. pomatia* Linn., see topmost shelf), is represented with foot extended, and with the shell containing the spiral portion of the body in normal position when the snail is crawling. The head has two pairs of tentacles, and the

black eyes are distinctly seen at the ends of the longer pair. No. 507 is a model showing the internal organs of *Helix pomatia* Linn. The various parts are marked; those on the left are the buccal body, esophagus, salivary glands, stomach, liver, intestine, and the pulmonary chamber; and those on the right the reproductive organs and slime glands.

The land Gastropods most specialized by reduction are the slugs, represented by *Limax* (Nos. 508-511). Here the shell is reduced to a thin, flat plate on the back (see model of *Limax maximus* Linn., No. 508), and this has become internal. The spiral body of most Gastropods no longer exists, but the body of the slug is long with the foot on the ventral side (No. 509, *L. flavus* Linn.). The preparation (No. 510) shows the general anatomy of *Limax rufus*, while the genital organs are seen in No. 511.

Section 9 of Case B is taken up with the Tectibranchs, Nudibranchs, Scaphopoda, Heteropoda, and Pteropoda. These are considered as so many groups of molluscs which have become modified, each in its own special and distinctive way, to meet the requirements of existence. The Pteropods are probably the most specialized, and the most closely related to the Cephalopods; but on account of their minute size, they are placed in the horizontal part of Section 9. Here they can be seen and studied more easily than in the erect portion, where, according to our system, they properly belong.

Some of the Tectibranchs have well developed shells, like Tornatella (No. 512, *T. solidula* Lam.) and Bullus (No. 513, *B. oblongus* A. Adams), while in others (Aplysia, No. 514, see erect part of Section, No. 515, and Pleurobranchus, No. 516) the shell exists only as a vestige. Tornatella (No. 512), reminds one of Oliva (No. 482) with its short spire and large body whorl. Bullus (No. 513) even when young shows no spiral form, but if a cross section of the shell is made near the posterior end the

spiral is seen within. Every whorl entirely conceals the preceding, as we have seen it in *Ultimus* (No. 492).

The "sea-hare," *Aplysia* (No. 514, *A. limacina*; No. 515, *A. inca* d'Orb.) has only the remnant of a shell on its back in the form of a concave plate, and this is concealed by a fold of the mantle. On the dorsal side the mantle grows out into two large folds, called epipodia (see Nos. 514, 515) which are used in swimming. The single branchia is on the back protected by the mantle. The model (No. 515) represents the animal as crawling on its long ventral foot. Garstang<sup>1</sup> has pointed out the interesting fact that young *Aplysiae* in migrating during growth from deep water to the shore pass through algae colored first red, then brown, and finally olive green, and that these animals change their colors from red to green in accordance with their surroundings.

The shell is reduced and concealed by the mantle in *Pleurobranchus* (No. 516, *P. grandis* Pease). *Lobiger* (No. 517, *L. picta* Pease), has a small shell on its back and two pairs of wing-like swimming organs extending from the sides of the body.

#### NUDIBRANCHS.

The Nudibranchs pass through a trochophore and veliger stage in their development. They possess a spiral or nautiloid shell before they leave the egg, and the body at this time is more or less spiral in form. During the growth of the larva the shell disappears and the animal extends lengthwise. The possession of a shell in the embryo is evidence that the Nudibranchs have descended from Gastropods with spirally coiled shells. According to Kingsley<sup>2</sup> the twisting or torsion of the body has not been carried to its full extent, which would indicate a primitive

<sup>1</sup> Journ. Mar. Biol. Assoc., n. s., I, 1889-90, p. 411.

<sup>2</sup> Stand. Nat. Hist., I, 1885, p. 295.

condition. But inasmuch as this torsion is greater in the embryo than in the adult, the less degree of twisting is a reduced rather than a primitive characteristic. The asymmetrical condition of the heart and the nephridium prove that the bilateral symmetry of the adult is also a secondarily acquired and not a primitive condition. Gilchrist<sup>1</sup> has shown that, while the original bilateral symmetry is apparently assumed, the organs which were lost on one side in the twisting of the straight body into a spiral are never again developed.

Not only has the Nudibranch lost its shell, but in some species the mantle has disappeared.

In other ways this group has become peculiarly specialized. Many Nudibranchs are without true tentacles, while most have organs called dorsal tentacles or rhinophores which are supposed to be organs of smell. The branchiae are not like the gills of most molluscs, but are secondarily acquired, respiratory organs, and are often called cerata to distinguish them from the primitive gill. These branchiae vary greatly both in shape and position and are often extremely beautiful organs.

*Eolis* (= *Aeolis*) *coronata* Forbes lays its eggs in a close-set spiral coil of four volutions (Pl. 518, fig. 1; fig. 2, a portion of the same magnified, showing the eggs imbedded in a gelatinous thread). The larva (fig. 3) is provided with a spiral shell (fig. 4), which is closed by an operculum. At this stage the larva has the two ciliated oral lobes which aid in locomotion. With the growth of the animal the shell and operculum disappear and the oral lobes are either modified or wholly absorbed. The mature *Eolis* (fig. 5, upper side; fig. 6, lower side; No. 519, *E. papillosa* Lovén), has a long slug-like body wholly unprotected by a calcareous or horny shell. The forward part bears a pair of tentacles, and also a pair of rhinophores or dorsal tentacles. Along the back the brilliantly col-

<sup>1</sup> Proc. Roy. Soc. Edinburgh, XX, 1895, p. 368.

ored branchiae are arranged in six clusters, each cluster consisting of many papillae. These branchiae are liable to fall off, and sometimes a whole cluster is wanting. In *Flabellina* (No. 520, *F. janthina* Angas), a related form, the branchiae are numerous and tube-like, as they are also in *Spurilla neapolitana* (No. 521).

The branchiae in *Glaucus longicornis* Reinh. (No. 522), are in the form of clusters of long slender filaments on either side of the tapering body. These branchiae are not only respiratory organs but are used for swimming when the little creature with ventral side uppermost darts through the water.

*Tethys leporina* Linn. (No. 523), is a Nudibranch of rare beauty. It is nearly transparent, with light and dark red spots. The forward part is broad and has a delicate fringe. The dorsal tentacles are leaf-like and the branchiae extend down the body on either side. At the posterior end the mantle is extended into an excurrent siphon. *Melibe* (No. 524, *M. fimbriata* Ald. & Hanc.) has the head differentiated from the body; it bears two prominent dorsal tentacles enlarged at the end. The body is covered with papillae, and along each side are large club-shaped branchiae, which after the first pair are placed alternately.

*Dendronotus arborescens* Müll. (No. 525), is similar in many respects to *Eolis*. When young it is nearly colorless, but the adult is subject to much variation in color; usually, however, it is reddish, as seen in No. 525.

The head is provided in front with branched appendages. Above are the dorsal tentacles which can be withdrawn into sheaths. Along each side of the body are the arborescent branchiae. The long tapering foot is well adapted for clasping seaweed and is used in this way as well as in crawling.

*Scyllaea marmorata* Ald. & Hanc. (No. 526), is a small Nudibranch with two pairs of gills. The animal resembles the *Sargassum* sea-weed in which it lives, and

its long narrow foot with thin and flexible sides is well adapted for clasping the stems of algae.

The branchiae in Pleurophyllidia (No. 527, *P. semperi* Bergh), consist of leaf-like organs on each side of the body between the foot and the dorsal portion of the mantle. In Doris (No. 528, *D. nubilosa* Pease) they form a circle around the anus and are retractile, while in Trevelyana (No. 529, *T. cristata* Bergh) and Plocamophorus (No. 530, *P. imperialis* Angas) they are not so completely retractile, although according to Eliot,<sup>1</sup> they retract when touched in the living animal, but remain outside in alcoholic specimens.

Among the Nudibranchs that have lost both shell and branchiae are Phyllobranchus (No. 531, *P. orientalis* Kol.) and Elysia (No. 532, *E. chlorotica* Gould); while in Pontolimax (= Limapontia) (No. 533, *P. capitatus* O. F. Müll.) no shell, branchiae, nor appendages exist.

It is interesting to note that the law of acceleration in development has brought about a condensation of embryonic stages in two Nudibranchs, *Cenia cocksii* and *Pelta coronata*,<sup>2</sup> so that the veliger stage with the ciliated velum and the shell is omitted from the ontogeny.

#### SCAPHOPODA.

The Scaphopoda are a small group represented by Dentalium (Nos. 534-536). The tube like shell of this genus is not made by the addition of successive layers to the margin of a cone-like embryonic shell, as a primitive Gastropod shell would be formed. On the contrary, the mantle at first consists of two folds which in the process of development come together on the ventral side and

<sup>1</sup> Proc. Acad. Nat. Sci. Phila., 1899, p. 520.

<sup>2</sup> Zool. Anz., XXIII, 1900; quoted in Science, n. s., XII, 1900, p. 824.

make a tube with an opening at each end. The shell formed by the mantle grows in the same way, and is a tube open at either end. No. 534 (*D. entalis* Linn.), shows the animal within the tube. From the larger or anterior end the foot projects. The mouth with the odontophore is at the base of the foot.

Plate 535 represents the fleshy animal as taken from the shell; fig. 1, dorsal view, fig. 2, ventral, and fig. 3, lateral view. The organ colored dark green in the model (No. 536) is the liver; the kidney is at the forward end of the liver, while the generative organs are on one side and are colored yellow.

#### HETEROPODA.

In the Heteropoda the foot is modified in different ways, sometimes being in the form of a vertical fin extending from the ventral side. The variability of the gills is shown by the fact that in this group they are present or absent in species of the same genus and even in specimens of the same species.<sup>1</sup>

*Atlanta peroni* Les. (No. 537), has a glassy shell which is a vertical spiral in the young animal, but which later becomes flattened in one plane. The last whorl increases rapidly in size, and the aperture is flaring. The fleshy body takes the coiled spiral form of the shell and can be wholly drawn into it and protected by the operculum. Around the outside of the shell there is a thin sharp keel which looks at first glance like a delicate membrane.

*Carinaria cristata* has a smooth coiled shell when young (Pl. 538, fig. 1, left side; fig. 2, right side; enlarged). When older the shell takes the form of a conical cap, seen in fig. 3, with flutings on the outer surface. No. 539 is the shell of the adult of another species, *C.*

<sup>1</sup> Tryon, Structural and Systematic Conchology, II, 1883, p. 348.

*lamarcki* P. & L., in which the early tendency to coiling is seen at the apex, while No. 540, *C. cithara* Bens., is suggestive only of the cap-like form. No. 541 is the fleshy animal (*C. mediterranea*), and Pl. 542, a drawing of *C. fragilis* Bory. It is drawn with the ventral side uppermost, the position it often takes in swimming. The body is long and the leaf-like fin (see No. 541) which is a modified foot is seen above, while below, the visceral mass consisting of liver, kidney, heart, reproductive organs, etc., is reduced in size and covered by the small shell (No. 541).

The more specialized Heteropods are represented by Pterotrachea (No. 543, *P. mutica*; No. 544, *P. coronata*; see lowest shelf) in which the body has lost its spiral form and become cylindrical, while the shell has wholly disappeared. The tentacles are also lost and the gills exist only as vestiges.

#### PTEROPODA.

Recent researches point to the conclusion that the ancestors of our present Pteropods existed in the early Palaeozoic times.

A near ally of Tentaculites, *Orygoceras* (Pl. 545, fig. 1, *O. dentaliforme* ?), had a plain unornamented shell. The protoconch is not represented in the figures of this species, but is finely shown in *O. cornucopiae* (Pl. 545, fig. 2). Succeeding the protoconch the young shell of this species is seen to be unornamented like the adult (fig. 1). As the animal grows older the shell becomes ridged by many circular rings (fig. 2).

*Tentaculites* (No. 546, *T. gyracanthus* Eaton; Pl. 547, *T. acuaris* Richt.), has a straight, cone-shaped shell like that of *Orygoceras*, with a simple circular aperture, and with concentric ridges of rings extending around the outside. These ridges are carried back nearly to the proto-



conch by the law of acceleration in development, so that Tentaculites comes naturally after Orygoceras in our classification.

Hyolithes (No. 548, *H. primordialis* Hall), is usually straight, but sometimes curved. Its aperture is triangular and is provided with an operculum. The shell is divided off in the interior by horizontal partitions.

Conularia (No. 549, *C. congregata* Hall), has a very thin straight shell with a four-sided aperture. According to Ruedemann<sup>1</sup> Conularia is at times a sessile form and is found attached to older individuals (Pl. 550, fig. 1, *C. gracilis* Hall,  $\times 2$ ) or sometimes to foreign objects. Pl. 550, fig. 2, exhibits the young of different ages attached.

The full and beautiful researches of Fol<sup>2</sup> upon Pteropods have given us much knowledge concerning the life histories of these interesting animals as well as their habits and structure.

The eggs of most species are laid at the going down of the sun, and the number produced by one individual is enormous.

When the Pteropod embryo of to-day leaves the egg it possesses a shell and a velum. In some genera the shell is present throughout life, while in others it is possessed by the larva only. The velum disappears, and the foot changes from a creeping to a swimming organ by developing two broad lateral expansions usually called wings, but which are really oar-like fins. According to Pelsenner these little creatures swim in a nearly vertical position with the head uppermost or slightly sloping, so that the foot is turned upward, while the fins move backward and forward.

The division of the group into Thecosomata and Gymnosomata is in accordance with the principle of a natural classification.

<sup>1</sup> Amer. Geol., XVII, XVIII, 1896.

<sup>2</sup> Arch. d. Zool. Expér. et Gén., IV, 1875.

Pelseneer, who has made a special study of the anatomy of these forms, admits that "the division established on the very empirical character of the presence or the absence of a shell, is quite justified by the anatomical differences."<sup>1</sup>

*Thecosomata.* The Thecosomata are among the more primitive forms. They possess a shell, and the animal adds new layers to it as it grows. The head is indistinct and the wing-like organs extend from it on either side and are joined at the anterior edge above the mouth. The anus is on the left side.

It may be that there are primitive forms among the straight, cone-shaped Pteropods living to-day, but judging from our present knowledge of the anatomy of these straight forms, one must consider them as secondary and specialized members of the Pteropod group, and the spiral forms living to-day as the more generalized.

The spiral condition is represented by *Spirialis australis* Soul. (No. 551; Pl. 552). Its tiny spiral shell protects a spirally twisted body and the aperture is closed by an operculum.

*Spirialis rostralis* Soul. (No. 553; Pl. 554), has a nautiloid shell with an umbilicus. The figures exhibit the forward part of the body with its appendages, the expanded wings, and the viscera enclosed by the mantle.

*Creseis acicula* Rang (No. 555, alcoholic specimen; Nos. 556, 557, shells; Pl. 558, figure of animal in shell), is provided when young like all Pteropods with a shell formed by the everted shell gland. In most members of the group this shell disappears and a secondary shell is formed. In *Creseis*, however, the primitive and secondary shells are both retained throughout life. The adult shell is smooth, cone-shaped, and bilaterally symmetrical, with a simple aperture.

It would seem that this bilateral symmetry was evi-

<sup>1</sup> Chall. Rep., Zool., XIX, part I, 1887, p. 1.

dence of a primitive condition, but the asymmetry of the internal organs proves, as already pointed out, that these forms have descended from spiral, asymmetrical Pteropods. The shell has become adapted for swimming, while the internal organs have not been so modified. To strengthen these views there are species of these usually straight forms which have the protoconch coiled dorsally, indicating a former coiled condition.<sup>1</sup> This genus exhibits the cone-in-cone structure plainly seen in *Creseis striata* Rang (No. 559; Pl. 560), which is large and finely striated on the outside. This straight cone may sometimes in the same species become horn-shaped, as seen in Pl. 560.

*Cuvieria columnella* Rang is like *Creseis* when a larva. No. 561 is a very rare specimen in which the small cone-shaped young is seen preserved. When older the animal builds a transverse partition across the slender tube, then advances and makes a much larger tube (No. 562). The young shell is usually broken off, so that only the part built by the adult is seen (Pl. 563).

*Cymbulia peroni* Cuv. (No. 564, animal; No. 565, model; Pl. 566), is a recent form, and has an external, spiral, operculated shell when a larva. This is thrown off and a secondary shell forms which is also cast aside. Finally in some species an internal cartilaginous shell is produced which is retained throughout life. The figure on the left in Pl. 566 is a view of the shell of *Cymbulia* from above with the wings expanded, and the figure on the right a side view showing the slipper-like form of the shell and the position of the animal within it. The model (No. 565) represents the adult with its delicate wings spread. *Tiedemannia neapolitana* (No. 567) is a nearly related genus with an internal shell.

The shell of *Hyalea* is essentially a hollow cone. The

<sup>1</sup> Chall. Rep., Zool., XXIII, Rep. on Pteropods, part 3, 1888, p. 36.

illustration shows the exquisite delicacy of *Hyalea globulosa* Rang with its blue shell and softly tinted wings. In this species the shell (No. 568) is nearly globular with the dorsal part projecting in front (Pl. 569) and the ventral part convex.

*Hyalea tridentata* Lam. (No. 570), is a much larger species with a golden shell (No. 571) and purple and golden wings (Pl. 572). The upper and lower parts of the shell, and the open spaces between the two are seen in the side view (Pl. 572, figure on the right).

*Cleodora cuspidata* Bosc. is protected by a glassy, nearly transparent shell (No. 573) with three projecting spikes. The visceral mass is colored in the figure (Pl. 574), while the other parts are nearly colorless. The alcoholic specimens (No. 575) show different ages of another species, *Cleodora pyramidata*.

*Balantium recurvum* Child (No. 576), is one of the larger Pteropods. Its shell is triangular in shape and terminates in a sharp point. Its delicate coloring and symmetrical transverse markings make it a beautiful object.

*Gymnosomata*. The larva of *Clio*, a member of the *Gymnosomata*, loses its primitive and secondary shell and its velum after which a second larval form appears with three bands of cilia encircling its body. This second larva is without a mantle and secretes no shell.

The adult (No. 577, alcoholic specimen; Pl. 578, *Clio* (= *Clione*) *borealis* Péron) has a long body with a distinct head. The latter bears two pairs of tentacles which are provided with a vast number of tiny suckers. The wings are distinct from the head and do not join in front, in which particulars the *Gymnosomata* differ from the *Thecosomata*. The foot is also distinct from the wings and consists of a posterior lobe with two smaller anterior ones. In all these forms the anus is on the right instead of the left side of the body.

*Pneumodermon peroni* Q. & G. loses its mantle and shell

like *Clio* (No. 577) and moves by means of bands of cilia. The adult (No. 579, No. 580, *P. violaceum* d'Orb.), possesses a distinct head which carries specialized tentacles having suckers similar to those of cuttlefishes. At the posterior end of the body there are external gills (No. 580).

*Clionopsis krohni* (No. 581; No. 582, *C. flavescens* Gegenbaur) has a barrel-shaped, shell-less body which is nearly transparent, and the visceral mass extends to the posterior end. The head is small with no mouth appendages.

#### Section 10.— CEPHALOPODA.

The Cephalopoda and Brachiopoda are perhaps the best groups that can be chosen at the present time to illustrate a natural classification based upon the stages of growth and decline. It is obviously impossible to follow out this classification in detail, to trace the numerous branches of the Cephalopod trunk to say nothing of the minute twig-like divisions and subdivisions of these branches. It is hoped, however, that such a series of specimens and drawings has been selected, and such an arrangement of these made, as will give the student a clear general view of the subject.

It is well to impress upon one's mind at the very outset the truth of the words: "A single shell, either from a living or fossil form, may present, accurately, the general history of the development of the young, the stages of the adult and of old age."<sup>1</sup>

<sup>1</sup> Hyatt, Fossil Cephalopods in the Museum of Comparative Zoölogy, Proc. Amer. Assoc. Adv. Sci., XXXII, 1883, p. 323.

## TETRABRANCHIATA. — NAUTILOIDEA.

When the Nautiloidea first appear in the Palaeozoic strata they are specialized in so many ways, the inference may be drawn that we are ignorant of the radical stock from which all the Cephalopods have descended. A study of the embryological and larval structure of living Nautiloids, however, leads to the conclusion that *Diphragmoceras*, *Piloceras* (Pl. 583), and *Endoceras* (No. 584) are among the generalized ancestors of the group. A knowledge of these genera and of the *Orthoceratites*, soon to be described, enables one to give an hypothetical ancestral form with a great degree of certainty.

*Diphragmoceras* is a nearly straight tube divided into a few chambers by simple plain partitions or septa. Through these septa runs a large tube or siphuncle which is divided by septa similar to those in the surrounding shell. The structure of the siphuncle is an important character in the classification of the Nautiloids, primitive forms and the young of specialized genera having large siphuncles, while those of adult specialized forms are small and contracted.<sup>1</sup>

Unfortunately the young *Piloceras* has not been described. The adult is both straight (Pl. 583) and curved. It is divided by septa and has a large siphuncle. Near the apex the siphuncle exhibits a cone-in-cone structure which is more developed in *Endoceras*. The latter genus, when young, may represent the full grown *Piloceras*. The adult *Endoceras* (No. 584; Pl. 585, vertical section of *E. proteiforme* Hall, greatly reduced), is a straight form with a shell divided into chambers by septa. Each septum extends downward beyond the one next below, forming funnels which taken together make a complete siphuncle (see Pl. 585). This tube is large, being sometimes

<sup>1</sup> See Hyatt, Proc. Amer. Assoc. Adv. Sci., XLVII, 1898, p. 363.

more than one half the diameter of the shell. Within the siphuncle are cones, one within another, which are much more plainly seen than in *Piloceras*. To understand this structure, one must consider the fleshy body of the animal. This occupied the outermost chamber of the shell. Extending backward a considerable distance from its posterior part was a bag-like prolongation which secreted shell in the form of a cone. At certain periods the body advanced and while resting built another cone, thus giving rise to the cone-in-cone structure seen in Pl. 585. Extending from the spire of the cones backward to the apex of the shell was a hollow tube, the endosiphuncle, also plainly seen in Pl. 585.

*Diphragmoceras*, *Piloceras*, and *Endoceras* represent generalized forms having huge siphuncles. These become only slightly contracted in later stages of growth. In fact the generalized members of this class do not pass through marked changes in external form and ornamentation or in internal structure; one genus, *Cyrtocera*, probably preserving its large siphuncle unchanged throughout life.<sup>1</sup>

Much more is known of the young of the genus *Orthoceras* than of the preceding genera. Its protoconch has been observed. Figs. 1-3 of Pl. 586 represent the protoconch of *Orthoceras elegans* Munst., from the front, side, and above; (a) protoconch, (b) shell; figs. 4-6, the protoconch of *Spyroceras* (= *Orthoceras*) *croतालum* Hall. This protoconch is a chamberless, septa-less shell, usually very much shrunken owing to the delicate substance — conchiolin — of which it was made. Here we have a clew to the radical form that gave rise to the Cephalopods, and probably to the Gastropods and Pteropods as well.

In figs. 4-6 not only is the protoconch distinctly seen but also the different substages of the nepionic stage.

<sup>1</sup> Hyatt, Genesis of the Arietidae, Smithsonian Contrib. to Knowledge, XXVI, 1889, p. 39.

The markings of the protoconch are carried over continuously to the beginning of the nepionic stage, proving conclusively that the shell or conch was formed on the edges of the protoconch. Usually the protoconch is broken off and in these cases a scar is left. Fig. 7 (*O. unguis*) shows the scar and the conch of the apex. Fig. 8 is a view of the apex of the same species after the protoconch has been accidentally broken off, fracturing the outer shell and exposing the scar.

The young has a large siphuncle which afterwards in the process of growth becomes contracted, but never develops the cone-in-cone structure, or an endosiphuncle. This tends to prove that *Orthoceras* descended from forms with a large siphuncle and that the small siphuncle is a secondary condition.

The position of the siphuncle is usually near the center of the septa, as seen in No. 587, which represents a portion of the adult shell. The septa are plain and concave towards the living chamber. The shell is straight and unornamented, with a simple aperture. It is marked by that genuine simplicity which characterizes primitive forms.

The tendency of the primitive straight shell to become coiled is shown in *Cyrtoceras* and *Gyroceras*. *Cyrtoceras* (Pl. 588) is more or less curved, but is never coiled. The septa are concave towards the forward part, the aperture is large, and the ventral sinus is distinct. In *Gyroceras* (Pl. 589) the process of coiling begins, but the whorls are not in contact, so that the result is a loose spiral. The aperture is simple and the septa are plain and concave.

There are fossil forms among the Nautiloids in which the whorls are closely coiled, as in *Nautilus dekayi* Morten (No. 590, showing septa and siphuncle) and *Nautilus intermedius* Sow. (No. 591). In some species these whorls are visible (No. 591; No. 592, *Nautilus umbilicatus* Lister; section of shell), and in consequence of this mode of growth the species has a deep umbilicus on either side.



The tendency towards becoming an involute shell is seen in *Nautilus stenomphalus* Sow. (Nos. 593, 594). The involute shell in which the earlier whorls are entirely concealed by the latest whorl is seen in *Nautilus pompilius* Linn. (Pl. 595; Nos. 596, 597). The development of this species is extremely interesting from a phylogenetic point of view. The first chamber of the shell of the young *Nautilus* has a linear scar (Pl. 595, fig. 2) which probably marks the spot where the protoconch was broken off. The protoconch itself has never been found in perfect condition in this group, though the scar bears strong evidence of its former existence. There are good reasons why the protoconch of *Nautilus* should be lost. It was probably made of frail material which would easily be broken while the animal was swimming about in the sea. Then again, when the young, nearly straight shell began to coil, the hard calcareous first whorl would come so close to the delicate protoconch that the latter could hardly fail to be destroyed. The protoconch was doubtless connected with the first chamber by an opening which is plugged up in the present *Nautili*, the scar marking its position.

In a section through a young shell of *Nautilus pompilius* Linn. (Pl. 595, fig. 1), the first living chamber is almost straight, while the rest is slightly curved. This chamber was occupied by the young animal after the protoconch stage. It was septa-less like the protoconch and without a siphuncle. In course of time the animal advanced and made a wall or septum behind it. This septum bent downward into the first chamber forming a coecum or the beginning of the siphuncle as seen in the figure. The second septum likewise is prolonged, and its coecum extends downward into the first coecum, the bottom of the coecum forming a septum across the siphuncle. This early condition of *Nautilus* represents the adult *Diphragmoceras* with its large septate siphuncle.

The third septum in *Nautilus* extends only to the sec-

ond septum, forming a long funnel with no septum at the bottom. The siphuncle begins to contract and from this time on is without septa, resembling the contracted septaless siphuncle of *Orthoceras* which arises in the same way; *i. e.*, by the formation of long funnels.

Fig. 2 represents the nepionic stage of *Nautilus* as seen from the front. The specimen has been obtained by breaking down a full grown shell. The vertical scar marking the position of the protoconch is distinct, while the circular siphuncle is of large size. Fig. 3 is the same seen from the side. It shows the increase in ornamentation from a comparatively smooth shell. The lines of growth do not bend backward in the middle of the ventral side but run nearly straight.

Fig. 4 shows finely the scar and the area of attachment of the protoconch; the siphuncle and first few septa are also plainly visible. The adult *Nautilus* is represented by No. 596, the shell; and No. 597, a section showing an alcoholic specimen of the fleshy animal within its shell.

The involute spiral form has been attained and the coiling has taken place in such a way that the ventral convex side is outermost and the concave dorsal side innermost. As the shell coiled, the newly formed, more or less plastic whorl came in contact with, and was pressed by the harder and older preceding whorl. The tighter the coiling the deeper we should say would be the impression. This impressed area in the dorsal side of the shell is known as the impressed zone, and is an important character in both Nautiloids and Ammonoids.

In the adult *Nautilus* the septa extend backward only a short distance, giving rise to short funnels in place of the long ones of more generalized forms. These funnels are connected by a porous tube secreted by the siphon, and the two taken together form the siphuncle. This is well seen in the section of the shell (Nos. 592, 597) running from the outermost chamber to the innermost. Its position is near the center of the concave septa. It will

be observed that the septa are much nearer together in the adult than in the young (Pl. 595, fig. 1). If a section of an old shell is examined the septa are sometimes found even nearer together than in the ephebic stage. This is especially interesting and exceptional, since just the opposite condition of things exists in the old age or gerontic stage from what has been described in the young stage.

A study of the young and the adult shell leads to a study of the fleshy parts of the animal. No. 597 is an alcoholic specimen of the Nautilus. It is placed in its natural position with the ventral side below. The large head and body of the animal occupy the outer chamber of the shell, and the long fleshy tube or siphon extends from the posterior part of the body backward to the innermost chamber. It is supposed by some that the chambers of the shell are supplied with gas and by others with liquid. On the ventral side the two flaps of the mantle have united, forming an ambulatory pipe or hyponome by means of which the animal is propelled through the water. The motions of this organ have caused a sinus in the aperture of the shell (see Nos. 592-594, 596), and the additional layers made to the shell, indicated by the lines of growth, bend backward running parallel with this sinus. As we have already said, no sinus occurs in the young Nautilus, so that probably at this stage it is not a swimming animal. The mouth of the creature is surrounded by arms for obtaining food, but these are without sucking cups.

The edges of the mantle make the shell already described, while the mantle on the posterior part of the body builds the septa during periods of rest. The short funnels of the siphuncle are made by the mantle, while the siphon secretes the porous wall which connects the funnels together.

In the group of Nautiloids there is no straight old age form, the involute form existing at the present time.

## AMMONOIDEA.

There are sufficient remnants of the early transitional forms left in the Silurian rocks to demonstrate the former connection of the Nautiloids and the Ammonoids.<sup>1</sup> The common ancestor for the two groups probably existed in pre-Cambrian times, but this form has not been discovered. Clarke<sup>2</sup> has described an *Orthoceras*-like form from the Devonian. It has a large, plump protoconch (Pl. 598, fig. 1) like that of Ammonoids, but the central position of the siphuncle (fig. 2) is like that of *Orthoceras*. According to Clarke this protoconch was probably derived from so young a shell that atrophy and wrinkling had not taken place, as is the case with the mature *Orthoceras* shells, all of which have been found in a later geologic formation. The connection of the protoconch with the conch is seen to be large, which is the case with the generalized Ammonoids, while it is narrow in the Nautiloids, as seen in Pl. 586.

*Bactrites* is probably the primitive straight form from which the Ammonoidea arose. The protoconch is seen in Pl. 599, fig. 1, while in fig. 2 it occurs with a few chambers.

When this protoconch is not present, the apex (fig. 3) is marked by a scar (figs. 3, 4). When the protoconch is broken off the opening of the siphuncle in the first septum (Pl. 599, fig. 5, somewhat broken), is seen to be intramarginal instead of being central as in *Orthoceras*, or marginal as in typical Ammonoids. Pl. 599, fig. 6, shows the protoconch and the enlargement of the shell which goes on until two chambers have been formed, after which the tube contracts.

An older specimen is figured in Pl. 599, fig. 7 (a dorsal

<sup>1</sup> Hyatt, Proc. Amer. Assoc. Adv. Sci., XXXII, 1883.

<sup>2</sup> Amer. Geol., XII, 1893, p. 112.

view of an internal cast), showing the long tube, the slightly oblique sutures, and the flaring aperture. As specimens are usually preserved the siphuncle appears to be distinctly marginal, but Clarke has shown that this is not the case, but that a narrow portion of the septum lies between the siphonal funnel and the shell wall. This is shown in fig. 8, which is the interior of a portion of the shell showing the intra-marginal position of the siphonal funnel.

*Mimoceras* (= *Goniatites*) *compressum* (Pl. 600), has a protoconch which is permanent throughout life. This is well seen in figs. 1-3. These figures show that the shell is nearly straight at first, and that the septa, and therefore the sutures, are primitive and similar to those of the Nautiloidea. The septa are, in fact, concave both in the young and in the adult. The siphuncle is nearer the center at first and later approaches the ventral side. The adolescent shell is loosely coiled (fig. 3), the whorls not being in contact. Later, however, the shell becomes closely coiled, as seen in figs. 4, 5; also figs. 6, 7 (*M. ambigena*). Fig. 5 shows the older septa with the siphonal lobe. The outline of the aperture of the shell is rounded on the dorsal as well as the ventral side (fig. 7). This is an important character showing the absence of an impressed zone at a late stage.

In these generalized forms of the Ammonoidea, significantly called the Nautilinidae, the Nautiloid characters are retained for a considerable length of time, but later new structural features appear which are distinctly Ammonoidal.

Adult *Goniatites* in general have the septa concave as in the Nautiloids, but the sutures though simple (No. 601, *Brancoeras ixion* Hyatt), have a few lobes (backward bendings of the septa) and saddles (forward bendings of the same parts). The aperture is simple with ventral sinus like that of *Nautilus*. The siphuncle is at first central in position and later reaches the ventral margin where

it makes a siphuncle lobe (No. 601, specimen on the right), which later in life in some species becomes divided, giving rise to the siphuncle saddle.

The Goniatites cease to exist in the Carboniferous age and the Ceratites appear. The specimen of Ceratites (No. 602, *C. nodosus* De H.), does not show the younger whorls but the sutures of the last whorl are finely seen. The number of saddles and lobes has increased but still can be easily counted. The bottom of the lobes is serrated, which may be seen in several places in the specimen.

The more primitive Ammonitidae are represented by *Deroceras* (= *Ammonites*) *planicosta* Hyatt. Here the protoconch is large and globular (Pl. 603, fig. 1). In this figure the shell is seen on the right with a few septa, and on the left it is broken exposing the cast of the protoconch. Fig. 2 is a section of the same. The contraction of the siphuncle is well seen. Fig. 3 is a section through the shell with the protoconch broken off. The coecum formed by the first septum is finely shown; three other septa are drawn. An organic deposit fills the siphuncle. Fig. 4 is a section through the shell of a related genus, *Pleuroceras spinatum* Branco, showing the protoconch in the center, the coecum and siphuncle, the first concave Nautiloid septum, and the remaining convex Ammonoidal septa. It is interesting to know that the septa of the first formed chambers are simply curved, while in the adolescent stage they resemble those of Goniatites, having few lobes and saddles (see fig. 5). In the whorls of the adult they are always folded (see outer whorl in fig. 5).

In this adult shell the ventral sinus of the aperture, so conspicuous in the Nautiloids, has disappeared and the lines of growth are continued straight across the ventral portion. This being the case we must infer that the organ which caused the sinus has disappeared. Hyatt<sup>1</sup>

<sup>1</sup> Genesis of the Arietidae, Smithsonian Contrib. to Knowledge, XXVI, 1889.

has pointed out that this change in structure indicates a change in habits whereby a swimming type of Cephalopod has been converted into a crawling type.

In *Dactylioceras* (No. 604, *D. commune* Hyatt), the whorls are closely coiled and in the same plane; all are visible and the ornamentation is similar.

These characters are seen on a large scale in *Ammonites parkinsoni* which, on account of its size, is placed at the back of the Section (see No. 605; No. 606, horizontal section of the same). A portion of the shell has been removed in No. 605, and the surface polished, thereby bringing out the sutures finely. In No. 606 the chambers and their walls are well shown.

*Asteroceras* (= *Ammonites*, also = *Arietites*) *obtusum* Hyatt (No. 607) has the whorls in one plane and all can be counted. The shell is tightly coiled and even the youngest whorls are ornamented with ribs. This specimen has most of the shell well preserved. The sutures are hidden, but where the shell is broken off the serrated or fluted edges of the septa are visible though more clearly seen in No. 608 where the outer shell is entirely gone. These sutures are complex as compared with those of *Goniatites*, *Ceratites*, or the primitive *Ammonites*. The siphuncle is seen on the edge and the specimen also shows how the dorsal side of the shell has become impressed by close coiling. The living chamber extends backward a considerable distance (No. 608), the last formed septum marking its posterior limit.

The complexity of the septa is seen in *Lytoceras jureense* Sitt. (No. 609), where the edges of the septa have been painted red to bring out their structure more plainly.

No. 610, *Stephanoceras tscheffkini* d'Orb., shows the tendency of a closely coiled shell to become involute. The last whorl spreads out laterally and partially covers the preceding whorls, leaving a deep umbilicus on either side. The dorsum is deeply impressed in this genus. Several of the specimens in No. 608 have a portion of the exter-

nal shell preserved which exhibits a brilliant iridescence. Where the shell is broken the septa and chambers are visible. The middle portion of the septum in the upper left hand specimen is seen to be nearly flat but the edges are deeply fluted. In the largest specimen on the right, the shell is mostly worn away, revealing the complex character of the sutures.

No. 611, *Perisphinctes*, belongs to another series in which the shell is compressed, but the younger whorls are not covered. The marginal siphuncle and the fluted sutures are remarkably well seen in this specimen. Another species of this genus, No. 612, *P. comptoni* Pratt, has long lateral processes or ears extending from the living chamber.

*Phylloceras heterophyllum* Suss. (No. 613). is not only compressed but involute. The shell has mostly disappeared, revealing the extremely complex character of the sutures. The section shows the protoconch in the center, the closely coiled young shell, the septa, and the chambers filled with mineral matter. As might be expected these extremely specialized Ammonites are not found in the ancient Palaeozoic strata but occur in the Mesozoic formations.

*Aturia zizac* Sow. is found in the recent Tertiary rocks, and is a compressed, involute form with specialized sutures, and differentiated, nearly dorsal siphuncle (No. 614; also Pl. 615, figs. 1-3). Growth in this genus is very rapid during the nepionic stage, the coiling is close, and the funnels of the siphuncle are flaring (see fig. 1). Fig. 2 is a front view, and fig. 3 a side view of the nepionic and half of the neanic stages. Fig. 2 shows the nearly dorsal position of the siphuncle, and fig. 3 the lobes of the first four sutures. No. 616, *Aturia aturi* Bast. is a valuable specimen obtained by breaking down the shell so that the funnels of the siphuncle are exposed.

It has been shown that the Nautiloids and Ammonoids both arose from straight *Orthoceras*-like shells, and in



their development passed through the loosely coiled, tightly coiled, and involute stages. The Nautilus was seen to be an involute form, but no reduced stage with a more or less uncoiled spire was described since no such form has been discovered.

Among the Ammonoids, however, a number of series have been traced from the straight primitive form through the involute stages to the straight reduced condition.

The Ammonites culminated in the Jurassic period. At the close of this period in all probability there was some great climatic change which caused reduction. The Nautiloids were somewhat affected, but not enough to cause them to become extinct. Those that died, did so slowly. The Ammonites, on the contrary, developed extraordinary reduced forms and afterwards became extinct.

The first indications of reduction are a lateral contraction in the whorl (see No. 617, *Sphaeroceras brochi* Sow.), attended with a diminution in the size and a decrease in the vertical height (No. 618, *Sphaeroceras wrighti*). In some cases the process is carried so far that the terminal portion of the last whorl separates from the preceding whorls and grows out straight, as seen in *Scaphites nodosus* Meek. The young Scaphites (No. 619, specimen on the left, and the section, No. 620) are closely coiled, but the older stage (No. 619, specimen on the right) has begun to uncoil. This is still better seen in No. 621, which is a cast of an aged specimen of *Eurystomites kelloggi* showing the free volution or whorl.

Another old age form is seen in No. 622, *Helicoceras stevensoni* Whitfield, where the asymmetrical spiral has partly uncoiled, and the last whorl has a secondary backward crook bringing the aperture of the shell near the base of the spire.

The uncoiled condition is carried still farther in *Crioceras bifurcatus* Quenst. (No. 623), in which the shape is more like a hook than a spiral.

Finally, the straight form is very nearly attained in *Baculites* (Pl. 624, figs. 1-10; No. 625), but this straight adult Ammonite has a tiny coiled shell when young. It is interesting to note that the protoconch has become modified, so that its shape is suggestive of a spiral when seen from the side (Pl. 624, fig. 1). The typical globular form has become broadly elliptical (fig. 2, front view) with a projection extending forward (fig. 1).

The earliest stage of the larval nepionic shell is seen in fig. 3. An older shell having four septa shows the siphuncle near the center (fig. 4). The aperture at this stage is broad, and the area of contact of the revolving whorl upon the preceding whorl is also broad, as shown by the dotted lines. The septa at first are simple. Fig. 5 represents a side view of the shell with six septa, and fig. 6 the first six sutures. Three of these sutures are simple, while the remaining three are similar to the sutures of *Goniatites*. A front view of a stage with thirteen septa (fig. 7) shows the siphuncle near the margin, the aperture and area of contact narrower so that the growing whorl envelops less of the shell. In a still older stage with seventeen septa (fig. 8) the siphuncle is close to the edge, the aperture is almost circular, while the area of contact is much narrower, as indicated by the dotted lines. When the shell has the diameter of one millimeter and consists of two or two and a half whorls with from twenty to twenty-five septa it begins to grow out in a straight line. Fig. 9 represents the adolescent (neanic) shell at this stage with the lines of growth and the rostrum at the opening.

The sutures, which are concealed in fig. 9, become more complex, passing from the *Goniatite* condition to the *Ceratite* (see lower suture in fig. 10) at about the thirtieth septum or after the shell has become straight. After this the lobes and saddles increase in number until the extremely complex sutures of the adult Ammonite are produced (upper sutures in fig. 10; see also No. 625).

In the history of the development of *Baculites* we have positive proof of the reduced character of the genus. Instead of being a relative of the primitive straight *Orthoceras* or of *Bactrites*, it is an extremely specialized form whose ancestors in their evolutionary history passed through the various stages of shell development. Of these stages the straight and loosely coiled stages are omitted in *Baculites*, so that the animal begins life with a tightly coiled shell, which, however, ceases to coil in the neanic stage, forming thereafter a straight cone.

#### DIBRANCHIATA. — BELEMNITIDAE.

The *Belemnitidae* begin in the Triassic period and are therefore more recent than the *Nautiloids* or the *Ammonoids*. We should expect to find them more specialized though still retaining certain characters of their ancestors.

We have seen in *Nautilus* the dorsal fold of the mantle which secretes the black pigment layer. In *Aulacoceras* (Pl. 626, figs. 1-3, *A. reticulatum* Hauer), the dorsal fold was nearly closed and secreted a shell with three principal parts: the chambered shell or phragmacone (fig. 1, *ph*); the guard (fig. 1, *g*; fig. 3), and a prolongation of the phragmacone, the pro-ostracum (see upper part of fig. 1), often called the pen, which is seldom preserved. The phragmacone has chambers, septa, and siphuncle (fig. 2, section). It corresponds with the shell of the *Tetrabranchiata*, but differs from the latter by being internal.

The more specialized form, *Belemnites* (No. 627), has a conical, chambered shell, at the anterior end of which on the dorsal side there was the shovel-like projection or pro-ostracum. The septa of the shell were plain (No. 627), concave, and were pierced by a siphuncle which does not show in the specimen. This shell is external in the young *Belemnite*. In time the dorsal flap of the mantle grows out and around the shell, its two edges not

meeting ventrally at first, but eventually coming together and joining. When this has happened, the mantle makes the first layer of the guard (No. 627). Successive layers are put on from without, thereby illustrating exogenous growth. In many genera the guard extends a considerable distance below the chambered shell and is the part most frequently preserved (see No. 628, *B. subquadratus* Roem.).

Thus it is seen that Belemnites carries specialization so far that the shell is enclosed and a secondary structure, the guard, is formed.

One of the descendants of the Belemnites is the beautiful living Spirula (Nos. 629, 630) which has lost both the pen and the guard. A perfect specimen of this animal is extremely rare,<sup>1</sup> but the alcoholic specimen (No. 629), though mutilated, shows that the shell is partly internal. It also exhibits a portion of the mantle and what some naturalists consider the disc of attachment.

The shell has a large, globular protoconch finely seen in No. 630. The plain concave septa are pierced by the marginal siphuncle which is made up of funnels that extend from one septum to another.

Belosepia, according to Zittel, connects the Phragmaphora (Belemnites, Spirula, etc.) with the Sepiophora (cuttlefishes and squids). It has a guard and the chambered shell is represented indistinctly.

The young cuttlefish of to-day, *Sepia officinalis* Linn. (Pl. 631, figs. 1, 2), has the interesting habit of fastening itself, for a day or two after hatching, by a portion of the lower side of the body and of the ventral arms. This sucker-like area is flat and nearly colorless, and reminds one forcibly of the foot of a Gastropod. Fig. 1 is a view of the animal drawn from below when attached to a glass plate; the arms are retracted. Fig. 2 is from

<sup>1</sup> According to Pelseneer (Nat. Sci., VII, 1895, p. 63) only five complete specimens are known.

above while in the same position. The line between the two figures represents the actual length of the animals.

After detaching itself, the young *Sepia* swims by means of the thin border of the mantle, and only when irritated uses the ambulatory pipe for darting backwards. The outer skin or integument of the disc of attachment is so thin that the ink bag can be clearly seen near the center of it. According to Bather,<sup>1</sup> one larval *Sepia*, when irritated, ejected ink twice within one minute of being taken from the egg-capsule. The ink, however, was not sufficiently dense to obscure the motions of the animal.

The adult (No. 632; No. 633, model of the same) loses the habit of attaching itself and of swimming by its mantle, while the ambulatory pipe becomes the chief means of rapid locomotion. The ink bag is large and an efficient means of protection. The pro-ostracum or pen is developed, being the calcareous portion familiarly known as cuttle bone. At its base there is a vestige of the chambered shell, while the guard has become nearly obsolete. These animals have short, stout, bag-like bodies with eight short arms and two longer ones. The alcoholic specimen, No. 632, exhibits the open mouth with its horny, beak-like teeth. There are two of these and the lower one is the larger. The ambulatory pipe is conspicuous. The cuttlefish possesses an ink bag which contains the sepia used as the basis of the pigment.

The squid is another living representative of the more specialized Cephalopods, which has lost both external and internal chambered shell and has nothing but a horny pen. This pen is situated in the dorsal part of the mantle and can be of little use to the animal. The eggs of the squid are in long, pod-like cases (No. 634), which are fastened together in large clusters. In its development, and in that of all Cephalopods, definite

traces of the veliger stage (which has been described in the Pelecypods and Gastropods) are entirely lost by the law of acceleration in development.

The squid (No. 635, *Loligo vulgaris* Lam.), has a long body covered with a leathery mantle with a fin on either side of the posterior end. At the forward end the mantle is free, so that the water passes into the cavity of the body, and bathes the two gills which are placed one on either side (see preparation, No. 636). After the water has flowed in, the mantle is applied closely to the neck so that the body cavity is a tight bag with only one opening, and that is the ambulatory pipe or hyponome which we found in the Nautilus. The forcible ejection of the water through this pipe sends the animal swiftly backwards. The waste products of the body and the inky fluid for protection are also discharged through this pipe. The head of the squid is provided with two eyes which are more highly organized than any other invertebrate eye, but have only a superficial resemblance to the vertebrate eye. The mouth has a horny beak and a lingual ribbon. It is surrounded by eight short arms and two long ones which have suckers. In the preparation (No. 636) an incision has been made along the middle of the ventral side, and the mantle laid back exposing the internal organs. A slender tube, the esophagus, extends from the mouth to the long, sac-like stomach which has a bag-like coecum near the pyloric or forward end. The intestine, another slender tube, is seen running forward from the stomach under the liver, and by the side of the duct of the ink bag. The anus and the outlet of the duct are near the base of the ambulatory pipe and directly in the path of the outgoing current of water which, as we have already said, carries away the products of both intestine and ink bag. The heart is situated near the base of the gills; back of it and occupying the greater part of the body cavity is the mass of eggs.

The embryo of Octopus has a shell sac on the forward

part of the dorsal side of the body, but as it develops this shell sac becomes aborted and neither the young (No. 637) nor the adult Octopus (No. 638) have a vestige of a shell. The animal is built upon the same plan of structure as the squid. The model shows the natural position of the Octopus with the mouth downward and long arms extending out on all sides, provided with the sucking discs that make this animal a formidable one. Above is the great rounded head with its prominent eyes.

The alcoholic specimen (No. 639) shows the large open hyponome, the arms surrounding the mouth, and the round plump body. The membrane that connects the base of the long tapering arms and the suckers are well seen in No. 640. The hyponome in this specimen is small.

In *Eledone aldrovandi* Delle Chiaje (No. 641), there is but one row of suckers on the arms. *Loligopsis verani* Fér. (No. 642), has a more slender body and two very long delicate arms.

*Argonauta argo* Linn., or the Paper Nautilus (No. 643, eggs, 2 females, 1 male) is related to the Octopus, the structure of the two animals being similar. Here we have no shell comparable with that of other Cephalopods. The male (No. 643, alcoholic specimen; No. 644, model) is without any protective covering, but the female (No. 643, alcoholic specimen; No. 645, model) has an egg case (No. 646) of exquisite beauty. This case is in the form of a spiral shell, and is developed late in a post-embryonic stage. It is composed of three layers, one made by the edge of the mantle, another by the whole mantle, and the outer layer by the two large arms (see No. 645). The last named layer does not occur in the shells of other Cephalopods.

The male is very much smaller than the female. One of the arms becomes modified and enclosed in a sac, as seen in No. 644. Later this sac splits and the arm is

free (No. 644). The two halves of the sac then reunite and the sac thereby formed becomes filled with spermatozoa. The arm with the sperm is detached and finds its way to the mantle cavity of the female. No. 645 shows the two large arms of the female that have become greatly modified in structure. In the alcoholic specimen these are much contracted. They are usually applied closely to the outer surface of the shell and are not carried as sails though often so figured in the books.

The Argonaut propels itself through the water in precisely the same way as the squid, having the same hydraulic apparatus.

The Mollusca constitute a subkingdom of immense size and unnumbered variations. Underlying these variations, however, there is a fundamental unity. Most Mollusca pass through a trochophore and a veliger stage in their development; most possess a shell gland the first product of which is a simple, unornamented, colorless or slightly colored, plate-like shell. If this plate-like shell divides into two parts the result is a bivalve shell, the distinctive character of the class of Pelecypods. If it becomes a spiral cone, the univalve shell and the class of Gastropods results. If the spiral cone becomes chambered, the product is the shell peculiar to the Cephalopods.

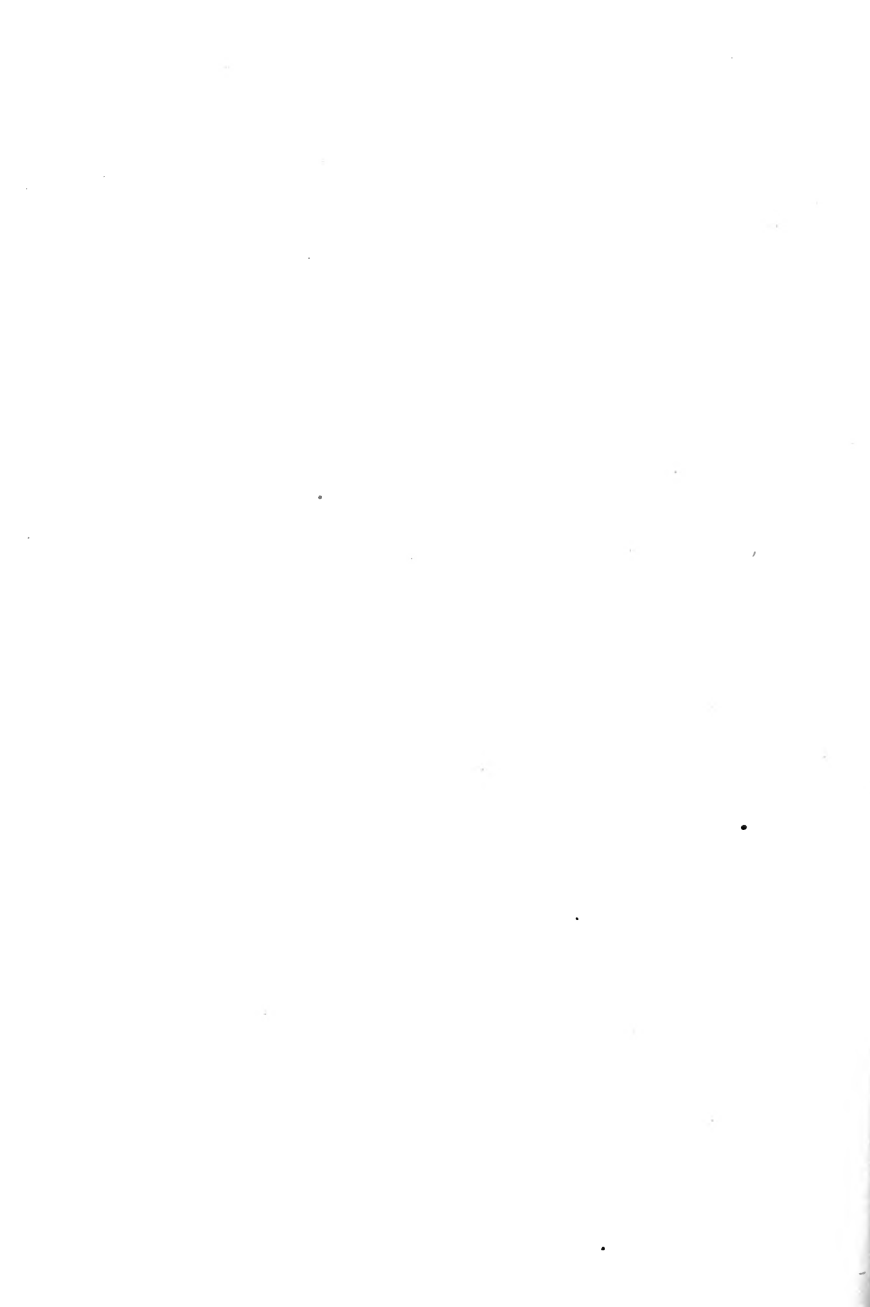
Free-moving, sedentary, and boring habits produce modifications in the shell. Among Pelecypods the free-moving species, as a rule, have equivalved, symmetrical shells, while the sedentary forms are unequivalved and asymmetrical. The boring habit in both Pelecypods and Gastropods tends towards the reduction of the shell, until only a vestige of it remains. Other causes have produced a similar reduction. The free-swimming habits of the Heteropods have resulted in the development of a fin-like organ, while the shell, being of little use, has become small and inconspicuous. The Nudibranchs carry the process still farther, since they possess a shell in the



embryonic stage only, which is quickly lost, so that the adult is without even a vestige of a protective covering.

The marine Gastropods probably gave rise to the specialized fresh-water and terrestrial species, transitional forms existing at the present time.

The Cephalopoda illustrate acceleration in development and specialization in structure. The external, chambered shell becomes internal and extremely modified; it may also exist as a vestige or be wanting altogether.



## VERMES.

## Section 11 and 12 (in part).

## BRACHIOPODA. — ATREMATA.

The class of Brachiopoda, as already stated, is one of the best for illustrating a classification based on the stages of growth and decline.

The ancestral form, Paterina, which Beecher described and figured,<sup>1</sup> is now considered by Walcott<sup>2</sup> to be identical with the genus Iphidea; and in the Iphidea, Walcott has found a rudimentary cardinal or hinge area. This fact prevents the Iphidea and the Paterina, if they be the same, from representing the most primitive form conceivable; that is, a shell without even the rudiment of a cardinal area. There is little doubt, however, that such a primitive form existed and in time will be discovered. To such a genus, when found, the name of Paterina should surely be given in consideration of Beecher's classic researches on the class of Brachiopoda. Until this new, theoretical form is brought to light, we will bear in mind that the Iphidea is the simplest form yet discovered and described, while at the same time we shall accept the shell as described by Beecher under the name of Paterina as representing the still more primitive form that is to be discovered.

This Paterina shell is simple in youth (Pl. 647, fig. 1, *P. labradorica* Billings, pedicle valve) and also in maturity (fig. 2, brachial valve), having two nearly equal valves which are semi-elliptical in shape. The hinge line is straight and nearly equal in length to the width of the

<sup>1</sup> Amer. Journ. Sci., (3), XLI, 1891; (3), XLIV, 1892.

<sup>2</sup> Proc. U. S. Nat. Mus., XIX, 1897, pp. 707-718.

shell. The lines of growth run parallel with one another and there is no ornamentation of any kind. The new layers of shell are added at the anterior<sup>1</sup> and lateral margins, so that the pedicle at the posterior end is always free.

The embryonic shell (uncolored in Pl. 647, figs. 1, 2) or protegulum (meaning early covering) is similar in form to the mature shell. As we have already said, the youthful (nepionic), adolescent (neanic), and mature (ephebic) stages are all alike (see Pl. 647, figs. 1, 2), so that it is impossible to tell where one stage ends or another begins.

The valves of the shell are not articulated together by teeth and sockets, but are held in place by muscles. The pedicle valve is slightly more convex than the brachial valve, so that an opening is produced through which passes the short pedicle. This opening, according to Beecher's figures, is shared alike by both valves, so that the pedicle is free. As already stated, Walcott has found the region between the two valves more or less closed by rudimentary cardinal areas.

Plate 648, figs. 1-4, represents Walcott's figures of *Iphidea*. The brachial valve is seen in fig. 1; fig. 2 is a summit view of the pedicle valve; while a side view of the same is shown in fig. 3. The imperfectly defined, rather narrow cardinal area is shown in fig. 4 with a broad plate, called the prodeltidium, just under the beak. The latter is formed by the pedicle and not by the mantle as is the case with the deltaria (see p. 277).

The ancestral species from the Cambrian and Lower Silurian, *Obolella polita* Hall (No. 649; Pl. 650, fig. 1), had a more or less circular form. This shape of the adult shell is peculiar to many young Brachiopoda, so that when

<sup>1</sup> In order to see the characteristic parts plainly, the specimens are mounted, and the figures are drawn, with the anterior end towards the observer. This is contrary to the usual rule which places the animal with the forward end away from the observer—the most favorable position when comparison with his own body is desired.

they attain this form they are said to be in the *Obolella* stage of development.

Each valve of *Obolella* had a rudimentary cardinal or hinge area in which a groove was scooped out for the pedicle. This groove is seen in an interior view of the brachial valve (fig. 2) and still more clearly in the pedicle valve (fig. 3). The markings in the interior of the valves (figs. 2, 3) are the scars left by the muscles.

One of the more progressive species closely related to *Paterina* and *Obolella*, is *Trimerella* (Pl. 651, fig. 1, *T. ohioensis* Meek, external view of pedicle valve; fig. 2, internal view) which has a large hinge area, finely seen in fig. 2, and a furrow bounded by ridges, the inner edges of which serve as teeth. This primitive mechanism is suggestive of the more perfect articulation by teeth and sockets of the more specialized *Brachiopoda*.

*Paterina*, *Obolella*, and *Trimerella* represent the *Atrēmata*, to which group of *Brachiopoda* *Lingulepis* (No. 652) and *Lingula* (No. 654) also belong. In *Lingulepis* (No. 652, *L. pinniformis* Owen, = *Lingula antiqua* Hall) the shape is rounded and similar to *Obolella*. The valves are also unequal, and in other structural characters this genus is intermediate between the *Obolellidae* and the more specialized *Lingulidae* represented by *Lingula*.

The power of resisting adverse conditions is so great in *Lingula* that it has come down to us essentially unchanged in structure from the early geologic period known as the Ordovician, which followed the Cambrian. Its persistence in time, according to Hall,<sup>1</sup> is "unequaled by that of any other known genus of organisms."

The embryonic shell of the *Lingula* living to-day is similar to that of *Paterina*. Pl. 653, figs. 1-3, represents a closely allied genus, *Glottidia albida* Hinds. Fig. 1 shows the *Paterina*-like shell (left unshaded in the drawing) and the long hinge line; also the youthful (nepionic)

<sup>1</sup> Pal. N. Y., VIII, part 1, 1892, p. 7.

stage when the shell has assumed the more rounded outline of *Obolella*. That this stage is more specialized than the *Paterina*-stage is proved by the fact, that, whenever the two stages occur in the development of a species, the *Obolella*-stage always follows the *Paterina*-stage. The hinge line grows narrower in the neanic (fig. 2) and the ephebic stage (fig. 3), while the shell becomes tongue-shaped in form.

The larva of the living *Lingula* is free swimming, but soon a pedicle is developed which becomes a long flexible organ in the adult (No. 654). This pedicle is not attached, but the end is buried in the sand and protected by a tube made of sand grains, after the fashion of the protective coverings of worms. According to Morse<sup>1</sup> the *Lingula* partially recedes into its sand tube after the manner of worms. The shell is in a line with the pedicle, and the length and flexibility of the latter organ allow the shell freedom of motion in any direction.

Beecher<sup>2</sup> has shown that physical forces acting similarly on all sides of a shell, which in this case is made possible by the long pedicle, tend to produce equal valves, such as are seen in *Lingula*.

Comparative simplicity of structure marks the internal organs as well as the external characters of the *Atremata*. The fleshy body takes up the greater part of the shell, while the arms or brachia (the characteristic organs which have given the name of *Brachiopoda* or arm-footed animals to the group) are without limy supports of any kind. Since these organs are of importance in determining the phylogenetic relations of genera, we will give figures to illustrate their stages of development. Their mode of growth "is alike in the larval stages of all *Brachiopods*." They first develop tentacles in pairs on each side of the median line in front of the mouth. This stage is repre-

<sup>1</sup> Proc. Boston Soc. Nat. Hist., XV, 1873, p. 372.

<sup>2</sup> Amer. Journ. Sci., (3), XLI, April, 1891.

sented in *Glottidia* and *Lingula* in Pl. 655, figs. 1-4. New tentacles are continually added at the same points, until by pushing back the older ones a complete circle is formed about the mouth (fig. 2), which later becomes introverted in front (fig. 3). From this common and simple structure are developed all the complicated brachia of the more specialized orders (Beecher). In the case of *Lingula* the growing points at which new tentacles arise, separate and the adult possesses two coiled arms one on each side of the median line (fig. 4).

We have already seen that members of the *Atremata*, *Trimerella* for instance, exhibit specializations of structure illustrating progressive tendencies, but the group contains no old age forms.

According to Beecher's classification, the *Atremata* are followed by the *Neotremata*, *Protremata*, and *Telotremata*, the first two being the more primitive orders and the last two the more specialized. This arrangement is in accordance with the geological history of the four orders, since the *Atremata* were the first to appear and the *Telotremata* the last.

Schuchert's classification<sup>1</sup> gives the following arrangement: *Atremata*, *Telotremata*, *Neotremata*, *Protremata*. This investigator makes a fundamental division of the class into two groups, the *Homocaulia* or those *Brachiopods* in which the pedicle is common to both valves, and the *Idiocaulia* in which the pedicle is restricted to one valve. The *Atremata* and *Telotremata* belong to the first division, according to Schuchert, and the *Neotremata* and *Protremata* to the second.

The fact that the *Atremata* and *Neotremata* are the most primitive of the four orders and are consecutive, is not considered a reason by Schuchert for placing the one after the other in a classification. Inasmuch as the line of descent is direct from *Atremata* to *Telotremata* and

<sup>1</sup> Bull. U. S. Geol. Surv., no. 87, 1897, pp. 118-135.

not by the way of the Neotremata or Protremata, he places the Telotremata next the Atremata.

The Neotremata and Protremata branch off from the Atremata at a much lower geological horizon than the Telotremata. According to Beecher the Neotremata have a protegulum like that of the Atremata and a Paterina stage when the pedicle passes out freely between the valves. According to Schuchert the pedicle opening in this order is restricted throughout life to the pedicle valve. Even if this be true with the forms so far described, we predict that other forms will be discovered which have the pedicle opening common to both valves in the nepionic stage.

For this reason we shall take up the Neotremata next, bearing in mind that more investigations are needed on the fossil forms belonging to this order, as well as on the early stages of development of existing species.

#### BRACHIOPODA.—NEOTREMATA.

One of the more primitive members of the Neotremata is *Paterula* (Pl. 656, figs. 1, 2, *P. bohémica* Barr.). It has a horny shell and when young is similar to *Paterina*, but later, layers are put on the brachial valve (fig. 1) posteriorly to the beak which cause the beak to become internal and the shell circular in outline. The pedicle valve (fig. 2) is differentiated from the brachial by having a notch in the margin which remains open in the adult (fig. 2). The arms or brachia in *Paterula* are two single spirals without limy supports.

Another genus, *Discinisca* (No. 657, *D. laevis* Sow.), has the protegulum of the brachial valve at the margin in the youngest stage and later near the margin, but with growth the protegulum becomes surrounded by more layers, as seen in No. 657. The edge of the pedicle valve (No. 657) is notched on the margin for the passage of the



pedicle, but this notch becomes surrounded by shell layers in the adult. This mode of growth is also peculiar to Discina, another member of the Neotremata, and when it occurs in the more specialized groups of Brachiopods it is usually called the Discinoid stage of development.

One of the most instructive forms is Orbiculoidea (No. 658, *O. lamellosa* Hall; No. 659, *O. minuta* Hall; Pl. 660, figs. 1-4, the same species; No. 661, *O. nitida* Phillips). Beginning with the protegulum, it passes through the Paterina stage (No. 659; Pl. 660, fig. 1) with its nearly equal valves, straight external or marginal hinge line, and its concentric parallel growth lines. The pedicle passes out freely between the two valves. This is the early nepionic stage. In the later stage, layers of shell have encircled the protegulum (No. 659; Pl. 660, fig. 2), causing the shell to become circular in outline, like *Obolella*, with no hinge line, and with the beaks internal though still near the margin.

In the neanic stage the beak is still farther from the margin (No. 659) while in the ephebic stage (No. 659) it is slightly less eccentric and would seem to be passing into the gerontic stage. The condition of the adult brachial valve as compared with that of the young is shown in Pl. 660, fig. 4.

The pedicle valve (No. 658, a, b; Pl. 660, fig. 3), has the protegulum at the center and an open pedicle notch as in the adult *Paterula*, but later the formation of circular layers of shell converts this notch into a hole through which the pedicle passes (No. 658, a, b). This hole becomes partly filled with a plate called the listrium (see No. 658, a, b).

It is probable that *Crania* (No. 662, *C. anomala*; No. 663, *C. tubinata* Poli) represents a reduced and specialized condition of the Neotremata. The complete life history of this genus has never been figured and described. It is known that, when young, the pedicle valve has an open notch like that of the adult *Paterula*. It is probable that

very early this notch is surrounded by shell layers, although no specimen showing this holoperipheral growth has been found. This is probably due to the fact that when very young the animal becomes attached to a rock (No. 663) by its pedicle valve which causes the pedicle to disappear and with it the notch and the circular layers if any such exist.

#### BRACHIOPODA.—PROTREMATA.

The Protremata may have arisen from some Paterina-like ancestor which lived in pre-Cambrian times, or may have branched off from the Neotremata at a later period. The forms known to us illustrate specialization of structure brought about through acceleration in development.

One of the more generalized forms is *Kutorgina cingulata* Billings (Pl. 664, figs. 1-3). Here the hinge line is straight (fig. 1), and there is a narrow rudimentary cardinal area on the pedicle valve (figs. 1, 2, *pv*). This valve (fig. 3) rises above the brachial (figs. 1, 2, *bv*) and a large opening is left for the passage of the pedicle (fig. 2) which is only slightly restricted by the deltidium. This plate in the Protremata is formed in the embryo and is a shell growth from the brachial side of the body which later becomes attached to the pedicle valve.<sup>1</sup> The teeth in *Kutorgina* are primitive and are situated at the outer ends of the cardinal area. Figures illustrating the stages of development are given under *Thecidium* (see p. 273).

The brachial valve in the Protremata, as in the other orders, is less differentiated than the pedicle valve, and shows the protegulum as in the Atremata. When extremely young, the shell probably passes through a long-hinged or Paterina stage, but in the early nepionic stage of most genera the pedicle is surrounded by shell layers

<sup>1</sup> See Beecher, Amer. Journ. Sci., (3), XLIV, 1892, pp. 142-147.

and the pedicle valve becomes circular in form, the shell passing through a stage similar to that which we have already described as the Discinoid stage of the Neotremata. This is shown in *Leptaena rhomboidalis* Wilck. (Pl. 665, fig. 1). As growth continues, the neanic stage (fig. 2) is marked by radiating lines. The peripheral layers are resorbed, so that the pedicle opening approaches the edge (fig. 2) and in the ephebic stage reaches it (fig. 3; see also No. 666). In this stage the cardinal areas of both the convex pedicle valve (No. 666) and the concave brachial valve are long, flat, and narrow with a triangular fissure for the pedicle which is partly filled by a deltidium. Finally the pedicle disappears altogether, and *Leptaena* is free as in its young condition. In old age the anterior and lateral portions of the valves bend at nearly right angles (No. 666) to the plane of the younger shell, and the layers of growth are crowded closely together (No. 667).

The arms or brachia in *Leptaena* and in the Protremata generally are not supported by a limy skeleton.

The only living representative of the Protremata is the genus *Thecidium* (= *Lacazella*). The cephalula stage (as it is called) is represented in Pl. 668, fig. 1, a dorso-ventral longitudinal section of *T. mediterraneum* Risso. The mantle lobes (fig. 1, *d* and *v*) are unequal. The limy dorsal valve (*ds*) and the shell-plate (*del*) begin to form; the latter on the dorsal side of the body. The larva transforms by the mantle lobes bending upward, which causes the shell-secreting surfaces (indicated by the heavy black lines) to come on the exterior (fig. 2). The shell-plate (*del*) is below the hinge line (fig. 2, *hl*). The adult (fig. 3) shows one valve and the deltidium (*del*), and the side view (fig. 4) gives both valves marked by concentric lines, the hinge line (*hl*) and the deltidium (*del*).

These figures show that the deltidium is formed on the brachial side of the body, as already stated, and on that

segment which subsequently becomes the pedicle; afterwards it is fastened to the pedicle valve. Thecidium is especially interesting as it is the only Brachiopod which retains a true deltidium at maturity.<sup>1</sup>

It is instructive to note that after the pedicle is lost, in several genera of this order, spines are developed for the purpose of anchoring the animal. In *Chonetes granulifera* Owen (No. 669), these spines are found only on the cardinal margin of the pedicle valve. *Productus nebraskensis* Owen (No. 670), however, inherits such a weak pedicle that this organ soon disappears, and spines are developed over the entire surface of the pedicle valve and sometimes are also found on the brachial valve. The animal lies on the pedicle valve fastened by its spines.

Vestiges of the cardinal areas and teeth are sometimes present in this genus, but are often wanting. The beak is high and curved, and no trace of a pedicle opening remains. Many of these characters are intensified in the old age stage (No. 671). The shell extends anteriorly and broadens outward at the same time. The beak of the pedicle valve is bent far inward and the pedicle opening has wholly disappeared. The ribs which are prominent and regular in the adult stage, partially die out and become more or less irregular (see No. 671).

Interesting specializations of structure are illustrated by *Orthis* (= *Platystrophia*<sup>2</sup>) (No. 672). We have here large cardinal areas and perfect articulation by teeth and sockets. The area of the pedicle valve has a large pedicle opening or delthyrium, and that of the brachial valve has a similar opening, the chelyrium. When young, these openings are partially closed by plates, the deltidium and chilidium. In the course of development, however, the plates are resorbed so that open passages remain in the adult (see No. 672).

<sup>1</sup> Hall and Clark, Nat. Hist. N. Y., Pal., VIII, part 2, 1894, p. 283.

<sup>2</sup> See Cumings, Amer. Journ. Sci., (4), XV, nos. 85, 86, 1903.

The changes which take place in the development of a Protrematous shell are well shown by *Bilobites varicus* Conrad (Pl. 673, figs. 1-12). It begins as a smooth, straight-hinged form with the hinge as broad as the shell and with a rounded front margin (figs. 1, 2). Occasionally while the shell is in the nepionic stage the deltidium of the pedicle valve is retained, as seen in fig. 3, which also shows the cardinal area and pedicle opening. The deltidium is lost in the neanic or the ephebic stage and the pedicle passes out of the large opening. Gradually the rounded front margin, seen in figs. 1, 2, becomes straight (fig. 4), and later a sinus is developed (fig. 5) which afterward becomes more pronounced (figs. 6-11).

The pedicle valve is at first shorter than the brachial, and for this reason is not seen in figs. 1, 2, 4-6; soon, however, it grows longer (fig. 7) and the cardinal area with its pedicle opening is distinctly seen (figs. 8-10). The adult shell (fig. 11) has a narrow hinge line, while the anterior portion of the shell is broad and strongly bilobed. In the old age or gerontic stage the sinus becomes nearly obliterated (fig. 12), and the anterior portion of the shell resembles that of the young stage represented in fig. 5.

One of the most differentiated members of the Protremata is the genus *Pentamerus* (No. 674, *P. oblongus* Sow.). The variation in form of this genus is shown by the specimens (No. 674, e, f) which are casts of the interior. The beaks even in the young stages (No. 673, a-d) are incurved, and so strongly is this the case in the adult (e, f) that the small pedicle opening is concealed. The deltidium when present (which is rarely the case) is concave.

This genus is an exception among the Protremata, inasmuch as the arms are supported by two limy processes called crura. These crura unite to form a plate, the crurulum, which is used for the attachment of muscles. The pedicle valve also has a large, strong, internal plate,

the "shoe-lifter" or spondylium, which serves the same purpose.

#### BRACHIOPODA.—TELOTREMATA.

One of the most primitive members of the Telotremata is *Protorhyncha aequiradiata* Hall (Pl. 675, figs. 1-3). We know nothing of the early development of this species, but the adult is primitive in its characteristics, so that it is reasonable to assume that the young stages must have been still more primitive. It has been ascertained in living genera of this order (Telotremata) that in the nepionic and early neanic stages the pedicle passes out freely between the two valves, the opening being shared by both as in the Atremata. In the later neanic period the shell layers extend entirely round the pedicle, so that this organ becomes restricted to the pedicle valve. In the adult or ephebic stage of *Protorhyncha* (figs. 1-3) the pedicle opening is triangular, and is rarely closed by plates of any kind.

There is no cardinal area in *Protorhyncha*, according to Schuchert,<sup>1</sup> while Hall and Clarke<sup>2</sup> figure a small rudimentary area (fig. 2). The adult shell is narrow at the beak or rostrate in form (Pl. 675, fig. 1, internal cast of the brachial valve; fig. 3, internal cast of the pedicle valve).

The arms of *Protorhyncha* are fleshy and not strengthened by limy supports; even crura, the parts to which the brachial supports are fastened, are not developed.

According to Schuchert<sup>3</sup> the oldest Rhynchonelloids are rostrate in form, like *Protorhyncha*, and the ontogeny of several living species of the genus has not revealed a long-hinged stage.

<sup>1</sup> Bull. U. S. Geol. Surv., no. 87, 1897, p. 87.

<sup>2</sup> 13th Ann. Rep. State Geol. N. Y., 1893.

<sup>3</sup> *Loc. cit.*, p. 83.

*Rhynchonella peregrina* (No. 676) from the Cretaceous, *Rhynchonella octoplicata* (No. 677), and *Rhynchonella psittacea* Dvds. (= *Hemithyris psittacea* Chemnitz) (No. 678; No. 679, shells of the same), living to-day, show no marked difference in form from the primitive Protorhyncha of the Silurian formation, although the size varies, *Rhynchonella peregrina* being the giant of the genus. This species exhibits the curved hinge line (No. 676), the prominent beak, and the pedicle opening which is partly closed by two plates called by Hall and Clarke deltaria. The origin of these plates is entirely different from that of the single plate, the deltidium. As we have already seen in the Protremata (see p. 272), the deltidium is a primitive character arising in the embryo or early nepionic stage of development, while the deltaria are formed in the neanic or the ephebic stage and are made by extensions of the mantle. Owing to this difference in origin and structure, and in order to save confusion, we prefer the name of deltaria to deltidial plates given by many naturalists.

The smooth, unornamented condition of the young *Rhynchonella* shell is seen in No. 677, while the later stages are marked by ribs and flutings. Along the margin, the layers are crowded closely together, an indication of the gerontic stage.

The specimen of *Rhynchonella psittacea* Dvds. (No. 678) is attached to a pebble. Unlike Protorhyncha, this genus has the arms supported by two short, simply curved processes, the crura (see No. 679, f; Pl. 680), which are attached to the brachial valve (see No. 678 specimen with arms extended).

Specialization of parts is finely illustrated in this order by the structure of the brachia and their internal limy supports or brachidia. Beginning with the simple, curved crura of the *Rhynchonellae* (Pl. 680, crura with the fleshy arms coiled), we pass to *Centronella* (*C. glansfagea* Billings; Pl. 681, fig. 1, dorsal view; fig. 2, ventral view;

fig. 3, side view), in which a primitive loop (fig. 4; fig. 5, side view of same) descends from the brachial valve. This is made by two leaf-like parts or lamellae which are attached to the crura and which unite in the median line to form the broad loop.

The hinge area with its ridges and the muscular scars are seen in fig. 6.

*Stringocephalus burtini* Deifr. (Pl. 682; No. 683) is a Devonian representative of a more specialized family. In the young shell (Pl. 682, fig. 1) the triangular pedicle passage or delthyrium is open or sometimes partly closed by partially developed deltaria; in the adult (Pl. 682, figs. 2-4; No. 683) it is wholly closed excepting the pedicle opening (fig. 2), while in the old age stage (fig. 5; No. 683, specimen on the right) the coalescence of the plates into one plate (called the deltarium and the pseudodeltidium) is almost complete, and the pedicle opening is greatly reduced in size.

The arm supports consist of a long loop which extends around the margin of the brachial valve. Its form and the radial filaments extending from it are seen on the left of Pl. 682, fig. 3. The strong cardinal process extending from the brachial valve towards the large median septum of the pedicle valve on the right is also well seen in fig. 3.

The changes which a *Centronella*-like loop often undergoes are well illustrated in the Palaeozoic Brachiopod, *Dielasma turgidum* (Pl. 684, figs. 1-5). Fig. 1 is the *Centronella*-like loop of the young. The pointed anterior portion is resorbed and two points extend forward (fig. 2). The process of resorption continues till the loop has the form of fig. 3. In the loop of the adult the two branches or lamellae diverge, as seen in fig. 4,  $\times 6$ ; fig. 5 is a side view showing the crus and loop on the right and the median septum on the left.

Among the instructive forms of the Telotremata living to-day are *Terebratula* and *Terebratulina*.

One of the forms of *Terebratula* (*T. insignis* d'Orb.;



No. 685) belonging to the Jurassic, was of remarkably large size. The pedicle opening and the deltarium are well shown in the specimen. The anterior margin exhibits the gerontic character of layers crowded closely together.

The position of a living *Terebratula* is well shown in No. 686, *T. vitrea* Born.; also No. 687, where the Brachiopod is attached to coral. The pedicle is tiny for the size of the valves, which are nearly erect. The brachial valve (No. 688, b) has the loop attached to it. This loop began as a primitive *Centronella* loop and passed through changes similar to those which will be described farther on in the closely related genus *Terebratulina*. The pedicle valve (No. 688, c) has a circular pedicle opening; the deltarium are small and concave, so that the brachial valve moves upon the pedicle, though the motion is limited, especially in the older, more rotund specimens.

The development of *Terebratulina septentrionalis* Couth. (Pl. 689, figs. 1-7; No. 690), throws light on several important points. The earliest stage observed after the egg-stage is represented in fig. 1, where the animal is extremely minute, the length of its shell being indicated by the line enclosed in the circle. It is attached to a rock, and rests upon its broad hinge area with the anterior margin uppermost, as seen in the drawing. The shell is comparatively broad and short, and there is a wide pedicle opening. Its form, however, changes rapidly, becoming like *Lingula* (fig. 2), though still retaining the wide anterior margin.

The pedicle is long, allowing freedom of motion to the valves which are seen in fig. 3 in a partial lateral view. The animal is able to "whirl quickly" on its pivot-like pedicle, and is represented in motion and at rest in fig. 4. When in motion, it is nearly erect with the valves open, and the cilia of the tentacles are active in catching food; while at rest, the valves are closed and the brachial valve often lies on the rock or other object of support. Further development causes the shell to broaden out anteriorly and to become ornamented by ribs (fig. 6).

A distinct line is seen in this figure marking off the nepionic, Lingula-like stage from the succeeding neanic stage. When the brachial valve is thrown open (fig. 5), the crura (*cr*), which have already begun to form, are seen supporting the crown of tentacles. The changes which take place in the external shell between the stage represented in figs. 5, 6, and the completed shell, fig. 7, were not figured by Morse. The development of the cardinal region of the pedicle valve, however, was given (Pl. 691, figs. 1-4). The pedicle opening becomes more circular in outline and truncates the beak of the pedicle valve (compare figs. 1-4 in Pl. 691; see also No. 692, *T. crassei* Dvds.). The deltaria are small and concave, while the teeth, which are prominent in the earlier stages (Pl. 691, figs. 1-3, *t*), are reduced in size in the adult (fig. 4, *t*). The development of the brachial loop is shown in Pl. 691, figs. 5-8. Beginning as little swellings or processes (fig. 5, *c*), the crura grow larger (fig. 6, *c*), reminding one of these parts in *Rhynchonella* (see Pl. 680; No. 678). Then the loop begins to form (Pl. 691, fig. 7), which is completed in the adult (fig. 8).

The development of the brachia in *Terebratulina* illustrates the development of these organs in the Telotremata generally. The first three stages are similar to those of *Glottidia* in the Atremata (see Pl. 655, figs. 1-3). The lophophore in the first stage is a simple crescent with few tentacles (Pl. 693, fig. 1); in the second stage the tentacles have increased on either side of the median line in front of the mouth and have been pushed backward until a complete ring has formed around the mouth (fig. 2). Next, the anterior edge of this ring bends inward (fig. 3). The development is carried still further in *Terebratulina* by the formation of a median unpaired arm (fig. 4). Fig. 5, *T. cancellata* shows a well developed spiral arm between the two lateral arms.

Certain gerontic peculiarities are seen in *Terebratulina cancellata* Koch (No. 694). The nepionic shells seen in

the little box are somewhat flattened and the beak of the pedicle valve is in a nearly normal condition. The pedicle opening is large, and the delthyrium is not filled with the deltarium. The older shells on the standard are thickened and have a sharp anterior edge. The pedicle has worn away a portion of the beak, while the deltarium have formed, and the suture indicating their line of contact can be plainly seen in the specimen in the lower right hand corner. In old age the shell becomes so rotund that the valves when separated are bowl-like in shape (see side view of the shell in the upper right hand corner). Each valve is thickened along the margin by many layers crowded closely together. The suture of the deltarium has disappeared, leaving apparently a single plate, the deltarium or pseudodeltidium. The brachial loop or ring is essentially the same in the youngest and oldest stages.

It now seems probable that *Tropidoleptus carinatus* Conr. (Pl. 695; No. 696) is an ancestral form of the family Terebratellidae. It is a thin shell with convex pedicle and concave brachial valve. The cardinal area is straight and narrow, and in the young (Pl. 695, fig. 1) longer than the greatest diameter of the shell, but in the adult (No. 696; Pl. 695, figs. 2-4) it is shorter. The pedicle passage is never closed by a deltidium (fig. 4; fig. 5, side view of cardinal area enlarged), but a chlidium is well developed on the brachial valve (fig. 5). The loop (fig. 6) consists of two descending branches or lamellae united to the median septum. These parts are still better seen in fig. 7, which is a side view of the septum loop and the two jugal processes extending from the lamellae.

*Cistella neapolitana* Scacchi, belonging to the generalized Terebratellidae, is living to-day. Its development tends to prove that Brachiopods are closely related to Worms. No. 697, with models 1-10, and pl. 698, figs. 1-10, illustrate the development of this genus. The egg (No. 697, 1) is unsegmented. Its division into two spheres is seen

in (2). These two stages represent the protembryo. The blastula or mesembryo is seen in (3), where there are many cells around a central cavity. The gastrula or metembryo (4) is formed in this genus by the turning inward of a portion of the outer layer, a process known as embolic invagination. In the first stage of the neoembryo (5; also Pl. 698, fig. 1) the embryo consists of two segments, the cephalic and the caudal. Then the thoracic segment develops (No. 697, 6; Pl. 698, fig. 2) with the eye spots and the four bunches of setae. A side view of this cephalula stage is given in Pl. 698, fig. 3, and a dorsoventral longitudinal view of the same stage in fig. 4. The mantle lobes now cover most of the caudal segment, and the cephalic segment is shaped like an umbrella (No. 697, 7). This is the completed neoembryo. The mantle lobes fold upward over most of the head segment, and the larva is transformed into the typembryo (see No. 697, 8; Pl. 698, fig. 5; fig. 6, longitudinal section of the same; No. 697, 9, the completed typembryo showing embryonic shell). The mantle lobes are now directed forward instead of backward, as in fig. 4, and the shell-secreting surfaces (indicated by the heavy black line) are on the outside instead of the inside. This stage develops into the phylembryo (No. 697, 10; Pl. 698, fig. 7); the latter figure shows the protegulum, the beginning of the tentacles on the band or lophophore (*l*), the hinge line, and the teeth (*t*) at the outer ends. The nepionic stage is represented in Pl. 698, figs. 8-10. The tentacles are now distinct (fig. 8), and also the mouth, stomach, and muscles are shown with the shell and the pedicle. The large opening between the valves (filled by the pedicle, *p*) is well seen in figs. 9, 10, which are a dorsal and a side view of the nepionic shell.

The family Terebratellidae is especially instructive as it offers interesting correlations. Beecher has brought out (see Pl. 699) the parallelism existing between adult, permanent generic structures of the more primitive mem-

bers of this family, and the stages in the ontogeny of the brachial supports of the specialized members; such, for instance, as *Magellania*. In *Gwynia capsula* Jeffreys (Pl. 699, A), one of the most primitive members of the Terebratellidae, the brachial supports never undergo a metamorphosis but remain essentially the same throughout life. They consist of two descending branches or lamellae which are not attached to the crura and which do not unite to form a complete loop. The crura from which the lamellae ultimately extend in most genera are seen at the posterior end of the valve in all the figures.

*Cistella neapolitana* Scacchi (Pl. 699, B), has a median septum with a calcified loop attached which is united to the crura.

A small ring appears on the septum in *Bouchardia rosea* Mawe (Pl. 699, C, Ca, side view), which is the beginning of the secondary loop. The parts become more united in *Megerlina lamarckiana* Davidson (D), while in *Magas pumilus* Sow. (E), the descending branches are completed, though the ascending have not united. *Magasella cumingi* Dvds. (F), shows the character of the descending and ascending loop more distinctly, which reaches a still more specialized condition in *Terebratella rubicunda* (G). Here we have the descending loop with the septum and connecting band or jugum and the completed ascending loop.

A further change takes place in *Magellania flavescens* Lam. (Pl. 699, H), in which the septum and connecting bands seen in *Terebratella* have been resorbed. These eight figures represent as many adults of eight different genera, ranging from the most primitive to the most specialized of the Terebratellidae.

When the life history of the last named genus, *Magellania*, is studied, it is found that it epitomizes in its own development the history of these genera, and in this way the history of the family to which it belongs.

The larval *Magellania* is without calcified brachial sup-

ports, but has a band or circlet of tentacles. This is the larval stage corresponding to the adult primitive Gwynia, and is therefore called the Gwyniform stage (Pl. 699, A<sub>1</sub>). Next the median septum appears, which is the Cistelliform stage (B<sub>1</sub>). The only advance over this condition shown by the adult Cistella (Pl. 699, B) is the calcification of the band which bears the tentacles, and its attachment to the crura.<sup>1</sup> The third stage shows a ring on the septum (C<sub>1</sub>, Ca<sub>1</sub>, side view of same) which is the Bouchardiform stage. A still more advanced condition is seen in the Megerliniform stage (D<sub>1</sub>, Da<sub>1</sub>, side view) which has the septum ring and in addition to these the "prongs" of the descending branches. It has been shown<sup>2</sup> that in "all genera where the median septum is highly developed the calcification of the lamellae of the brachidium begins quite as soon from the lateral wall of the septum as from the crural bases on the hinge-plate. Calcification thus proceeds both posteriorly and anteriorly."

The Magasiform stage exhibits the completion of the descending branches (E<sub>1</sub>). This stage and also the Magaselliform stage (F<sub>1</sub>) which follows, show the union of the ascending branches, and in this particular differ from the adult Magas (E) and Magasella (F).

The Terebratelliform stage (G<sub>1</sub>) is similar to the adult of Terebratella (G). At last the final stage is reached, as we have already stated, by the resorption of the connecting band and the septum (H<sub>1</sub>, *Magellania venosa* Sol.).

The family of Atrypidae is represented by *Zygospira* and *Atrypa*. *Zygospira* is the most primitive spire-bearing genus known. Figs. 1-11 of Pl. 700 represent *Zygospira recurvirostra*, *Z. modesta*, *Z. headi*, and No. 701 is a small colony of *Zygospira modesta* Hall, in which the shells are preserved in natural position.

<sup>1</sup> Beecher, Trans. Conn. Acad. Sci., IX, part 2, 1895, p. 393.

<sup>2</sup> Hall and Clarke, Nat. Hist. N. Y. Pal., VIII, part 2, 1894, p. 305.

The brachial support in the young *Zygospira* is a Centronelliform loop (Pl. 700, fig. 1; fig. 2, side view of the same). With the growth of the shell the descending branches of the loop diverge, while the resorption of the central portion of the loop causes the formation of the cross band or jugum, as seen in figs. 3, 4. Both the loop and the jugum become more slender (Fig. 5), while the projections on the descending branches of the loop are the beginnings of the spiral cones. These projections grow longer (fig. 6) and begin to coil. Fig. 7 represents a young individual in which there are one and a half turns to each spiral. In the mature form (fig. 8) there are about three volutions in each spiral. The adult *Zygospira modesta* Hall (figs. 9, 10) has five volutions, while the species *Z. headi* Billings (fig. 11), has six whorls.

At the same time that the whorls have increased in number, the jugum has moved posteriorly (figs. 9-11), until in *Z. headi* it is seen to be posterior to the brachia (fig. 11). The spiral arms and the jugum are both seen in the two microscopic preparations (No. 702) of the shell of *Zygospira*.

The largest number of whorls of any member of the family Atrypidae is reached in the genus *Atrypa*. In *A. reticularis* Linn., from the Silurian, sixteen volutions have been counted in each cone, while in Devonian specimens (Nos. 703, 704; Pl. 705) twenty-four volutions have been found. These are directed towards the median dorsal region and fill the brachial cavity. The cross band or jugum is continuous in the young but becomes disunited in mature specimens. No. 704 shows the club-shaped ends of the jugum posterior to the apices of the whorls (see Pl. 705).

One of the most specialized families of the Telotremata is the Spiriferidae, represented by *Spirifer* (No. 706, *S. granulosus* Conrad; No. 707, *S. mucronatus* Conrad). Here we have a broad shell with well developed cardinal

areas and straight hinge line. The deltarria are formed and become united into one plate, but with age they are removed by accident or resorbed, so that usually the delthyrium is open.<sup>1</sup> In the old age stage some species form a callosity in the pedicle cavity which extends across the delthyrium and reaches in extreme cases nearly to the cardinal margin. The median septum in the pedicle valve is found in the young but seldom in the adult.

The very young stages of some species of *Spirifer* have a *Centronella*-like loop which passes through a metamorphosis. The descending branches in this genus are between the spiral cones (Nos. 706, 707), and the apices of the latter point outward and upward (No. 707). The spiral cones (No. 706, lower left hand corner, two single specimens from two shells) may have a greater number of volutions in the adult or the old age stage than any other genus, as many as thirty-five having been counted.

The jugum is discontinuous and is represented by two short processes, one of which is seen in the right hand lamella of No. 707. A faint median septum is sometimes present in the brachial valve.

*Meristina* is another specialized form. No. 708, *M. maria* Hall, is a vertical section through the outer shell revealing one spiral cone and cut to show the position of the loop. In No. 709 these cones are seen to point outward on each side and to consist of many whorls.

Enough has been said to show that there is a far greater degree of specialization among the *Telotre mata* than in the other three orders of *Brachiopods*. The arm supports are extremely complex, and the devices which have arisen to meet the needs of the muscular system are novel and various. Unlike the *Atremata* there are numerous examples of old age forms in this order.

<sup>1</sup> 13th Ann. Rep. State Geol. N. Y., 1893, II, p. 752.



## POLYZOA.

The young stages of Polyzoa, also called Bryozoa, are similar to those of Brachiopods, which is one good reason for placing these two groups near each other. The Polyzoa develop from a trochophore and with one exception become colonial forms. Their calcareous skeletons, consisting of numberless little cavities or chambers, are often seen encrusting seaweed. Other genera are like miniature trees, branching coral, and the like.

Loxosoma is the only single Polyzoan known, but inasmuch as it is a commensal living with other animals, the strong probability is that, though single, it is a specialized form, a reduced descendant of some colonial ancestral species. For this reason we consider *Pedicellina* (No. 710, *P. cernua* Pall.) as the more primitive. Here we have a comparatively simple colony. No. 710, a-h, represents eight members; (a) and (b) are very young stages; (c) is also young with its tentacles drawn in; (d) is a vertical section showing mouth (*m*), stomach (*s*), and anus (*an*); (e) and (f) have the tentacles expanded; (g) is just losing its old cup-like body wall or calyx and another bud is beginning to grow; in (h) the primary calyx has been lost and a new one is developing.

It is seen that the alimentary canal is complete, and that it makes a turn, bringing the anus near the mouth within the circle of tentacles. This position of the anus is characteristic of the generalized Polyzoa, since it is found outside the circle of tentacles in the specialized forms.

When the colony of *Pedicellina* dies there are left little stalks that rise from a creeping stolon, but in the specialized Polyzoa an innumerable number of tiny cavities or zoecia remain, each one of which represents an animal.

Many Polyzoa are of exquisite beauty, as shown in

some of the species (Nos. 711-721). These illustrate different modes of growth in colonial forms. *Cellularia* (No. 711, *C. rigida*) is an erect species with its many branches made up of joints. The beautiful *Catenicella* (No. 712) has delicate curling branches, while *Bugula* (No. 713) is tree-like in form and some species show a spiral mode of growth. Peculiar modifications of structure are found in these specialized Polyzoa, such as the birds' heads or avicularia, which are remarkable organs of uncertain function.<sup>1</sup> The avicularia are well illustrated by *Bugula* when seen under the microscope (Pl. 714). One avicularium (b) is seen with jaws closed, and another (b') with the lower jaw open. These little organs have been seen to catch small animals.

*Biflustra perfragilis* (No. 715) is an extremely fragile specimen growing in a circular form. In *Tessaradoma* (No. 716, *T. magnirostris*) there is one layer of zooecia, while in *Adeona* (No. 717, *A. grisea*) the zooecia are in two layers. In general form *Adeona* resembles the fan coral, *Rhipidogorgia*. The colony is attached by a slightly flexible stem, but in *Adeonellopsis* (No. 718, *A. australis*) there is a rigid base.

*Lepralia* (No. 719) forms a large colony, and the flattened branches unite irregularly. In *Filogrina* (No. 720, *F. implexa*) the branches appear to be made of strands.

Among the fresh-water Polyzoa are *Retepora* (No. 721, *R. phoenicea*) and *Cristatella*. The latter has the power of locomotion, though it is probably descended from some marine stationary form.

#### ANNELIDA. — CHAETOPTERA.

The record left by the early ancestors of our present worms is scanty and unsatisfactory. It offers another

<sup>1</sup> Hertwig, *Man. Zool.*, transl. by J. S. Kingsley, 1902, p. 323.

illustration of the fact that only under exceptional conditions can traces of soft-bodied animals be preserved.

Such conditions were realized in Mesozoic times by the peculiar clay of the present lithographic slates of Bavaria, the extreme fineness of which made it possible for an impression to be taken and preserved of even so delicate an animal as a jelly-fish. The Palaeozoic formations, however, have no lithographic slates, and the occasional indefinite trails (Pl. 722, *Nereites cambrensis* M'Leay), the filled-up burrows (Pl. 723, *Planolites vulgaris*), and the like, are but uncertain evidences in regard to the ancient fleshy progenitors.

When, however, the descendants of these fleshy ancestors became specialized to such a degree as to possess masticating organs in the form of chitinous jaws, then these hard parts would be preserved. The fact that such remains (Pl. 724, figs. 1, 2, jaws of *Eunicites*, greatly enlarged<sup>1</sup>) exist in the lower Palaeozoic rocks proves that worms originated in the early geologic times. Corroborative testimony on this point is given by Dr. Hobb's discovery of worm borings and worm teeth in the pre-Cambrian rocks of eastern Massachusetts.<sup>2</sup>

Though we know little of the Palaeozoic predecessors of our present worms, the Bavarian lithographic slates help us greatly in regard to the Mesozoic ancestors. Remains are preserved with sufficient clearness to enable us to determine many of their characteristics. These worms (Pl. 725, fig. 1, *Eunicites avitus* Ehl.), had long bodies divided into a large number of segments (more clearly seen in fig. 2, *Ctenoscolex procerus*). The greatest breadth of the worm is at the anterior end, and the body tapers towards the posterior extremity which is not preserved in fig. 1, but is seen in fig. 2. On either side of

<sup>1</sup> Most of these jaws do not average more than one twelfth of an inch in length.

<sup>2</sup> See Amer. Geol., XXIII, Feb., 1899, p. 109.

the body the bristles or setae are distinctly seen (fig. 1), but it is not definitely known whether these worms possessed locomotive paddles called parapodia. The jaws are found in place (fig. 1) and in some species of Eunicites (*E. dentatus*, fig. 3) they bear prominent teeth, reminding one of the toothed jaws of the Palaeozoic species, *Eunicites simplex* H. (Pl. 724, fig. 1) and *E. clintonensis* H. (fig. 2).

Doubtless naked worms with primitive structural features exist or have existed in the abyssal depths of the sea, but these could hardly be brought to the surface in perfect condition. Most of the worms so far obtained have been protected by a tube, and are specialized by the possession of numerous organs. There is evidence, furthermore, that many of these forms have migrated from shallow water to the deep sea, and therefore they possess a combination of adaptive characters which renders them puzzling and of little phylogenetic value.

In default of fossils representing pre-Cambrian or Cambrian fleshy forms, and of primitive deep-sea species, we should naturally turn, as we have done already in several groups under similar circumstances, to the embryonic and larval stages of development of a primitive, marine, and free-swimming member of the class under consideration.

There are many reasons for considering *Dinophilus* as a primitive worm, although its development has not been worked out in detail nor the trochophore (if one exists) figured, yet the young stage (Pl. 726, fig. 1, *D. taeniatus*) is little more than a trochophore. There is no metamorphosis, and it does not appear that the larval stages peculiar to those forms that pass through a metamorphosis are skipped in the development of this worm. We should say, on the contrary, that these stages have never occurred in the ancestors of *Dinophilus* and that the embryo develops gradually from the egg to the young form (fig. 1). In this stage the body is transparent, and

is divided into a few distinct segments. Both the young and the adult (fig. 2, *D. gigas*) are without tentacles and no parapodia are developed. Neither are setae found, and locomotion is effected by the bands of cilia clearly seen in figs. 1, 2. Practically, according to Harmer,<sup>1</sup> the adult is a trochophore, or, as Benham<sup>2</sup> puts it, "the adult is more like a larval Polychaete than a full grown worm."

While it is true that there is a marked difference in size between the male and the female of some species (which is one reason why some naturalists consider *Dinophilus* as a secondary rather than a primitive form), nevertheless there are other species, like those figured in Pl. 726, figs. 1, 2, where, excepting the sexual organs proper, the sexes are alike.

Most Annelida arise from a trochophore which does not differ essentially from that of Mollusca. As we have already seen, this trochophore stage is common to several groups of animals, — Pelecypods, Gastropods, Cephalopods, Pteropods, Brachiopods, — and for this reason we maintain that it must be of phylogenetic importance.

When the ancestors of the trochophore which were active swimmers, gave up this mode of locomotion and became crawlers, it is not unlikely that the body elongated. Surely it is not difficult to conceive that such a change of habitat and of habit would produce a long, more or less flattened and unsegmented body. Neither is it hard to see that, as time went on and the habit of creeping was established, it would be an immense advantage to such a crawling animal to have its body capable of the greatest possible freedom of motion. This freedom might be gained through purely mechanical means, whereby the sinuous movements of the body would bring about a division into parts or segments of greater and less mobility.

<sup>1</sup> Journ. Mar. Biol. Assoc., n. s., I, 1889, p. 141.

<sup>2</sup> Cambridge Nat. Hist., II, 1896, p. 243.

The boundaries of the segments would in time become definite and the segments themselves be capable of moving freely upon one another. While this may be an explanation of the origin of segmentation, there is as yet no evidence to prove it in embryology. Granted, however, that this explanation be correct, it is doubtful whether the flattened, unsegmented stage of development is represented by adult living worms of to-day. The unsegmented Nemerteans and Turbellaria (p. 317) are considered by many naturalists as the nearest living representatives of ancestral forms, but there are so many reasons for considering these as secondary and not primitive groups (see p. 317) that we prefer to place them as terminal branches rather than trunk forms of the great genealogical tree of Vermes.

The process by which at the present time a many-segmented worm arises from a trochophore is shown more plainly in *Polygordius* than in any other worm so far described. For this reason we shall consider it here, but provisionally, since it is not yet clear whether *Polygordius* is a primary or a secondary form. As a rule such uncertain species are omitted in this Guide, and an exception is made in favor of *Polygordius* only because it illustrates the subject far better than any other known worm. Its trochophore, familiarly known as "Lovén's larva" (Pl. 727, fig. 1, seen from the side), is free-swimming and similar to the trochophore of Mollusca. It is spherical and transparent. The mouth (fig. 1, at the left) is on the ventral side and in front of it is the pre-oral lobe, and also the pre-oral band of cilia. Parallel with this band, and just back of the mouth, is another band of cilia which are much shorter than those in front. This band is seen more plainly in fig. 2, which is a drawing of an older larva.

The digestive system consists of a mouth, stomach, and intestine ending in the anus which is at the posterior end (figs. 1, 2). Soon the trochophore begins to elongate (fig. 3) by adding segments to the posterior end, while the

pre-oral lobe in front of the mouth decreases in size (fig. 4). This process goes on until the form of the mature larva (fig. 5) is attained. The body is now made up of similar segments; the mouth is on the ventral side, and there is an ocellus on either side near the forward end, while it possesses (in addition to the young larva) a pair of short tentacles (fig. 5). These are its only appendages, and as there are no locomotive organs in the form of chitinous setae or fleshy paddles, the animal moves by means of cilia only. Neither does this worm possess external breathing organs in any form, for the skin probably performs the work of respiration.

The adult (Pl. 728, fig. 1, natural size; fig. 2, enlarged) does not differ essentially from the mature larva. Some of its features enlarged are shown in figs. 3-5. The body is segmented, the segments showing more plainly in the enlarged section (fig. 3) than in figs. 1, 2. The pre-oral lobe bears the pair of hairy tentacles (fig. 4) and back of this lobe is the mouth (fig. 4). The anus is still at the posterior end of the body (fig. 5) surrounded by a circle of papillae.

The worms which are best known and which are exhibited in the Synoptic Collection belong for the most part to one of two groups. Either they are broadly differentiated by the possession of many parts and organs, or they are extremely specialized by the reduction of organs. The first group to be described consists mainly of marine and shallow-water forms, and many are found for a longer or shorter time under stones or burrowing in sand. They have become more or less adapted to their environment, so that some of their organs are secondarily acquired and these of course throw little light on phylogenetic relationships. The second group, however, consists mostly of parasites, and their structure has undergone such a profound modification that they are much farther removed from the primitive ancestral forms than are the members of the first group. They have become adapted to the

most varied situations, and their organs have passed through such a complete change that they are of no phylogenetic value.

Aphrodite or the "sea-mouse" (No. 729) belongs to the first group. It is unique in possessing an almost innumerable number of delicate hairs and larger setae, which reflect the most brilliant prismatic hues, making the worm a marvel of beauty. Alcohol has no power to rob this animal of its gorgeous tints. The mechanical cause for the coloring lies in the extremely fine lines on the surface of the hairs which break the light into its component elements, but the reason for the file-like surface and the "forest of prisms" is not so clear, especially as it is said that these worms are usually covered with clay so that their beauty is hidden from the sight of other animals.

No. 730 is a preparation of Aphrodite showing the scale-like respiratory organs. These are situated on the back of the worm and are protected by a felting of hair (see No. 729). The water passes through the felting and bathes the scales, after which it is expelled from the posterior end.

A relative of Aphrodite is found in the scale-bearer *Phyllodoce* (Pl. 731, *P. maculata* Oersted). The young larva (fig. 1; fig. 2, side view of the same) has a band of cilia and the body is segmented. Gradually the worm lengthens (fig. 3; fig. 4, ventral view of same), the paddles become distinct and also the setae, though the cilia still persist. The tentacles grow out and the large mouth (fig. 4) is back of the band of cilia. The body continues to grow longer (fig. 5). The head now possesses eight tentacles, as in the adult (fig. 6).

*Sigalion squamatum* (No. 732) is also provided with scales on many of the segments. This is such a peculiar-looking worm that at first sight it seems as though the body wall had been removed exposing the internal organs and that these consisted of a long, double, vertebral rod



with an infinite number of brush-like setae attached on either side and enclosing laterally a double row of delicate leaf-like parts. In reality, the long double rod is the ventral side of the worm, and the leaf-like parts are scales or peculiar modifications of the dorsal surface. In this case, gills exist with the scales. The head is differentiated from the body. Its anterior portion including the slit-like mouth is dark brown in color, indicating that it performs hard work.

*Psammolyce arenosa* (No. 733) covers the upper part of its body with coarse sand, so that at first sight there appears to be a protecting tube. The under side, however, is not covered in this way so that the median groove of the body is distinct and, in lesser degree, the sutures between the segments. Clusters of setae extend down both sides of the body and are useful in locomotion.

The species of *Nereis* are typical members of the group of shallow-water worms. The larva of an undetermined species is seen in Pl. 734, fig. 1. At this early stage it is transparent and consists of a few distinct segments. The head (figs. 1, 2) is provided with five pairs of appendages and three pairs of eyes. The large, toothed mandibles (figs. 1, 2) are well developed, and even in this early period they can be seen distinctly through the body wall. The setae are prominent, but the parapodia have not yet taken on the form peculiar to the full grown animal. Although the adult *Nereis virens* Sars (No. 735; Pl. 736, figs. 1-4), makes a loose flexible tube for itself<sup>1</sup> by fastening grains of sand together with a secretion of its body, it never attaches itself, but is extremely active, burrowing in sand during the day and often swimming at night. The body is made up of numerous segments of which the forward ones are differentiated into a head (Pl. 736, fig. 1). This part in this species bears six pairs of tentacles and two pairs of eyes (fig. 1). The mouth con-

<sup>1</sup>Trans. Conn. Acad. Arts and Sci., III, 1878, p. 265.

tains a sac called a proboscis (fig. 2) which can be turned outward as seen in the figure. It is armed with many fine horny teeth and two stout hooked teeth already seen in the larva.

Along each side of the body there is a row of fleshy, unjointed, and two-lobed organs, the parapodia (figs. 1, 3, 4) which are continuations of the body wall (fig. 4). They serve as efficient paddles in locomotion, and the lobes are also differentiated into breathing organs. In the living worm these lobes are bright red in color, owing to the blood contained in them. Extending beyond the edge of the paddles are horny setae (fig. 3) which in reality originate within the body cavity and pass outward piercing the body wall (fig. 4). The division of the body cavity into segments, which is one of the chief characteristics of worms, is well shown in fig. 3, representing the forward end of *Nereis* with the proboscis in place. The dorsal part of the body wall has been removed so that six muscular partitions are exposed, dividing the cavity transversely into as many compartments. There is, moreover, a marked tendency towards the repetition of the paired organs in each compartment, such as the nephridia, the bundles of muscles, and the ganglia of the nervous system.

The relative position of the three important systems of organs in this class of animals is shown in Pl. 736, fig. 4. The digestive system represented by the large central circle takes up the greater part of the body. Immediately above and below it are the long tubes of the circulatory system, cut across in fig. 4. Below the ventral blood vessel is the nerve cord which runs the whole length of the body.

*Autolytus cornutus* Ag., (Pl. 737, figs. 1-13), is especially interesting as it is one of the few worms that illustrates alternation of generations. The eggs pass from the body cavity of the mother into a bag or pouch which has grown out from the lower side of her body. Here they remain and are brooded over by the parent until the

embryos hatch; the pouch then breaks, and the larvae are set free.

The larva just after hatching (fig. 1) has a flattened, unsegmented body which shows no differentiation into regions. Very soon, however, the beginnings of segments (fig. 2) are visible, and the head is marked off by a slight constriction. The segments become more apparent (fig. 3) and the three regions are clearly marked (fig. 4). The tentacles bud out (fig. 5) and the bristles grow from the middle region (fig. 6). The tentacles increase in size and the setae in number (fig. 7). Later the posterior organs, known as cirri, grow longer (figs. 8, 9). The mature asexual form, called the "parent-stock," is represented in fig. 10. It multiplies either by division or by budding. If by the former process the anterior end remains asexual while the posterior end develops into either a male (fig. 11, male ready to separate from parent-stock; fig. 12, forward part of a male) or a female (fig. 13). Larger drawings of the mature *Autolytus* are framed and placed over the Section. The figure on the left represents the asexual parent stock dividing in two; the middle figure is the female with the egg-bag, and the figure on the right the free male. These two sexually mature individuals produce the fertilized egg which in turn develops into the sexless parent stock (fig. 10). The latter produces more than one offspring, for after this has left, the anterior end buds out new segments until a posterior part is formed which in time is ready to be thrown off and to develop into either a male or a female.

*Autolytus* is placed with the free-swimming forms since the adult male and female are found at the surface of the sea. The parent stock also is free-swimming when the sexual individual is attached to it. At other times it makes a delicate tube which it leaves at will.

The development of *Autolytus* which we have just traced is exceptional in one particular, namely, in the flattened, unsegmented state of the very young larva. In conse-

quence of this early condition, it may be urged that here is a proof of the descent of the segmented Annelids from the group of flat, unsegmented worms.

We must not lose sight of the fact, however, that this unsegmented larval state is accompanied by a specialized mode of reproduction, as already shown. The formation of a pouch for the young, the brooding by the mother, the various changes in the development of the asexual and sexual individuals, all indicate secondary instead of primary conditions, so that it seems most probable that this flattened state of the young larva is an adaptive character.

The proboscis which we have seen in *Nereis* is sometimes of great size, as in *Rhynchobolus siphonostoma* (No. 738), a large, distinctly segmented worm. In this finely preserved specimen the proboscis is extended and the four dark horny teeth are seen at the swollen anterior end. One row of tiny parapodia with setae extending from them is seen on either side of the body.

Some of the worms of this group of Chaetopods have the head so slightly differentiated that the two ends of the body resemble each other, as in *Eteone siphonodonta* (No. 739). They are tapering and terminate in a blunt point; the forward end, however, differs from the posterior in having short tentacles.

The locomotive organs in *Eteone* are prominent, consisting of a double row on each side of the body. The upper and longer organs end in flattened leaf-like parts, while the lower have clusters of setae. These enable the worm to move swiftly through moist sand and also to penetrate clay and fissures in rocks.

Another worm with an inconspicuous head is *Halla parthenopeja* (No. 740), which is of great size with a large number of apparent segments. Florence Buchanan<sup>1</sup> has shown that in a few Annelida (Chaetopods) cases occur of intercalation of half segments and of spiral segmenta-

<sup>1</sup>Quart. Journ. Micr. Sci., XXXIV, 1893.

tion, which are probably variations from the normal segmentation. This variation of a spiral segmentation is illustrated by Halla, and since it occurs in Oligochaeta (see p. 305) and in Cestodes, especially in *Bothriocephalus latus*,<sup>1</sup> it indicates a tendency toward secondary and adaptive specialization. Both the upper and lower surfaces of Halla are iridescent. On either side are the parapodia with bunches of projecting setae.

Besides the species of worms already described as free-swimmers there are many others which are free-swimming when young, but which later in life make tubes and fasten them to foreign objects either temporarily or permanently. Although the worms are never organically connected with the tubes, yet most remain in them for the greater part of the time, and in this new position develop structural characters fitting them for a sedentary life.

These worms are usually grouped together under the name of the Sedentaria in contrast to the Errantia or free-swimming forms. It must be borne in mind, however, that there is no sharp line of demarcation between these groups, since some Errantia (Eunicidæ, some Polynoids) make tubes and some Sedentaria are tubeless (Polycirrus). Broadly speaking, nevertheless, the division holds good, and the Sedentaria, having acquired many secondary characters, are naturally placed after the Errantia.

One of these sedentary worms is *Arenicola marina* Linn. (No. 741, model). Although not permanently settled, *Arenicola* makes a U-shaped tunnel for itself in the sand and remains in it much of the time. The parapodia not being needed have disappeared, and the anterior segments bear setae only. The central segments are provided with setae and gills; the latter are protected in some degree by the setae that extend beyond them, and also by the swollen anterior end of the body which

<sup>1</sup> Buchanan, *loc. cit.*, p. 541.

enlarges the burrow as the animal moves along. Furthermore, this burrow is lined with a mucous secretion from the body which soon hardens so that the sand does not come in contact with the gills while the worm is in its home.

Since *Arenicola* digs its own tunnel it could not have the delicate gills on the segments near the mouth, but the anterior region in many of these tube inhabiting worms is provided with a profusion of long, slender feelers and branchiae, while in the middle and posterior parts of the body only a few of these organs occur. This is the case with *Audouinia filigera* (No. 742), a handsome and graceful worm. Extending the whole length of the body of this Annelid are four rows of setae.

Most curious of all this group of worms is *Chaetopterus variopedatus* Ren. (No. 743). It never leaves its tube<sup>1</sup> and therefore its body has become modified in various ways. The outer skin is delicate and light colored. The segments and fleshy appendages of the middle and anterior regions of the body are more specialized than those of the posterior region, since it is these that are modified for the purposes of catching food and for holding the animal in its tube. As *Chaetopterus* does not require locomotive paddles and setae, these organs are not developed, though there are stiff hairs and plates which aid the animal in moving up and down its tube.

*Terebella* (= *Amphitrite*) *conchilega* Pall., is naked and free-swimming when young (No. 744 a-c). There is no marked differentiation of the body in these stages, but the appendages are developed in the form of clusters of setae on either side. The mouth opens on the ventral side (b) and in front of it is developed a very long feeler (b, c). Other feelers grow out (c) until in the adult (No. 745, model) there are many of these delicate organs besides bushy branchiae; the latter are usually red (as

<sup>1</sup> Benham, Cambridge Nat. Hist., II, 1896, p. 323.

represented by the model), owing to the blood contained in them. The tube (No. 745) of the adult *Terebella* is sometimes fifteen inches long and is usually made of fragments of shells, sand grains, etc., cemented together by a secretion of the body. These substances the worm prefers, and it shows discrimination in selecting materials, refusing certain substances altogether, as pointed out by Dalyell.<sup>1</sup> From the larger end the many extremely long feelers and the feathery, brilliantly colored gills are extended, as already stated; the latter are borne on only a few of the anterior segments. One of the tentacles has become differentiated into an operculum or "stopper" which closes the tube in time of danger.

The bristles are found on the forward segments only, having disappeared from the posterior region of the body where they would be of no use to a tube-inhabiting animal.

*Stylarioides monilifer* (No. 746), is an instructive form. The plump, rounded, anterior region of the body has nearly lost the boundary lines of the segments, though these are distinct on the tapering posterior region. The head is extremely differentiated. The tentacles are surrounded by long bristles which reflect the most brilliant prismatic hues. Many of the setae on the anterior region of the body exist as vestiges like the lines of demarcation between the segments, while the setae on the posterior region are more regular and bushy.

*Cistenides*, or as it was formerly called, *Pectinaria* (No. 747), has a symmetrical tube reminding one in shape of the shell of *Dentalium* (see No. 534). It is made of tiny pebbles which are fitted together with extreme neatness. There is an opening at the smaller posterior extremity, and the head extends from the larger anterior end; this is provided above with prismatic bristles. Though placed with the *Sedentaria*, *Cistenides* is not a sedentary worm, since it travels about freely, carrying its tube with the smaller end pointing upward.

<sup>1</sup> Ann. and Mag. Nat. Hist., (6), XIII, 1894, p. 11.

A worm that buries its long quill-shaped body with the exception of a few of the anterior segments is *Sabella penicillus* Linn. (No. 748, model). Its tube is leathery, and is formed by a secretion of the body; from its opening the branching gills, which are supported by a cartilaginous skeleton, are extended. The model shows the animal out of its slender tube, so that the body with its setae and parapodia as well as its long, delicate branchiae and tentacles can be clearly seen.

Many of these tube-inhabiting worms have large, segmented bodies, while the paddles and setae are more or less reduced in size. Such a worm is *Spirographis spallanzani* (No. 749), in which these lateral appendages are tiny. The feelers, on the other hand, are active working organs and are finely developed.

Two tubes of *Branchiomma koellikeri* (No. 750), are shown in No. 751. One is made of sand and tiny pebbles; it is symmetrical and well put together. The other is composed of similar materials throughout about three fourths of its length, but the remaining fourth has pieces of rock of surprising size incorporated in it. Its extreme irregularity reminds one of the experimental work in shell-making seen among the Protozoa (see *Saccamina*, Pl. 15), and sponges (*Prophysema*, Pl. 60). It is remarkable that the cementing material is sufficiently strong to hold these fragments in place, especially as only a small portion of their surface is in contact with the tube. From the anterior end of the tube many delicate tentacles are put forth. Along each side are short setae without paddles. According to M<sup>r</sup>Intosh<sup>1</sup> one species of this genus, *Branchiomma vesiculosum*, has the surface of the greatly enlarged eye minutely dotted as if furnished with corneal facets analogous to those of Crustacea and Insecta; the eye has proximally a kind of peduncle.

The tubes already described have been formed mechani-

<sup>1</sup>Chall. Rep., Zool., XII, 1885, p. 494.



cally by the animal picking up such materials as it could find and working them over; but the tubes of *Serpula* (No. 752, *S. contortuplicata*); are made by a chemical process and are composed wholly of carbonate of lime.

In this genus the setae are reduced in size. The gills (see No. 752) are borne on the forward segments of the body and can be withdrawn into the tube, while the opening is closed by a tentacle, the end of which has become differentiated into an operculum.

The habit of living attached and in chemically formed tubes was acquired by some genera very early in geologic times. The Palaeozoic formations yield specimens of *Spirorbis* which resemble those living to-day (Pl. 753, *Spirorbis omphalodes* Goldf.). Usually in these fossils the tube is hollow throughout, but sometimes the shell is divided into a few chambers by limy walls. Not only do tightly coiled forms occur as represented by Pl. 753, but some species, like *Spirorbis laxus* (Pl. 754, figs. 1-4), exhibit old age or gerontic characters. The worm on reaching maturity (Pl. 754, figs. 1, 2) begins to untwist (fig. 3) and in rare cases this process goes on until the whole tube is uncoiled excepting the apical portion (fig. 4). It is interesting to note that the round aperture of this tube is smaller than in the mature or ephebic shell (figs. 2, 3) which we have already seen is the case in certain gerontic stages of Cephalopods (see Nos. 617, 618). The descendants of *Spirorbis* are found living to-day in great numbers.

The larva of *Spirorbis spirillum* Gould (Pl. 755, figs. 1, 2), is free-swimming at first, but only for a few hours. It then settles down and begins to build its tube. The tentacles and setae develop early (fig. 3), the former branch rapidly and one becomes specialized into an operculum (fig. 4, *p*). Thus it is seen that the tendency towards the sedentary habit is inherited so early in the life of the individual that the young *Spirorbis* (fig. 4) completes its development within the tube. This ex-

plains why the posterior region of the body is small and without well developed appendages.

The adults are often attached to seaweed by one side of the shell (No. 756, *S. nautiloides* Lam. ; No. 757, *S. lucidus*). An examination of this large settlement (No. 757) shows a great variation in the tube. If one were unfamiliar with fossil forms, it would seem as if here was a spiral shell in process of making ; as if, in short, a straight tube coiling round the delicate stem of an alga became in time a loose spiral. When, however, one observes that as a rule the young tube at the apex is closely coiled, as we have seen in the specialized fossil species (Pl. 753), and that it is the adult stage which is usually straight, then one sees he is dealing with secondary and not with primitive conditions. The spiral of the young tube in *S. lucidus* and *S. laxus* is doubtless inherited from spiral-tubed ancestors, but the tendency to coil loosely around stems is evidently an adaptation to surroundings. This view is strengthened by the fact that those specimens of *Spirorbis* which are found on the flat fronds of the *Fucus* (No. 756) are seldom if ever uncoiled to such a degree as those upon stems.

On a small specimen of *Fucus* we have seen upwards of three thousand tubes of *Spirorbis* (2,800 were actually counted, and there were a few hundred more in the hollows) not one of which was uncoiled. The whorls of the close spiral of the young tubes could be traced from the inside in many places, where only a portion of the tube had been broken away owing to the strength of the cement by which it was fastened to the *Fucus*.

The breathing organs of the living *Spirorbis* extend from the opening of the tiny coiled tube (No. 756), and are protected when within the tube by the operculum (also seen in No. 756).

## ANNELIDA.—OLIGOCHAETA.

Transitional forms between the marine Chaetopoda and the terrestrial Oligochaeta may be represented by *Manayunkia speciosa* Leidy. This little tube-worm inhabits fresh water, while at the same time, according to its discoverer, it is related to the marine worms, especially to Fabricia, a near ally of Terebella.

In the development of *Manayunkia* the free-swimming stage is skipped and even the embryo (Pl. 758, figs. 2, 3) that develops from the egg (fig. 1) has lost its cilia. The different stages of the larva (figs. 4-6) are passed within the tube, and thus the young are "retained under the care of the parent until sufficiently developed to be able to care for themselves."<sup>1</sup> Both larvae and adult (fig. 70) are divided into a small number of segments. The adult is abundantly supplied with tentacles. There are no parapodia, but each segment is provided on either side with a cluster of setae. These organs are small and generally few in number, as compared with the numerous strong bristles of Chaetopods; hence the name of Oligochaeta.

The terrestrial Oligochaeta are represented by the common earthworm, *Lumbricus terrestris* Linn. (Nos. 759, 760). Although a land animal, it is able, according to Romanes<sup>2</sup> to live in water nearly four months.

The eggs of the earthworm are laid in cocoons or egg-cases and the free-swimming larval stages are wholly skipped, so that the worm acquires the form of the adult before leaving the egg.

The peculiar iridescence already observed on marine worms is well seen when the earthworm is immersed in water and placed in the sunshine.

<sup>1</sup> Leidy, Proc. Acad. Nat. Sci. Phila., 1883, p. 209.

<sup>2</sup> Nature, XXIV, 1881, p. 553.

The body is segmented. Late in life<sup>1</sup> each segment may become ringed, making it difficult to determine the exact number of segments, but the secondary rings are superficial, not being represented by muscular partitions in the body cavity.

The two ends of the body are similar, since the forward end is not differentiated into a head and there are no tentacles nor eyes. The mouth leads into a proboscis which is not armed with teeth.

The worm is well supplied with locomotive organs in the form of hooked setae which extend, with the exception of a few segments, in four double rows from one end of the body to the other.

The structure of the earthworm is an illustration of specialization by the suppression of parts. The cause for this suppression is found in the habits of the animal. No longer swimming freely in the sea like its early ancestors, it has for some reason or other taken to crawling through the earth. In such a situation what use is there for paddles, eyes, or tentacles? Eating soft, partly decayed organic matter in the earth, what use has the worm for horny teeth like those of its marine relative, the greedy Nereis?

The forward end of the body is pointed for tunneling, and the setae with the supplementary muscles can easily pull the long body through the earth. Thus the worm is adapted to its environment and it is seen that the adaptive organs are secondarily acquired.

The earthworm is an hermaphrodite, although self-fertilization does not take place. The worms mate and the breeding season is indicated by the swollen clitellum or saddle (see No. 759 and also No. 760, specimen on the right; these preparations were made according to Semper's method). The development is accelerated as we have shown, and in this way the Oligochaeta differ from the Chaetopoda.

<sup>1</sup> Cambridge Nat. Hist., II, 1896, p. 394.

## ANNELIDA. — HIRUDINIA.

Some of the non-parasitic members of this class resemble the Oligochaeta. *Nephelis* (Pl. 761, the young), for example, is cylindrical in form similar to the earthworm, and its suckers are smaller than in most members of its class. Its intestine is not differentiated into numerous large sacs as is the case with the more specialized Hirudinia to be hereafter described.

The eggs of *Nephelis* are deposited in cocoons in fresh water, but the adults often leave the water and live under stones on the shore.<sup>1</sup>

The land leech, *Haemadipsa japonica* (Pl. 762, fig. 1, at rest, dorsal view; fig. 2, ventral view; fig. 3, another worm stretched out, dorsal side; all natural size), lives in moist places among mountains and never goes to the water, not even to lay its eggs. As in all leeches the segments are ringed, making it difficult to determine the exact number (fig. 4, posterior, and fig. 5, anterior end, both figures enlarged). A shortening of the body at either end has taken place in *Haemadipsa*, as in most land leeches, brought about by a reduction of the number of rings in a segment.

The eggs of the European medicinal leech, *Hirudo medicinalis* Linn. (in America, *Macrobdella decora* Say, No. 763, is often used in place of *Hirudo*), are laid in cocoons which are placed in holes that the mother has made above water level in the soft, moist banks of the pond she inhabits. The cocoon usually contains about twenty eggs and is filled with albumen. The young remain in the cocoon, feeding upon the food prepared for them until they have attained the form of the parent. The free-swimming larval stage is therefore omitted, so that the development is accelerated.

<sup>1</sup> Johnston, Cat. Worms Brit. Mus., 1865, p. 43.

The segments of the adult are obscured, the secondary annular markings obliterating the division lines of the true segments. Paddles and setae are not developed in *Hirudo*, the animal either swimming by means of the thin edges of its body or crawling by aid of its suckers. It is, however, a sluggish creature, so that it often remains attached by its suckers for a long period of time.

*Hirudo* may be a descendant of the land leeches, like *Haemadipsa ceylonica*. The fact that its eggs are laid in earth above water-mark would indicate such a descent.

This is probably the case with another fresh-water leech, *Clepsine* (No. 764; Pl. 765, fig. 1), which is a fish parasite.<sup>1</sup> Although the eggs of this leech are not laid in cocoons, yet they are covered after attachment to some water plant, with a fluid that soon hardens and which serves for protection. The parent covers the eggs with her body and also carries the young about with her<sup>2</sup> until they are old enough to care for themselves. The development illustrates, according to Whitman,<sup>3</sup> ontogenetic concentration in which the earlier phases of one stage appear before the later phases of the preceding stage are completed. It is in a worm with this accelerated development that we find the segments of the body distinct in the young and indistinct in the adult. Pl. 765, fig. 1, is a drawing of *Clepsine* when seven days old and when it has nearly attained the form of the adult. The internal organs of a species of *Clepsine* (*C. complanata*) are well shown in fig. 2, which is a dissection that has been treated with reagents. The portions colored pink and blue constitute the sacculated digestive system which begins at the mouth and ends in the rectum (see figs. 1, 2). The dark red organs are the excretory organs or nephridia which are in pairs (fig. 2).

<sup>1</sup> Whitman, Quart. Journ. Micr. Sci., XVIII, 1878, p. 224.

<sup>2</sup> Whitman, *loc. cit.*, p. 225.

<sup>3</sup> *Loc. cit.*, p. 272.

There is a marine leech, *Pontobdella muricata* Linn. (No. 766, No. 767, model) which not only attaches itself to another animal, the skate, but even fastens its eggs to the fish, showing that the parasitic habit has become stronger in this leech than in *Hirudo* which lays its eggs in earth, or in *Clepsine* which deposits its eggs in water.

The indistinct segments of the body of the adult *Pontobdella* are covered with warts, but a short distance from the head a few segments are comparatively smooth. There is a large anterior sucker, provided with papillae round its edge by means of which the animal becomes attached.

The Hirudinia have much in common with the Oligochaeta, as already stated, but their semiparasitic habits and consequent change of environment have brought about peculiar modifications of structure. Having given up very largely the swimming mode of locomotion, the parapodia have disappeared and some of the segments of the body have become modified into an anterior and a posterior sucker which are used chiefly for the purposes of attachment, though they are also efficient organs in creeping.

#### GEPHYREA.

The trochophore of the Gephyrean *Echiurus* (Pl. 768, fig. 1), has all the typical characters of the trochophore of the Chaetopods, and it is also similar to the trochophore of Mollusca. The larva (fig. 2) is segmented in the posterior part of the body, but early in the development the segments disappear (fig. 3, side view of an older stage than fig. 2) and no trace of them is seen in the young *Echiurus* (fig. 4) which is essentially like the adult.

In this genus the mouth is at the anterior end and the anus is terminal as in the Chaetopods. There are no parapodia, but ventral setae occur, and two circles of bristles at the posterior extremity. Besides these organs

there are also regular rows of papillae encircling the body (figs. 3, 4).

It is interesting to note that the larva of another Gephyrean, *Phascolosoma vulgare* Dies. (No. 769, model), possesses setae which are lost before the animal attains adult size. This is probably owing to the habit of the worm of living in a shell, usually a univalve, that it has found on the beach. The opening being too large, the animal builds out a long tube composed of mud and sand cemented together by a secretion of its body. The large plump body stays within the shell, while the long proboscis is put out of the tube.

The development of Sipunculus is remarkably abbreviated (Hatschek). Even the larva shows no trace of segments, such as we have seen in the larva of Echiurus.

This genus differs from the majority of worms by having distinct longitudinal ridges extending from one end of the body to the other. The shape of the body is peculiar. The extreme forward end from which the proboscis extends (No. 770, *Sipunculus tessellatus*) is small as compared with the rest of the anterior region, which is greatly swollen. Near the middle, the body decreases in size only to swell out at the posterior end. The mouth is surrounded by tentacles, and the anus is situated on the dorsal side of the anterior region.

The preparation (No. 771) shows the long alimentary canal which in the animal coils and bends upon itself and ends in the anterior region as already stated. The four large retractor muscles of the oral sac and their points of attachment to the wall of the body are also clearly seen.

Besides these muscles, Sipunculus is unusually well supplied with locomotor muscles, having three sets, circular, oblique, and longitudinal.

The nerve cord is visible in the preparation (No. 771) as a white thread extending from one end of the body to the other.

One species of this genus, *S. nudus* (No. 772) is pro-



vided with an embryonic membrane, the amnion, when passing through its development, which is evidence of acceleration in development. The shape of the body of the adult *Sipunculus nudus* is more nearly equal throughout than in *S. tessellatus*. The tentacles are clearly seen in the specimen (No. 772), and also the anus near the anterior end.

#### NEMATODES.

Free-living Nematodes are extremely abundant in the sand of beaches and of rivers. One from the Mediterranean is represented by *Tricoma cincta* (Pl. 773, figs. 1, 2, greatly enlarged). While it is true that most Nematodes are without segments or appendages, yet there is, according to N. A. Cobb,<sup>1</sup> a repetition of the order of arrangement of certain organs, both external and internal. This observer mapped the position of all the hairs on the anterior half of several specimens of a species of *Spilophora*. A comparison of the results showed that the hairs were arranged in almost exactly the same order in each case, and that there was a faint trace of repetition of arrangement such as is commonly observed in segmented worms. *Tricoma cincta* (Pl. 773, A, the head; B, the posterior end of the body) shows external "annulation" which is certainly similar to segmentation, though this does not extend to the internal organs. The body cavity of the Nematodes is hollow and similar to that of Annelida generally.

Besides the free-moving species there is a great number of parasites. Many of these spend their early larval life in water and afterwards become parasitic for a shorter or longer time as the case may be.

<sup>1</sup> Parasites of Stock, New South Wales Dept. Agric., Misc. Publication 215, 1898, p. 18.

The class illustrates great variation in the process of development, not less than fourteen different modes having been described by von Linstow. Accompanying this widespread variation there is a marked development of adaptive characters, the cause lying in the fact that the Nematodes "display a variation in the conditions under which they live greater than that of any other group of Helminths."<sup>1</sup> For these reasons they are placed among the more specialized of the subkingdom of Vermes, although not at the extreme end of the genealogical record, since their structure is not profoundly modified and the adults have not departed so far from their young as those of the Acanthocephala, Trematodes, or Cestodes, to be described farther on.

It would seem, indeed, as though the parasitic habit had not been long acquired by the members of this class, and that therefore the effects of this habit had not become fixed in the organization to such a degree as to cause its complete modification.

The hair worm, *Gordius* (Pl. 774; No. 775, ♀), lays its eggs in water where a portion of the first larval life is spent.

The embryo of *Gordius subbifurcus* while still within the egg (Pl. 774, fig. 1) has the body divided into two regions, both of which are segmented (clearly seen in fig. 3). At the anterior end the proboscis forms; this is retracted in fig. 2 but is thrown out in fig. 3; the latter figure shows also the well developed head. In this condition the embryo escapes from the egg and swims freely about.

Some members of the family to which *Gordius* belongs have two larval stages. The first is segmented and has the body divided into a distinct head, middle, and posterior region; but the second stage, though still segmented, is without a head. These immature stages are mostly

<sup>1</sup> Leuckart, Parasites of Man (translation), 1886, p. 53.

passed in the body cavities of insects; afterward *Gordius* becomes free in water, where it sexually matures. The body of the adult (No. 775, *Gordius varius* taken from a well) shows no vestiges of segmentation nor of distinct regions.

Ascaris (= Angiostomum) (No. 776) is one of the parasites of man, being found usually in the small intestine. The eggs pass from the intestine and develop in water or moist earth, and the larval life is spent in this environment. It is not known how the larva reaches its place of final development. The adult has lost its segmented structure, also its locomotor and external respiratory organs. The body is more or less cylindrical and tapers at both ends, the head not being differentiated. The digestive system is present with the mouth in front and the anus at the posterior end. In this condition the animal is an hermaphrodite. No. 777 is a preparation of a female Ascaris (*A. lumbricoides*) showing the intestine and generative organs. The female is ten to fourteen inches long, while the male is only from four to six inches in length.

Another Nematode worm, *Filaria epinocaudata* (No. 778) is parasitic in the seal, those of No. 778 being found in the right ventricle and at the base of the pulmonary artery of *Phoca vitulina*. The thread-like body is without segmentation, distinct head, branchiae, or locomotor organs. *Filaria insiginis* (No. 779) was taken from the foot of a raccoon.

The guinea-worm of hot climates, *Filaria medinensis*, passes its earliest stages in the water, but its later larval life is spent in the little crustacean, Cyclops. The latter, in drinking water, is swallowed by man. The parasite then finds its way to the outer integument of its host, where just under the skin of the leg or the shoulder it becomes encysted. In time it matures sexually and produces living young which bore through the skin and find their way to the water.

## ACANTHOCEPHALA.

The development of *Echinorhynchus* (No. 780), a member of the Acanthocephala, is instructive as showing what changes a parasitic mode of life may bring about in the embryo. The egg, in cleaving, forms four protective embryonal membranes. At a very early stage the embryo develops a disc with hooks, and the anterior end of the body on which they are situated can be retracted. In this condition the embryo still enclosed in its envelopes leaves the parent while in the intestine of the hog (*E. gigas*) or the fish (*E. angustatus*) and from the intestine is ejected with the faeces. The embryos of *E. gigas* are swallowed by the larvae of *Cetonia aurata* while eating. In the stomach of this beetle the envelopes soften and the enclosed embryo becomes free. It now pierces the intestine of this intermediate host and undergoes a most complicated change of structure resulting in a stage similar to the adult. This adult, however, does not become sexually mature until its intermediate host, the beetle, is devoured by its permanent host, the hog: in the intestine of the latter animal its final development is reached.

This worm is an excellent example of specialization by the suppression of parts. The process has gone so far that not only is the adult worm without a mouth and alimentary canal, but the digestive tract is not even indicated in the embryonic development. This tends to prove that the ancestors of *Echinorhynchus*, near and remote, have led an endoparasitic life, living upon a supply of already digested food which has been absorbed by the walls of the body.

Another change has taken place in these worms, whereby the ventral side of the body cannot be distinguished from the dorsal side, — a most unusual modification of structure.

The Annelida (consisting of the Chaetopoda, Oligo-

chaeta, and Hirudinia), the Gephyrea, Nematodes, and Acanthocephala, may be considered as one division of worms in which the Chaetopods are the most primitive, though at the same time they are examples of specialization by addition, while the Nematodes and Acanthocephala through the habit of parasitism are the most modified, and offer good illustrations of specialization by reduction.

The next division, including the Nemertea, Turbellaria, Trematodes, and Cestodes, consists of secondary forms which illustrate in a marked degree acceleration in development and extreme specialization by the suppression of parts.

#### NEMERTEA.

The Pilidium larva (Pl. 781, *Lineus lacteus*) peculiar to some Nemertines, has an incomplete digestive system and when older its structure is complicated by having the young worm enclosed within (Pl. 782, *Pilidium gyraus*), the development of which is abbreviated.<sup>1</sup>

Most Nemerteans enclose their eggs in cocoons and the embryo is sometimes protected by a membrane, the amnion. There are various modes of development, but the majority are without a metamorphosis, the development indicating a concentration of stages. Some are even viviparous, and this process is usually the result of acceleration in development.

Most Nemerteans are unsegmented though there are some species that show traces of segmentation (Balfour), and the segmented condition is indicated in various systems of organs.<sup>2</sup>

While the young are usually free-swimming, the adults are generally found under stones on the shore. These

<sup>1</sup> Balfour, Comp. Embryol., I, 1880, p. 169.

<sup>2</sup> Gegenbaur, Elem. Comp. Anat., 1878, p. 130.

characters indicate secondary and not primary conditions.

The group is represented in the Synoptic Collection by *Cerebratulus*, *Meckelia*, and *Borlasia*.

*Cerebratulus marginatus* (No. 783), has an extremely long body which is indistinctly segmented. The forward end is small and a long slender organ, the proboscis, which is characteristic of the Nemertines, extends from it (Pl. 784, *C. tristis* Hubr.). The figure shows that this proboscis is not thrown out of the mouth but has a separate opening above the mouth. It is provided with a sheath and sharp spines and is thought to be an organ of defence. The head also possesses deep lateral slits or olfactory organs.

There are no locomotive organs on the sides of the body. It is generally stated that these worms move by the cilia which cover the whole body, but according to M'Intosh,<sup>1</sup> this statement is incorrect. This author maintains that the adhesion of the body to the mucus which is secreted by the worm gives the animal sufficient purchase for the use of its facile muscles, so that it is muscular rather than ciliary action which causes locomotion. Many of these worms, however, lie for hours in what would seem to be a torpid state, and *Cerebratulus*, although a good swimmer, has the habit of frequenting empty bivalve shells in which it remains quiescent.

*Meckelia macrorrhochma* Schm. (No. 785, model), is large in the anterior region but is without a distinct head and the body tapers posteriorly. It is without external locomotive or respiratory organs. Like *Cerebratulus* it possesses the proboscis enclosed in a sheath which has a distinct opening just above the mouth.

Other Nemertean worms are *Borlasia trilineata* Schm. (No. 786, model), and *Nemertes flaccida* O. F. Müll. (No.

<sup>1</sup> Monograph on Brit. Annelids, part 1, 1873, p. 6. (Ray Society.)

787). *Borlasia* unlike *Meckelia* tapers at both ends, making it difficult at first sight to tell which is the anterior region. These worms possess the same general characters as *Cerebratulus*, though, as compared with this giant, they are diminutive members of their class.

### TURBELLARIA.

The Nemertea and Turbellaria have been considered by many naturalists as the representatives of the ancestral forms of not only the Platyhelminthes or group of Flat Worms, but of the whole subkingdom of Vermes. The reasons why they are here regarded as derived rather than primitive forms are the following:—

First: The trochophore stage of development is not found in the Turbellaria nor in other Platyhelminthes. Now, since this stage occurs in the early development of many classes of animals and in the Annelida, as we have already seen, we consider it of great phylogenetic importance.

Secondly: The Turbellaria (excepting the Polyclads) are either fresh-water or terrestrial animals, and, therefore, show in their structural features and mode of development the specializations peculiar to animals with such a habitat. The rest of the class of Platyhelminthes are extremely specialized by the suppression of parts. In fact, this class offers some of the best illustrations of specialization by reduction to be found in the whole animal kingdom.

Thirdly: While it is true that most of the Turbellaria are unsegmented in both the young and the adult condition, nevertheless there are members of the class which are segmented when young and which lose this feature on approaching maturity. This tends to prove not only that the Turbellaria and Platyhelminthes belong to the great group of animals with segmented bodies, but also that

the segmented condition is characteristic of larval stages and consequently of ancestral forms, and is lost through semiparasitic and parasitic habits.

Fourthly: The Turbellaria have a complicated digestive system. The reproductive organs are also complex, as shown by Gamble.<sup>1</sup> The embryo is retained in the uterus and the young resemble very early the adult.

Fifthly: When the trochophore larva of an Annelid is compared with the Pilidium larva of a Nemertean or with Müller's larva of a Turbellarian (see Pls. 727, 782, 789), the Annelid trochophore is the more primitive so far as we are able to judge. This is, as we have seen, a spherical body surrounded by bands of cilia and containing a digestive system with a mouth and an anus. This trochophore passes into the worm by changes which are comparatively simple and easily followed. The Pilidium, on the other hand, has a bell-shaped part from which hang two lobes. The mouth opens between the lobes and the anus ends blindly. Within this organism the worm is formed by complex changes, after which it leaves the Pilidium and the latter continues to live some time.<sup>2</sup>

Müller's larva, as will be seen (Pl. 789), is elongated in shape and is provided with eight finger-like prolongations. Numerous changes are undergone before this larva assumes the adult form (see p. 319).

Sixthly: Most Chaetopods pass through a trochophore stage while only a comparatively small number of Turbellaria (the Cotylea and a few Acotylea of the Polyclads) go through the stage represented by Müller's larva, while the rest of the Polyclads, the Triclads, and the Rhabdo-coela have either a modified Müller's larva or are without this larval form, the stage being skipped altogether through acceleration in development. The remaining classes of the Platyhelminthes (Trematodes, Cestodes)

<sup>1</sup> Quart. Journ. Micr. Sci., XXXIV, 1893, p. 438.

<sup>2</sup> Balfour, Comp. Embryol., I, 1880, p. 167.



are remarkable for complicated processes of development which illustrate in the majority of cases great abbreviation in the life history.

The marine Turbellaria or Polyclads are mostly littoral animals, but a few genera are pelagic.

*Alaurina composita* Metsch. (Pl. 788), was found at the surface of the sea. Its body is segmented<sup>1</sup> and is long, narrow, and covered with cilia. It has a tactile organ, the proboscis, at the anterior end. There are stiff hairs at the posterior end, and sometimes paired setae occur on the sides.<sup>2</sup>

The life history of those Turbellaria which pass through a metamorphosis begins (after the embryo is free from the egg) with the stage known as Müller's larva (Pl. 789, fig. 1, dorsal view; fig. 2, ventral view; probably figures of the genus *Thysanozoön*<sup>3</sup>). The body is somewhat elongated and possesses eight finger-like lobes around which extends a band of cilia. Three of these lobes are dorsal (fig. 1, the posterior pair of lobes and the single median lobe just back of the eyes), two lateral (fig. 1, the anterior pair), and three ventral (fig. 2, a short pair and a single one just back of the eyes). The mouth is in the center of these three lobes, and can be seen in fig. 2 and also through the body in fig. 1. When this swimming larva changes into the creeping adult, the lobes grow smaller till they disappear altogether, the ciliated band is absorbed, and the form becomes flattened.

The more complete development of a Turbellarian is shown in Pl. 790, figs. 1-10 which represent *Yungia aurantiaca* (figs. 1-8) and *Thysanozoön brocchi* (figs. 9,

<sup>1</sup> Metschnikoff, Ann. and Mag. Nat. Hist., (3) XVIII, 1866, p. 61; Huxley, in his Invertebrata, 1897, p. 157, says, "None are divided into distinct segments except the genus *Alaurina*, in which there are four."

<sup>2</sup> Quart. Journ. Micr. Sci., XXXIV, 1893, p. 449.

<sup>3</sup> Korschelt and Heider, Text-book of the Embryology of Invertebrates, part 1, 1895, p. 166.

10). The very young larva (fig. 1, dorsal view; fig. 2, ventral view) is provided with eye-spots and ciliated lobes. The body and lobes increase in size, and the larva (fig. 3, dorsal view; fig. 4, ventral view) is found swimming freely at the surface of the sea. The body elongates (fig. 5, dorsal, and fig. 6, ventral view), and the lobes begin to be resorbed (fig. 7, dorsal, and fig. 8, ventral view). Finally by the suppression of the lobes, the young sexual form (fig. 9, dorsal, and fig. 10, ventral view) resulting from the metamorphosis is produced. This form is essentially like that of the adult.

The broad, flat, marine *Leptoplana gigas* Schm. (No. 791, model), has, like *Thysanozoön* and most of its group, an unsegmented body with the mouth near the center of the ventral side. The digestive system is extremely complicated, as shown by Pl. 792, *L. alcinoi*. The central stomach gives off intestinal branches which fill the body cavity and end blindly, there being no anus. These animals are often called solid-bodied worms and are contrasted with the hollow-bodied forms, such as the Chaetopods, Nematodes, and the like.

Among the Triclad marine Turbellaria, *Planaria angulata* is interesting since it differs from most of its class by having a segmented cylindrical body (Pl. 793, figs. 1, 2) which in the course of development loses its segments and becomes flattened.

A fresh-water Triclad Turbellarian, *Planaria lactea* Baer (No. 794, model), is a flat and nearly transparent worm. Extending down the back is the digestive system which is characteristic of the Turbellaria, as we have already shown. It consists in this genus of a median tube which gives off two branches. Near the middle of the body this median tube divides into two large branches which extend backward giving off smaller branches. At the point where the median tube divides there is a good-sized bag, the proboscis, which seizes the food. As in the Polyclads, the intestine in the Triclads ends blindly, there being no anus.

Although many naturalists, as we have said, place the Platyhelminthes as primitive worms, yet at the same time it is stated that even the Triclad's belonging to the most generalized division of this group, the Turbellaria, deposit their ova in chitinous cocoons which contain, beside the ova proper, large numbers of amoeboid cells originating in the pouches of the parent and serving as food for the young embryo. In association with this condition of affairs many peculiarities of segmentation and growth occur in the Triclad embryos all of which must be considered as secondary adaptations.<sup>1</sup> These facts being true, it is evident that the Triclad's cannot be primitive worms.

The Turbellaria include not only marine and fresh-water forms but also many terrestrial species.

#### TREMATODES.

The Trematodes are built upon the same plan of structure as the Turbellaria but this plan is greatly modified by parasitism. All the group excepting the Temnocephala are either external or internal parasites, and there are numerous adaptive characters and complicated modes of development. A good illustration of the Trematodes which pass through a metamorphosis is found in the fluke worm, *Distomum* (Pl. 795; No. 796, a specimen taken from the liver of the red deer). The eggs of most flukes pass from the intestine of their host into water, where, as in the case of *Distomum hepaticum* (Pl. 795, figs. 1-6), they become ciliated larvae (fig. 1). Very soon this larva bores into the body cavity of a snail (*Limnaeus minutus*). In this cavity it loses its cilia and becomes a sac-like body or sporocyst (fig. 2). Its germ cells, seen in fig. 2, grow large and divide, giving rise to

<sup>1</sup> McMurrich, *Invertebrate Morphology*, 1894, p. 140.

new sporocysts which differ from the original sporocyst by having a mouth with a sucker and an intestine, but no anus. The new sporocysts are called Rediae or "parent-nurses" (fig. 3). The wall of the sporocyst breaks and the Rediae migrate to the other organs of the snail, especially the liver, and there develop into Cercariae (fig. 4) which are provided with tails (fig. 5, a single Cercaria showing the anterior and ventral sucker). In this stage the Cercaria works its way through the tissues of its host and seeks the water, where, however, it stays only a brief time. It fastens itself to the plants on the shores of the pond and becomes encysted. In this state it is swallowed by sheep; in the stomach of this animal the cyst is dissolved and the freed worm, finding its way to the liver (fig. 6, a young fluke in which the intestine has begun to branch), develops into the sexually mature *Distomum hepaticum* (fig. 7). The eggs find their way through the bile duct to the intestine and escape.

One of the most remarkable instances of acceleration in development is found in *Gyrodactylus elegans* (Pl. 797). Not only do the eggs of this worm develop into sexually mature embryos while within the body of the parent, but the embryos thus formed also develop embryos which in turn produce eggs in process of development, so that four generations are represented by a single specimen.

Certainly no better example of acceleration in sexual maturity need be offered than these viviparous "young," as they are called, containing offspring which are themselves in the act of developing eggs.

The figure shows the adult with one embryo enclosed. The esophageal bulb of the mother and embryo are seen; also the posterior sucker with the two great hooks.

## CESTODES.

All Cestodes are internal parasites and illustrate extreme specialization by a profound modification of some organs and by the total suppression of others.

The important fact that there is no mouth and no digestive system in either the young or the adult Cestode proves how far removed these parasites are from the primitive ancestral forms.

The tape-worm, *Taenia solium*, found in the intestine of man, is an instructive example.

Its eggs do not develop in water nor in earth, like those of the tape-worm's remote ancestors, but within the body of another animal, the hog. Thus the environment has changed throughout the whole life of the worm, and with this complete change in physical surroundings there has followed a complete change in structure. The eggs, which may be seen in the little bottle at the bottom of the jar (No. 800), leave the intestine in faecal matter and are swallowed by swine which are often kept in unclean places. The young of the tape-worm originally described as *Cysticercus cellulosae* Auct. are bladder-like and for this reason are often called bladder-worms. The figure (Pl. 798, fig. 1) shows the bladder with just the beginning of the head. In fig. 2 the head is turned inward, and in fig. 3 outward; between the head and bladder the neck has developed. In time the head or scolex of this larva is provided with hooks and suckers. (No. 799 is the young of another species of *Taenia* which is found in the liver of the rat. These are swallowed by the cat in whose intestine they develop.)

The larvae of *Taenia solium* bury themselves in the flesh of the hog, which is often eaten by man in a raw or half-cooked condition. In this new situation the worm develops rapidly. The bladder is cast off. The head (Pl. 798, fig. 4) has a double circle of hooks and four

suckers (fig. 5) for the purpose of attachment. From the neck, which is smooth in front and irregularly wrinkled behind, grow out sections divided by regular joints. This process continues until an immense number have been formed, those nearest the neck always being the youngest and those at the posterior end the oldest.

Weinland<sup>1</sup> has pointed out that the articulation of a Cestode is by no means homologous with that of an earthworm or any true segmented animal.

When we consider how these sections develop into sexual organisms or proglottids (fig. 6), how these break away from the chain and live for a while as independent individuals (Van Beneden), we see how very far removed they are from the true segments of the typical worm. They serve the one function of reproduction, containing such an incredible number of eggs that it may be said "in no group of the animal kingdom do we find any fecundity to be compared to this of a cestode worm."<sup>2</sup>

A specimen of *Taenia* now in the possession of the Boston Society of Natural History measures thirty feet, but this is incomplete, not having the head; while the complete specimen, No. 800, measures sixteen and a half feet. The tiny, knob-like, and reddish brown head is seen on the right of No. 800, a short distance from the bottom of the jar. The youngest sections are small and narrow, but the oldest are large and sexually mature. Not only is the adult without a mouth and digestive system,—the fluid being absorbed through the body wall,—but no nervous system has been discovered.

<sup>1</sup> Tape-worms of Man, 1858, p. 9.

<sup>2</sup> Van Beneden, Animal Parasites and Messmates, 1876, p. 208.

## CRUSTACEA.

Section 12 (in part), Section 13, and Section 14  
(in part).

## ENTOMOSTRACA.

The Worms with the remaining large classes of Invertebrates — the Crustacea, Arachnozoa, Myriopoda, and Insecta — were formerly grouped together under the name of the Articulata or animals with articulated bodies. Afterwards the Worms were placed in the subkingdom of Vermes, and the other classes, taken collectively, were known as the Arthropoda or animals with jointed legs. Of late years there has been much discussion on the question, "Do the Arthropoda constitute a natural group?" That is, have these different classes descended from a common ancestor? The tendency is toward a negative answer, and the giving up of the name Arthropoda, while the classes are considered separately, each having its own ancestral forms. This course we have followed in the Guide.

The trilobites of Cambrian times may be ancestral forms of the Crustacea. They are certainly a generalized group, possessing characters in common not only with the Crustacea but also with the Arachnozoa. This being the case, it may be that some pre-Cambrian trunk form gave rise to both groups which developed and spread out into separate branches reaching down to the present day, while the parent group — the Trilobita — became extinct in Palaeozoic times.<sup>1</sup>

The relationships, however, between the trilobites and

<sup>1</sup>See Woodward, Quart. Journ. Geol. Soc. London, LI, 1895, p. lxxi.

Limulus of the Arachnozoa are so natural, and the bonds uniting Limulus with the scorpion and spiders so close, that we have placed the trilobites as the primitive Arachnozoa instead of the primitive Crustacea.

Among the generalized living Crustacea are the marine pelagic Copepods which may be taken to represent the ancestral form of the group. These exist in inconceivable numbers both in the tropical waters and the arctic seas. Calanus (= Cetochilus) (Pl. 801, figs. 1-3, *C. septentrionalis* Goodsir; Pl. 802, figs. 1, 2, *C. propinquus* Brady), begins life with few parts and organs, and the changes which convert the larva into the adult are of the simplest (Kingsley). The larva, called the nauplius (Pl. 801, fig. 1), has a body consisting of one part, the cephalothorax, which is provided with a median simple eye and three pairs of appendages corresponding to the two pairs of antennae and one pair of mandibles. The abdomen grows out (fig. 2) and more appendages are developed (fig. 3). This continues until, after several moults, the adult form is attained.

The body of the adult Calanus (Pl. 802, fig. 1, dorsal view of female; fig. 2, side view of the same), which is less than a quarter of an inch in length, is made up of segments most of which are distinct and freely movable. The cephalothorax is not covered by a carapace, peculiar to more specialized forms, though the anterior segments are more or less fused together. The abdomen is provided with terminal appendages only, but the cephalothorax has two pairs of antennae, four pairs of mouth parts, and four or sometimes five pairs of swimming-feet.

The anterior pair of antennae are long (fig. 2), equalling the length of the body, and are adapted for a purely natory life. They are spread out, according to Brady<sup>1</sup> "at right angles to the body, acting like the wings of a hovering bird and so suspending the animal at almost perfect

<sup>1</sup>Chall. Rep., Zool., VIII, 1883, p. 30.



rest in the water." At other times they are used as oars and each powerful stroke propels the animal a considerable distance through the water.

The second or posterior pair of antennae are divided into two branches and supplied with long hairs. These are also adapted for swimming. The mouth parts consist of a pair of strong mandibles, one pair of maxillae which carry long branchial filaments, and two pairs of well developed maxillipeds. The five pairs of rowing feet aid the antennae in locomotion, and thus it is seen that the pelagic Copepods are preeminently swimmers.

Besides the marine forms of Copepoda there are many related fresh-water species, the most familiar of which is Cyclops (Pl. 803, fig. 1, *C. brasiliensis*, ♂; fig. 2, *C. vitiensis*, ♀). In the fresh-water forms the first pair of antennae are much shorter than in Calanus, and consequently the animals are not such good swimmers. The setae of the second pair open and close like the fingers of a hand, so that by means of these organs Cyclops can attach itself to objects. In the middle of the forward part of the cephalothorax there is an eye that appears to be single but which in reality is double.

The fifth pair of legs exist as vestiges and usually have but one joint.

The female (fig. 2) carries the two sacs of eggs about with her for a time, and the young are hatched as nauplii.

Nearly every group of Crustacea has its parasites illustrating specialization by the reduction of some organs and the modification of others. The Copepoda are no exception to this rule; indeed, they offer some modified forms which are far removed from their primitive ancestors. Such are *Chondracanthus* (No. 804; Pl. 805) which lives in the gill chamber of a fish; *Penella* (No. 806) and *Lerneæ* (No. 807).

The body of *Chondracanthus* (No. 804; Pl. 805, *C. gibbosus*, side view) has lost its distinct segmentation, while the abdomen exists as a vestige only. The eyes

have disappeared and the appendages are for the most part jointless and lobe-like. The antennae are tiny and indistinctly jointed (Baird). The mouth parts are adapted for piercing and sucking, instead of for biting as in non-parasitic Copepods.

Another parasitic form of this group is *Penella* (No. 806), which bores into the body of a fish and lives partly imbedded in the flesh. Its long, tubular body is indistinctly segmented. At the anterior end there are several pairs of vestigial appendages, while at the other extremity a large number of thread-like organs extend beyond the end of the abdomen and give a plume-like aspect to this part of the body.

One of the most modified Copepoda is *Lernea branchialis* Linn. (No. 807; Pl. 808, figs. 1, 2, drawings of the same), found on the gills of codfish. Parasitism has brought about such complete changes in this species that it is only the young stage (fig. 1) which enables one to place it among the Crustacea. In this stage it is seen to have a cephalothoracic region with a pair of eyes and three pairs of jointed appendages.

The body of the adult (No. 807; Pl. 808, fig. 2) has lost all trace of segmentation and is an S-shaped sac with two long egg masses hanging from it. There are no eyes and no jointed appendages, the antennae even having disappeared. The mouth parts are horny, root-like organs which are buried in the flesh of the fish, and the fluid food is obtained by suction.

*Phyllopoda.* The group of Phyllopoda is of special interest since it contains two genera, the brine *Artemia* and the fresh-water *Branchipus*, which have been transformed the one into the other, by changing their environment.

*Artemia salina* M. Edw. lives in salt lakes. By gradually decreasing the density of the salt water during several generations, it has been converted into the fresh-water genus *Branchipus*. By increasing the density of

the water in which *Artemia salina* M. Edw. was living, it was transformed into another species, *Artemia mühlhausenii* M. Edw. Again, this brine was diluted and *Artemia mühlhausenii* was changed back to *Artemia salina*.<sup>1</sup> In this way it has been proved that not only one species can be converted into another species, but that the same is true of genera.

Figures of the two animals would not bring out these changes since they take place in the details of structure (such as the number of the abdominal segments and the bristles and knobs of the terminal abdominal appendages), but they are clearly represented in Pl. 809, figs. 1-8. The long terminal segment of the abdomen of *Artemia salina* is seen in fig. 1; this becomes divided into two segments (fig. 2), as in the abdomen of *Branchipus*. Figs. 3-8 show the gradual reduction of the bristles of *Artemia salina* (fig. 3) to the knobs of *Artemia mühlhausenii* (fig. 8).

The American species of *Artemia* (*A. gracilis* Verrill) (Pl. 810, fig. 1) lives in Great Salt Lake, and the New England species of *Branchipus* (*B. vernalis* Verrill) (fig. 2), is often found during the spring and autumn in ponds that dry up in the summer time. They are graceful little creatures that swim on their backs with great rapidity, their light colored bodies contrasting prettily with their brightly tinted locomotor organs which combine the function of feet and gills.

*Apus lucanus* Packard (No. 811) is a fresh-water specialized Phyllopod. The anterior part of the body is covered with a large carapace which, however, is not soldered to the thoracic region. When this carapace is removed the segmented body is exposed beneath. It consists in this genus of not less than sixty-nine segments.

<sup>1</sup> For further information see Zeitschr. f. wiss. Zool., XXV, Suppl., 1875; also 12th Ann. Rep. U. S. Geol. and Geogr. Surv., 1878, part 1, pp. 466-514.

Bernard<sup>1</sup> maintains that this large number of segments is one of many proofs that the Apodidae, and with them all the Crustacea, have arisen from carnivorous worms. He takes great pains to bring out the resemblances of Apus to a carnivorous worm, but in doing this he is dealing with adults, and is attempting to connect the mature forms of one subkingdom with those of another.

On the other hand, Packard<sup>2</sup> considers the excessive number of segments in Apus and the irrelative repetition of abdominal feet as signs of a vegetative repetition of parts in a type which has culminated and is subject to decline and extinction. He finds that the Phyllopods as a whole, especially the Apodidae and Branchipodidae, are a comparatively recent, extremely specialized group which was developed under exceptional biological conditions in salt lakes or in bodies of fresh water. He also points out the important fact that although fossils of Phyllopods are found in the Palaeozoic rocks, they appear to have been fresh-water forms, since their remains occur in fresh-water strata.<sup>3</sup>

The eyes of Apus are prominent. Extending from the ventral side are the two pairs of long, slender antennae. Back of these are the mouth parts and swimming-feet (No. 811).

One of the modified Phyllopod crustaceans is *Estheria californica* Pack. (No. 812). No one could imagine at first sight that this animal was in any way related to a Gammarus, lobster, or crab. The fleshy organs are covered by a bivalve shell (Pl. 813, fig. 1, enlarged; the line shows true length of shell) which is provided with a hinge, with small umbones placed near the anterior end, and with what appear to be distinct lines of growth.

<sup>1</sup> The Apodidae, 1892, p. 18 (Nature series).

<sup>2</sup> 12th Ann. Rep. U. S. Geol. and Geogr. Surv., 1878, part 1, p. 418.

<sup>3</sup> *Loc. cit.*, p. 419.

Packard<sup>1</sup> states that these so called "lines of growth" are superficial like the tubercles and spines on other Crustacea, and that therefore they are probably a kind of ornamentation. The shell is in reality a modification of the carapace which bends downward and encloses the whole body. The fleshy animal (fig. 2, with one valve removed) has the segmented body and jointed appendages which prove that it does not belong to the class of Pelecypods. The thoracic and abdominal segments are similar and bear twenty-two pairs of feet. Most of these are alike in structure, but the first two pairs in the male are provided with claspers. The head segments are soldered together.

#### CIRRIPIEDIA.

Barnacles have undergone numerous modifications which have carried them far from the primitive ancestral form. The young, however, is a free-swimming nauplius (Pl. 814, fig. 1) similar to that of other generalized Crustacea. It possesses the two pairs of antennae and the mandibles which are locomotor organs as in other members of its class. After moulting twice it appears as seen in fig. 2. It now has a segmented abdomen which serves as a rudder and the cephalothoracic appendages are larger. In the still older larval stage (fig. 3, side view), when the barnacle is preparing to settle, the parts and organs which are useful in swimming become reduced in size or are dispensed with altogether. Thus the abdomen is a mere vestige, while the compound eyes and one pair of antennae, wholly disappear. The cement duct in the remaining pair of antennae, which connects with the cement gland in the stalk, pours out its cement whereby the barnacle is fastened by the anterior part of its head to a rock.

<sup>1</sup> *Loc. cit.*, p. 377.

If a barnacle belongs to the pedunculated Cirripedia like *Lepas* (No. 815), the stalk or peduncle grows long and the shell forms at its farther end; if, on the other hand, it is one of the sessile Cirripedia, like *Balanus* (Nos. 816-818), the shell is fastened directly to the rock and the barnacle looks as figured in Pl. 814, fig. 4. A slightly older stage is represented in fig. 5, with the thoracic appendages extended.

The adult *Lepas anatifera* Linn. (No. 815) is provided with a long contractile stalk by which it is usually attached to some floating object. At the end of this stalk is the shell which is made of five plates. The shell protects the viscera, the mouth with its mandibles and two pairs of maxillae, and the six pairs of feathery thoracic legs which have become transformed into organs for catching food. It was the discovery of these jointed appendages which caused the barnacle to be removed from the Mollusca and placed with the Crustacea.

In the specimens (No. 815), as in the undisturbed living *Lepas*, these organs are seen extending from the shell; when the animal is disturbed they are withdrawn and a transverse muscle draws the valves tightly together.

The segments of the body are very indistinct, while, during the period the animal was becoming adapted to a sedentary life, the abdomen became a mere vestige and its appendages disappeared.

*Lepas*, like the Cirripedia generally, has no heart or specialized circulatory organs and probably no respiratory system.

The more common form of barnacle is sessile, the stalk not being developed. In the specimen (No. 816) several of these barnacles have made their home upon one valve of *Pecten*. The opening of the pyramidal shell of the barnacle is closed by four valves; in some of the specimens, however, these valves are open and the cirri are extended. These delicate organs are still more plainly

seen in No. 817, *Balanus hameri*, where they occur so large in size that they can be easily studied.

Variation in the color and ornamentation of the shell is well shown by *Balanus tintinnabulum* Linn. (No. 818). In three specimens the shell is smooth, while the specimen on the right is ridged.

Sometimes barnacles attach themselves to a whale and become imbedded in its skin. This is the case with *Coronula diadema* Blainv. (No. 819). The usual conical shell may become modified into a tube, as in *Tubicinella balaenarum* (No. 820). It is made of eight vertical sections and is marked by circular ridges and perpendicular striae. At the top the four valves are open in No. 820, as when the thoracic appendages or food-catchers are put out.

The barnacle *Conchoderma aurita* Olf. (No. 821) is a peculiarly modified form. The young, represented by four specimens in the bottom of the bottle, have a short peduncle and a body that is similar in shape to that of *Lepas* (No. 815), though it is never covered by a shell. In the two youngest specimens this body is colorless, but in the two older ones it is distinctly banded with brown. As *Conchoderma* grows older the peduncle becomes long and the body less compressed, while both are dark colored. From the upper side of the body grow out two tubular organs which are very conspicuous in the adult (No. 821). Their function is not known with certainty, though Kingsley thinks they may be respiratory organs.

#### MALACOSTRACA.

An ancestral form of the Malacostraca may be represented by *Palaeocaris typus* M. & W. (Pl. 822, fig. 1, enlarged three diameters). The body is long and excepting the head, is made up of distinct and similar segments which are uncovered by a carapace. The two pairs of

antennae are largely developed and these were probably used as locomotor organs. The mouth parts are not preserved, so that their structure is not known. The thoracic legs extend forward; they are undivided at their ends, and the anterior pairs are apparently not differentiated into organs of prehension or mastication, but all are useful as swimming organs. Most of the abdominal segments bear a pair of appendages which are simple in structure (fig. 2, enlarged four times), and like the thoracic appendages were used in locomotion. The last segment or telson carries a pair of swimmerets (fig. 3) which indicate that this portion of the abdomen is a true segment, and which also give additional proof that *Palaeocaris* was a good swimmer.

It is generally conceded that the Malacostraca can be traced back to the group described by Packard as the Phyllocaridae, the only living representative of which is *Nebalia*. One of the ancestors of *Nebalia* is probably *Ceratiocaris* (Pl. 823, *C. papilio* Salter), in which a carapace covers the thorax and a part of the abdomen. The antennae are obscure and are indicated in the figure by broken lines. The anterior projection of the carapace or the rostrum (Pl. 823) has separated from the carapace. The resemblance of *Ceratiocaris* to *Nebalia* is marked. The latter is a generalized form combining Copepod, Phyllopod, and Decapod features.<sup>1</sup> The development is without a metamorphosis and the young and adult resemble each other. *Nebalia bipes* Fabr. (No. 824; Pl. 825, figs. 1-6, *Nebalia geoffroyi*) is a marine form which has the segments of the thorax and abdomen similar and distinct, though all of the former and four of the latter are covered by a carapace (fig. 1, nearly natural size). In fig. 2 one side of the carapace has been cut away exposing the body beneath. The eight thoracic segments can be easily counted, and each carries a pair of appendages in the

<sup>1</sup> Woodward, Quart. Journ. Geol. Soc. London, LI, 1895, p. lxxxiii.



form of leaf-like, gill-bearing thoracic legs (fig. 3). The eight abdominal segments are also distinct. The first four of these carry each a pair of swimmerets consisting of a basal stem and two leaf-like parts (fig. 4); the fifth and sixth pairs of appendages are small, and the last two segments are without swimmerets, though the terminal segment carries a pair of spines. There is no telson in *Nebalia*, and in this respect the genus differs from most Crustacea.<sup>1</sup>

The segments of the head are consolidated, but as there are six pairs of cephalic appendages it is inferred that this region of the body is made up of as many segments. The dorsal and lateral portions of these segments have grown backward forming the carapace which not only covers the thoracic region but also four of the abdominal segments, as already stated. In front, a movable plate, called the rostrum, is hinged to the carapace which the animal can move up and down at pleasure. The appendages of the head are a pair of eye-stalks and two pairs of well developed antennae (fig. 2), a pair of mandibles (fig. 5), and two<sup>2</sup> pairs of maxillae (figs. 6, 7), making six pairs attached to the head.

*Stomatopoda.* The young of *Squilla*, first described as *Alima* (Pl. 826, fig. 1, *Squilla empusa* Say), has a long, loosely articulated body. The posterior thoracic segments are not covered by the carapace and these segments are without appendages, none being developed after the large grasping legs which correspond with the second pair of maxillipeds.<sup>3</sup> The flat abdomen is greatly extended and bears a few pairs of swimmerets.

<sup>1</sup> According to Claus (Ann. and Mag. Nat. Hist., (6), III, 1889, p. 441) the last two segments of the abdomen represent the telson of the Malacostraca.

<sup>2</sup> Lang says one pair, making five pairs to the head. Packard describes and figures six pairs (12th Ann. Rep. U. S. Geol. and Geogr. Surv., 1878, part 1). Woodward says three pairs of mouthparts (Quart. Journ. Geol. Soc. London, LI, 1895, p. lxxxiv).

<sup>3</sup> Faxon, Mem. Mus. Comp. Zool., IX, no. 1, 1882, explanation of Pl. vii.

All the appendages of this Stomatopod are adaptive even at this early age, and Brooks<sup>1</sup> has shown that during the long larval life the larvae have undergone many secondary modifications which have no reference to the life of the adult and are therefore unrepresented in the adult organism. Indeed, the larvae differ among themselves, says this investigator, "more than the adults, thus reversing the general rule that larvae are less specialized and exhibit clearer evidence of genetic relationship than mature animals." At the same time Brooks has shown that the changes which convert the larva into the adult are very gradual, and that the development may be regarded as the simplest expression of the extremely complicated metamorphosis of the specialized Crustacea. Inasmuch as the changes are slight compared with those of most stalk-eyed Crustacea,<sup>2</sup> we have a sufficient reason for placing *Squilla* among the more generalized Malacostraca.

When fully grown, *Squilla* (No. 827, *S. nepa* Latr.) excavates holes in the sand, and one species, *Lysiosquilla excavatrix*, buries itself with the exception of the tips of its eye-stalks while waiting for its prey. The body of *Squilla*, like that of the larva, is long and made up largely of distinct and movable segments. When viewed from the dorsal side (No. 827, specimen on the left) only a few pairs of jointed appendages are seen, but a ventral view (No. 827, specimen on the right) exposes a large number of these paired organs extending from one end of the body to the other.

The preparation (No. 828) shows more plainly the parts that make up the external skeleton. There are seven distinct segments in the posterior or abdominal

<sup>1</sup> Chall. Rep., Zool., XVI, part 45, 1886, p. 4.

<sup>2</sup> Brooks, Johns Hopkins Univ., Stud. Biol. Lab., I. In this volume is included Chesapeake Zool. Lab. Scientific Results of season of 1878, p. 152.

region. Six of these are similar, while the seventh or terminal segment is larger, rounder, and flattened on the edges. The five anterior abdominal segments carry five pairs of similar jointed swimming-feet, while the sixth bears a pair of modified swimming-feet. The slight variation in the structure of all the swimming-feet excepting the last two indicates that they perform a similar function. Each swimming-foot is made of two leaf-like parts fastened to a stem; the former are fringed with long hairs. Attached to the base of each swimming-foot is a gill made up of filaments. The last pair of swimming-feet are longer and stronger than the others. They consist of more sections and joints, and the basal section does not bear a gill. These two swimming-feet with the large terminal segment, which is without appendages, constitute an efficient organ for propelling the animal through the water.

In front of the abdomen are four similar segments which are much smaller and narrower than the abdominal segments already described. Three of these segments bear slender little organs resembling walking-legs, while the remaining segment bears a pair of appendages very different from the walking-legs, but similar to the two pairs of appendages in front of them. The segments bearing the mouth parts and one pair of antennae are consolidated and covered in part by the carapace, so that the number can only be inferred by the number of appendages.

In front of the walking-feet are three pairs of organs that are alike in shape and which terminate in a curved movable jaw. Then come the large grasping organs and in front of them a slender pair of appendages. These five pairs are the maxillipeds. In front of the maxillipeds are three pairs of small maxillae and one pair of short antennae.

The first two segments of the body bearing the eye-stalks and first pair of antennae are freely movable, and in this respect *Squilla* differs from other Crustacea.

Having found twenty pairs of appendages, it is to be inferred that there are twenty segments in the body. These are usually divided into seven abdominal, eight thoracic, and six cephalic.

In the preparation (No. 829) the nervous system is shown.

*Amphipoda.* *Gammarus locusta* M. Edw. (No. 830; over Section 12 large figures of *G. ornatus* M. Edw.), like the Amphipods in general, has a body made up of similar segments uncovered by a carapace. The seven abdominal segments bear the six pairs of swimming-feet, the eight thoracic (the first one of which is represented only by remnants of its ventral and lateral portions) bear the thoracic legs and maxillipeds. The eyes of *Gammarus* are sessile or in other words set in the head. Various parts of *Gammarus* properly labeled are drawn on a large scale in the plate over Section 12.

*Laemodipoda.* *Caprella* (No. 831; see also large figures over Section 12) is a remarkable crustacean in appearance when seen running or climbing over algae, hydroids, or starfishes. The body is made mostly of the thoracic region, the abdomen being reduced to a mere tiny knob. The long, slender segments of the body are distinct and so loosely put together at the joints that the animal can double upon itself. At the forward end there are two pairs of antennae, one long and one short, which probably aid in catching food (Gosse). Back of these are two pairs of appendages which are finely adapted for seizing prey; the last section but one is enlarged, while the terminal section shuts down upon it as the blade of a pocket knife closes into the handle.

In the middle of the body two pairs of respiratory organs take the place of feet; these also form a pouch for the young during the season of oviferation. At the posterior end are three more pairs of long spiked and bladed feet which take hold of objects when the creature is in action.

One of the external parasitic Crustacea is represented by the whale louse, *Cyamus ceti*, Latr. (No. 832). Its flattened body is reduced to a few segments. Most of the appendages are provided with hooks whereby the crustacean fastens itself upon the whale. This is the case with the arms which have no claws, but the movable jaw is modified into a sharp curved hook. The third and fourth apparent segments bear long tubular branchiae.

*Isopoda. Idotea wosnessenski* Brundt (No. 833), has the body flattened from above and divided into seven distinct thoracic segments and an indistinctly segmented abdomen. The head is provided with a pair of small sessile eyes and two pairs of antennae, one pair being much smaller than the other. Then follow seven pairs of similar jointed feet placed far apart on the lateral edges of the ventral side and adapted for walking. Between these legs the respiratory leaves are snugly folded over the eggs. The abdomen is supplied with leaf-like swimmerets and the first pair are modified into a cover for the other.

The segments of the depressed body are similar from one end to the other, there being slight differentiation between the thoracic and the abdominal regions.

The head with its pair of sessile eyes is inconspicuous but it carries one pair of long antennae. The thoracic region has three pairs of jointed feet followed by two segments without feet, and these in turn are succeeded by three segments with feet. The respiratory organs are leaf-like and enclose the young larvae. The thoracic appendages are followed by several pairs of abdominal leaf-like organs.

The fresh-water *Asellus communis* Say (No. 834) is a little crustacean with a long, narrow, depressed body composed of similar segments, none of which is covered by a carapace. The head is provided with two pairs of antennae. The thorax consists of seven segments and carries seven pairs of walking-feet. The terminal seg-

ment is large and has three pairs of leaf-like organs attached to the ventral side.

The many peculiar modifications of *Serolis* (No. 835) are interesting. The body is flattened out and nearly circular in outline as compared with most Crustacea. The thoracic segments are narrow near the median line and spread outward and downward surrounding the shortened abdomen. Neither carapace nor rostrum is present. The eyes are set in the head on the dorsal side and the two pairs of antennae are flattened and closely applied to the thoracic segments. These are the only appendages visible from above. The mouth parts and legs are all flattened and the latter are wide apart on the edges of the body.

*Lygia dilatata* St. (No. 836, dried specimen; No. 837, alcoholic specimen), has a shortened depressed body covered like most of its kind by a chitinous exoskeleton. This is divided into a small number of segments most of which are distinctly seen, since *Lygia* has no carapace. The head is small and fits into the first thoracic segment, which is scooped out in front for this purpose.

The seven thoracic segments are similar and constitute the larger part of the body, while the six visible abdominal segments are narrow and are crowded closely together.

The thoracic and abdominal segments are prolonged laterally beyond the body proper, and the separate side pieces thus formed are so freely movable that the body can double upon itself. They also serve to protect the appendages (excepting the first and last pair), so that these are not seen in a dorsal view (No. 836) when the crustacean is resting.

The eyes are compound and are set in the head. One pair of antennae are long and the other pair are very short. The mouth parts are small and compact. The seven pairs of jointed thoracic legs perform a similar function and are similar in structure.

Packed closely together under the abdomen are the leaf-like respiratory organs, while the sixth or terminal abdominal segment bears a pair of caudal appendages.

#### MACROURA.

Lucifer (Pl. 838) is one of the few Macrouran Crustacea which pass through a nauplius stage (Pl. 838, fig. 1). It possesses at this time the three pairs of locomotor appendages and an ocellus, but as yet there is no carapace nor compound eyes.

The nauplius develops into the zoëa stage (fig. 2), when the antennae and mandibles are still used for swimming. The abdomen and its telson have developed and the cephalothorax is provided with a carapace.

In the next or Schizopod stage (fig. 3) the antennae and mandibles have lost their locomotive function and stalked eyes appear with the ocellus.

When this Schizopod larva moults the Mastigopus or young Lucifer stage (fig. 4) reveals a marked change in the forward part of the cephalothorax. The segments bearing the eye-stalks and two pairs of antennae are carried far forward, while the hinder segments of the cephalothorax bear the mouth parts and thoracic legs. The adult does not differ essentially from Pl. 838, fig. 4. The anterior segments extend farther forward; the first pair of thoracic legs are vestigial, while the remaining four pairs are adapted for swimming, being abundantly supplied with hairs. The abdominal appendages borne on the six abdominal segments also aid the thoracic legs in swimming.

Penaeus, like Lucifer, leaves the egg in a nauplius condition. The adult *Penaeus canaliculatus* Oliv. (No. 839) is larger than most shrimps and it has elaborated some of the typical features of this group. The long pointed rostrum of the carapace is notched on the upper

side like a saw and provided with short hairs. The eyes are prominent, flattened, and black in color. The antennae are the most conspicuous organs, the scales of the second pair extending beyond the rostrum. These organs and the mouth parts are fringed with hairs, giving an elegant appearance to *Penaeus*. The first two pairs of thoracic legs are much smaller than the remaining three pairs and are provided with claws.

The abdomen tapers to a sharply pointed telson and carries good-sized swimmerets that serve as a protection for the masses of eggs.

Most of the groups of Crustacea, although composed largely of marine forms, yet have also fresh-water and terrestrial members, and it is interesting to note that one species of *Penaeus* (*P. brasiliensis* Latr.) is often found in brackish waters, and even ascends streams to points where the water is nearly or quite fresh.<sup>1</sup>

The fresh-water prawn, *Palaemon carcinus* Oliv. (No. 840, on upper shelf) is remarkable for the extreme length of its antennae. It is indeed surprising that organs of such delicacy and length can be of use.

The second pair of walking-feet in this genus are the arms and claws, and these are also greatly prolonged. The first pair, according to Gosse,<sup>2</sup> are used as brushes to clean the ventral side of the thorax and abdomen. The carapace is short and without a median suture; it is armed in front with an elegant curved rostrum having a double notched edge. In the species *Palaemon serratus*, Leach found that the point of the rostrum was notched in three thousand specimens, while the notch was wanting in only two specimens,<sup>3</sup> certainly a good example of the persistency of a structural character. The eyes of *Palaemon* are small and on slender stalks. The large swimmerets of the abdomen show finely in No. 840.

<sup>1</sup> Stimpson, Ann. Lyc. Nat. Hist. N. Y., X, 1874, p. 133.

<sup>2</sup> Quoted by Adam White, Pop. Hist. Brit. Crust., 1857, p. 131.

<sup>3</sup> Malac. Podoph. Brit., no. 15, 1817.



Interesting adaptive characters are found in *Alpheus heterochelis* Say (Pl. 841; No. 842). It is a burrower and one of its arms has an immense claw (No. 842) which is fully as large as the cephalothorax. The wonder is that so small a body and so delicate a basal portion of the appendage can control the movements of such a large organ. That this organ is an adaptation of the adult animal to the life it leads is proved by the fact that in the young *Alpheus* (Pl. 841, fig. 1, greatly enlarged) the claws are not developed. In the more advanced stage, however (fig. 2, enlarged), they are of considerable size. Fig. 1 gives the color of the young *Alpheus* which changes with growth (fig. 2).

In *Evatya crassus* Smith (No. 843), the abdomen tapers and the last segment is small. The swimmerets of the forward segments (excepting those of the first segment) are unusually large, broad, and hairy organs. The small thoracic legs have horny spikes at their ends. Then comes a pair of enormously developed legs covered with dark horny knobs; the terminal hooks are still darker and everything indicates that these organs perform hard work.

The eyes of this species are inconspicuous but the second pair of antennae are extremely long and slender.

The shrimp (*Crangon franciscorum* Stimp.) (No. 844) has the segments of the abdomen tapering to a long, narrow telson. The cephalothorax is small and the rostrum weak. The swimmerets are long, slender organs and in one of the specimens (No. 844) they hold the mass of eggs in place. The last pair of swimmerets are large and efficient swimming organs. The last two pairs of legs are the strongest and these are used in digging holes when the shrimp buries itself in the sand. The second and third thoracic legs are slender; they are not provided with claws but the terminal section of the arms bends upon the next lower section like the blade of a knife upon the handle. The antennae have large basal scales

that extend forward and lie horizontally, concealing from sight the two arms and the mouth parts.

Leach says that *Crangon vulgaris* or the common shrimp often enters estuaries, especially during the breeding season, and it sometimes ascends rivers with the tide and is left in great quantities in the saline marshes.

The lobster, *Homarus americanus* M. Edw. (Pl. 845), passes through the nauplius state in the egg, and when hatched is surrounded by a thin membrane which is moulted before the little creature enters upon a free-swimming life. The first larval stage (Pl. 845, fig. 1) is little over a third of an inch long. It is marked by the presence of a comparatively large cephalothorax, big compound eyes, and a prominent frontal spine; it also has a segmented abdomen with a fan-like telson. The cephalothorax bears appendages which are two-branched; the outer branch or paddle is flattened and provided with long hairs, while the inner branch is prehensile. These appendages resemble the swimming organs of the Schizopods so closely that this stage is often called the Schizopod larva. The abdomen is without appendages, though their rudiments can be seen under the skin from the second to the fifth segments. In the next larval stage (fig. 2) the cephalothorax and its appendages are similar but the rudiments of abdominal swimmerets have developed. At the fourth moult (fig. 3) the swimming paddles are reduced to vestiges (fig. 4), while the inner branches have developed into walking-legs. The lobster still stays at the surface, swimming forward by its abdominal swimmerets and backward by its abdomen. At the sixth moult the thoracic swimming organs are wholly lost and before the seventh moult is passed the lobster leaves the surface of the sea, going to the bottom and approaching the shore where it lives among the rocks. Its larval life is now over. During the first year the lobster may moult from fourteen to seventeen times, and at the end of this time it is from two to three inches long.

It is not sexually mature until it is ten or eleven inches long and this growth probably requires four or five years. It exhibits the typical crustacean characters on a large scale, and for this reason we shall give its structure in greater detail, thereby summarizing in part what has already been said. Many of these characters may be seen in the spiny lobster, *Palinurus ehrenbergi* Heller (No. 846), and in the preparation (No. 847, *Homarus americanus* M. Edw.). The cylindrical body is covered by a hard crust or exoskeleton and divided into two distinct regions, the cephalothorax and the abdomen.

The abdomen has the more primitive characters, since its six circular segments and seventh flattened segment are distinct and movable. To each of the six segments is attached on the ventral side a pair of appendages, the swimmerets. These appendages, excepting the first and sixth pairs, are composed of three parts, a basal stem and two leaf-like portions. Similarity in structure suggests a similarity in function, and we find that these organs are used in swimming forward and in floating from below upward. The first pair of swimmerets is modified for reproductive purposes, and the last pair, which are larger and stronger than the others, supplement the telson and muscular abdomen in propelling the animal swiftly backward through the water.

The cephalothoracic segments are consolidated so that it is impossible to make out their boundaries with absolute certainty. They are mostly covered by a carapace which bends downward on the sides, covering the branchiae or gills. The number of cephalothoracic segments can be inferred from the number of paired appendages attached to it.

In front of the swimmerets are four pairs of walking-feet which are jointed in such a manner as to be efficient organs in walking, pushing, and pulling. They are armed at the end with a spike (fourth and third pairs counting from the forward end) or with a movable and useful claw

(second and first pairs). In front of these walking-legs there are a pair of arms which in the embryo cannot be distinguished from the other walking-legs, but which in course of development twist and stretch out forward, becoming arms for catching food and for anchoring.

Sometimes these organs through injury, by accident, or through other unfavorable conditions, become deformed and often in such cases the specimens show the strong hereditary tendency possessed by the claw to produce its like. In the thirty-five specimens of deformed lobsters' claws in the collection of the Boston Society of Natural History there are five which have developed an additional claw with a movable jaw. This jaw is fastened invariably either to the immovable jaw of the lobster's claw or to the section from which the latter grows. In no case does the movable jaw make a mock claw with the true articulated jaw.

In front of the arms are the three pairs of maxillipeds and one pair of maxillae which are used in obtaining food and carrying it to the mouth. These nine pairs of appendages belong to the thoracic region. The segments to which they are attached are immovably consolidated, as we have said, and their dorsal portions have disappeared, owing probably to the fact that the dorsal and lateral portions of the fifth segment have grown out backward in the form of a carapace, thereby covering them and making their dorsal portions unnecessary.

In front of the maxillae is another pair of leaf-like maxillae and in front of these a pair of hard mandibles. The mouth parts—maxillipeds, maxillae, and mandibles are placed snugly together, when at rest, but when the animal is eating they are all in active motion.

In front of the mouth parts are the two pairs of antennae, one long and one short, and the pair of movable eye-stalks with the compound eyes at their ends. The last five pairs of appendages described belong to the cephalic region and their segments are consolidated like

those of the thoracic region, while their dorsal and lateral parts extend backward to form the protecting carapace. Since fourteen pairs of appendages have been found attached to the cephalothorax, this part is supposed to be made up of as many segments, which with the seven abdominal segments and the six pairs of appendages make in all twenty-one segments and twenty pairs of appendages.

The circulatory system of the lobster is shown in part in the preparation (No. 847); portions have been cut away on the ventral side, exposing the sternal artery which gives off branches that pass to the limbs.

*Nephrops norwegicus* Leach, or the Norway lobster (No. 848), is a peculiarly delicate and graceful crustacean. The cephalothoracic region is more slender than in most genera and the abdominal segments are finely sculptured. With the exception of the sixth pair of swimmerets the appendages are likewise long and slender; especially is this true of the second pair of antennae which extend backward beyond the body and are thread-like in structure. The eyes are large and kidney-shaped, while the stalks are small.

One of the fresh-water crustaceans which closely resembles the salt-water lobster in structure is the crayfish, *Cambarus acutus* God. (No. 849). It is in fact a miniature lobster in general appearance, having the same number of segments and appendages. The position of the legs when the animal is walking is shown in the specimens. The body of the male (specimen on the left) is smaller than that of the female (specimen on the right), but his arms, especially the claws, are much longer than hers. The fifth pair of legs are without branchiae. The development of this fresh-water crustacean is accelerated and the nauplius stage is passed through in the egg, evidence of which is found in the membrane or delicate cuticle that is formed and afterward shed, while the embryo is still in its case.<sup>1</sup> When

<sup>1</sup> Huxley, *The Crayfish*, 1880, p. 215.

hatched the crayfish resembles the adult in general characters, though differing in details. The male of *Cambarus* has two forms and these are considered by Faxon<sup>1</sup> as alternating stages in the life of the same individual, one phase being assumed through the breeding periods, the other during the intervening seasons of sexual quiescence. Crayfishes abound in the middle and western states, but few know that they are also found in Massachusetts. The little creature seen in No. 850, *Cambarus bartoni* Gir., came from a small brook in North Grafton where for a number of years we obtained them for purposes of instruction.

Another species of this genus is the blind crayfish, *Cambarus pellucidus* Tellk.<sup>2</sup> (No. 851) found in Mammoth Cave. Living under these unfavorable conditions its body is smaller and the eyes which its ancestors possessed have gradually disappeared, although the eye-stalks remain (Kingsley).

Peculiar modifications of structure have taken place in *Galathea rugosa* Fabr. (No. 852). The exoskeleton is ridged and many of the ridges are provided with hairs. The abdomen is shortened and tapers posteriorly, while the cephalothorax has a swollen, puffed-out appearance. The latter region is much darker in color at the anterior end and this with the hairy ridges gives the crustacean a hardy aspect. A distinct groove on each side of the carapace divides this protecting covering into a median and two lateral parts. The last thoracic segment is not fastened to the others but is freely movable.

The appendages of the cephalothorax like the body are covered with hairs. The three pairs of small walking-feet extend forward and are provided with spikes instead of claws; the last pair are vestigial and are not

<sup>1</sup>Amer. Journ. Sci., (3), XXVII, 1884, pp. 42-44.

<sup>2</sup>*Cambarus pellucidus* Erichson. Smith, Rep. U. S. Comm. Fish and Fisheries, 1872-'73, p. 639.

seen in a dorsal view, since they are doubled up within the branchial cavity, and are attached to the movable thoracic segment.

The two arms are similar but differ greatly from these organs in other genera. The sections are very nearly the same in breadth and terminate in a claw, the two jaws of which are about equal in size and armed with sharp fine teeth. The arms extend straight out in front as seen in No. 852. All these peculiarities suggest that the habits of *Galathea* are very different from those of the typical *Macroura*.

An unusual modification of the external skeleton is found in *Callianassa grandimana* Gibbes (No. 853). It is membranous and looks at first sight as if it were the soft unhardened skin which appears when the crustacean has just shed its crust or shell. The fossorial habit of living in tunnels which it excavates in the sand is doubtless the cause for this condition of the skeleton. The tunnel or "tubular domicile" extends vertically downward to a considerable depth, according to Say,<sup>1</sup> and its compact sides project half an inch or more above the surface, like a chimney which contracts to a small opening.

*Callianassa* has a long, broad abdomen which takes up two thirds of the body. The cephalothorax is correspondingly short and the rostrum consists of two pieces hinged to the carapace. It is interesting to note how the terminal sections of most of the cephalothoracic appendages are furnished with dark brown hairs which grow on these parts that perform the hardest work in digging.

The hermit crab, *Eupagurus* (No. 854, *E. bernhardus* Brandt.; No. 855, the same, showing nervous system), is a modified form with adaptive characters. The young of some species of *Eupagurus* have a symmetrical abdomen like that of a shrimp, with swimming-legs on the

<sup>1</sup> Journ. Acad. Nat. Sci. Phila., I, 1817, p. 240.

second, third, fourth, and fifth segments,<sup>1</sup> and the external skeleton of the body is quite firm.

In the stage preceding the moult when the animal seeks a shell, the distinctly segmented abdomen has lost its symmetry; the feet are largest on the right side and the abdomen begins to curve away from the longitudinal axis. With the next moult, the abdomen is soft and the segments indistinct, while some of the abdominal appendages are lost (Pl. 856, *Eupagurus pollicaris*).

The adult usually lives in a Gastropod shell (No. 854; No. 857, *Petrochirus granulatus* Stimp., see lower shelf) and in this way the abdomen has become extremely soft, light-colored, and indistinctly segmented. Its appendages have lost all those characters which are natatory, and have either disappeared or have taken on secondary structural features. Thus the first segment has no appendages; the second, third, and fourth have limbs on the left side only for holding the eggs during the egg-bearing season; the fifth appendage is a mere vestige, while the sixth pair are modified for holding the crab in its shell.

The cephalothoracic appendages, though less modified than the abdominal, still have undergone changes in structure. The arms are used for walking, for getting food, and for closing the aperture of the shell; the second and third pairs of legs for walking only, while the fifth and probably the fourth pair aid in holding the animal in its shell.

Many interesting modifications of structure may be seen in the burrowing crustacean, *Hippa talpoida* (No. 858; Pl. 859). The smooth, more or less tubular cephalothorax is well fitted for a burrowing animal. Four of the abdominal segments can be seen from above, while most of the remaining portion that is bent under the cephalothorax is apparently composed of one piece, the segments

<sup>1</sup> Verrill, Rep. U. S. Comm. Fish and Fisheries, I, 1871-'72, p. 530.



having become consolidated without leaving a trace of the sutures. In this way a wedge-shaped implement is produced which is an efficient organ in burrowing. It is also aided in the work by the short, stout cephalothoracic legs. Thus equipped, the creature burrows backward into its hole with great rapidity and is wholly hidden save the tips of its small antennae.<sup>1</sup>

Although the adult *Hippa* is more of a burrower than a swimmer, nevertheless when undisturbed it will leave its burrow and swim about by means of its thoracic and abdominal feet. The antennae of *Hippa* are unique organs. When extended they curve like the horns of a deer and are provided with long hairs on the outer side. These are seen in No. 858, but more plainly in Pl. 859, where they are extended. When living, the animal usually carries them folded about the mouth, and, according to Smith, one of the principal offices of these organs is to keep the anterior appendages — mouth parts, etc. — free from all foreign substances.

A relative of *Hippa* is found in *Raninoides levis* M. Edw. (No. 860). Here the entire carapace has many irregular serrated markings. The front edge is provided with slender pointed teeth and the rostrum is composed of two parts and appears to be movable. The front of the cephalothorax is hairy. The last pair of legs are reduced in size and pushed up on the back. The arms have become flattened and twisted, till the movable jaw of the claw is inside instead of outside or above.

One of the most remarkable and interesting modifications of structure is found in *Dromia vulgaris* M. Edw. (No. 861), which lives with the sponge or sometimes in coral. The external skeleton has become soft and horny

<sup>1</sup> Smith, Trans. Conn. Acad. Arts Sci., III, 1876, pp. 311, 313. According to Verrill (Rep. U. S. Comm. Fish and Fisheries, I, 1871-'72, pp. 338, 339) *Hippa talpoida* burrows like a mole, head first, instead of backward.

and is covered with a thick coating of hairs which in color and texture resemble the fibers of the sponge. In this way, whether by conscious mimicry or by an instinctive adaptive power, the crab is perfectly protected.

Even the naked jaws of the claws are not hard or limy but so soft that they crush in the fingers. According to Bell<sup>1</sup> the young have the carapace entirely covered with a sponge which also conceals the two hinder pairs of legs as these are pushed above the others and are closely pressed against the back. The function of the legs that have been pushed out of their natural position is to assist in holding the sponge on the crab's back, and consequently sharp hooks have developed at their ends.

The plump, rounded appearance of the front of the cephalothorax which extends forward beyond the sponge, with the deep-set eyes in their circular sockets, gives an almost cat-like expression to the crab which is amusing.

The little *Porcellana ocellata* (No. 862) is interesting for the reason that its telson bears a pair of appendages. The telson itself is small and pointed; the appendages are fastened to it on its sides and also united to each other in the median line behind the point of the telson. These appendages with those of the sixth abdominal segment, together with the broad, well-developed abdomen which turns under the cephalothorax, enable this little animal to swim; hence the popular name of "crab-lobster." But, although it can swim on occasion, it prefers to stay under stones or in narrow crevices, and the structure of its body is well adapted to such an environment, for both the cephalothorax and abdomen and also the appendages give one the impression that *Porcellana* has been pressed out flat.

*Lithodes* (No. 863, placed towards the back of the Section) is one of the giant crabs of the group represented by the hermit crab. Armed with spines and knobs it is

<sup>1</sup> Brit. Stalk-eyed Crustacea, 1853, p. 371.

a formidable animal. The small abdomen is bent under the triangular cephalothorax so that it resembles that of the true crab soon to be described. There are, however, but four pairs of functionally useful walking-feet, the fifth pair being reduced in size and fastened to the last unconsolidated segment of the cephalothorax, as in the hermit crabs. *Lithodes* has given up the habit of swimming and is found creeping along the bottom with sluggish motion.<sup>1</sup>

*Birgus latro* Linn., or the palm crab, is an animal of great interest, since it has not only changed its habitat from the sea to the land but has also succeeded in converting a part of its gill chamber into an air-breathing lung. Pl. 864, fig. 1, is a diagrammatic representation of the lungs and the circulation in this crab. The heart is in the center and the lung cavities on either side. The anterior blood vessels are the veins, and the large posterior vessel, the artery. Fig. 2 is a diagram of a vertical section of the same, showing the branchia and the lung cavity with the pulmonary villi or tufts on the inner surface of the wall. The dark circular spots are blood vessels which have been cut across and which connect with the heart.

This crab spends its adult life on the land far from water, but it goes to the sea to deposit its eggs and the young are free-swimming creatures which breathe the air dissolved in water.

#### BRACHYURA.

The development of our common crab, *Cancer irroratus* Say (Pl. 865; Nos. 866–868), illustrates the mode of development of most crabs. The nauplius stage is passed through in the egg, the crab hatching as a zoëa (Pl. 865, fig. 1; the line indicates natural size; see also figure on

<sup>1</sup> Dana, Crustacea U. S. Explor. Exped., I, 1852, p. 428.

the left of the large plate over Section 13). The three enlarged figures represent different stages in the life of the young crab. In this larval condition the plump, rounded cephalothorax is provided with a long dorsal and frontal spine. The compound eyes are sessile, while the appendages of both regions of the body are adapted for swimming. The zoëa develops into the so called Megalops stage (Pl. 865, fig. 2; see also the middle figure of the plate over section 13) which resembles the lobster in the general shape of the body. The appendages of the abdomen are still adapted for swimming, but those of the cephalothorax have become transformed into organs for walking and more efficient instruments for catching food. The claws are developed, but at this stage are equal in size. The large, compound eyes are now on short, stout eye-stalks.

After moulting again, this swimming animal becomes a walking crustacean and is found at the bottom (see figure on the right of the plate over Section 13).

The adult crab (Nos. 866-868) is a fine illustration of concentration of parts and organs. This is shown most forcibly when this animal is compared with the lobster. Here the body is short, broad, and flat. The abdomen is reduced to a thin, small, often colorless, and altogether insignificant part of the body, consisting of a limited number of segments and usually hidden away under the cephalothorax. Its appendages are likewise limited in number and are used almost wholly for carrying the eggs. The terminal pair of swimmerets has disappeared and the telson is scarcely more than a vestige of its former self. The reduction of the abdomen is suggestive of the cause that has produced it; *viz.*, the change of habit from a swimming to a walking type of animal. The effects of this habit are still further illustrated by the shape of the cephalothorax and the structure of the well developed walking-legs.

All the appendages of the cephalothorax — the four

pairs of walking-legs, one pair of arms, six pairs of mouth parts, two pairs of antennae, and one pair of eye-stalks — although the same in number as in the lobster, are crowded together. The maxillipeds have lost their foot-like appearance, but are distinctly mouth organs, the third pair being folded like a lid over the other pairs.

The internal structure as well as the external parts reveal remarkable concentration. The internal skeletal portions of the cephalothoracic segments are consolidated (No. 866, vertical section), while the carapace, extending backward on the dorsal side, covers them completely from view. The nervous system, especially, is consolidated in the cephalothorax in a most surprising manner. No. 867 exhibits the great nerve mass in the center of this region with the nerves radiating from it to the different parts of the body. The stomach and intestine belonging to the digestive system are well seen in No. 868.

We have already seen that the Crustacea offer extremely interesting modifications of structure brought about by the varied habits of the animals. There still remain in the Synoptic Collection numerous examples of Brachyura which have been chosen to illustrate more fully the instructive adaptations of this group.

*Callinectes hastatus* Ord, the "edible," "blue," or "soft-shelled" crab (No. 869; a, male; b, female) can swim rapidly, and for this purpose the last pair of legs is converted into a pair of flattened paddles. These are such strong organs that they are able to propel the body forward in spite of its unwieldy proportions.

The abdomen of the male tapers abruptly to a mere vestige of its former condition and lies locked by two teeth into a deep groove in the ventral side of the cephalothorax. The abdomen of the female, on the other hand, is broad and adapted for carrying the eggs. The sharply notched carapace and the spiked arms of this genus offer a strong defence against its enemies.

*Eriphia gonagra* M. Edw. (No. 870), has the outer side of its arms and the forward part of the cephalothorax thickly studded with knobs, while the inner and ventral portions of the arms are smooth. The eyes in this genus are wide apart and the front of the cephalothorax is broad, while the region as a whole is quadrilateral. No. 870 b, c, represent the male and female. The most marked difference between the two is in the abdomen, that of the male (b) being small and narrow, while that of the female (c) is broad and fringed with hairs for the purpose of carrying the eggs.

*Calappa granulata* Fabr. (No. 871), has a convex triangular carapace with its greatest breadth at the posterior part. It is light in color with a luster as if polished. The abdomen is very narrow and in a dorsal view wholly concealed by the cephalothorax and carapace which also cover the largest sections of the legs. The claws are unique organs; they are flattened vertically and the immovable section of the claw rises higher even than the cephalothorax.

*Corystes dentatus* Fabr. (No. 872), is one of those crabs that have a cephalothorax longer than broad. It is found, according to Bell,<sup>1</sup> in rather deep water and has the habit of burying itself in the sand with the exception of the tips of the antennae. It is evident that a long, pointed, more or less tubular cephalothorax is more convenient for a burrowing animal than one that is broad, flat, and truncated at the forward end. The body is light colored, and the long, slender arms extend forward rather than sideways.

*Cardiosoma guanhumii* Latr. (No. 873), has a hard, tough, dark brown shell covering a body of unusual thickness, and also its prodigious right arm which in the male is out of all proportion to the rest of the appendages. The claw is provided with two blunt, knob-like teeth placed

<sup>1</sup> Brit. Stalk-eyed Crustacea, 1853, p. 161.

opposite each other; the other teeth are minute and can be of little use. The eye-stalks are long and prominent and when the animal is alarmed it withdraws them into deep sockets.

*Pseudothelphusa dentata* Latr. (No. 874), looks brown and hardy as if it were accustomed to weathering storms. The cephalothorax is nearly triangular in form, with a broad, straight front, tapering posteriorly towards the abdomen. The first segment of this region is narrow and is flanked on either side by the basal joint of the fifth pair of legs, but the remaining segments in the female broaden out for use in the breeding season. The arms are formidable looking organs and in this case the left arm is larger than the right. The abdomen in the walking crabs is bent under the cephalothorax, as we have already seen, and therefore cannot be used as a locomotor organ. It is, in fact, of little use excepting in the female, where it serves as a cover for the eggs which are fastened to its appendages. We should expect, therefore, to find this part in the female much more developed than in the male, and this is the case, as shown by *Grapsus maculatus* Catesby (No. 875).

The cephalothorax of this crab is unusually flattened; it approaches a circular form excepting in front where it is truncated. All the parts are clearly seen in No. 876, which is a dissection to show the exoskeleton. The seven segments of the abdomen are unusually large and the four pairs of hairy appendages are of considerable size. In this crab the three hinder pairs of walking-legs are the largest, while the second pair is comparatively small and the arms are short and stout. The six pairs of mouth parts are similar to those of most crabs, but the antennae are extremely minute and the eye-stalks are short. The sternal portion of the cephalothorax with the genital openings on the third segment are seen in the preparation. The front portion of this region of the body bends vertically downward, giving the truncated appear-

ance to the otherwise circular outline, as already pointed out.

The carapace sometimes becomes ornamented with spines, as seen in *Pericera cornuta* M. Edw. (No. 877). Two long divergent spines extend forward, while the next longer pair protect the closed tubes for the eye-stalks. The walking-legs (not seen in the specimen) are free from spines.<sup>1</sup>

The spider crab, *Metoporphapis calcarata* Stimp. (No. 878), resembles a spider in having a small cephalothorax and extremely long legs. The former appears to have been pushed upward in front, so that the slender, sharp rostrum, instead of extending forward as in most Crustacea, points almost vertically upward. The posterior part of the cephalothorax also appears to have been crowded upward and forward with the result of bringing the last or fourth pair of legs very nearly over the third pair. In the process the carapace has been shortened, so that the last segment of the thorax is exposed. The arms with their claws are slender and extend forward. The rostrum and the large spikes of the legs are tipped with two tiny spines.

A relative of the spider crab is *Dorippe lanata* Bosc. (No. 879). In this case the hind pair of walking-legs are pushed up on the back and being of no use for locomotion in this position they have become vestigial. The third pair of legs are undergoing the same process, being much smaller and shorter than the first and second pairs. The latter are long and spider-like. The claws are little organs and their position indicates that they offer efficient aid to the mouth parts.

One species of *Dorippe* (*D. facchino*) is of especial interest, since it is never found without a sea-anemone (*Cancerisocia expansa* St.) on its back. This is an admirable illustration of commensalism, since neither animal is ever found excepting in each other's company.

<sup>1</sup> Miers, Journ. Linn. Soc. London, XIV, 1879, p. 664.



Ixa (No. 880) is protected by a sharp pointed spike which extends outward on either side of the cephalothorax. The arms are flattened vertically so that the movable jaw of each claw moves up and down instead of horizontally. These organs when at rest are folded over the front of the ventral side of the carapace and have the same knobs and markings, as seen in No. 870.

*Maia squinado* Latr. (No. 881), has a spiny and hairy cephalothorax that is pointed in front and extremely narrow behind where it passes into the flat and spineless but hairy abdomen. The arms in *Maia* are surprisingly small and weak, while the claws are almost wholly free from spikes and hairs, although the walking-legs are all hairy. According to Leach, *Maia* is extremely common in deep water and is called by the fishermen the thorn-back. This same author states that the young often approach the shore.

Belonging to the same family of spider crabs as *Maia* is *Hyas araneus* Leach (No. 882), which has a carapace without spines and the four pairs of walking-legs well developed.

The reduction of the walking-legs is carried still further in *Lambrus* (No. 883). Although most of these organs are wanting in the specimen, yet enough of one leg is left on the right side to show how short, small, and smooth they have become. The arms, on the other hand, are more than three times the breadth of the cephalothorax, and are provided with spines from one end to the other,

Another peculiarly modified form is *Cryptopodia fornicata* M. Edw. (No. 884), in which nothing but the carapace, arms, and small, partly hidden eyes are to be seen in a dorsal view. The walking-legs are wholly concealed by the carapace that is greatly extended laterally. The eyes are protected by the flattened rostrum which has a row of tiny dots along its edge.

The fiddler crab, *Gelasimus vocator* Martens (No. 885), is a small crab with a quadrangular cephalothorax and in

the female (No. 885, c, d) a broad rounded abdomen (c). The arms in this sex are similar; both are small with small claws (c, d). The males (No. 885, a, b, e, f), however, have one arm much larger than the other, while the claw is greatly developed. This arm may be on the right side (b) or on the left (a, e, f). It is carried across the front of the body in a somewhat similar position to that of the arm of a fiddler, hence the name of fiddler crab. The movable jaw of the big claw in (f) has apparently been broken off and another piece has grown out and beyond the immovable jaw. These crabs are fighters and often an arm is lost in the fray. They walk and run sideways, but they spend much of their time in burrows which they make by removing the sand and carrying it out of the opening with the three anterior legs on the rear side, while they climb out of the burrow by the legs of the side in front. This front side may be either the right or the left side of the crab, but in the male it is usually the side with the big claw.

*Gonoplax rhomboides* Desm. (No. 886), like *Gelasimus* has a four-sided cephalothorax with the greatest breadth in front. The stalked eyes extend out laterally nearly to the edge of the carapace. The arms are long, slender organs, as is the case with some burrowers, *Gonoplax* having the habit of excavating burrows in the hardened clay which are open at either end.

It has been shown that the Crustacea offer numerous and remarkable examples of adaptation of structure to habit. They are also instructive in showing how a swimming type of animal may be converted into a walking type. In this process the law of cephalization or head-development operates, and the organs, especially the nerves and ganglia, are concentrated in the anterior part of the body. They possess many characters in common with the next group, the Arachnozoa.

## ARACHNOZOA.

## Section 14 (in part).

*Trilobita.* The trilobites and the king or horseshoe crabs with their allies, the Arachnida, form a group intermediate between the Crustacea and Myriopoda. Trilobites are primitive in structure and offer good illustrations of generalized segmented animals bearing jointed appendages. They also constitute one of the few groups which well illustrate a natural classification. As Beecher<sup>1</sup> has pointed out, the principles of such a classification can be best applied in a group of animals which has a geological history more or less complete, and which is not wholly parasitic or greatly reduced.

The trilobites have a long geological history covering the time from the pre-Cambrian to the Permian. Their structure is generalized and quite uniform, and no sessile, stalked, parasitic, fresh-water, or land species is known. We are therefore dealing with primitive, free-swimming, marine forms.

The stage in trilobites corresponding to the protoconch of Cephalopods and the protegulum of Brachiopods is known as the protaspis (Pl. 887, fig. I, *Sao hirsuta* Barande). At this time the trilobite consists almost wholly of the head region or cephalon, covered by a dorsal shield and with a central axis clearly defined. The abdominal segments — which consolidated are called the caudal shield or pygidium — are now only indistinctly outlined. The free cheeks are situated on the ventral side and therefore cannot be seen in a dorsal view; only the eye-lines which in older stages extend from the central axis to the eyes are now visible from above (see fig. 1).

<sup>1</sup> Amer. Journ. Sci., (4), III, March, 1897, pp. 97, 98.

In an older protaspis (fig. 2,  $\times 30$ ) the central axis is segmented; the pygidium has developed, and is distinctly segmented. The free cheeks, though narrow, are at the margin so that they can be seen in a dorsal view (fig. 2). In a still older protaspis (fig. 3,  $\times 30$ ) the pygidium is complete but the thoracic segments are not yet formed. When the protaspis stage has passed into the nepionic stage the eyes and free cheeks have migrated to the dorsal side of the cephalon (fig. 4, cephalon, pygidium not drawn. The shaded parts are the free cheeks; the crescent eyes are seen at the ends of the eye-lines).

The thoracic segments form between the cephalon and pygidium, as seen in the adult (fig. 6,  $\times \frac{1}{2}$ ). They are freely movable, while those of the caudal shield are consolidated. The free cheeks become larger and the eyes are farther from the margin (fig. 5). The central portion of the head region, or in other words, the forward part of the axis, is known as the glabella, and the fixed cheeks are situated between this part and the free cheeks. Other characters of the adult trilobite are better seen in *Triarthrus*, the next genus to be described.

The protaspis of *Triarthrus* differs somewhat from that of *Sao*, since the central axis of the cephalon does not extend to the anterior edge (Pl. 888, fig. 1), and the eye-lines run from the first segment to the margin. A restoration of the ventral side of the protaspis at this time is represented in fig. 2. Since the head region has five segments it is inferred that it has as many pairs of appendages, and that the pygidium has two pairs for the same reason. The first pair of appendages are unbranched and are probably sense organs, but the remaining pairs are two-branched and adapted for swimming. The segments of the pygidium increase in number, as seen in fig. 3.

The adult (No. 889; Nos. 890, 891, models; also Pl. 888, fig. 4) has a small cephalon, while the thoracic and abdominal regions are divided into distinct segments (No.

890, dorsal side). The body is also divided longitudinally into three lobes—central axis with pleurae on either side—and hence the name of trilobite.

The cephalon is provided with compound unstalked eyes. These eyes have migrated, as we have already said, from the ventral side over the margin and are now on the inner side of the free cheeks some distance from the margin. Each segment bears a pair of appendages, most of which are similar in structure and adapted for swimming or for crawling on the sea bottom.

In front a pair of long, jointed antennae have been discovered. These are clearly seen extending forward in No. 889, a specimen taken from the lower Silurian formation.

A deep groove runs through the middle of the ventral side of *Triarthrus becki* (No. 891), and the mouth parts and long, jointed feet fastened to the axis conceal the trilobed character of the body. These feet are made up of a stem and two branches, one of which is adapted for swimming, having long hairs, while the other is fitted for crawling. The appendages of the pygidium are especially fitted for locomotion, having flattened leaf-like sections and very long hairs.

According to Beecher<sup>1</sup> no traces of any special respiratory organs have been found in *Triarthrus* and their existence is doubtful, though the fringes on the locomotor organs may have served as gills, since in many forms the functions of locomotion and respiration were combined.

In some genera of trilobites the central axis is broad, while the cephalon is small and granulated, as seen in *Lichas boltoni* Hall (No. 892). Many of the hairy appendages are well preserved in this fossil, and are seen lying on either side of the large flat body. The glabella has a swollen lobe in front besides lateral lobes, and the eyes are seen near the margin.

<sup>1</sup> Amer. Journ. Sci., (4), I, April, 1896, p. 253.

In the large order with *Triarthrus* and *Lichas*, is found *Isotelus gigas* DeKay (No. 893). This genus exhibits the three regions of the body very distinctly. The cephalon and caudal shield are smooth and unornamented, showing only slight evidence of segmentation. The eight thoracic segments, on the other hand, are distinct. The central axis is unusually broad in this genus and the glabella is not lobed. Close to the glabella, on either side, the eyes stand out prominently (No. 893). These trilobites had the habit of doubling upon themselves (No. 894), probably for safety. If this specimen were turned over, the posterior part of the dorsal side would be seen as represented by the figure (Pl. 895). When doubled up in this way the ventral side of the animal is completely hidden.

In the most specialized order, as given by Beecher, we have *Calymene* (No. 896) and *Dalmanites* (No. 897).

The body in *Calymene* is more or less ornamented. The thoracic region is the longest, consisting of thirteen segments, while the caudal shield is tapering and bends downward at nearly right angles to the body. The glabella is deeply grooved (No. 896) and its lobes are sometimes mistaken for eyes. The latter organs are on the free cheeks and are comparatively small.

The body of *Dalmanites* (No. 897, *D. limulurus* Hall) extends backward in a long spine (not shown in the specimen). The dorsal shield is also carried back on each side as a sharp spine. The eyes in this genus are generally large and are always faceted. The free cheeks on which they are borne unite in front, making a complete segment which Beecher regards as the ocular segment.

*Merostomata*. The horseshoe or king crab, *Limulus polyphemus* Latr. (No. 898; Pl. 899; Nos. 900-903), is the only representative of the *Merostomata* that is living at the present time. In its development it passes through a trilobite stage. This is seen in No. 898 and in Pl. 899, figs. 1-3. The dorsal view of the embryo just

before hatching (fig. 1) shows the anterior region (which in this case is the cephalothorax) and the three-lobed abdomen. The anterior segments of the abdomen at this stage are separate, and the posterior part has segments that are distinctly seen. The ventral view of the same embryo (fig. 2) exhibits the six pairs of appendages attached to the cephalothorax (also seen in fig. 3, side view) and two pairs of leaf-like organs to the abdomen (fig. 2).

The adult *Limulus* (No. 900, A, dorsal side; B, ventral side) is protected by a chitinous exoskeleton, the parts of which have been separated in the preparation (C). The cephalothoracic region is horseshoe-shaped, while the abdomen lies behind and extends backward into a long, sharp, movable spine. A flexible membrane at the junction of the cephalothorax with the abdomen enables the animal to bend its body. Traces of segmentation are seen on the dorsal side of the cephalothorax (No. 900, A) and more plainly on the abdomen, where seven segments can be made out in part. The consolidated portion behind these segments is supposed to consist of five segments soldered together so that even their sutures are lost.

*Limulus* has a pair of single eyes situated one on either side of the anterior median spine. The compound eyes are aggregations of single eyes and quite different from the more specialized compound eyes of Crustacea and insects. They are situated far back on the cephalothorax and are widely separated.

The cephalothorax bears six pairs of appendages and the short metastoma or under lip situated back of the mouth (No. 900, C). The first pair of appendages are in front of the mouth and bend backward over the opening. The succeeding five pairs are adapted for walking and seizing food. All excepting the sixth pair, which is used in pushing and in propping up the body, terminate in a claw, and their inner section carries a leaf-like part thickly covered with hair.

The spines on the sides of the abdomen differ from those on other parts of the body by being movable. The abdomen is provided with a so called operculum which consists of a pair of appendages soldered together and of five pairs of thin plate-like swimmerets (No. 900, C) chiefly used as respiratory organs. On the under side of these plates are hundreds of leaves which are supplied with blood vessels.

The tubular heart with the larger blood vessels is seen in the preparation (No. 901). The upper portion of the exoskeleton has been cut away and the circulatory organs distended with wax. In No. 902 the arteries which arise from the anterior end of the heart are exposed. These unite to form the sternal artery. The latter is seen in the preparation No. 903 with the branches that run to the limbs.

Allied to the Merostoma on the one hand and to the Arachnida on the other are the Eurypterids, of which *Pterygotus bilobus* Salt. (No. 904) is a representative. The body is long and distinctly segmented, excepting the forward part which is covered by the small, short carapace.

The first pair of appendages are in front of the mouth, as in the trilobites, and are provided with claws. These are followed by several pairs which were used for catching food and for locomotion, while the largest pair, which extend outward on either side like wings, were powerful swimming organs.

#### ARACHNIDA.

The resemblances between *Limulus* and the scorpion of the Arachnida are shown in the preparations (Nos. 905, 906). The cephalothorax of both animals is probably made of six segments, while there are twelve in the abdomen.



The single eyes are in the anterior part of the cephalothorax, but in the scorpion there are three pairs on the anterior edge and one pair situated farther back.

The number of appendages attached to the cephalothorax and abdomen is the same (Nos. 905, 906). These consist of a pair of mandibles, or chelae as they are called in the scorpion; a pair of maxillae or pedipalpi, provided in the scorpion with nippers; and four pairs of similar walking-legs (in the preparation one leg is wanting). The first pair of abdominal appendages are represented in both animals by the operculum which conceals the median genital opening. The second pair have become peculiarly modified in the scorpion to form comb-like organs (see No. 906) which are probably tactile in function (Shipley). The four following abdominal segments of the scorpion have slit-like openings or spiracles which lead into sacs containing the breathing organs or lung-books. There are four pairs of these internal organs (No. 906), each consisting of hundreds of leaves. The embryo scorpion has external appendages on these segments but in the process of development they are replaced by the lung sacs. The latter organs therefore correspond to the last four pairs of external branchiae of *Limulus*.

The terminal, postanal section of the scorpion is provided with two poison glands, and the poison is discharged through the opening at the end of the sharp, pointed spine which is in reality the poison fang.

The spiders are the most specialized of the Arachnida. This specialization is shown most strikingly in the adult condition, while the embryo spider exhibits certain characters possessed by the scorpions and probably by the earliest ancestors of the group. The adult is without even vestiges of abdominal legs, but the embryo has them clearly marked (Pl. 907, fig. 1, *Clubione* coiled, and fig. 2, the same unrolled) as six pairs of bud-like projections. The four pairs of cephalothoracic feet and the two pairs

of mouth parts are indicated at this stage by larger buds (figs. 1, 2). The latter continue to grow, while the abdominal feet are soon lost.

Comparatively speaking, the order of Arachnida does not exhibit those marked variations of structure which are seen in most orders. While, however, the general features remain essentially the same, the details vary according to the habits of the different families. One of the oldest fossil spiders, *Arthrolycosa antiqua* Harger (Pl. 908), while possessing the form and the appendages of most Arachnida, yet apparently has certain other structural features which ally it with the more generalized spiders of the present day, such as *Eurypelma* (= *Mygale*) (No. 909, ♀ ; No. 910, ♂).

The position and character of the mandibles in this ancient spider (Pl. 908) seem to indicate that these organs moved vertically like the mandibles of the hairy *Eurypelma*. The four pairs of walking-feet are also similar to those of *Eurypelma*, and altogether it is most probable that both genera belong to the same suborder, the *Tetrapneumones*, which has four air sacs like the scorpions and only four spinnerets, two of which are long and bent up behind the abdomen. These organs are not so useful in these hairy spiders as in some of the more specialized Arachnida, since they do not spin elaborate webs for catching their prey, but live in nests made in the ground. One genus (*Cteniza*) of this group makes the ingenious trap-door nest (No. 911). These nests are usually constructed in the moist earth which afterwards hardens; they are lined with soft silk from the spinnerets, and the door is skillfully hinged, fitting snugly into the opening. By means of the claws on the feet or the fangs of the mandibles<sup>1</sup> the trap-door (see No. 911) is raised and the spider backs down the tube, the door clos-

<sup>1</sup> McCook says "apparently the fangs." Amer. Spiders and their Spinning-work, III, 1893, p. 30.

ing upon her. When within the nest the occupant is safe, for the external appearance of the door is like the surrounding surface. "If the bank is bare," says McCook, "the top of the door is also bare; if the bank is covered with lichens the spider cuts a crop of minute lichens and glues them with nice judgment to the outside of her door, thus disguising the entrance."

It is an interesting fact that the habit of nest-building has become so strongly fixed in the organization of the adult that it is inherited at an extremely early age by the offspring. "That so young and weak a creature," says McCook, "should be able to excavate a tube in the earth many times its own length and know how to make a perfect miniature of the nests of its parents, seems to be a fact which has scarcely a parallel in nature."<sup>1</sup>

The difference in the sexes is not so marked in these more generalized spiders (compare No. 909, ♀, with No. 910, ♂) as in the more specialized forms (see Nos. 913, 915, 916, 919, 921, 922), in which the male is extremely reduced in size.

The brilliantly colored,\*unnamed spider (No. 912) is allied to *Eurypelma*. Its abdomen is covered with a thick coating of hair and two long, light colored spinnerets extend outward while the other pair is short.

Among the spinners the tube-weavers are represented in the Collection by the common grass spider, *Agalena naevia* Walck. (No. 913, ♀, ♂), and the orb-weavers by five genera of the Epeiridae: *Nephila*, *Epeira*, *Argiope*, *Mahadeva*, and *Acrosoma*.

It is the grass species, *Agalena*, that makes the horizontal webs (Pl. 914) on grass that are brought into view by the sparkling dew of the early summer mornings, but which in reality are on the grass all the time, often remaining for months in favorable localities. Pl. 914 shows the tube at one side of the web where the spider

<sup>1</sup> *Loc. cit.*, II, 1890, p. 251.

stays and from which the forward part of its body is put out. The web is so close and tight that according to Emerton<sup>1</sup> "one can hear the footsteps of the spider as she runs about on it."

When the web is finished she waits in the tube until an insect is caught in the snare when she runs out, catches her prey, and retires into the tube to eat it.

Just as the young *Cteniza* knows how to construct its trap-door nest, so the young *Agalena* possesses a knowledge of the art of web-making inherited from its ancestors near and remote.

*Nephila* (Pl. 915, *N. plumipes* Koch) differs from the other orb-weavers in having an abdomen much longer than the cephalothorax. In life this spider is brilliantly colored and provided with hairs of a silvery luster. The difference between the sexes, which is generally great, is seen in this genus, the male (fig. 2) being about a tenth as large as the female (fig. 1).

The common spider, *Epeira sclopetaria* Clerck (= *E. vulgaris* Hentz), (No. 916, ♀, ♂; Pl. 917, figs. 1, 2) carries the art of web-making to great perfection. It selects a window-frame, fence, or some other favorable locality and spins a line across the space where the future web is to be. Then it spins radial threads as seen in Pl. 918 from the center to certain fixed points on the circumference. When this is done it makes a spiral scaffolding from the center to the outside, then retracing its steps, it spins a closer spiral of adhesive threads (see Pl. 918) behind it while it tears down the scaffolding in front of it. On approaching the center it allows the scaffolding of non-adhesive threads to remain,<sup>2</sup> evidently because it is here at the center that the spider stays much of the time. When the prey is caught in the web the spider

<sup>1</sup> The Structure and Habits of Spiders, 1878, p. 55.

<sup>2</sup> Campbell, Trans. Hertfordshire Nat. Hist. Soc., I, part 1, 1880, p. 44.

runs down the radial non-adhesive threads to get it, or when alarmed it hurries down a special thread, made for the purpose, to its nest (in the upper right hand corner of Pl. 918.)

The characters of this genus are typical. As in most spiders, the small, flattened cephalothorax is connected with the large, plump abdomen by an extremely narrow waist (Pl. 917, fig. 1; fig. 2, *a*). The eyes in all Arachnida are single, and in this species there are eight (fig. 1) of which six are figured near the front edge of the cephalothorax. The Peckhams<sup>1</sup> have shown that different species of spiders can see from one or two inches to twelve inches, and in the opinion of these investigators they have the power of distinguishing colors.

*Epeira*, like all spiders, has no antennae, but according to Emerton, both the palpi and first pair of legs at times perform the function of these organs. The mandibles are strong, black organs (fig. 2, *d*) which move laterally and are provided with sharp fangs through which the poison flows. The only other mouth parts are the two maxillae (fig. 2, *e*) which bear the palpi that are enlarged in the male (No. 916, specimen on the right) and used as organs of copulation.

The long seven-jointed legs (Pl. 917, fig. 2, *b*) are provided with claws that are admirably adapted for walking on a web.

The abdomen bears three pairs of spinnerets (fig. 2, *s*) which represent as many pairs of legs. The third pair are short and not distinctly seen until the other two pairs are separated. Each of these spinnerets bears many minute horny tubes from which the jets of liquid matter issue, almost immediately solidifying, while the feet of the spider unite the strands into a cord of cobweb. The anus (fig. 2, *u*) is situated a little behind the

<sup>1</sup>The Sense of Sight in Spiders, Trans. Wisconsin Acad. Sci. Arts and Letters, X, 1894, p. 249.

posterior pair of spinnerets. The genital opening (fig. 2, *j*) is at the anterior end of the abdomen, and on either side of this opening there is a horny patch of skin which marks the position of the two air-sacs or lungs (fig. 2, *h*). Besides these lungs the spider is provided with air-tubes or tracheae opening in a single spiracle, just in front of the spinnerets (fig. 2, *k*).

One of our largest spiders is the brightly colored *Argiope cophinaria* Walck. (= *Epeira riparia* Hentz) (No. 919, ♀, ♂), which is abundant in certain places along our coast, no less than three hundred and forty having been collected in an hour at Beachmont, Massachusetts.

This spider hangs out from the middle of its web and being brightly colored is a conspicuous object; for this reason it would seem that it would fall an easy prey to its enemies. It has, however, protected itself in a most ingenious way. On either side or in front of its web (Pl. 920) it spins many irregular threads. The spider has such a delicate sense of touch that if one but lightly place his finger on a thread, "she falls like a shot to the ground, where with her back down, and her legs drawn in she is difficult to find, unless you have followed the drop with your eye. Or approach the web without touching it; your shadow, the sound of your footstep, or perhaps the vibration of the ground warns her; still, the danger does not seem imminent; she has time to make use of another power — she will render herself invisible. The web begins to sway backward and forward; the rapidity of the motion increases; the outlines become indistinct, and within a few seconds of the first movement, spider, web and all have vanished from sight!"<sup>1</sup>

Another species of *Argiope* (No. 921, *A. argyraspides* Walck., ♀, ♂) from Long Island in Casco Bay, Maine, is conspicuous for its size, light color, and banded legs.

<sup>1</sup> Peckham, Occasional Papers, Nat. Hist. Soc. Wisconsin, I, 1898, pp. 72, 73.

Peculiar modifications in the shape of the body are seen in *Mahadeva verrucosa* Hentz (No. 922, ♀, ♂; Pl. 923, fig. 1, ♀; fig. 2, ♂). The abdomen is triangular and nearly as wide in front as the body is long. The male (No. 922, specimen on the right; Pl. 923, fig. 2) has extremely long fore legs, while the second pair are provided with remarkable clasping spines.

Acrosoma (No. 924, *A. gracile* Walck., dorsal and side views; also Pl. 925, figs. 1-4) has a very different form from the others already described. The cephalothorax of the female (No. 924; Pl. 925, fig. 1, upper side) is small, glossy, and dark colored, while the abdomen is broad at the posterior end and provided with spikes on each side (fig. 1; fig. 2, lower side,  $\times 4$ ). It is flattened above and is light colored (fig. 1), while the ventral side is darker colored and the spinnerets extend forward in a conical peak to the middle of the abdomen (fig. 1; fig. 3, side view of the same,  $\times 4$ ), giving a most peculiar appearance to the animal. The male (fig. 4,  $\times 4$ ) is very much smaller than the female (fig. 2,  $\times 4$ ) and is distinguished by the enlarged palpal organs.

Among the more differentiated spiders are the runners like the Lycosidae and the leapers or Attidae. They have a well developed cephalothorax and keen organs of sense. According to the observations of the Peckhams,<sup>1</sup> the sense of sight is especially strong in these families.

The runners, like *Lycosa* (No. 926) have long hind legs, enabling their possessors to run swiftly while catching their prey. The leapers, like *Phidippus galathea* Walck., (= *Attus audax* Hentz) (No. 927), have short legs, the first pair being the stoutest. The Lycosidae have three pairs of spinnerets, like the orb-weavers. Though they do not spin webs for catching prey, they construct homes for themselves in the earth, line them with silk, and over them erect a chimney.

<sup>1</sup>The Sense of Sight in Spiders, Trans. Wisconsin Acad. Sci., Arts and Letters, X, 1894.

These spiders, notably the Lycosidae, take especial care of their young. Not only are the eggs protected by a cocoon, as in most spiders, but the mother *Lycosa* carries the cocoon about with her until the larvae are hatched. Rather than desert it, she will carry or draw it after her, and will defend it to the last (Campbell). McCook<sup>1</sup> records an instance of maternal ingenuity on the part of one species of *Lycosa* (*L. tigrina*) whereby a nest was provided with "a window." The builder had a cocoon attached to her spinnerets and she would put herself in a position to let it lie against the window where it received the warm rays of the sun. For three weeks her daily occupation was holding her egg-sac in the sunlight.

When the eggs hatch, the larvae moult their first skin within the cocoon. Sometimes a second skin is shed before the larvae get on their mother's back. She carries them until the third and sometimes the fourth skin is moulted, when they are able to take care of themselves.

Among the Saltigrades is the interesting *Synageles picata* Hentz (Pl. 928), which strikingly resembles an ant. This is probably a case of protective resemblance. The first pair of legs extend forward and resemble antennae so that only three pairs extend outwardly, although there are four pairs in all, — the characteristic number among spiders.

The Arachnida which are most specialized by the reduction of some parts and the modification of others are the mites. These are represented by several species. Atax (No. 929, *A. bonzi*, fig. 1, ventral view of larva) is a water mite, living in the gills of *Unio*. The larva in this case has the same number of feet as the adult (fig. 2, dorsal view). Tetranychus (No. 930, *T. telarius*; fig. 1, larva; fig. 2, adult) is found on plants in greenhouses, while another genus, Tyroglyphus, includes the cheese and sugar mites. The latter have scissors-like mandibles

<sup>1</sup> Amer. Spiders and their Spinning-work, III, 1893, p. 25.



and the feet are provided with claws and suckers. *Tyroglyphus setiferus* (Pl. 931) has long bristles or setae extending from the body. This figure also exhibits the digestive system, though the anus is not seen, as it is situated ventrally near the posterior end of the body. Four eggs are seen on the ventral side (Pl. 931).

Another more specialized form is the itch mite, *Sarcoptes scabiei* Latr. (Pl. 932, figs. 1-4). The larva (fig. 1) has a nearly circular body in which cephalothorax and abdomen are indistinguishable. It is provided with needle-like mandibles, and, like the larvae of most mites, with three pairs of feet, the two forward pairs having suckers for clinging to the host even at this early age.

The female (fig. 2, upper side; fig. 3, lower side) is essentially like the larva in form, but has four pairs of feet; the two forward pairs having large suckers (figs. 2, 3) and the two hinder pairs long bristles. The male (fig. 4) is smaller than the female, but like her has four pairs of legs; each of the third pair ends in a sucker, and each of the fourth pair in a bristle.

The members of one family of mites, the Ixodidae, are usually called ticks. One of the common examples of this group is the cattle tick, *Boophilus bovis* Riley (Pl. 933, figs. 1-6). The six-footed larva (fig. 1, greatly enlarged) looks like a minute seed, having a body in which the cephalothorax and abdomen are united in one mass. These larvae fasten themselves on cattle and develop into the adult (fig. 2, ♀, natural size when gorged with food; fig. 3, ♀, enlarged; fig. 4, ♂). The mandibles (fig. 5) are fitted for piercing the hide, and as their hooks extend backward they enable the tick to hold tightly while sucking the blood of its victim. The feet of the tick are also adapted for clinging to its host, the hind feet (fig. 6) having two claws and a sucking disc as well as a double spur.

*Boophilus* illustrates the law of acceleration in development since it is able to lay eggs any time after it is half

grown,<sup>1</sup> and a mite, *Sphaerogyna ventricosa*, carries the process still further if it is true that it produces sexually mature animals which are fertilized as soon as born.<sup>2</sup>

It is probable that the parasitic habit of the larva of many species of mites tends to reduce the number of legs in this stage, and this view finds confirmation in the fact that some of the mites of the family Oribatidae which are terrestrial, living in moss, under stones, and the like, are said to have four pairs of legs when hatched.<sup>3</sup>

While most mites have four pairs of legs in the adult stage, it is interesting to note that the gall-making species, *Phytoptus pyri* Scheuten (Pl. 934, fig. 1), which bores into leaves and lives in the cavities or galls that it makes, has only two pairs of these organs.

Among the mites, the sea-spiders or Pycnogonida may be placed, though there is a diversity of opinion among naturalists in regard to their true position. Morgan<sup>4</sup> has shown, however, that the younger stages of the Pycnogonids tend to prove a relationship with the Arachnida. This group is represented in the Collection by Phoxichilidium (No. 935, upper specimens on the tablet) and Pycnogonum (No. 935, lower specimens). In these forms the abdomen is a mere vestige, while the anterior part of the body extends forward into a proboscis which is used for sucking. In reality, there is scarcely any body, the animal being almost wholly made up of legs into which extend, apparently of necessity, some of the internal organs. The more typical members of the group, like *Nymphon stromi* Kröyer (Pl. 936, fig. 1, ♂) have besides the proboscis a pair of clawed appendages (fig. 1) which are considered antennae by Wilson and mandibles by

<sup>1</sup> Bull. 24, Texas Agric. Exper. Sta., 1892, p. 242.

<sup>2</sup> See Shipley, Zool. of the Invert., 1893, p. 420.

<sup>3</sup> See Kingsley, Stand. Nat. Hist., II, 1884, p. 102.

<sup>4</sup> Johns Hopkins Univ., Stud. Biol. Lab., V, no. 1, 1891, pp. 25-33.

others; these are sometimes followed by a pair of palpi (fig. 1). Back of these appendages there is a pair of accessory legs in both the male and the female. Singularly enough the work usually done by the female of carrying and thereby protecting the eggs is performed in Pycnogonids with a single exception by the male (Kingsley).

There are four pairs of walking-legs<sup>1</sup> which are extremely long and hooked at their ends. Phoxichilidium has, in common with Nymphon, the antennae and accessory legs.

Pycnogonum (No. 935; Pl. 936, fig. 2), on the other hand, is without antennae in the adult stage, though the larva possesses them. The legs of the male for carrying the eggs are very small (see Pl. 936, fig. 2), while they are wanting altogether in the female. This genus has much stouter and shorter walking-legs than Nymphon, and they end in larger claws.

The Pycnogonids differ from the spiders in having no tracheae nor lung sacs, respiration being carried on by the general surface of the body.

One of the puzzling forms of animal life is Linguatula (Pl. 937; No. 938). It has been placed among the Worms, the Crustacea, and at present is considered as a near ally of the mites and, therefore, placed among the Arachnida. Its parasitic habit has completely disguised the adult, and were it not for the larva one would be wholly unable to classify it. This larva (Pl. 937, fig. 1, lower side; fig. 2, upper side of *L. proboscidea* Rud.) is an internal parasite. Its body shows no separation into cephalothorax and abdomen. The jaws are horny; the two pairs of jointed legs are similar in shape and are provided with hooks. The larva finds its way to the liver or the lungs of its host — a reptile, the python, in this case — and becomes encysted (fig. 3; fig. 4, taken from the cyst; fig. 5, the same enlarged).

<sup>1</sup> In regard to the different views held concerning the third and seventh pairs of appendages, see Morgan, *loc. cit.*, p. 31.

In the process of growth the animal elongates (No. 938) and the body wall becomes constricted, forming ridges or raised rings throughout nearly its whole length. The mouth parts are represented by two pairs of horny hooks only, on either side of the mouth (No. 938; Pl. 937, fig. 5), and the feet have wholly disappeared. In addition to this loss of external organs, *Linguatula* is without a heart, tracheae, or lung sacs, respiration being effected by the skin.

The life history of *Linguatula proboscidea* Rud., is not so well known as that of *L. taenioides* Rud. The mature female of the latter species is found in the nasal passages of the dog where the eggs are laid. These are expelled by sneezing and are scattered on the grass. The latter is eaten by some herbivorous animal. The embryo develops into the four-footed larva which has mouth parts adapted for boring. By means of these the larva finds its way to the liver or lungs of its host and there becomes encysted. When the herbivorous animal is eaten by a dog the cyst is ruptured and the mature female makes its way to the nasal passages, when the process is repeated.

## MALACOPODA.

### Section 14 (in part).

One of the most interesting animals is *Peripatus* (No. 939, *P. edwardsi* Blanch, or *P. trinidadensis*; Pl. 940, figs. 1-4, *P. capensis*, drawn from life, life size). It is a synthetic form, combining characters of Mollusca, Annelids and Malacopods. It is "an animal of striking beauty," says Adam Sedgwick.<sup>1</sup> "The exquisite sensi-

<sup>1</sup> Stud. Morphological Lab., Univ. Cambridge, IV, part 2, 1888, p. 155.

tiveness and constantly changing form of the antennae, the well-rounded and plump body, the eyes set like small diamonds on the sides of the head, the delicate feet, and, above all, the rich coloring and velvety texture of the skin, combine to give these animals an aspect of quite exceptional beauty. Of all the species which I have seen alive, the most beautiful are the dark green individuals of *Capensis*, and the species which I have called *Balfouri*. These animals, so far as skin is concerned, are not surpassed in the animal kingdom. . . . I shall never forget my astonishment and delight when on tearing away the bark of a rotten tree-stump in the forest on Table Mountain, I first came upon one of these animals in its natural haunts."

*Peripatus* has been considered rare, but, according to J. E. Duerden,<sup>1</sup> it has been found in great numbers on the eastern side of the Island of Jamaica. It is cylindrical in form (No. 939; Pl. 940, fig. 1). The color in *P. capensis* varies from dark green to bluish gray, with a light band at the bases of the legs which extends the whole length of the body (fig. 1). There are no distinct segments but the skin is thrown into numerous fine ridges that bear papillae, each one of which is provided with a tiny spine (fig. 2).

The forward part of the body is not differentiated into a distinct head, although it bears the eyes, the jointed antennae, and the mouth parts (fig. 2). The eyes consist of a group of ocelli and are therefore simple and unstalked. The mouth parts consist of a pair of mandibles or jaws, colored reddish yellow in fig. 2, placed on either side of the opening; each of these jaws has a pair of sickle-shaped claws at its free extremity. On the upper or dorsal side of the mouth is the tongue, seen in fig. 2, extending downward between the jaws. On either side of the mouth, near the base of the antennae, are the oral papillae.

<sup>1</sup> Nature, LXIII, March 7, 1901.

In speaking of segments Mr. Scudder says,<sup>1</sup> "The entire body [of *Peripatus*] is of a leathery texture with no external signs of segments. . . . The same is true when the internal structure of the body is examined, for neither in the disposition of the muscles nor of the tracheal apparatus does it appear that one could judge whether a pair of legs represented one or more segments of the body; even in the nervous system it is only indicated by a small ganglionic swelling next each pair of legs. The tracheae are like extended cutaneous glands, independent of one another and scattered over the body, and the longitudinal muscles show no segmental breaks." This weakness of segmental divisions is evidence of specialization by reduction, and we therefore place *Peripatus* among those forms that have become more or less modified from the ancestral type by the suppression of certain characters, such as distinct segmentation of the body and distinctly jointed legs. We have already pointed out many cases, especially among parasites, where there is a marked weakness in segmentation.

*Peripatus* when disturbed secretes a quantity of slime, the slime glands opening at the end of the oral papillae. The mouth is encircled by a lip which is raised into papillae, and these adhere to the food while the jaws probably tear it in pieces.

The different species of *Peripatus* are determined in part by the number of paired walking-legs, *Peripatus capensis* (Pl. 940, fig. 1; fig. 3, leg enlarged) having seventeen pairs and *Peripatus edwardsi* (No. 939) having from twenty-nine to thirty-four pairs. These legs are similar in function and therefore in structure. They are obscurely jointed;<sup>2</sup> and since *Peripatus* lives in damp

<sup>1</sup> Mem. Boston Soc. Nat. Hist., III, no. 9, 1884, p. 287.

<sup>2</sup> Scudder, Amer. Journ. Sci., (3), XXIV, 1882, p. 166, says, legs "obscurely jointed, the joints being perceptible only at the extreme tip and on the apical half of the inner side."

places, preeminently under the bark of decaying stumps, the legs are soft and fleshy; hence the name of Malacopoda. The leg proper is provided with many rings of papillae and at its lower end are three pads. The foot carries two claws and several papillae (Pl. 940, fig. 3). At the bases of the feet on the ventral surface the paired excretory organs or nephridia open. The presence of these organs in *Peripatus* recalls the similar organs we have already found in Worms.

*Peripatus* breathes by means of tracheae which, however, do not appear until the animal is hatched.<sup>1</sup> The spiracles are scattered irregularly over the body, each spiracle (Pl. 940, fig. 4) leading into a tracheal pit which spreads out into a bundle of tracheal branches (see fig. 4) that never unite.

*Peripatus* is viviparous, the period of gestation covering thirteen months; this being the case, a comparatively small number of individuals is produced and these resemble the parent at birth excepting in color. While the adults of *P. capensis* are of a rich green, the little ones are nearly white with green antennae. According to Steel, the animals cast their skins like many insect larvae, and the cast skins are generally worked over with the jaws and finally swallowed.

The general more or less slug-like appearance and the possession of a nervous system similar to that of *Chiton* caused some naturalists to place *Peripatus* among the Mollusca. Its closer resemblance in form to the Worms, the possession of paired appendages along the whole length of the body, and still more the presence of rows of paired nephridia caused naturalists later to place *Peripatus* in the subkingdom of Vermes.

The discovery of true tracheae and spiracles, the possession of jointed antennae and legs, the existence of appendages modified as jaws, and of certain important

<sup>1</sup> Packard, Text-book of Ent., 1898, p. 15.

resemblances in internal structure, place *Peripatus* to-day among the articulated animals with jointed appendages.

Its worm-like affinities together with its scattered spiracles and the single pair of jaws seem to take *Peripatus* from the Myriapods—probably its nearest allies—and to place it in a class by itself.

It may be that *Peripatus* is the survivor of a primitive type which, however, has lost some of its primitive characters, and become more or less specialized by the suppression of parts. The loss of segmentation and the obscure jointing of the legs would point to this conclusion, while the power possessed by *Peripatus* of bringing forth its young alive is an indication of specialization of structure. The retention of paired nephridia suggests its possible remote origin from some worm-like form, while the possession of tracheae proves that it is far removed from the Worms and is doubtless near the Myriapods and Insects.

#### MYRIAPODA.

##### Section 14 (in part).

“The relations of ancient to modern forms of life,” says Scudder,<sup>1</sup> “prove far more important and interesting in the myriopoda than in either the arachnida or the hexapoda.”

This eminent authority points out that the embryology of living forms of Myriapods is inadequate to explain the origin of the complex structure of the segments, and that we must look to the palaeontologic record for light on this

<sup>1</sup>The Geological History of Myriopods and Arachnids, Psyche, IV, Jan.-March, 1885, p. 245; see also Bull. U. S. Geol. Surv., no. 31, 1886.



puzzling problem. Here we find forms in which simple distinct body segments without any trace of subdivisions follow one another, each segment bearing one pair of jointed appendages (Pl. 941, fig. 1, *Palaeocampa anthrax* Meek and Worthen). The boundaries of these segments can be determined, as each is made up of a single dorsal and a single ventral plate. The number of segments is small and each segment bears a pair of jointed legs which are similar in structure. On the upper side are tubercles which carry clusters of slender needles (see Pl. 941), probably used as means of defence. The head of *Palaeocampa* is small but distinct and composed apparently of only one segment.

The Chilopoda of to-day probably descended from *Palaeocampa* of forms similar to it, but these Myriapods are more specialized in certain important features than the Diplopoda, another group of living Myriapods, which in all probability descended from Archipolypoda described by Scudder.

It may be that future investigations into the pre-Cambrian or the early Palaeozoic rocks will bring to light the common ancestor of the *Palaeocampa*-like forms, and of the Archipolypoda.

The segments of the Archipolypoda are composed of one dorsal and two ventral plates, but in some of the types the dorsal plate is distinctly seen to be made of two plates, which indicates that one apparent segment is in reality composed of two segments.

The Diplopoda, embracing the Millipeds, of which *Julus* (No. 942) is a good example, have a distinct head and a plump cylindrical body (which is not divided into thoracic and abdominal regions). A dorsal view (No. 942, specimen on the right), exhibits a succession of similar segments of nearly equal size extending from one end of the body to the other, while a side view shows the unusual thickness of the body and the small size and great number of jointed, single-clawed legs fastened near the median line of the ventral surface.

The preparation of *Julus* (No. 942, specimen on the left), gives the ventral view and exhibits the segments separated from one another. Most of these segments have two ventral plates instead of one apparent plate as in the dorsal view. These ventral plates are extremely small and so narrow that the legs which are fastened to them are crowded closely together.

It is seen that the three complete anterior segments (which are probably thoracic) carry one pair of legs, while the remaining segments which are abdominal, excepting the first (the appendages of which are modified for reproductive purposes), and last, carry two pairs of these appendages.

The light thrown on the structure of Myriapods by *Palaeocampa* and *Archipolypoda* enables one to see that each apparent abdominal segment of the *Diplopoda* is most probably made of two segments, the dorsal plates of which have become fused. Furthermore, the two ventral plates of each thoracic segment have likewise fused into one plate, and at the same time one pair of legs has disappeared. The present condition of these segments is therefore not primitive but rather secondary and specialized.

The head of *Julus* is free, as we have said, but is so bent down as to be concealed under the body in a dorsal view. It bears a cluster of ocelli on each side, one pair of jointed antennae, a labrum or upper lip, a pair of mandibles, and one pair of maxillae. In the preparation the sternal plate of one of the cephalic segments is seen.

The *Julidae* breathe by means of tracheae which do not arise until the animal is hatched (Packard). The openings of spiracles occur on each of the ventral plates. The tracheae are in the form of tufts of tubes which never join.

The *Diplopoda* leave the egg in a very immature condition when only three pairs of legs are formed. These are small, partially developed, and are not fastened to consecutive segments, one segment being skipped.

A metamorphosis is correlated with this immaturity, as we have seen in other groups of the animal kingdom. The larval stage seems to be adaptive and therefore of comparatively little phylogenetic value. In time, the thoracic legs become fully developed and the abdominal legs grow out until finally the adult stage is reached.

The Chilopoda or Centipedes and the like are represented by Scolopendra (No. 943). They have a depressed body consisting of fewer segments than are found in the Diplopoda. Each apparent segment bears one pair of single-clawed legs. These appendages are on the sides so that they are widely separated.

It is probable that each segment in the Chilopods was originally two segments, one of which with its pair of legs became atrophied. This condition is farther removed from the primitive state as seen in Palaeocampa than the condition of the Diplopods, and therefore the Chilopods may be considered the more specialized. There is a difference of opinion in regard to the mouth parts of Chilopods, some maintaining that there are three pairs and others that there are four pairs. The former consider that the first pair of legs are modified into poison fangs, while the latter consider them as mouth organs.

The breathing organs in the Chilopods are more specialized than in the Diplopods. They consist of tubes which unite to form long tracheal trunks that run nearly the whole length of the body. The number of spiracles varies, but they generally open on alternate segments.

The Chilopods do not leave the egg in an immature condition, like the Diplopods, but this is passed within the egg, and the animal when hatched is usually fully formed with all the legs developed. There is accordingly no metamorphosis, the development being accelerated.

## SYMPHYLA.

The Symphyla is represented by the interesting little *Scolopendrella* (Pl. 944, fig 1, enlarged; natural size indicated by vertical line) which Ryder considers may be the last survivor of an ancestral form from which insects have descended. It is a synthetic type, combining characters of Myriopods and Insects, the insectean features predominating.

The body of *Scolopendrella* consists of a limited number of segments which have the appearance of plates on the dorsal side. The head (Pl. 944, fig. 1; fig. 2, ventral side, enlarged) is distinct and movable. Twelve of the segments bear jointed legs that terminate in two claws instead of one, as in the Myriopods.

The antennae (fig. 2) are longer than those of Myriopods and in structure are essentially different. They resemble a series of glass cups strung upon a delicate rod (Wood-Mason). There are a pair of mandibles and two pairs of maxillae, the two parts of the second pair uniting to form a lower lip or labium. The first two pairs of mouth parts are not fastened to the head or skull by a hinge joint as in Myriopods and most insects, but are withdrawn into the head and are buried in the muscles of the mouth, so that only the tips appear outside.<sup>1</sup>

The appendages of the last segment are modified into organs called cerci (fig. 2); at the end of each of these is the opening of the silk glands, the ducts of which can be seen in fig. 2. At the bases of the legs there are movable vestigial ones (fig. 2) which probably represent the second pair of legs similar to those found in *Diplopoda*.

The internal organs are similar to those of insects. A small pair of spiracles are situated in the front of the

<sup>1</sup> Packard, Amer. Nat., XV, 1881, p. 701.

head near the insertion of the antennae, and the tracheae (colored blue in fig. 2) are simple air tubes without spiral threads, which extend only a short distance back into the trunk.

Besides these organs there are nine or ten pairs of ventral sacs or "blood gills" (colored red in fig. 2), which are situated within the body near the vestigial feet but which can be turned outward as seen in fig. 2.

Unfortunately, the embryology of *Scolopendrella* is unknown (Packard, 1898), but it is most probable that the larva has six legs like the Diplopods, and like them develops more legs with growth.

The Symphyla introduces us naturally to the next and last group of invertebrates, the Insecta.



## INSECTA.

## Sections 15 and 16.

## Order 1. — THYSANURA.

No ancestral form of insect has been discovered among the pre-Cambrian or Cambrian rocks so primitive in structure as the living Campodea of the order Thysanura. This genus is therefore one of the best living representatives of that extinct ancestral type that gave rise to the great group of Insecta. The embryology of Campodea exhibits no such vestiges of a more specialized condition as have been seen in many genera, but the characters are primitive and the changes in structure are progressive.

The larva develops in a primitive way without a metamorphosis or marked change of any kind. It sheds its skin only once (quoted by Packard after Grassi) and has no resting period during life. The external appearance of the larva is preserved in the adult, so slight is the specialization attending growth.

The very small adult (Pl. 945, fig. 1, greatly enlarged)<sup>1</sup> has a long, somewhat flattened (Meinert) body divided into segments that are uniform in breadth. A slight differentiation of these segments has brought about a grouping into three regions, which is characteristic of insects, but not found among Myriapods. The anterior region is the head (fig. 1; Pl. 946, fig. 1, seen from below), which is generally considered to be made up of an uncertain number of consolidated segments. According to the

<sup>1</sup> On account of the minute size of many insects, or because they are rare and difficult to obtain it has been necessary to have a large number of drawings made. These drawings as well as nearly all in the Synoptic Collection have been made by Miss L. R. Martin, assistant in the Museum.

observations of Folsom,<sup>1</sup> however, the head of insects is composed of seven segments, each of which, excepting the first (which carries the eyes), bears a pair of appendages. This naturalist discusses the morphology of the biting mouth parts of insects and their nearest allies, the Crustacea, Arachnida, and Myriapoda, upon anatomical and embryological evidence derived from the most primitive insects. The student in search of the natural relationships of animals reads with satisfaction the following: "It seems almost superfluous to insist that highly specialized organs can be but imperfectly understood unless studied in egg and larva as well as imago; that generalized types illuminate specialized forms; and that equivalent groups are linked together through their more generalized members; yet too often these accepted principles are not applied."<sup>2</sup> Folsom finds in *Anurida maritima* Guér., an insect belonging to the Collembola of the primitive order Thysanura, seven cephalic segments. The first or ocular segment carries the compound eyes which this investigator homologizes with the compound eyes of Crustacea. The second segment bears the antennae (Pl. 947, fig. 1, *at*; ventral aspect of a portion of the germ band at stage 1,  $\times 480$ ) homologous with the antennules or first pair of antennae of Crustacea; the third segment a pair of premandibular appendages (fig. 1, *pr'md*) homologous with the second pair of antennae of Crustacea. These mouth parts are rudimentary and are not even seen when the specimen is magnified 150 times (fig. 2). The fourth segment bears the mandibles (fig. 1, *md*) homologous with the same organs in Crustacea; the fifth a pair of superlinguae (fig. 3, *sl*, ventral aspect of cephalic region of germ band at stage 3,  $\times 480$ ) homologous with the first pair of maxillae in Crustacea; and the sixth and seventh segments bear the two pairs of maxillae homol-

<sup>1</sup> Bull. Mus. Comp. Zool., XXXVI, no. 5, 1900.

<sup>2</sup> Folsom, *loc. cit.*, p. 87.



ogous with the second pair of maxillae and the first pair of maxillipeds in Crustacea.

The view that the head is made up of seven segments is strengthened by the fact that seven ganglia are found in the cephalic region of the embryo. Since the pre-mandibular and superlingual appendages are either embryonic or difficult to detect as compared with the mandibles and maxillae, we will consider only these latter organs in this general treatment of insects.

The middle region or thorax of *Campodea* (see Pl. 945, fig. 1) is made of three distinct and movable segments named respectively the prothorax, mesothorax, and metathorax. The posterior region or abdomen is composed of ten segments, likewise distinct and freely movable.

The body is hairy and is without scales or feathers; it extends longitudinally and there is little concentration of parts. The junction of the head with the thorax is a soft unchitinized portion of the body wall which forms a functional neck, while the junction of the thorax with the abdomen is nearly as broad as the body itself, and for this reason the abdomen is said to be sessile.

The head is without eyes according to Westwood, Meinert, Lubbock, and Oudemans, while Nicolet and Grassi state that they are present.<sup>1</sup>

The appendages like the body are primitive in most of their characteristics. The head is provided with a pair of long, hairy antennae (Pl. 945, fig. 1) and with three pairs of distinct mouth parts. These latter organs are the hollow mandibles (Pl. 946, fig. 2, one mandible with the muscles that move it; fig. 3, the tip of the mandible enlarged), first pair of maxillae (fig. 4, showing the inner lobe, (*d*), of the right maxilla, and the outer lobe, (*e*), with its palpus (*f*), of the left maxilla; the lingua,

<sup>1</sup> On this subject see, Viré, *Le Campodea staphylinus* Westwood, et ses variétés cavernicoles; Bull. Mus. d'Hist. Nat. Paris, 1897, no. 3.

hypopharynx, or tongue, (*t*), is seen in the median line, drawn without the supporting chitinous frame-work), and the second pair of maxillae or labium (fig. 1, *l*; palpus of same enlarged in fig. 5).<sup>1</sup> Comparatively speaking, these mouth parts are but slightly differentiated, since Campodea feeds upon soft substances and has no need of hard, specialized mouth organs. They are set in muscles (some of which are seen in Pl. 946, fig. 2) within the cavity of the skull, like those of Scolopendrella, and may be used for either biting or sucking, although they are more allied to the biting type. They are, in fact, generalized structures and are probably similar to those that gave rise to the complicated organs for cutting, piercing, and sucking of the more specialized insects. This view is strengthened by the fact that the mouth parts of Neanura, one of the Thysanura of the suborder Collembola, have become modified into suctorial organs.<sup>2</sup>

The three pairs of legs attached to the thorax (Pl. 945, fig. 1) are well developed and similar in structure, since they are all used in running. They are jointed and provided at their ends with two tiny hooks for taking hold of objects. These legs are the only appendages of the thorax and, furthermore, there are no vestiges or indications of any kind that the Campodea or the Thysanura ever possessed appendages in the form of wings. This is one of the important reasons why the group is entitled to the position of the most primitive order of insects.

According to Uzel the embryonic Campodea has ten distinct abdominal segments of which the first nine are provided with appendages. In the adult each of the first

<sup>1</sup> According to Uzel these are not the labial palpi but the outer lobes of the labium. This author differs from Meinert in his interpretation of the other parts of the second pair of maxillae (see Zool. Anz., XX, 1897, p. 234).

<sup>2</sup> Folsom, The Anatomy and Physiology of the Mouth Parts of the Collembolan, *Orchesella cincta* L.; Bull. Mus. Comp. Zool., XXXV, no. 2, 1899, p. 35.

seven segments of the abdomen has a pair of similar appendages (Pl. 945, fig. 2), while the last segment bears a pair of long appendages called cerci which resemble the antennae in structure.

The most characteristic system of internal organs in insects is the tracheal system, but it is subject to great variation owing to the widely different physical conditions under which insects live. According to Meinert, *Campodea* has three pairs of spiracles, one pair to each thoracic segment, while the abdomen is without spiracles. In *Japyx*, a closely allied genus, the abdomen has seven pairs of these openings. The thoracic spiracles lead into tracheae (colored blue in Pl. 945, fig. 2) which do not unite but simply form six small independent subsystems, three on each side; of these the anterior subsystem gives off branches to the head, and the posterior one to the forward segments of the abdomen (see fig. 2).

Bearing in mind that the general typical features of *Campodea* represent the characters of the archetype of the class *Insecta*, we pass to some of its near allies.

*Lepisma saccharina* Linn., or the "silver witch" (No. 948; Pl. 949,  $\times 4$ , drawn from life), has a more flattened body than *Campodea* and in this particular respect it is probably nearer the ancestral form. Its body is not only provided with hairs like that of *Campodea*, but many hairs have become modified into delicate sculptured scales (No. 950; Pl. 951, fig. 5).

The regions of the body are less uniform in breadth than in *Campodea*, the abdominal segments tapering away from the much broader thorax (see Pl. 949). The head is free and of considerable size.

The eyes of *Lepisma* are compound but they have only twelve facets (Packard), so that they are primitive in structure.

A pair of extremely long antennae (see Pl. 949) are attached to the head and a pair of maxillary palps extend forward. The mouth parts in *Lepisma* are hinged to

the skull by an imperfect articulation and not buried within the cavity of the skull as in Campodea. They consist of a pair of mandibles (Pl. 951, fig. 1) and two pairs of maxillae (figs. 2, 3); the two parts of the second pair are united to form the labium (fig. 3). At the tip of the labial palpi are three sense organs.

The legs are similar in structure and are flattened, especially the large basal sections, which enables this little animal to glide in and out of crevices. Each leg ends in a pair of claws. The forward abdominal appendages of Campodea are replaced in *Lepisma* by clusters of stiff hairs, but the seventh, eighth, and ninth segments have abdominal appendages (Pl. 951, fig. 4), and the extremity of the abdomen is provided with three long hairy bristles and a pair of short curved bristles; hence the name of Thysanura or bristle-tails. In the female there is an ovipositor (fig. 4) composed of four parts.

The tracheal system of *Lepisma* consists of ten pairs of spiracles, and the tracheae are united into one system consisting of two longitudinal trunks and of cross tubes.<sup>1</sup> The tracheae are strengthened by delicate spiral threads (Fernald).

It has been shown that *Lepisma* is more specialized than Campodea in having a scale-protected body, external mouth parts, a well developed ovipositor, and a complete tracheal system.

Campodea and *Lepisma* are representative Thysanuran insects, having the abdominal bristles which give them the name of bristle-tails. In this same order is the suborder Collembola represented by the Poduridae or spring-tails, some of which have at the posterior end of the abdomen a peculiar spring for leaping. This is seen bent under the body in Pl. 952, which is a side view of *Papirius fuscus* Lubbock. In this genus the leaping organ extends far forward and the tips are white. Besides the

<sup>1</sup> Sharp, Cambridge Nat. Hist., V, 1895, p. 186.

spring, many of the Poduridae have a sucker attached to the basal portion of the abdomen (see Pl. 952), by means of which the insect attaches itself. According to Uljanin quoted by Cholodkowsky<sup>1</sup> the springing-fork of the Poduridae arises from two abdominal appendages which are in every respect similar to legs, so that their homology with the thoracic limbs is hardly open to doubt. The ventral tube also develops from two anterior abdominal appendages which are probably homologous with the thoracic legs. The tiny leapers that sometimes blacken large patches of our snow, making it appear as if covered with animated coal dust, are spring-tails (Pl. 953, *Achorutes nivicola* Fitch, possibly unnaturally swollen). It is surprising to watch the leaps of these minute animals, sometimes covering several feet (Comstock) and again jumping many times their height into the air. Although bluish black when full grown, they are white when young.<sup>2</sup>

There are other Poduridae which have a spring in the larval stage but which lose it on reaching maturity. One of the springless forms is *Lipura maritima* Guér. (Pl. 954). This is one of the few insects that adapt themselves, for short periods at least, to salt water. It is found on the surface of tide pools and immersed in the water, but when in this situation it is said to be protected by a layer of air that envelops its body.<sup>3</sup>

We cannot but think that some of the primitive wingless ancestors of insects, which in all probability were essentially like the Thysanura, developed in the course of many generations the wing sacs or pads that finally became efficient organs of flight. It is true, as before stated, that so far winged insects of as primitive a nature as the Thysanura have not been found in a fossil state, but it may be that still older rocks than the Devonian

<sup>1</sup> Ann. and Mag. Nat. Hist., (6), X, 1892, p. 434.

<sup>2</sup> Packard, 5th Ann. Rep. Peabody Acad. Sci., 1872, p. 30.

<sup>3</sup> Cambridge Nat. Hist., V, 1895, p. 195.

will reveal insect forms that are marked by Thysanuran simplicity of structure, and by the possession of one or two pairs of wing sacs. Until there is more light on the subject we may suppose, as Packard<sup>1</sup> points out, that the dorsal parts or nota of the two hinder segments of the thorax grew out laterally in some running or leaping insect, and that these expansions became of use in aiding to support the body in its longer leaps. Then by continual use they would become articulated to the body and, growing larger, would in time develop into permanent flying organs or wings.

Order 2.—EPHEMEROPTERA. (EPHEMERIDA, Comstock.)

One of the earliest winged insects found in America, known as *Xenoneura antiquorum* Scudd., was a synthetic form which possessed affinities with several generalized families, among them the Ephemeridae or mayflies. Although the wings are the only parts of these ancient insects preserved, yet nevertheless they have become trustworthy aids in determining the relationships of the insects once possessing them.

The wing of *Xenoneura* (Pl. 955, a composite drawing from different specimens) exhibits primitive characters and simple venation, indicating slight differentiation of structure.

Another Devonian insect, *Platephemera antiqua* Scudd., was, with little doubt, an ancestor of the present Ephemeridae. The wings (Pl. 956, the dotted lines indicating the probable form of the wing) possess unmistakable resemblances to the same organs of our present mayflies. The drawing is made to show the expanse of the wings, which was probably about 135 mm., proving that this ancient mayfly was much larger than recent species.

<sup>1</sup> 3d Rep. U. S. Ent. Comm., 1880-'82 (publ. 1883), pp. 268-271.

In the Carboniferous rocks of Commentry an insect, *Homaloneura bonneri* Brong., (Pl. 957, a restoration) has been discovered which Brongniart considers an ancestor of our Ephemerae. It has a large, elongated, and plainly segmented body, a sessile abdomen terminated by long caudal setae and two pairs of wings of equal size. Besides these appendages of the mesothorax and metathorax, the prothorax has a pair of scale-like appendages which according to Brongniart may represent prothoracic wings. This investigator suggests that sometime there may be found in the ancient strata an insect with six wings or rather six expansions which served only as parachutes, and that later the expansions of the mesothorax and metathorax developed into useful organs of flight while those of the prothorax were atrophied.

The living Ephemerae in a very early larval stage have an open tracheal system like that of Campodea, with thoracic spiracles.<sup>1</sup> This is one proof of their descent from ancestral forms possessing an open tracheal system. In changing their habitat from land to water they have adapted themselves to their new surroundings, and in so doing have gradually converted the open tracheal system into a closed one. At the same time external gills of varying form and structure have developed. In fact, so many complex modifications have arisen in these insects, in response to the changed environment, that it is difficult to place them among the most generalized orders unless we bear constantly in mind the general features of the group. These are, in the larvae, a long body (Pl. 958, fig. 1, *Chloëon dimidiatum* Lubbock) divided into freely movable regions; a large thorax with slight consolidation of the prothorax, mesothorax, and metathorax; simple antennae; and three pairs of similar legs.

An extremely slow development is often attended with numerous sheddings of the skin, so that no sharp line of demarcation can be drawn between larva and pupa.

<sup>1</sup> Packard, after Dewitz, Text-book of Ent., 1898, p. 460.

In Chloëon as many as twenty moults may take place. Up to the ninth moult there is no indication of wings, according to Lubbock. At the twelfth stage the posterior angles of the mesothorax and metathorax have grown out (fig. 3). The mesothoracic angles grow faster than the metathoracic and cover the latter completely (fig. 4). These figures are interesting as showing the origin of the wing pads of the pupa. When the last skin but one is thrown off, the winged insect (fig. 5) flies away, but still another skin must be shed before full size is attained (fig. 6, *C. dipterum* Lubb.). The last skin is often got rid of while on the wing. We shall see that in most insects this slow process of development is more or less shortened by the law of acceleration. While there is no resting period, there is a metamorphosis which transforms the wingless insect into the winged creature. It is evident that this metamorphosis is more specialized than the primitive development of the Thysanura.

The generalized characters of the adult (Pl. 958, fig. 6; see also No. 959, *Hexagenia bilineata* Say) are a long, unconsolidated body; an abdomen without an ovipositor and with the genital openings paired; a thorax without secondary sutures and with wings that are simple in their venation.

The adaptive and secondary characters, on the other hand, are seen as soon as the young larva develops tracheal gills (Pl. 958, fig. 2; see also figs. 3, 4) on each side of the abdomen. These fit it for an aquatic existence and the larval and pupal life may last three or four years. The long caudal setae also aid as respiratory organs, and the terminal blood vessel in the body is so made as to drive the blood backward into the canals of the setae,<sup>1</sup> where it is purified by the air in the water.

<sup>1</sup>Zimmermann, Zeitschr. f. wiss. Zool., XXXIV, 1880, p. 404. See also Creutzburg, Ann. and Mag. Nat. Hist., (5), XV, 1885, p. 494.



An advanced pupal stage of *Chloëon dipterum* Linn.,<sup>1</sup> is seen in Pl. 960. The wing pad on the left side and the gills on the right side have been cut away. In addition to these gills the pupa has caudal gills which also serve as good swimming organs.

The adult (Pl. 958, fig. 6, *C. dipterum* Lubbock; No. 959) is specialized by reduction, so that the mouth parts are wholly incapable of taking food. The insect in this stage lives only a few hours or at most a few days; hence the name Ephemeroptera (signifying short-lived insect and wing) given to this order. When the function of reproduction is performed the insect dies. The loss of efficient mouth parts is correlated with a loss of the second pair of wings (Pl. 958, figs. 5, 6; No. 959) and with a peculiar modification of the compound eyes. These organs are divided in *Chloëon* so that there appear to be a pair of stalked eyes (which, however, are not united at their bases) and a pair of sessile eyes (fig. 7). Besides these eyes there are three ocelli (fig. 7).

Peculiar modifications of structure are found among the more specialized Ephemeridae. An extreme case of specialization in the pupal stage is seen in *Prosopistoma foliaceum* Fourcroy (Pl. 961, fig. 1,  $\times 12$ ). Here a portion of the mesothorax and metathorax with the anterior wing pads has formed a carapace that covers the dorsal part of the body with the exception of the four posterior abdominal segments and the caudal swimming organs. This carapace conceals from view the respiratory chamber with its five pairs of gills supplied with tracheae. The water passes into the respiratory chamber at two openings, seen on either side in the ventral view (fig. 2, *v*) and flows out at the dorsal opening (fig. 1, *d*). In the ventral view (fig. 2) the last segment with its

<sup>1</sup> *Cloëon dipterum* Linn., a synonym for *Chloëon dipterum* Lubbock; see Eaton, Trans. Linn. Soc. London, (2), Zool., III, 1888, pp. 183, 188.

hairy appendages is drawn completely into the ninth segment of the abdomen.

Specialization by reduction is illustrated in the adult stage by *Caenis* (Pl. 962, *C. macrura*) in which the second pair of wings have disappeared and the insect resembles the two-winged Diptera.

### Order 3. — ODONATA.

These insects, like the Ephemeroptera, have become adapted to aquatic life. There can be little doubt, however, that their ancestors were terrestrial, air-breathing animals with an open tracheal system like that of Campodea.

A dragon-fly, *Palaeophlebia superstes* (Pl. 963, fig. 1, with the wings on one side and with two legs removed) has been discovered in Japan, which possesses, perhaps, more primitive characters than any other member of its order. Unfortunately the larval form is unknown, but judging from the adult, the larva must be more primitive than most young dragon-flies. The broad head, the separated eyes (fig. 2), the nearly equal wings, with their simple venation (fig. 1), are all generalized characters. Although it is true that the larvae of the Odonata do not resemble Campodea so closely as the larvae of the Ephemeridae, nevertheless, the body in the most generalized family, represented by *Calopteryx* (spelled also *Calepteryx*) *virgo* (Pl. 964, fig. 1; No. 965, an allied form, Hetaerina) is long with little concentration of regions and but slight modification of the thoracic segments. Like the young mayfly, the young *Calopteryx* has three caudal appendages (fig. 1) which serve both as locomotor and as respiratory organs.

The second pair of maxillae or labium have become modified into a mask (fig. 2), so called because in the more specialized genera it entirely conceals the mandibles

and first pair of maxillae. It can be thrown out as represented in the figure, and the teeth at the end serve to catch the prey.

According to Packard,<sup>1</sup> it was owing to the fact that the second pair of maxillae were armed with teeth that the name Odonata (from the Greek meaning tooth) was given to this order. Calvert<sup>2</sup> remarks, however, that the name refers "presumably to the toothed mandibles."

The adult has small eyes, comparatively speaking; the labium is reduced in size and the parts are more concentrated than in the larva, although much more loosely connected than in the specialized dragon-flies.

In many ways Agrion (No. 966) resembles Calopteryx. Its young is provided with three caudal gills. The head of the adult is broad with the eyes on the sides, and the labium is short. The wing venation is simple and the flight is not swift. The long slender abdomen is used as a rudder and is sometimes brilliantly colored in both genera.

The most specialized Odonata are represented by Aeschna and Plathemis (= Libellula). Aeschna (Pl. 967; No. 968) is one of our largest dragon-flies. The eyes are separated in the larval and pupal (Pl. 967, *A. grandis* Linn.) stages but meet on top of the head in the adult (No. 968, *A. heros* Fabr.). The wing muscles are strong and the flight is swift, the insect darting like an arrow.

Plathemis is another swift flier. Its eggs, like those of most Odonata (see No. 969), are laid on aquatic plants or dropped in the water. The young (No. 970; Pl. 971, fig. 1) possesses the long unconsolidated body and the similar thoracic segments of the adult Thysanura and the larval Ephemeridae, but in many respects it has become specialized. The labium is modified into a mask (No. 972) that completely covers the other mouth parts. The

<sup>1</sup> Ent. for Beginners, 1889, p. 346.

<sup>2</sup> Trans. Amer. Ent. Soc., Phila., XX, 1893, p. 153.

young *Plathemis*, it may be a larva or a pupa (Pl. 971, fig. 2), looks extremely innocent until a little crustacean or insect passes by, then suddenly the mask is darted out, as seen in No. 972, also Pl. 971, fig. 2, and the prey is secured. The legs of both larva and pupa are extremely long. The rudiments of wings appear after the third or fourth moult<sup>1</sup> and with their development the segments of the thorax become greatly modified.

The larval and pupal *Plathemis* breathes by tracheal gills situated in the rectum at the posterior end of the body. These gills are in the form of lamellae (fig. 3, *Plathemis vulgate*) which are richly supplied with tracheae (fig. 3). Instead of having three caudal gills at the end of the abdomen, like the young *Calopteryx* and *Agrion*, *Plathemis* has three chitinous valves (Pl. 971, figs. 2, 5; No. 972). When these open, water fills the rectum and the tracheal gills rob it of its air; then it is thrown out with such force as to send the insect swiftly forward. In this way the water serves the double purpose of locomotion and respiration.

The pupal life lasts eight or ten months and during this time several moults take place. Pl. 971, fig. 4, is a side view of the last pupal skin shed by a male *Plathemis trimaculata* De Geer, and fig. 5 is a dorsal view of the pupal skin (No. 973) shed by a female of the same species. The former was drawn from a dry specimen, the latter from No. 973, which had then been in alcohol a short time. Both figures show the four tracheal threads that extended from the inner side of the pupa skin to the emerging dragon-fly, and which were shed with the skin when the dragon-fly escaped.

The adult *Plathemis trimaculata* De Geer (No. 974, ♂; No. 975, ♀; Pl. 976, dissection of ♀), retains the primitive character of the ten distinct abdominal segments, but various remarkable modifications have taken place in the

<sup>1</sup> Quoted from Poletaiew by Calvert, *loc. cit.*, p. 197.

head and thorax whereby the insect is fitted for its aerial life. The unusual habit of catching its food while on the wing has caused the head to become extremely mobile. It seems, indeed, as if the dragon-fly could turn this part of its body completely round without the slightest injurious effect. The head is aided by the long slender legs (Pl. 976, fig. 1) which have lost their function of walking and changed their position, being much farther forward on the thorax than in other insects, as seen in the side view (fig. 2). Calvert<sup>1</sup> states that the first pair of legs are usually employed in holding the food while it is devoured.

These peculiar habits have doubtless brought about the complex structure of the thorax. The prothorax (fig. 1, *p*) which in the larva (Pl. 971, fig. 1) was about the size of the other two segments of the thorax, has become a tiny ring, while the mesothorax (Pl. 976, figs. 1, 2, *ms*) and the metathorax (figs. 1, 2, *mt*) are large and consolidated. These contain the powerful muscles that control the action of the wings. The two pairs of wings (fig. 1) are similar in size and structure, and each pair is free from the other, which is unusual in fast fliers. To understand fully what a complicated machine it is that produces the flight of dragon-flies, one needs to examine von Lendenfeld's figures<sup>2</sup> of the thorax and wings of these insects. It is indeed surprising that such complexity is found to exist among the more generalized orders of this class of animals.

Authorities differ in regard to the tracheal system of the Odonata, but according to Calvert<sup>3</sup> there are two pairs of spiracles in the thorax and a pair in each of the abdominal segments from the second to the eighth inclu-

<sup>1</sup> *Loc. cit.*, p. 162.

<sup>2</sup> Sitzungsber. k. Akad. d. Wiss. Wien, LXXXIII, Th. 1, 1881, pp. 289-380, pls. 1-7.

<sup>3</sup> Trans. Amer. Ent. Soc., Phila., XX, 1893, pp. 161, 170.

sive. It is interesting to note that even in these more generalized insects the social instinct is developed in so far that the migrating habit has been acquired, *Plathemis quadrimaculata* Linn., having been seen frequently migrating in large numbers.

#### Order 4. — PLECOPTERA.

The larvae of the stone-flies or Perlids resemble in a general way the Thysanura and also in their adaptive features the larvae of the Ephemeridae. Like the latter they are fitted for an aquatic life, as seen in Pl. 977, which is the larva of a species of *Perla* showing Thysanuran characters and in addition the adaptive tracheal gills.

The motions of the larva and pupa are slow. The pupa (Pl. 978, fig. 1, *Perla virescens*), however, has no resting period and, although the skin is shed several times, the form of the larva is preserved essentially in the adult (fig. 2, with the wings extended; see also No. 979). When the wings are folded (fig. 3) they are plaited and hence the name Plecoptera, from the Greek signifying plaited wing.

It is unusual for the tracheal gills of the larva to be retained by the adult, but this is the case in *Pteronarcys* (Pl. 980, ventral side), where there are eight sets of branchial tufts. According to Hagen,<sup>1</sup> these vestiges are in a shriveled condition and are functionally useless.

Among the Perlids, the genus *Nemoura* or the willow-fly contains a species (*N. postica* Walk.) with well developed wings, while the male of another species (*N. trifasciata*) has the forward pair existing only as vestiges. In this genus the mandibles are horny and provided with teeth, while in most of the Perlidae they are membranous.

<sup>1</sup> Quoted by Sharp, Cambridge Nat. Hist., V, 1895, p. 402.

As a rule among insects, whenever there is a decrease in the size of the wings, it occurs in the female, while the wings of the male are often remarkably large, but there is a species among the Plecoptera, the *Isogenus nubecula* (Pl. 981, figs. 1, 2), in which the wings of the female (fig. 1) are large, while those of the male (fig. 2) are reduced to remnants.

#### Order 5. — PLATYPTERA.

The termites possess certain Thysanuran characters in the larval state, while in maturity they are developed physiologically to a greater degree than any other members of the generalized orders of insects.

The larva of *Termes* (No. 982; Pl. 983, fig. 1, *T. lucifugus*) has distinct thoracic and abdominal segments and the two regions are broadly connected. It is white and even the hooks of the feet are colorless, while the mandibles are tinted only slightly. This condition indicates that the larvae do little work, and this is the case, since they are nursed and carefully tended when young and are not obliged to shift for themselves.

The pupae (No. 984; Pl. 983, fig. 2) are essentially like the larvae excepting in possessing wing pads.

When, however, the adult forms are considered, we find conditions wholly different from anything so far described. The law of variation has acted, and specialization in function has produced modifications in structure. At the same time the social instinct has developed to a remarkable degree so that there appears, as a result, a colony consisting of groups of many individuals, each group having its special work to perform.

If the course of development had been typical, that is to say, if it had been similar to that of most insects, the pupae would develop in every case into the male or the female winged insect (No. 985, ♂; No. 986, winged

form; also see Pl. 983, fig. 3) with two pairs of wings. It so happens, however, that this occurs with only comparatively few members of the colony. The winged insects swarm; that is, they leave the nest together, and after this "marriage flight" new colonies are probably founded, although Grassi<sup>1</sup> concludes after prolonged investigations that no further result attends swarming than a wholesale slaughter of the individuals. This view is strengthened by Hagen<sup>2</sup> who witnessed a swarm of termites attended by fifteen species of birds, and some of these were so gorged with termites that they could not close their beaks.

While it may be true, as heretofore generally stated, that the colonies of some species are founded by the wingless and helpless king and queen that re-enter the nest after "the flight" just mentioned, it seems now more probable that these two are not in such a weakened condition as described, but that they gradually become so after remaining in the nest and being waited upon by the workers. Generally speaking, Grassi considers that when the vitality of the queen is exhausted (which probably is not the case for several years) one of the complemental females (Pl. 983, fig. 5), which are always kept for the purpose, is substituted in her place, and thus the continuation of the species is secured.

The king when found in the royal chamber of the nest is wingless (No. 987, *T. bellicosus* Smeath). Pl. 988, fig. 1, represents the wingless king of a species of *Termes* from Singapore. The queen found with the king is seen in fig. 2, both natural size.

The body of the queen becomes enormously distended with eggs (Pl. 983, fig. 4. *T. lucifugus*; No. 989, queen of *T. bellicosus* Smeath.; No. 990, royal chamber of the same). According to Sharp growth actually takes place

<sup>1</sup> Atti Accad. Gioenia, Catania, VI, 1893.

<sup>2</sup> Proc. Boston Soc. Nat. Hist., XX, 1881, p. 118.



after the metamorphosis which is the only instance known among insects. This growth does not affect the chitinous segments which are close together before egg-bearing begins, and afterward far apart (Pl. 983, fig. 4; see also Pl. 988, fig. 2).

Besides the young and the winged and, later in life, the wingless males and females, there are workers and soldiers in the colony of *T. lucifugus*. The larvae which produce these different forms are all alike, and it is probable that the duties which have devolved upon certain members of the colony, generation after generation, have been one cause of the loss of wings. The more immediate cause lies in the physical condition of food which is of such a nature as to divert the larvae from the usual course of development and to equip the adults for a special work.

Although the worker of *Termes* (Pl. 983, fig. 6; No. 991) is apparently more like the larva than the winged insects, yet in reality it is farther removed from the larval form, since its ancestors were doubtless winged creatures whose descendants gradually lost their wings by ceasing to fly, and by becoming laborers for the colony in the way of building and repairing nests, storing food, feeding the young, etc. In doing this work they have become more hardy and are provided with dark-colored mandibles and feet.

Still greater specialization along the same line results in the termite soldier (Pl. 983, fig. 7; No. 992). Its head is immense for so small a body, and all its parts are more or less modified. The mandibles are powerful and the whole organization is that of a fighter.

According to the view just stated the worker and soldier are termites which have come to their present condition by a process of specialization, and are not illustrations of arrested development as maintained by some naturalists. If they were such illustrations, they might be placed side by side with the larvae. But, on the con-

trary, they are adults which are differentiated in a peculiar way for a particular sphere of action, thereby becoming examples of specialization by the suppression of organs.

An interesting modification in structure for the purpose of defence is found in the soldier of the genus *Eutermes* (Pl. 993, figs. 1-6). Its head (fig. 5; fig. 6,  $\times 25$ ) extends forward into a beak or "gun" and from this beak the animal discharges glutinous pellets or shot<sup>1</sup> which are so sticky that its enemy is quickly disabled. *Eutermes* is one of the smaller termites; the figures of the worker (fig. 4) and of the soldier are enlarged five diameters, and the remaining three figures are natural size. The winged female is seen in fig. 1, and the wingless queen, before the period of egg-bearing begins, in fig. 2, while fig. 3 is the mature queen with her body distended with eggs.

The wings of the termites when extended are broad, and hence the name of *Platyptera* (meaning broad wing). When spread they give an unusually broad effect to the insect. They are about equal in size and structure in the termites and hence the name *Isoptera* which is often given to this order.

*Oligotoma michaeli* McLachlan (Pl. 994, fig. 1, larva; fig. 2, "starved" pupa; fig. 3, adult) of the family *Embiidae*, is interesting for the reason that it represents a case among insects in which both pairs of wings are developed, but which are so weak that they are practically useless. The thoracic segments to which these inefficient organs are attached are unconsolidated and the insect is described as "feeble." It seems as though the wings were ready to drop off and in time *Oligotoma* would become wingless.

The *Psocidae* are like the termites in many ways but the arrangement of the veins of the wings differs from that of any biting insect (*Comstock*) and these organs

<sup>1</sup> Dudley, Trans. N. Y. Acad. Sci., VIII, 1889, p. 87.

are not of equal size (Pl. 995, *Psocus venosus* Burm.), although when extended they give a broad effect to the insect. When not flying the wings are held roof-like and almost vertically over the body.

Very little is known of the life history of the Psocidae, but it is interesting to note that they spin a web as a covering for their eggs. They are further represented by *Psocus fasciatus* F. (Pl. 996, fig. 1), *Mesopsocus unipunctatus* Müll. (fig. 2, ♀), and *Atropos divinatoria* Müll. (fig. 3). *Psocus* is provided with four delicate wings; the male *Mesopsocus* has the same number, while the female (fig. 2) has only vestiges of these organs (white in the drawing), and *Atropos* is altogether destitute of them. Large numbers of the latter genus are sometimes found gnawing books and papers and for this reason they are known as "book-lice," although they are not parasites and have not the structure of true lice.

In England the *Atropos* is called the "death watch," on account of a ticking sound the insect is supposed to make. The Psocidae bear a striking resemblance to the Aphides of the order Hemiptera, but unlike the Aphides the Psocidae have biting mouth parts.

The family Mallophagidae we place provisionally as the most specialized of the Platyptera. The ancestors and primitive forms of the family are as yet unknown, and the life history of the group has not been worked out completely, but enough has been discovered to show that these insects differ essentially from the well established orders. This has caused many entomologists to place them as an independent order, the Mallophaga. This word is from the Greek, meaning to eat wool, and refers to the habit which some of the species have of eating the wool or hair of sheep and goats. Most of the species, however, live upon the feathers of birds. All the forms are parasitic throughout life and are examples of specialization by reduction. Pl. 997, figs. 1-4, illustrates one of the "bird-lice," *Lipeurus forficulatus* N.,

found on the pelican, and which is related to *Nirmus claviformis* Denny (Pl. 998, fig. 1), and to the common hen-louse, *Menopon pallidum* Nitzsch (the color of the last species is shown in figure 2 of Pl. 998, while the details of structure are better seen in Pl. 999). According to Kellogg,<sup>1</sup> to whom we are indebted for most of the facts in this description, the eggs of *Lipeurus* are fastened singly to the vanes of the feathers of the host, and the young (Pl. 997, fig. 1) is a parasite at start. Its head is large in proportion to the size of the body, and the thorax, even at this early stage, is apparently made of only two segments, the mesothorax and metathorax being united without visible suture. This union is doubtless a vestige of the time when the insect possessed two pairs of wings and was a flier; it is also a proof that *Lipeurus* is a secondary and not a primitive animal.

In the main, the young (fig. 2, an older stage) and the adult (fig. 3, ♀; fig. 4, ♂) resemble each other. This resemblance, however, cannot be compared with the resemblance of the larval and adult Thysanura, since in this case of the Mallophaga we have not primitive simplicity but on the contrary a specialized larva fitted for a parasitic life. The body is extremely flattened and hardened by chitin. The biting mouth parts are modified for cutting feathers or hair, bits of which are seen in the crop through the semitransparent walls of the body. In some species the upper lip serves as a scraper and the mandibles are provided with sharp teeth. The feet terminate in claws for clinging, while the fore legs are used as foot-jaws for carrying food to the mouth.

The wing muscles are greatly reduced in size and there are no indications of wings in any stage of any species of the group.

While it is true that these insects are parasites, they

<sup>1</sup> Leland Stanford Junior Univ., Contrib. Biol. Hopkins Seaside Lab., IV, 1896.

are not so extremely modified as many among the more specialized orders, such as, for instance, *Melophagus ovinus* Linn., the sheep-tick of the Diptera. The Mallophaga still have the generalized type of mouth parts and the power of locomotion.

#### Order 6. — EUPLEXOPTERA.

The larval characters of this order are mostly primitive and generalized, but little is known of the development or life history of the group.

Unlike most insects the mother earwig does not die soon after laying her eggs, but according to Kirby she broods "over her eggs and young almost like a hen."<sup>1</sup>

Pl. 1000, fig. 1, is the larva of the common earwig, *Forficula auricularia* Linn. The thorax and abdomen are distinctly segmented, and the junction of the two is broad. The caudal appendages, even at this early stage, are in the form of forceps.

The adult (Pl. 1000, fig. 2; No. 1001) retains the long body of the larva, the distinct thoracic segments, and the biting mouth parts. There is a peculiar imbricated arrangement of the segments, however, which we have not seen in the insects so far described.

The wings of the adult are unique. The anterior pair are reduced in size and are chitinous covers for the hind wings, which are large and rounded when spread (Pl. 1000, fig. 3), but which by an ingenious method can be folded and almost wholly packed away under the wing covers (fig. 4); hence the name of the order Euplexoptera, meaning to fold well and wing. The projecting portions of the wings, unlike the remaining parts, have the same texture and sculpturing as the wing covers.

No one knows what has caused the earwig to fold its

<sup>1</sup> Text-book of Ent., 1885, p. 81.

wings in this fashion, and the subject becomes more interesting when we consider that "it is probable that the majority of the individuals of this species may never make use of their organs of flight or go through the complex process of unfolding and folding them."<sup>1</sup> If this is the case this species of earwig is an illustration of an animal that possesses absolutely useless organs. These organs occur, however, in an order of insects all of whose members have vestigial fore wings, and many of whose members are without either pair of wings. One may, therefore, reasonably predict that in time *Forficula auricularia* Linn., will be wingless.

The forceps which have given the name of Forficulidae to the family probably represent the cerci of many insects. They vary greatly in form from symmetrical to distorted organs and little is known in regard to their function. It is now probable that the peculiar insect, *Hemimerus talpoides* Walk. (Pl. 1002, fig. 1, young; fig. 2, adult), is a near relative of *Forficula*. According to the observations of Hansen,<sup>2</sup> this insect has not four pairs of mouth parts, as has been stated, but the normal number of three pairs.

*Hemimerus* is a blind, wingless creature, that is found living among the hairs of the rat, *Cricetomys gambianus*, Waterh. Its development is accelerated, so that it brings forth living young, but it differs from other viviparous insects by giving birth to only one at a time. Probably several days intervene between the birth of the small number of offspring. Fig. 1 represents the young as taken from the mother, showing the coiled position and the ragged end of a process, extending from the neck, which Hansen thinks connects the embryo with the mother. When uncoiled the young *Hemimerus* is nearly as large as the parent, and differs from it only in the number of antennal joints and in the structure of the posterior abdominal segments.

<sup>1</sup>Sharp, Cambridge Nat. Hist., V, 1895, p. 207.

<sup>2</sup>Ent. Tidskr., XV, 1894.

The Euplexoptera are placed by many entomologists among the Orthoptera, the next order to be described, but it will be seen that, while they possess certain characters in common with that order, they are in other essential respects very dissimilar.

Until at least there is more knowledge in regard to the life history of the Euplexoptera it seems better to place them in a distinct order next the Orthoptera.

#### Order 7.— ORTHOPTERA.

The ancestors of the Orthoptera or straight-winged insects are found in the Carboniferous and possibly in the Silurian formations. Pl. 1003 represents one of these primitive forms, *Progonoblattina columbiana* Scudder, which is related to the Blattidae or cockroaches of to-day.

The body in these ancient cockroaches was elongated and the thoracic segments were of nearly equal size, while the junction of the thorax and abdomen was broad.

The antennae were thread-like and the mouth parts were of the biting type. The legs were adapted for running, and the two pairs of wings were of more nearly equal size and texture than the wings of their descendants. The venation of these organs was less differentiated than in modern types, though there was a general resemblance, the principal veins and their branches running to the outer margin.

Some points in the embryology of the cockroaches of to-day are instructive. In these cockroaches the eggs and embryos are protected by an egg-case in which are placed sixteen eggs or eight on each side. Pl. 1004, fig. 1, gives an external view of this case, and fig. 2 an internal view showing the eight eggs on one side. According to Cholodkovsky<sup>1</sup> the segmentation of the

<sup>1</sup> Zeitschr. f. wiss. Zool., XLVIII, 1889.

anterior part of the body of the cockroach may be seen at first distinctly. In the course of the development a pair of appendages appears on each segment. Pl. 1005, fig. 1, shows one pair of antennae, three pairs of mouth parts, three pairs of thoracic legs, and eleven pairs of abdominal appendages, making in all eighteen pairs. These are alike when first formed and appear before the dorsal portion of the body is completed. Most of the abdominal appendages (which we have already found in the adult Thysanuran insects) quickly disappear, as shown in the older embryonic stages (figs. 2, 3). The body shortens but the distinctness of the segments is preserved. The eyes (fig. 3, *c*) are plainly seen in this stage. The larvae (No. 1006, *Blatta* (= *Periplaneta*) *orientalis* Linn.) have ancestral and Thysanuran characters, but in addition the adults have certain marked adaptive features. Some of these features are particularly well shown in *Blatta orientalis* Linn. (Nos. 1007, ♂; 1008 ♀) and in the large Cuban cockroach (No. 1009), because in these species the features have been intensified by domestication. The body and leg sections are extremely flattened, and the freely movable segments of the abdomen can be extended or shortened by telescopic action, thus enabling the insect to crawl into narrow crevices. The head is reduced in size and turned under the large prothorax, so that it is scarcely seen in a view from above. The biting mouth parts are hard and dark colored, since the cockroach feeds upon almost any substance that comes in its way.

Both pairs of wings are well developed in certain genera of this family, *Blabera* for instance (Pl. 1010, fig. 1, A, anterior wing; B, posterior wing), but in *Blatta* the wings of the male (No. 1007) are diminished in size, while in the female (No. 1008) the forward wings are vestiges and the hinder pair have wholly disappeared.

Among the more generalized Orthoptera the "praying mantis" (No. 1011, egg-case; Nos. 1012, 1013, adults)



and the walking-stick have acquired unique specializations. The prothorax of the adult *Stagmomantis carolina* Linn., (Nos. 1012, 1013), is a long, slender segment, on the forward end of which are borne the extremely large fore legs that are adapted even in the larval state for seizing living prey, and which are usually raised in readiness to act whenever occasion offers. The other two pairs of legs are locomotor organs and are slightly modified. The wings of Mantis are too small to be of use, and the motions of this walking type are extremely slow.

Certain species of Mantis and also of the walking-stick (No. 1014, *Cythocrania gigas*) have remarkable plant-like features in the form of leaf-like wings, but in the single species found in New England, *Diapheromera femorata* Say (No. 1015), the wings have wholly disappeared.

These insects are among the good illustrations of what is known as protective coloration. In the spring time their color is a vivid green, but as autumn approaches they take on brownish tints. Whatever may be the cause of these changes, whether due to conscious or unconscious adaptation of the insect to its environment, to the direct effects of heat and cold, to the age of the animal, or to some unknown cause, they certainly render the insect less conspicuous and in this way serve to protect it against its enemies. One of the most remarkable cases of this kind is seen in the genus *Phyllium* (No. 1016, *P. scythe*). The anterior wings of the female resemble leaves and their hues change with the changing seasons.

Among the more specialized Orthoptera are the Acrididae or locusts, the Locustidae or grasshoppers, and the Gryllidae or crickets.

The Acrididae are good type forms not only of the Orthoptera but of the class Insecta. The larva (No. 1017; Pl. 1018, fig. 1) possesses the similar thoracic and abdominal segments that are comparable with those of the Thysanura. The mouth parts are the same in

number and function as in all the most generalized groups, but the running type of insect has changed into the leaping type, and this is true not only of the adult but also of the young larva.

With the development of wings the pupa (No. 1019, Pl. 1018, fig. 2) takes on some of the features of the adult. The first thoracic segment becomes differentiated, serving to protect the parts, and the two hinder segments become consolidated until in the adult (No. 1020, *Melanoplus femoratus* Scudd., ♂; No. 1021, ♀; Pl. 1022, fig. 1, side view of ♂; fig. 2, dorsal, with view of dissection of ♀), they are so complex in structure that it is difficult to make out their boundaries with absolute certainty.

The abdomen (Pl. 1022, figs. 1, 2) retains essentially its primitive simplicity, though a fold has appeared on either side above which, near the anterior edge of the segment are situated eight pairs of spiracles, while there is a pair in each of the posterior segments of the thorax (fig. 3).

The Acridiidae have a tracheal system consisting not only of air tubes but also of a large number of air sacs (fig. 3). When the tubes and sacs are filled with air, the body is greatly lightened and the insect is able to fly considerable distances. The second pair of wings (fig. 2) are most useful in flight. When at rest these organs are folded lengthwise like a fan and lie straight with the body; hence the name of Orthoptera or straight-winged insects. The hind wings are often large and handsomely colored, as in one of our largest Locusts, *Dissosteira carolina* Linn. (No. 1023, ♂; No. 1024, ♀, with wings spread).

The ovipositor (Pl. 1022, figs. 2, 3) of the female consists of horny spike-like organs situated at the end of the abdomen and well fitted for digging holes in the earth in which to place her eggs.

Most of the parts of the locust exist on a large scale in *Dictyophorus reticulatus* (No. 1025), and for this reason

the genus is especially helpful to teachers and students. The wings in this locust, however, are useless vestiges.

One of the interesting specializations occurring among the Acridiidae is in the case of the grouse locust, *Tettix*, (No. 1026). Here the prothorax has grown backward, usurping the place and function of the wing covers, which, no longer needed, have dwindled to tiny remnants.

The Locustidae are represented by the true grasshopper, *Orchelimum vulgare* Harris (No. 1027). It lives in grassy meadows and fields, and is a vivid green in color, while the katydid, *Cyrtophyllus concavus* Say (No. 1028), also green in color, frequents trees and shrubs. In these insects the unconsolidated condition of the thorax is correlated with the weak legs and wings. The latter organs are leaf-like and have no stiff anterior veins. In the katydid the forward wings are so large and concave that they encircle the posterior part of the body like a cylinder. The insect opens these wings suddenly and brings them together in such a way as to produce the familiar note "Katydid, she did, Katy didn't." The cone-headed katydid, *Conocephalus ensiger* Harris (No. 1029), has the head extending forward in the shape of a cone.

The female of *Orchelimum* (No. 1027) can be readily distinguished from the male by the sword-shaped ovipositor.

Among the specialized Orthoptera are the Gryllidae or crickets. The body in both the larva (No. 1030) and the adult *Gryllus* (No. 1031) is shortened and black in color. The first pair of wings (No. 1031) are small, horny wing covers, while the second pair are useless in flight. The cricket is provided with an ovipositor and a pair of long cerci.

A remarkable example of adaptation of structure to habit is offered by the mole cricket, *Gryllotalpa vulgaris* Linn. (No. 1032, dorsal and ventral side). It is ex-

tremely interesting to note that before the first moult this insect has the power of leaping several inches<sup>1</sup> but after this moult it is more sluggish. Living and burrowing in the earth, there is no need of leaping legs, and therefore these have become essentially like the second pair.

The habit of excavating tunnels while in search of food has modified the forward legs into powerful digging implements which are seen in the mature larva as well as in the adult. This same habit has produced a similar structure in the mole of the Mammalia.

Although these crickets do not possess the power of leaping in the adult stage, they can swim, and, according to Fletcher,<sup>2</sup> "their little shining black eyes, velvety coats and flexible bodies recall strongly the appearance of the otter particularly when emerging from the water or crawling over stones."

#### Order 8. — THYSANOPTERA.

The larva (Pl. 1033, *Parthenothrips dracaenae* Heeg) of the Thysanoptera has the general features of the Thysanura. These are seen still more plainly in *Limothrips* (= *Thrips*) *tritici* Fitch (Pl. 1034, fig. 1). The pupa (Pl. 1033, fig. 2), however, and especially the adult (Pl. 1033, fig. 3, and Pl. 1034, figs. 2, 3) are farther removed from their own larvae than the adults of the Euplexoptera or the Orthoptera. The mouth parts (Pl. 1035, fig. 1) have become modified for sucking. There are still three pairs of these organs and the labrum (fig. 2, *a*) but the mandibles (fig. 2, *b*) are more like the bristles of the Hemiptera, the next order to be described, than the horny teeth of the Orthoptera. The first pair of maxillae (fig. 2, *c*) and the maxillae of the second pair, which

<sup>1</sup> Doran, Can. Ent., XXIV, 1892, p. 271.

<sup>2</sup> Can. Ent., XXIV, 1892, p. 25.

united make the labium (fig. 2, *d*), are very unlike the typical mouth parts although both pairs have palpi (see fig. 2, *c*, *d*). According to Osborne,<sup>1</sup> the Thripidae are vegetable feeders, and the carnivorous habit when present, as in *Thrips phylloxerae*, is acquired or but recently developed in the species.

The beautiful wings with their long delicate fringe (Pl. 1036, *Heliothrips haemorrhoidalis* Bouché) have given the name of Thysanoptera or fringe-winged insects to the order. In Pl. 1034, fig. 2, these wings are folded over the back.

The male of Limothrips has become specialized by reduction, having lost its wings altogether (see Pl. 1034, fig. 3).

#### Order 9. — HEMIPTERA.

The Hemiptera have probably descended from some Campodea-like ancestor, though many of the stages of descent are wholly skipped in the development of existing forms. Even the most generalized members of the order are far removed, as regards the mouth organs, from the Thysanura and also from the orders so far described.

While this is true, there are nevertheless certain indications here and there that the sucking apparatus of the Hemiptera, which is so perfect in most of the members of the order, is an adaptation of the original biting mouth parts of the ancestral Thysanura. For instance, in the mouth organs of *Zaitha* (*Z. margineguttata*) the second pair of maxillae which form the sucking tube are provided with palpi (Pl. 1037, fig. 1). These have also been seen in *Benacus griseus* Say (fig. 2), *Gerris najas* (fig. 3), as well as in *Nepa*, *Ranatra*, and *Belostoma*.

As we already know, an important feature of biting

<sup>1</sup> U. S. Dep. Agric., Insect Life, I, no. 5, 1888, p. 142.

mouth parts is the possession of palpi, and the discovery of these organs by Leon<sup>1</sup> tends to confirm his statement that there is a complete homology between the Hemipterous mouth organs and those of biting insects.

The Hemiptera are divided into two groups, the Heteroptera and the Homoptera. The Heteroptera are the more generalized, inasmuch as they have more direct development than the Homoptera, and the thoracic and abdominal regions are more like those of larval cockroaches.

The larvae and adults of some of the water-inhabiting Hemiptera bear a greater resemblance to the Thysanura in the general proportions of the body than do the terrestrial forms like the typical *Anasa* or squash-bug. For this reason they will be considered first.

The generalized characters of Notonecta are seen in the larva. Besides these both the larva and the adult (No. 1038) possess adaptive features fitting them for aquatic life. The back is shaped somewhat like the bottom of a boat and the insect swims with it downward hence the name of back-swimmer. The hind pair of legs have become efficient oars; concomitantly their structure has changed and they have become long, flattened organs fringed with hairs.

The water-inhabiting Hemiptera, like all water insects, breathe air. Notonecta often comes to the surface and stows away a supply under its wings, while another water boatman, *Corixa* (No. 1039), is enveloped in a film of air which gives it a silvery appearance.

The largest Hemipterous insect is the giant water-bug, *Belostoma americanum* (No. 1040, dorsal and ventral side), which on account of its size is particularly helpful to the student.

The segments of the thorax in this insect are free like those of the abdomen. The head is flat and placed hori-

<sup>1</sup> Zool. Anz., XX, 1897, p. 73.

zontally; the antennae are concealed from view, being hidden under the eyes. The jointed sucking tube extends backward and consists of the two parts of the second pair of maxillae united. Within this tube are the mandibles and first pair of maxillae, which are sharp bristle-like organs used for piercing the flesh of animals. The legs are greatly modified; the forward pair are provided with claws, one jaw of which closes upon the other like the blade of a knife upon its handle. These legs are strong enough to catch small fish and to hold them, while the sucking tube draws the blood of the animal. The hind legs are powerful swimming organs. The anterior pair of wings exhibit the peculiar structure of the typical Hemipterous wing, having a horny basal portion, while the remaining part is membranous; hence the name Hemiptera, meaning half and wing. The posterior wings are membranous throughout, and are useful flying organs; both pairs of wings lie flat on the body, their tips crossing. When wings are present in these water insects, they aid in seeking out a favorable habitat for the dissemination of the species; *Belostoma* is capable of long sustained flights,<sup>1</sup> and *Zaitha* (Nos. 1041, 1042) resembles *Belostoma*. *Zaitha* has, however, the habit of fastening its eggs on its back (No. 1041). According to Slater,<sup>2</sup> it is the male that carries the eggs, and the ovipositor of the female is too short to place the eggs on her back, as has been supposed. The wing covers are concealed, as seen in No. 1041, so that these organs are useless for locomotion until the young are hatched.

The spiracles in *Belostoma* and *Zaitha* are apparently closed, but they have valvular openings which admit the air.

*Ranatra* (No. 1043) has besides the spiracles a pair of respiratory tubes at the end of the abdomen. This insect

<sup>1</sup> Dimmock, Ann. Rep. Fish and Game Comm. Mass., 1886, p. 70.

<sup>2</sup> Amer. Nat., XXXIII, 1899.

has a long body and long legs like the walking-stick of the Orthoptera, and the wings are reduced in size, while in *Hygrotrechus* (No. 1044), an insect that lives on the surface of the water, the wings have disappeared.

In striking contrast to these long-bodied and long-legged Hemiptera is the *Galgulus oculus* Fabr. (No. 1045), which inhabits marshes. On account of its short, broad body and projecting eyes it is often called the toad-shaped bug. It is a good leaper and its color harmonizes with its surroundings.

The terrestrial Hemiptera are well represented by the squash-bug, *Anasa tristis* De Geer (No. 1046, eggs, larva, pupa, adult; No. 1048, adult). In the larva (No. 1046; Pl. 1047, fig. 1) the thoracic segments are unequal in size, although they are freely movable. The head, antennae, and legs are dark-colored, presenting a striking contrast to the light-colored body and indicating that these appendages perform hard labor. The posterior lateral angles of the mesothorax and metathorax grow out (No. 1046) until the distinct wing pads of the pupa (No. 1046; Pl. 1047, fig. 2) are formed. One can often find all the stages of the developing wings in the squash-bugs that infest a single plant.

The prothorax in the adult (Nos. 1046, 1048; Pl. 1047, fig. 3, *p*) has grown backward and covered the larger part of the mesothorax, which is also seen in Pl. 1047, fig. 4, where the prothorax (*p*) is raised exposing the mesothorax (*ms*); the latter is large and its posterior part, the scutellum, conceals the dorsal part of the small narrow metathorax (fig. 3, *mt*).

The jointed sucking tube (fig. 3, *su*; No. 1048, with tube extended) is essentially the same in the larva and adult. It is seen in fig. 5, where the bristle-like mandibles and maxillae are drawn out of the tube or second pair of maxillae (fig. 5, *mx''*).

The distinctive characters of the wings of *Anasa* and of the Heteroptera generally are well seen in fig. 3. The



basal portion is chitinous and has few veins, while the terminal part is membranous and is richly supplied with veins. The under wings (fig. 3, *w''*) are membranous throughout but have few veins. Both pairs of wings lie flat upon the back and their tips overlap.

Peculiar specializations are found in many of the adult Heteroptera, the reasons for which are not always known, owing chiefly to the fact that much information in regard to the habits of the insects is wanting.

The thread-legged bugs like *Emesa* (No. 1049) have the habit of hanging to twigs by their long legs and swinging backward and forward. The fore legs are provided with claws for seizing their prey and are well fitted for this purpose.

Especially attractive is the lace-bug, *Corythuca arcuata* Say (No. 1050). This insect lives on the under side of oak leaves where its eggs (Pl. 1051, fig. 1) are laid. The larva (fig. 2) has such a spiny thorax and abdomen that it looks like "a lobe of a prickly cactus" (Comstock). The adult (fig. 3) is distinguished from other insects by the exquisite gauzy appearance of the body. This is due to the wing covers that are formed of a nearly transparent membrane netted with veins.

*Prionidus cristatus* Linn., or the wheel-bug (No. 1052) destroys great numbers of caterpillars and other insects. Both as larva and adult it is a hardy, rapacious creature, and it may be that the cog-wheel crest of the thorax (No. 1052) gives strength to the animal when making its attacks.

In *Scutellera* (No. 1053) the scutellum of the mesothorax has developed for some reason so that it covers both pairs of wings and resembles, at first sight, the horny wing cases of the beetles.

Among the more specialized Heteroptera is the bed-bug, *Acanthia lectularia* (No. 1054). It is adapted to its habitat by having a flattened body, strong mouth parts, and a thorax that is almost entirely unencumbered by wings.

The prothorax is of good size and aids the head and mouth organs, but the mesothorax is reduced in size and bears the tiny scales which will probably in time wholly disappear, while the metathorax is already a vestige without appendages.

Most specialized of all the Heteroptera are the parasitic lice. Here the thoracic segments are fused together and even the sutures are indistinct (Pl. 1055, the body louse, *Pediculus vestimenti* Nitzsch; hair line indicates natural size) or apparently wanting (Pl. 1056, the swine louse, *Haematopinus suis* Leach) until brought out by staining reagents. When thus brought into view, they are proofs of the evolutionary history through which these parasites have passed and demonstrate that the position of these insects in a natural classification must be with the secondary and specialized forms. Associated with this specialization of the thorax is the loss of compound eyes and the absence of both pairs of wings. The sucking tube has lost its joints, is fleshy and capable of extension by rolling inside out. The feet have ceased to be running or leaping organs, but are provided with claws for climbing upon hairs or for clinging to the flesh of the host.

The generalized Homoptera are represented by the Cicadidae. The seventeen-year species, *Tibicen septendecim* Linn., often called cicada (Pl. 1057, larva; No. 1058, adult), requires that period of time for its development in the north, and thirteen years in the south; *Cicada marginata* Say, (No. 1059, pupa skin; No. 1060, ♂; No. 1061, ♀) probably develops in a shorter time, while our common dog-day cicada, *C. canicularis* Harr. (Pl. 1062, probably larva; No. 1063, pupa skin and adult) reaches the adult stage in two years (Comstock). There is little in the larva of this insect that suggests the Thysanuran stock form, although in certain characters the larva of the seventeen-year cicada when newly hatched (Pl. 1057, fig. 1) approaches the Thysanura nearer than the proba-

ble larva of the two-year cicada (Pl. 1062). The resemblance is seen especially in the similarity of the thoracic segments.

At the time of hatching, the fore legs are fitted for burrowing (Pl. 1057, fig. 1), having strong digging claws at their ends. These are needed when the larvae, which hatch from eggs laid in the branches of trees, drop to the ground and begin to burrow downward to the roots. Development is so extremely slow that in six years the larva of the seventeen-year species has hardly attained one fourth its full size (Riley). There are probably twenty-five or thirty moults, the body gradually shortening, thickening, and growing darker with age.

The larva lives on the sap of roots and the moisture in the earth, which it takes by means of its strong sucking tube. Much of the time it lies in an oval cell which it has made for itself by using its claw as one would use a pick. It never passes into a quiescent pupal stage in which structural changes are gone through quickly; nevertheless, it lies in a cell, as we have said, and is able to live a considerable time without taking nourishment. In these ways it approaches pretty closely to the quiescent condition of the more specialized insects. Gradually wing pads are developed and the pupa (Pl. 1057, fig. 2) works its way to the surface. "To witness these pupae in . . . vast numbers . . . swarming out of their subterranean holes and scrambling over the ground, all converging to the one central point, and then in a steady stream clambering up the trunk and diverging again on the branches, is an experience not readily forgotten and affording good food for speculation on the nature of instinct. The phenomenon is most satisfactorily witnessed where there is a solitary or isolated tree."<sup>1</sup> In about an hour after rising and settling, the transformation

<sup>1</sup> Riley, Rep. of the Entomologist, U. S. Dep. Agric., 1885, p. 237.

begins, and usually several hours pass before the insect is ready for its aerial life. It is to be noticed that during the transforming process the wings lie flat on the back before they slope, roof-like, at the sides.

The development of our species of cicada is accelerated so that it is accomplished in two years. The larva has a shortened cylindrical body like a grub. The segments of the thorax are unequal in size, the metathorax being much narrower than the prothorax or mesothorax, and the segments of the abdomen are tapering.

The fore wings of the adult cicada and of all Homoptera differ from those of the Heteroptera in being membranous throughout, as seen in Nos. 1058, 1060, 1063. The adult male produces the shrill piercing note so often heard in July and August. This sound is made by means of two "drums" on the lower side of the basal part of the abdomen. These drums are covered by flaps which are much larger in the male (No. 1060) than in the female (No. 1061). In *Cicada tibicen* Linn. (= *pruinosa* Say) (No. 1064) there is a white pubescence on the lower side.

The Homoptera include insects that have become modified in most peculiar ways. For instance in the lantern fly, *Fulgora*, (No. 1065) the forward part of the head is greatly enlarged and extends in front, forming a rostrum which is luminous at night. A nearly related form, *Hotinus*, (No. 1066) is armed on the head with a long curved horn, which appears to be an organ of offence and defence.

The most specialized of the Hemiptera are the Aphides (No. 1067, Aphis) and the scale insects or Coccidae. The life history of the hop-plant aphid, *Phorodon humuli* Schrank, has been worked out more fully than that of many species.

Whether we begin with the fertilized egg or with the sexually mature male and female, we are dealing with specialized conditions, since in this Aphid the fertilized

egg develops into a form far removed from its parents and from the ancestral Hemiptera, while the apparently normal sexually mature male and female develop from the unfertilized eggs of agamic individuals.

The unfertilized eggs may be in a certain sense hermaphroditic, but without going into a discussion<sup>1</sup> of the subject of parthenogenesis, or the development of living organisms independently of the male, it is evident that the sexually mature male and female which pair and give rise to fertilized eggs are nearer the primitive insects, and also the ancestral forms of nearly all the groups above the Protozoa, than the exceptional agamic forms which bring forth living young. In the latter case acceleration in development has caused the embryonic and larval stages to be passed within the body of the parent, and the young when born may be compared to active pupae which are so specialized that they never acquire wings, but in a few days are mature insects and ready in their turn to bring forth living Aphides.

Unfortunately, a figure of the larva of the male Phorodon cannot be given, but the pupa (Pl. 1068, fig. 1) has the rudiments of wings like the pupae of most insects. These pupae develop into the male (fig. 2) which has two pairs of wings, although the posterior pair are small in size. The sexually mature female is more specialized than the male, inasmuch as it never possesses wings. Its young, which is probably the specialized wingless pupa, is seen in fig. 3; the adult with the body distended with eggs is represented in fig. 4 and with the body shrunken during egg-laying in fig. 5.

These fertilized eggs are laid upon the branches of plum trees. Each develops into a wingless female often called the "stem mother" (fig. 6), which in a few days produces living young, entirely independent of the male. This second generation (fig. 7) gives rise in the same

<sup>1</sup> See Weismann, Brooks, Geddes, Adler.

way to a third generation (fig. 8, pupa ; fig. 9, adult), but these are winged agamic females. These "winged migrants" fly from the plum tree to the hop plant. The fourth generation or the first on the hop plant is represented in the act of crawling in fig. 10. Several generations may be produced parthenogenetically on the hop vine, fig. 11 representing the normal parthenogenetic female of the sixth generation. In the autumn, winged females (fig. 12, pupa ; fig. 13, adult) are again developed and these "return migrants" fly back to the plum. They are agamic and soon produce young which, however, develop into the sexual wingless females already described. Later the winged males appear and sexual reproduction follows.

This remarkable specialization in development is correlated with specialized structures and with social habits. The thoracic segments, which, generally speaking, are distinct in the Hemiptera, are more or less fused together in these forms; especially is this the case with the mesothorax and metathorax, the boundaries of which are difficult to make out.

The dorsal tubes on the abdomen of both the sexual and the parthenogenetic forms which discharge the sweet liquid, "honey dew," is a unique adaptation on the part of the Aphides which brings them into harmonious relations with other insects that are remotely connected with them genetically, such as ants.

The grape aphid, *Phylloxera vastatrix* Planchon, has carried specialization so far that there are several phases or types of the species, and it is probable that in one type, *Gallaecola* or the gall-inhabiting form, the male has ceased to exist.

According to Riley<sup>1</sup> the first galls that appear on the grape leaves in the spring time are formed mainly by young *Phylloxera* that hatch on the roots of the grape

<sup>1</sup> 6th Ann. Rep. Nox. and Benef. Insects Mo., 1874, p. 37.

vine. We will therefore begin with the root-inhabiting type or, as it is called, the *Radicicola*. This type produces two forms, the sexually mature winged form and the parthenogenetic or wingless form. Since the sexually mature form is nearer the ancestral type than the reduced parthenogenetic form, we will consider it first. Its larva (Pl. 1069, fig. 1) has distinct tubercles; it develops into the pupa (fig. 2, dorsal view; fig. 3, ventral view), which crawls to the surface of the ground and in summer transforms into the winged insect (fig. 4, dorsal view; fig. 5, ventral view). These winged forms are mostly females. Among them is a smaller, shorter form (fig. 6) which may be the male, although this is not proved. The winged females lay from two to five eggs above ground and die on the approach of winter. Their eggs live through the winter and in the spring the larvae climb to the leaves of the vine and there make galls. Since, however, most of the galls are made by the second or parthenogenetic form of the *Radicicola*, we will describe it next. Its larva (fig. 7) which is at first without tubercles, develops them later, as seen in fig. 8, dorsal view; fig. 9, side view. This form, however, never acquires wings and as it grows it becomes more specialized by reduction; it hibernates in the larval state, but when the sap starts in the spring, it matures and lays parthenogenetic eggs which develop into wingless females. It is chiefly these females that give rise to the gall-inhabiting type or the *Gallaecola*. They make their way out of the earth and to the leaves of the vine which they pierce on the lower side, thereby causing the formation of abnormal growths or galls. The eggs are laid in these galls. They hatch into plump, six-legged larvae (fig. 10, dorsal view; fig. 11, ventral view) which leave the gall and find their way to the leaves of the vine. These they in their turn pierce and the resultant gall becomes the home of the adult (fig. 12, dorsal view; fig. 13, ventral view; fig. 14, side view). In this situation the antennae and legs

become reduced in size. The body distends with unfertilized or parthenogenetic eggs. These are laid until the gall is crowded, the mother shriveling in the process, and dying at its termination. Five or six generations are produced parthenogenetically during the summer and the number of individuals born is enormous. Since each individual repeats the process of making its gall-home and filling it with eggs, the number of galls is also very large. With the fall of the leaves in the autumn, the *Gallaecola* that remain, quit the vines and finding their way to the roots of the grape become *Radicicola*. It is interesting to note that the newly hatched larvae which develop from the eggs of the root-inhabiting type cannot be distinguished from those of the gall-inhabiting type (compare fig. 7 with fig. 10), but in time the former develop tubercles, as already stated, and the two types become distinct, although so closely connected genetically that they are one and the same species.

We have here apparently the unusual phenomenon of parthenogenetic individuals of two different types carrying on the principal rôle in the life history of a species, and the sexual females and possible males playing such an unimportant part that it seems as if they could be dispensed with altogether. It may be, however, that the "problematical male" (fig. 6) is more necessary for the continuance of the species than it appears, or possibly *Phylloxera* has "a true sexed generation of minute, wingless" forms, as in the wooly aphid (*Schizoneura lanigera* Hausmann), of the apple.<sup>1</sup>

In one important structural feature *Phylloxera* differs from the hop-plant aphid: it never secretes "honey dew," and consequently is without the honey tubes.

The Coccidae or scale insects are in certain ways unique among insects. The newly hatched larva of the

<sup>1</sup> Marlatt, U. S. Dep. Agric., Div. Ent., Circular no. 20, ser. 2, 1897, p. 3.



female cottony cushion-scale, *Icerya purchasi* Maskell (Pl. 1070, fig. 1, dorsal side; fig. 2, lower side, colored from life), has club-shaped antennae each bearing four long hairs. It would be interesting to know the cause of the elaborate development of these organs. The eyes are situated on the margin of the head (see fig. 2) and are raised on short tubercles. There are rows of pores and many hairs on the body. In the second stage (fig. 3) and also the third (fig. 4) the antennae are shortened, and the eyes are no longer on the margin but on the ventral side of the head. The pores and hairs are scattered irregularly over the body. The adult female (fig. 5, dorsal view) is provided with tufts of black hairs around the edge and with an immense number of pores. The wax filaments that issue from the pores are curly. Besides these wax threads the animal produces glassy-like filaments and from one large pore in the back globules of honey dew are ejected. When ready to lay her eggs, the female lies flat on the back, the edges of the body turned slightly upward, and the waxy material of which the sac is composed begins to issue from countless pores on the under side of the body, but more especially along the sides below. As the secretion advances, the body is raised, the forward end being still attached, until, near the completion of the sac, the insect is apparently standing on its head nearly at right angles to the surface of attachment (fig. 6, dorsal view; fig. 7, side view, showing the pale greenish gray form, and with part of the white egg-covering torn away, showing the eggs stained with carmine). The egg-laying begins as soon as a thin layer of the secretion has formed on the under side of the abdomen, and it continues during the formation of the sac (Riley). The egg-sac is snowy white, in striking contrast with the reddish colored insect. From the middle of the under side of the sac the larvae make their escape soon after hatching.

The male is less specialized by reduction than the

female, inasmuch as it passes through a normal larval, pupal, and winged adult stage, but it is more specialized by having a quiescent pupal stage and an indirect development unlike any of the insects in the large group of Insecta including orders 1-9, which we have been describing. The quiescent pupa (fig. 8) is, in fact, here met for the first time, as is also its covering or cocoon (fig. 9), which in this case is made of wax so that it melts readily when heat is applied.

Associated with this specialization in development there is the loss of mouth parts in the adult male (fig. 10), and the reduction of the second pair of wings to organs that resemble the halteres or balancers of the Diptera, the most specialized order of the class of Insecta.

#### Order 10. — COLEOPTERA.

The more generalized members of the Coleoptera have larval characters in common with the Thysanura, while the adults are similar in certain features to the Euplexoptera, Orthoptera, and Hemiptera. The most specialized Coleoptera, on the other hand, have lost completely the larval Thysanuriform characters and the adults are far removed from their generalized ancestors.

For the sake of clearness we will consider, first, those beetles whose larvae resemble more or less the Thysanura; secondly, those which have larvae in the form of soft, cylindrical, and active grubs, possessing three pairs of feet; thirdly, those whose larvae are elongated, with minute feet, suggesting in their general aspect the caterpillars of the more specialized order, the Lepidoptera; and, fourthly, those whose grub-like or caterpillar-like larvae have become specialized by reduction, so that they are soft, cylindrical and inactive, having only vestiges of feet, or in some cases being wholly without these organs.

This arrangement not only holds good for the order

but in some of the families, the Chrysomelidae for instance, the Thysanuriform, grub, and caterpillar-like larvae can all be found.

Many of the Carabidae or ground beetles have elongated, chitinous, more or less flattened larvae. The body is of nearly equal breadth throughout and the segments are distinct.

The Thysanuriform characters are plainly seen in *Patrobus longicornis* Say (Pl. 1071), although the adult (No. 1072) has become specialized by the loss of its second pair of wings.

Calosoma is another Carabid whose larva is elongated but more plump in aspect than that of *Patrobus*. The pupa has its parts free, while the adult (No. 1073, *C. scrutator*) is a brilliant beetle with well developed wings.

The Coccinellidae or lady-birds are similar to the Carabidae in many respects and they too have elongated Thysanuriform larvae (Pl. 1074, fig. 1, *Coccinella novemnotata* Herbs.). These larvae fasten themselves by the posterior end of the body and develop into pupae (fig. 2, with the larval skin attached at the anal end). The pupae are often brightly colored as well as the adults (No. 1075, dorsal side; No. 1076, ventral side; Pl. 1074, fig. 3), which in this species have nine spots. Sometimes the adult in this family has a uniform color and a fine pubescence of short hairs, as seen in *Scymnus punctum* LeC. (Pl. 1077, figs. 1, 2, 3, larva, pupa, and adult), a shining black Coccinellid with yellow antennae. These beetles are not only extremely pretty insects but they are also extremely useful in devouring pests such as Phylloxera and the like.

The fast-running tiger beetles of the Cicindelidae have Thysanuriform larvae which, however, are peculiarly modified by habit. These larvae live in holes and while there catch their prey. For this purpose the head is large and strong, the mandibles long and curved, while two tubercles on the abdomen, each with a recurved hook, hold the insect in any part of its burrow. The adults (No. 1078, *Cicindela sexguttata*) are often brilliant in coloring.

The larva of *Amphizoa lecontei* Matth., (Pl. 1079, fig. 1, dorsal view; fig. 2, ventral view) is Thysanuriform in general aspect and is strongly chitinous above. When the larva is extended, the body is much longer and resembles the larvae of the Carabidae. The larva and adult live along the sides of rapid mountain streams, floating on sticks in eddies or crawling among stones. "It gives the impression," says Hubbard,<sup>1</sup> "of a terrestrial beetle with amphibious or semiaquatic habits."

Dytiscus is a water beetle whose larvae (Pl. 1080, fig. 1, *D. marginalis* Ahr.) breathe by means of two spiracles at the end of the abdomen. The air is taken in at the surface of the water, as is also the case with the adult (No. 1081, *D. verticalis* Say, dorsal side; No. 1082, ventral side) which stores its air away under the wing covers.

The larva is remarkable for having primarily solid mandibles modified into hollow organs (Pl. 1080, fig. 2, showing the opening at the smaller end) through which the juices of its prey are sucked. Here, then, we have a mandibulate type of insect converted into a suctorial type.

The Gyrinidae are also aquatic beetles in both the larval and adult states, and possess other specializations for such a habitat. Along each side of the abdominal segments of the larva (Pl. 1083, *Orectochilus villosus* O. F. Müll.) there are branchial organs used for respiration and locomotion. The adults (No. 1084, *Gyrinus*) are usually seen upon the surface of the water swimming by means of their paddle-like feet. They are provided with a pair of eyes that are divided in such a way that it is thought that one part looks upward into the air (Pl. 1085, fig. 1, dorsal view) and the other part downward into the water (fig. 2, ventral view).

The long, flattened larvae of the Silphidae or burying beetles (Pl. 1086, *Necrophorus tomentosus* Web.) feed upon

<sup>1</sup> Proc. Ent. Soc. Washington, II, no. 3, 1892, p. 344.

carion which the adults (No. 1087, *Necrophorus carolina*) have provided.

According to Kirby,<sup>1</sup> a pair or sometimes more than one pair of these insects hunt together. When a dead bird or mouse is found, the pair dig the earth away from under it, thus sinking it; the female then allows herself to be buried with the carcass until after her eggs are laid, when she finds her way to the surface. The sense of smell is very acute in these beetles, and they exhibit much intelligence.

The rove beetles or Staphylinidae (No. 1088, *Staphylinus fossator*) have become specialized by reduction, the wing covers or elytra being short though still performing the same function, since the large wings can be folded and packed away snugly under them.

Still more reduced are certain species of Adranes which live in ants' nests. These are blind, with vestigial mouth parts. They are carefully tended by the ants, and in return they secrete a substance which collects on the tips of the elytra and the end of the abdomen.<sup>2</sup>

Among the beetles some of whose larvae are more or less like the Thysanura, those of the Lampyridae are especially interesting, owing to a peculiar modification in their structure whereby light-giving cells are produced. The common fire-fly, *Photuris pennsylvanica* De Geer, (No. 1089, adult) is luminous in all its stages, though most brilliant in the adult. The light-producing cells are in the abdomen, and they are surrounded by a network of tracheal tubes. The cells contain yellowish white granules which combine with the oxygen brought by the tracheae and thus combustion produces light. This chemical process does not depend wholly upon the life of the insect, since the cells when taken from a dead beetle and crushed in the air are luminous for a time.<sup>3</sup>

<sup>1</sup> Text-Book of Ent., 1885, p. 29.

<sup>2</sup> Can. Ent., XXXIII, Jan., 1901.

<sup>3</sup> See Watase, Woods Hole Marine Biol. Lab., Biol. Lectures, 1895.

The female of *Lampyris splendidula* has neither elytra nor wings; these females, and the larvae of *Lampyris* generally, are luminous and are called "glow worms," though incorrectly, since they are not worms but true insects.

The Scarabaeidae represent the more typical Coleoptera, many of whose larvae are cylindrical and six-footed grubs. The type selected is the common June or May beetle, *Lachnosterna fusca* Fröhl. Its white larva (No. 1090; Pl. 1091, fig. 1) lives in the earth. Its head is small and chitinous, and the thoracic and abdominal segments are wrinkled. This wrinkled appearance is increased by the habit the creature has of coiling and lying partly on one side (fig. 1) in an irregular cavity which it has formed. It also moves on one side, and according to Lockwood<sup>1</sup> the larva of a closely allied form, the brilliant goldsmith beetle, *Cotalpa lanigera* (No. 1093), travels on its back with quite a rapid serpentine movement.

The grub is very destructive, eating the roots of grass, corn, grain, etc. (Pl. 1091, fig. 2). After two or three years the larva makes a well defined oval cavity and lines it with a secretion from its own body; it then changes to a pupa (fig. 3) in which the parts are free. Soon after, the pupa becomes a beetle, which, according to Riley is white and soft at first but remains in the earth until hardened. Often swarms rise from the earth at once, and begin immediately to eat the leaves of trees.

The short body of the beetle (No. 1092; Pl. 1091, fig. 4, dissection of same) like that of the other typical forms is divided into the three regions. The head is small and capable of being withdrawn under the prothorax so far as the eyes; when extended, the short neck allows the head little freedom of motion, as compared with carnivorous insects like the dragon-fly. The prothorax (fig. 4, *p*) is

<sup>1</sup> Amer. Nat., II, 1869, p. 190.

large and, excepting the small mesothoracic scutellum between the bases of the wing covers, is the only part of the thoracic region seen from above. It forms with the head a wedge-shaped portion of the body of advantage to the insect when digging its way through the earth.

When the elytra and wings are removed the small mesothorax (fig. 4, *ms*) and the large metathorax (fig. 4, *mt*) are seen. The junction of the thorax and abdomen is broad like that of most of the types so far described.

The antennae of the Scarabaeidae, the family to which the May beetle belongs, are leaf-like or lamellate at the end and hence the name Lamellicorns often given to the family. The antennae are usually tucked away under the eyes and are extended only when needed.

The mouth parts are of the biting type and are similar to those of the Orthoptera. The six legs are adapted pre-eminently for running. The wing covers or elytra are characteristic organs giving the name of Coleoptera, meaning sheath and wing, to the order. These elytra are usually considered as the anterior pair of wings which have become horny, but in which, according to Dimmock,<sup>1</sup> the remnants of veins can often be seen. According to Comstock,<sup>2</sup> their structure "resembles that of the body wall rather than that of wings, and in some beetles (*e. g.* *Dytiscus*) rudiments [remnants] of the fore wings exist beneath the elytra." The wing covers are of little use in flight and hence the small size of the mesothorax which bears them; on the other hand, the wings are useful flying organs and the metathorax is consequently large and strong.

There is no external ovipositor and the abdomen of the male and female are alike, excepting that in the former the ventral side of the seventh segment has a transverse ridge. Each of the first seven abdominal segments has a

<sup>1</sup> Stand. Nat. Hist., I, 1885.

<sup>2</sup> Manual for the Study of Insects, 1895, p. 494.

pair of spiracles.<sup>1</sup> The May beetle like all beetles is without a stinging organ.

Some of the beetles allied to the Scarabaeidae have greatly developed mandibles like those of *Cladognathus* (No. 1094).

Among the large beetles of the United States is *Dynastes* (No. 1095, larva; No. 1096, *D. tityrus* Linn.). The thoracic and abdominal regions of the larva are immense as compared with the head. The legs are small since this stage of the insect's life is passed in rotten wood.

*Coscinoptera dominicana* Fabr. is an interesting form. It fastens its eggs on long, slender stalks (Pl. 1097, fig. 1; fig. 2, egg, magnified) and its larva (fig. 3) makes a case for itself out of the egg shell and particles of earth (fig. 4) which it carries about. Fig. 5 is the beetle enlarged.

The potato beetle, *Doryphora decemlineata* Say, of the family Chrysomelidae, is another good type of the Coleoptera, but it is much smaller than *Lachnosterna*. The larvae (No. 1098) are short, plump grubs that are extremely active. They burrow into the ground where the pupae transform to the adult (No. 1099, alcoholic specimen; No. 1100, dried).

The larvae of some of the Chrysomelidae when young combine characters of the Thysanuriform type with those of Coleopterous grubs, while the full-grown larvae would be called caterpillars by those not knowing that this term is restricted to young Lepidoptera. The three pairs of legs in the young larva are prominent on each side (Pl. 1101, fig. 2, elm-leaf beetle, *Galerucella luteola* Müll.; fig. 1, eggs of same), while the body is rounded and grub-like. The feet in the full-grown larva (fig. 3), however, are not seen from above but only in a side view and the general aspect is decidedly that of a caterpillar.

When full grown, the larva finds a sheltered place in

<sup>1</sup> Willcox, *The Observer*, July, 1896.



the crevices of the bark or on the ground and transforms to a pupa (fig. 4) which in a shorter or longer time, according to whether the month is July or October, develops into the beetle (No. 1102; Pl. 1101, fig. 5). There may be two and possibly three broods in a season and as both larva and adult feed upon the elm great injury is done.

Still more striking is the caterpillar-like larva of *Haltica chalybea* Ill. (Pl. 1103, fig. 1), the adult (fig. 2) of which is the small shining blue or sometimes greenish beetle found on grape vines in early spring.

The caterpillar-like larvae of beetles may be hairy in some species and naked in others. An illustration of the former is found in the carpet beetle, *Anthrenus scrophulariae* Fabr. (No. 1104; Pl. 1105, fig. 1), of which, although its shape is unlike that of a caterpillar, the feet are small and hidden from a dorsal view. This being the case, it resembles more closely a hairy caterpillar than a Thysanuriform larva or a typical Coleopterous grub. It is this larva which does most of the damage to carpets and woolen goods. The larval skin serves as a case for the pupa (fig. 2, dorsal view with the larval skin split down the back; fig. 3, the pupa removed from skin). If the pupa transforms normally, its skin splits lengthwise and it crawls out leaving the two skins.

The wing covers of the beetle are provided with scales of different colors, black, brick-red, and white (No. 1106). The beetles (No. 1106; Pl. 1105, fig. 4) leave our houses and feed upon the blossoms of rhubarb; they are especially fond of single tulips, particularly the yellow shades.<sup>1</sup> Unfortunately for us, the beetles return to our houses and lay their eggs upon the food which their young love best.

The larvae of some species of the family Dermestidae have a brush of long hairs at the end of the body (Pl.

<sup>1</sup> 13th Rep. State Ent., N. Y. State Mus., 1897, p. 359. This pamphlet is reprinted from the 51st Ann. Rep. N. Y. State Mus., I.

1107, fig. 1, *Attagenus piceus* Ol.). In this species the larva is a reddish brown, while the pupa (fig. 2) is white covered with a delicate pubescence. The adult (No. 1108; Pl. 1107, fig. 3) is nearly black and is common on window sills in spring and early summer.

Many of the Elateridae or spring-beetles have naked larvae, as seen in *Alaus oculus* Linn. (No. 1109, larva, pupa, and adult). The adult is conspicuous on account of the scales on the prothorax which are arranged in two black velvety spots encircled by white rings. The beetles of this family, when they have fallen on their backs, can right themselves by springing into the air.

Other Elaterid larvae are long, cylindrical, and wire-like in shape with a smooth, tough cuticle, such as the larva of *Ludius attenuatus* Say (No. 1110).

Phosphorescence is not limited to the Lampyridae among insects but is found in members of other families. The most beautiful luminous insect we have seen is *Pyrophorus noctiluca* Linn. (No. 1111, *P. physoderus*) of the Elaterids. When flying or when disturbed, its light is given out from two spots on the prothorax and one on the ventral surface. This light is not intermittent as in the fire-fly, but is steady, strong and of an exquisite greenish tint.

The larvae of some of the Tenebrionidae, *Eleodes gigantea*, for instance, have the abdominal segments flattened at first, but gradually after several moults of the skin they acquire the typical wire-like shape and become darker in color.<sup>1</sup> No. 1112 is the adult of *Eleodes tricostata*.

*Tenebrio molitor* Linn. (Pl. 1113, fig. 1, larva; fig. 2, pupa; fig. 3, adult; No. 1114, adult) is a well known genus of this family, since its larva, one of the so called "meal worms," is often found in flour and meal.

The life histories of the parasitic Coleoptera, Meloidae

<sup>1</sup> Bull. Brooklyn Ent. Soc., I, no. 1, 1878, p. 19.

and Stylopidae, are instructive inasmuch as they throw light on the life history of the group, while they also illustrate the changes that parasitic habits may produce on insect structure.

The Meloidae are represented by *Epicauta vittata* Fabr. (Pl. 1115; No. 1116). It lays its eggs (Pl. 1115, fig. 1) in the ground, generally near the egg-pods of locusts. In about ten days the larva, known as the triungulin (fig. 2), hatches. It is soon light brown in color and very active. Its flattened body with its well developed legs and its cerci give it a Thysanuriform aspect. This larva burrows through the mucous neck of a locust's egg-pod, *Melanoplus differentialis* (fig. 3, egg-pod of *M. differentialis*), and sucks out the contents of an egg. In time the skin splits along the back and the second larva (fig. 4) appears with the legs much reduced in size. Fig. 5 is a side view of this same larva, showing its natural position within the egg-pod. The last stage of the second larva is shown in fig. 6. It now leaves the egg-pod and forms a cavity in the earth in which it lies motionless, and is known as the coarctate larva, called by Fabre pseudopupa (fig. 7, with the skin adhering behind; fig. 8, dorsal view of same). The legs in this stage are little more than tubercles. The insect usually hibernates in this condition. In spring the third larva appears, which is very similar to the coarctate larva excepting that it is active; but, although active, it seems to take little or no nourishment. In a few days this larva transforms to a pupa (fig. 9, pupa of *Epicauta cinerea* Forst.) and in five or six days the imago (No. 1116; Pl. 1115, fig. 10) is fully developed.

Thus it is seen that the Thysanuriform larva with well developed legs becomes, by the laws of variation and adaptation governing animals, a creature with a grub-like form and small tuberculous legs. Specialization by reduction, however, is not carried so far as to produce a footless larva.

The young of Meloë (No. 1117), a common genus in Massachusetts, eat the eggs of the bee (*Anthophora*) to which they are borne by clinging to the hairy body of the mother. The second larva feeds upon the honey in the cells intended for the larval bee. The coarctate stage gives rise to an active fourth (usually called the third) larval form which eats its way out of the cell and becomes a pupa from which the dark blue beetle emerges. The latter has small elytra and no wings, while another member of this family, *Hornia minutipennis* Riley, is without wings in both the male and female and practically without elytra as these are extremely small.

One of the members of this family, *Nemognatha* (No. 1118), is of especial interest since its mouth parts are similar to those of the Lepidoptera. The two maxillae are long and hollowed out on the inner side so that, when pressed together, they form a sucking tube for obtaining the sweet juices of flowers.

Specialization by reduction is carried further in the Stylopidae than in the Meloidae, since the larvae which are at first active Hexapod insects finally become footless grubs, while the adult female Stylops is little more than a bag-like creature without legs or wings. Pl. 1119, fig. 1, represents the young active larva of *Stylops childreni* Westw. The adult male Stylops (fig. 2; fig. 3, side view; Pl. 1120, enlarged more than fig. 2 of Pl. 1119) is unique among insects, since it possesses a pair of club-shaped organs on the mesothorax which resemble the metathoracic halteres of the most specialized group of insects, the Diptera. The wings are large and fan-shaped. The female Stylops is parasitic in the abdomen of bees (Pl. 1119, fig. 4, dotted line shows its body in natural position; fig. 5, taken from abdomen). It is without compound eyes, legs, or wings, and is viviparous.

We now come to those Coleoptera which have skipped the Thysanuriform larval stage and also the active grub stage, and which at the start have only the vestiges of thoracic feet or are wholly without these organs.

Most of the Cerambycidae are tree-borers in the larval stage and the young live in narrow galleries where there is little need of feet. These organs, therefore, are reduced in size so that they are not seen from above (Pl. 1121, fig. 1, *Orthosoma brunneum* De Geer), but only in a ventral view (fig. 2, probably the same species).

The structure of these small thoracic legs is better shown in Pl. 1122, fig. 2, which is the limb, greatly enlarged, of the oak pruner, *Elaphidion villosum* Fabr. (No. 1123; Pl. 1122, fig. 5). The larva (fig. 1) burrows in the wood under the bark and packs the burrow with its sawdust-like castings. It selects, as a rule, a small twig consuming the wood in such a way that the winds easily sever the twig so that it falls to the ground with the larva. The opening at the severed end the larva plugs with castings and in this closed cell transforms to a pupa (fig. 3, longitudinal section of twig; fig. 4, cross section of same) which in a shorter or longer time, according to temperature, changes to a beetle that cuts its way out through the plug of castings.

Some of the Cerambycidae have footless grubs like the *Saperda candida* Fabr., or the round-headed apple-tree borer (Pl. 1124, fig. 1, dorsal view; fig. 2, side view). It feeds when in the larval state upon the sap-wood, but by the end of the second year it reaches the solid heart-wood. The third year the larva gnaws outward to the bark and makes a cell for itself. Here the pupa (fig. 3) transforms to the adult (No. 1125; Pl. 1124, fig. 4) which cuts its way out of the tree by its sharp mandibles.

*Chalcophora virginica* Drury (No. 1126), of the family Buprestidae, is another species with footless larvae. These live in the pine and have the forward part of the body broad and flat. The adults have brilliant metallic hues (see No. 1127, ventral side of same species).

The Ambrosia beetles of the Scolytidae are interesting forms, since, according to Hubbard,<sup>1</sup> they exhibit charac-

<sup>1</sup> U. S. Dep. Agric., Bull. Div. Ent., n. s., no. 7, 1897, p. 9.

teristics in the care they take of their young that are utterly foreign to most Coleoptera and such as we shall find farther on in the social Hymenoptera.

The female of *Platypus compositus* deposits her eggs in the galleries which are made by the beetles in the heart-wood of trees. Here young (Pl. 1128, fig. 1) and old (fig. 2) live together, and the galleries are always kept clean and free from wood-dust. The larva is footless, but its ridges and tubercles enable it to move rapidly through the galleries. It feeds upon Ambrosia, a kind of fungus (fig. 3) which is carefully propagated by the beetles as their only food supply. The species of Ambrosia eaten by *Platypus* has erect stems with swollen cells or conidia at their ends. Hubbard says that "young larvae nip off these tender tips as calves crop the heads of clover but the older larvae and the adult beetles cut the whole structure down to the base from which it soon springs up afresh." The Ambrosia is started by the mother beetle upon a carefully packed bed or layer of chips. In some species it is grown only in certain brood chambers, and in others "it is propagated in beds near the cradles of the larvae." The excrement of the larvae is used to form new beds for the propagation of the fungus. The older larvae assist their parents in excavating the galleries; in this case not only do the adult beetles care for their young, but the larvae "show evident regard for the eggs and very tender young which are scattered at random through the passages, and might easily be destroyed by them in their movements. If thrown into a panic the young larvae scurry away with an undulatory movement of their bodies, but the older larvae will frequently stop at the nearest intersecting passage" to let the little ones pass, and will "show fight to cover their retreat."<sup>1</sup>

The beetles that are most specialized by reduction, are the Curculionidae or weevils. The tiny strawberry weevil,

<sup>1</sup> *Loc. cit.*, p. 15.

*Anthonomus signatus* Say (Pl. 1129, figs. 1-4, greatly enlarged), although only one tenth of an inch in length, is an extremely clever insect and exhibits the characters of the family.

The female, with her long snout, parts the petals of a nearly matured bud and in the hole thus made deposits her egg. The sepals and petals close, never to open into a blossom. The beetle then crawls, according to Chittenden, to the stem below the bud and with her microscopic but scissors-like mandibles cuts it in such a way that the part bearing the bud hangs by a mere shred and soon falls to the ground (fig. 1, showing buds ready to fall). The development of the bud is thus arrested long enough for the larva to feed on the pollen and the food is kept moist by the earth. The larva (fig. 2, full grown) is footless and fleshy tubercles have taken the place of the jointed legs. After devouring the pollen, it feeds upon some of the harder parts of the bud. In three or four weeks it utilizes the more or less hollowed-out bud for a cocoon, transforming to a pupa (fig. 3) and finally to a beetle (fig. 4). The latter feeds a few days upon the strawberry blossoms but seldom eats the leaves and never the fruit. It would seem that hibernation begins in July, as the beetles are seldom seen after the middle of this month.

The structural features seen in the strawberry weevil are peculiar to most weevils. The larvae are footless though sometimes tubercles or bristles are developed. The young larva of *Epicaerus imbricatus* Say (Pl. 1130, fig. 1, side view of young larva; fig. 2, adult, both enlarged), has a pair of stout bristles on each thoracic segment, and these aid in locomotion. In the adult the head is extended into a longer or shorter snout, which carries the straight or elbowed antennae. The mouth parts are usually reduced in size and are borne at the end of the snout. The latter organ is of unusual interest, since it has acquired the function of an ovipositor, and for this

reason doubtless has grown remarkably long in some species.

The elytra are more chitinous than in most beetles, being so hard that it is difficult to thrust an insect pin through them. They are sometimes furnished with scales, as in the diamond weevil, *Entimus imperialis*, for instance, which are extremely brilliant microscopic objects.

*Cionus scrophulariae*, like some other weevils, spins a cocoon from a secretion of its body. This cocoon is strikingly like the seed capsule of the *Scrophularia nodosa*, the plant upon which *Cionus* feeds, and it is usually fastened to a pedicel of the seed pod.

The chestnut weevil, *Balaninus proboscideus* Fabr. (formerly *B. caryatipes* Bohm.), (No. 1131) is exceptional among insects owing to the fact that its mandibles are vertical instead of horizontal. Its proboscis is also longer than in other weevils, often being in the female twice the length of the body. It is used for piercing the burr and the husk of the chestnut when both are young. One or more eggs are then laid in the nut and the small puncture soon heals. The footless larva feeds upon the chestnut until ready to pupate, when it leaves the nut and enters the ground.

#### Order 11. — NEUROPTERA.

The Neuroptera includes insects which have Thysanuriform larval characters, although combined with these characters are many peculiar modifications of structure that ally the insects with the more specialized order, the Lepidoptera.

The larva of *Corydalus cornutus* Linn. (No. 1132), of the family Sialidae, has the elongated body, the distinct and freely movable thoracic and abdominal segments, and the three pairs of well developed legs of the Thysa-



núra. It also has the biting mouth parts of the generalized insects. But in addition to these structural features, *Corydalus* has nine pairs of long branching filaments extending from the sides of the abdomen, and seven pairs of sponge-like masses also used for respiration (see No. 1132), or it may be to aid the animal in attaching itself to the surface of stones at the bottom of swift-flowing streams.<sup>1</sup> Besides these branchial organs the larva is provided with the tracheae which its ancestors possessed, and which are useful during the pupal stage that lasts about a month and is spent in a cell in the earth under some stone or log. The adult (No. 1133, ♂; No. 1134, ♀) is a giant among insects. The mandibles of the female are used for obtaining and masticating food, while those of the male are weapons and also clasping organs. The wings expand six inches (Packard) but as the thoracic segments which bear them are unconsolidated, we should predict that the flight of the insect would be slow, and this is the case.

The wings have an open network of veins. The name Neuroptera, meaning nerve and wing, was formerly given to an order of insects whose typical form was the dragon-fly, and the significance of the term is much more apparent when we consider the fine network of veins peculiar to the dragon-fly wing than it is when we examine the *Corydalus* wing. Now, the dragon-flies are placed in an order by themselves, the Odonata, and the name Neuroptera is retained for the Sialidae, Hemerobidae, and the like, which pass through an indirect development.

One of the interesting Neuroptera is the lace-winged fly or aphid-lion, *Chrysopa perla*. The female has the habit of fastening her eggs at the tip end of long stalks. In order to do this she secretes from her abdomen a drop of a tenacious substance which she draws out into a thread; at the end of this thread she places a knob of

<sup>1</sup> Riley, 9th Rep. Benef. and Inj. Insects Mo., 1877, p. 128.

cement to which she attaches an egg (No. 1135; Pl. 1136, fig. 1). The larva (fig. 2) crawls out and is Thysanuriform in general aspect. The mouth parts, however, are specialized for sucking. Each mandible is grooved on the lower side, and the maxilla fits into it in such a way that a tube is formed through which the blood of the prey is sucked. The eggs are laid where Aphides abound, so that the larvae find their food close at hand. When ready to transform, the larva spins a silken cocoon (fig. 3). The adult (No. 1137; Pl. 1136, fig. 4) cuts a lid in this cocoon and crawls out. It has brilliant golden eyes, biting mouth parts, and gauzy wings of large size compared with the body; but the flight of the insect is slow.

Among the Coleoptera we have found the larvae of the tiger beetles watching for their prey in burrows; so the larval *Myrmeleon immaculatus* De Geer, or ant-lion of the Neuroptera digs a pitfall (Pl. 1138, fig. 1, lower portion, showing insect; fig. 1 a, upper portion of same) in dry loose sand and buries itself at the bottom with the exception of its stout mandibles which are wide apart ready to seize whatever insect falls in. The mouth opening of *Myrmeleon* is not of the usual character but is compressed and its mandibles are like those of *Chrysopa*, so that the unfortunate victim that has fallen down the pit is held by the mandibles until its juices are sucked out, when the empty skin is thrown some distance beyond the pit by means of the ant-lion's head.

The mature larva makes a cocoon by fastening grains of sand together with silk spun from its spinneret. The adult (No. 1139; Pl. 1138, fig. 2) has biting mouth parts. Though its wings are large, its flight is weak and it flies chiefly at night. The antennae of the ant-lion are slightly swollen at the ends, but this tendency is carried so far in *Ascalaphus* (Pl. 1140) that it possesses knobbed antennae like those of butterflies of the order Lepidoptera. In short, this insect strikingly resembles a butterfly, hav-

ing besides the antennae a short, thick abdomen and large, gaily colored wings.

A good example of differentiation in the second pair of wings is found in *Nemoptera ledereri*. These organs are extremely long and narrow, swelling out at their ends and appearing like paddles. They doubtless aid the insect in flying.

As the development of *Epicauta* threw light upon the life history not only of the Coleoptera but also of the whole class of Insecta, so the development of *Mantispa* illumines the life history of the Neuroptera and strengthens our hypothesis in regard to the life history of insects in general.

*Mantispa* begins its life as a Thysanuriform larva (Pl. 1141, fig. 1, *M. styriaca* enlarged). This larva finds an egg-case of a spider — it may be a *Lycosa* — and making a small opening, crawls into the sac. There, as the eggs hatch, it devours the young spiders. The habitat within the spider's egg-case causes marked changes in structure. The body becomes caterpillar-like in form (fig. 2) and the head small. The legs are reduced in size and in the mature larva are useless vestiges, while the antennae are shortened. The larva spins a cocoon within the egg-sac and the pupa develops under the larval skin. The adult No. 1142, having much the same habit as the praying mantis (see Nos. 1012, 1013), has a similar structure. The prothorax is greatly extended and the fore legs are attached at the forward edge. These legs are long and are adapted for seizing and holding prey, being held in the same attitude as in mantis.

#### Order 12. — MECOPTERA.

The larvae of the Mecoptera, as represented by the type, *Panorpa communis* Linn. (Pl. 1143, fig. 1), are caterpillar-like in general aspect. In fact, all the Mecoptera larvae,

so far known to us, are caterpillar-like in the young as well as in the mature larval stage, though some species may yet be found that passes through a transient Thysanuriform stage. This is the more probable, since the Mecoptera have biting mouth parts and in this way are more generalized than the Lepidoptera, a group which we shall see has the Thysanuriform stage represented in the life history of one of its generalized members (see p. 461).

The larva of *Panorpa* (fig. 1) is not only provided with thoracic legs, but it has also eight pairs of jointed prop-legs on the abdomen, and an organ called the anal fork at its end (see fig. 1). The prop-legs seem to be of little use,<sup>1</sup> but locomotion is accomplished by the thoracic legs and anal fork, the latter being capable of supporting the body. Besides the prop-legs, the young larva has spines which disappear in the mature larva, excepting those on the eighth, ninth, and tenth segments. Like caterpillars, *Panorpa* has a pair of spiracles in the prothorax, but none in the mesothorax or metathorax, while there is a pair in each of the first eight abdominal segments.

The larva burrows in the ground and there becomes a pupa. The head of the adult (No. 1144, ♂, ♀; Pl. 1143, fig. 2) is extended into a beak, at the end of which are the mouth parts. According to Felt,<sup>2</sup> feeding is a combination of biting and sucking, and only wounded or dead animals were eaten by the species under observation.

The long abdomen of the male is provided with a pair of forceps-like claspers and is bent over the back, giving the insect somewhat the appearance of a scorpion, although the two animals are very different.

Another member of the Mecoptera is *Bittacus tipularius* which is a slender insect with remarkably long legs, but without the forceps-like abdominal appendages of *Panorpa*.

<sup>1</sup> Felt, 10th Rep. N. Y. State Ent., 1895.

<sup>2</sup> *Loc. cit.*, p. 466.

The legs are, in fact, so long that the insect never stands upon them, and therefore never alights but suspends itself from a twig by its long fore legs, sometimes using also its second pair. In this situation it has cleverly adapted its hind legs for seizing, using them as hands (Brauer). The mouth parts are better fitted for piercing than those of *Panorpa*, and living insects, preferably flies, are the diet.

The wingless condition is represented in the Mecoptera by the female *Boreus hiemalis* (Pl. 1145), which is sometimes found on snow. The head is extended into a beak, as in the other Mecoptera, and the female has an external ovipositor while the hind legs are adapted for leaping.

#### Order 13.—TRICHOPTERA.

The Phryganidae or caddis-flies are the only members of the Trichoptera. The larvae are caterpillar-like from the start, although their aquatic life (together with the habit of carrying a protective case about with them) has caused such modifications in structure that they are not so strikingly like caterpillars as the larvae of Mecoptera. They are, however, nearer the caterpillar than the Thysanuriform type.

The adults do not closely resemble the imagoes of any of the orders so far described, but their resemblance to moths of the order Lepidoptera is most marked.

*Anabolia* is a common genus in New England. The forward part of the body of the larva (No. 1146; Pl. 1147, fig. 1) is chitinous owing to exposure, while the posterior part, being covered with a case, is soft and light colored. The case (No. 1146; Pl. 1147, fig. 2) in this genus is made of sticks and stones, and is fastened to the body by means of two hooks at the end of the abdomen, while it is probable that the three tubercles on the first abdominal segment also aid in this work. As the larva

drags its case about with it by means of its legs and sometimes its mandibles, these parts are well developed. The case is large enough for the respiratory filaments on each side of the abdomen (fig. 1) to move freely in the water. In fact, the larva is able to turn itself in its case so that its head appears indiscriminately at either end.<sup>1</sup> The larva is exceptional in having no antennae and at the same time small eyes, for when the former organs are absent the eyes are usually well developed.

When the larva is ready to become a pupa (fig. 3), it closes both ends of its tube with silk spun from the spinneret which is near the mouth, as in Lepidopterous caterpillars. During the pupal stage the antennae develop, the mouth parts become reduced in size, though the mandibles still persist, and the respiratory filaments disappear.

The appendages of the pupa are free as in all the pupae so far described.

The adult (Pl. 1147, fig. 4) has a small head, a collar-like prothorax, a comparatively large mesothorax, and a slender abdomen — characters which we shall see are shared by moths. The caddis-fly (No. 1148, *Neuronia*, one of our largest species) also possesses hairy wings (hence the name *Trichoptera*, meaning hair and wing), which sometimes become scale-like. The two wings on each side are fastened together so that they act as one thereby increasing the power of flight. When at rest the wings are held roof-like over the body.

The mouth parts of the adult are transitional between the biting and sucking type. The mandibles are obsolete, and in some genera, according to Hagen,<sup>2</sup> the mouth

<sup>1</sup> McLachlan, *Trans. Ent. Soc. London*, (3), V, 1865; p. 11.

<sup>2</sup> Quoted by Packard, *Ent. for Beginners*, 1889, p. 90.

organs form a proboscis which is adapted for probing flowers and obtaining the sweet nectar.

The cases of caddis-flies are exceedingly varied and ingenious little objects. *Leptocerus* (Pl. 1149, fig. 1) builds a straight tube of sand. *Limnephilus vittatus* Fabr. has a slightly curved tube of the same substance (fig. 2), while *Helicopsyche* makes the young or nepionic part of its case straight, while the older or ephebic portion (fig. 3; Pl. 1150, fig. 2) is coiled like a snail shell. Fritz Müller<sup>1</sup> says, that "when preserved in adult specimens the oldest portion [in reality the young shell] peeps out from the top of the heliciform case like a little chimney."

The body of the caddis-fly is not spiral like that of the snail but symmetrical like that of other Trichopterous larvae, as shown in Pl. 1150, fig. 1. When ready to transform, the larva (fig. 2, in its case) spins an operculum (fig. 3) which has concentric lines like many of the opercula of Gastropods, but unlike the latter this operculum has a slit for the admission of water.

Some caddis-flies, like *Setodes tineiformis*, do not select foreign substances for their cases, but spin them entirely of a secretion from their own bodies, popularly known as "silk."

The caddis-fly larvae already described are free-moving and live in comparatively still water, but there are others living in swift flowing streams that attach their habitations to stones and the like. One of the most ingenious of this group is *Hydropsyche* (Pl. 1151). It builds its case of sand or of bits of plants, fastening it to a stone so that the latter forms the lower part of the case (Pl. 1152). Close to the opening of the case it erects a vertical framework across which it stretches a net. The food brought down by the current is caught by the net and the larva can eat its meal without wholly leaving its house (see Pl. 1152).

<sup>1</sup> Trans. Ent. Soc. London, 1879, p. 132.

In the family of Limnophilidae, the members of which have slightly curved horn-like cases, as seen in Pl. 1153, fig. 2, there is one genus, *Enoicyla pusilla* Burm. (Pl. 1153, figs. 1-3), that lives on the land. This is the only Trichopterous insect so far known that is terrestrial. The figure of the larva (fig. 1; fig. 2, larva in its case) does not exhibit any vestiges of respiratory filaments which we should expect to find if the ancestors were aquatic. It may be, however, that a sufficient period of time has elapsed for the terrestrial habitat to cause the complete disappearance of the branchial filaments. This seems the more probable since the female (fig. 3) is specialized by reduction, having lost both pairs of wings. If this is not the case, then the insect is primary and should be placed as the most primitive of the Trichoptera.

#### Order 14. — LEPIDOPTERA.

The caterpillar-type of larva has now become so fixed in the insect organization that it is found with scarcely an exception in the members of this immense order of Lepidoptera. The variations that occur are mainly in the minor details of structure, while the fundamental form and characters remain essentially the same. Although this is true speaking broadly, we shall see farther on that there is one moth, *Melittia satyriniformis* Hbn, which throws light on the genealogy of the order, since it passes through a stage when first hatched that is comparable with the Thysanuriform stage of the more generalized insects. This stage, however, is brief, and the larva has attained the caterpillar form when half grown. As we have stated elsewhere the common custom of calling caterpillars "worms" is misleading and therefore has not been followed in this work. The word was given because the caterpillar, like the worm, is cylindrical and segmented, but if all cylindrical, segmented animals were to



be called worms, our classification would be most erroneous. When it is borne in mind that the caterpillar is a specialized animal, as compared with the worm, having well developed mouth parts, jointed legs, adaptive prop-legs, and embryo wings, it becomes evident that the retention of "worm" as descriptive of young Lepidoptera leads only to a confusion of ideas which is always to be avoided.

The moths constitute the more primitive group of the Lepidoptera or scaly-winged insects, while the butterflies are more specialized. This arrangement, based on structure and development, is in harmony with the palaeontological record of the order.

*Fugatae.* *Eriocephala calthella* possesses characters allying it with the Neuroptera, Mecoptera, and Trichoptera. The caterpillar (Pl. 1154,) is provided with eight pairs of abdominal prop-legs, each ending in a curved spine and resembling the similar prop-legs of the *Panorpa* larva. It is specialized by addition in possessing rows of odd ball-like appendages. The adult has the collar-like prothorax, while the mesothorax and metathorax are long and slightly consolidated. These two thoracic segments are of nearly equal size, like the two pairs of wings which they bear. These wings are similar in their venation and are fastened together by a membranous lobe, the jugum (see Pl. 1157, fig. 1, *j*), extending from the posterior basal part of the fore wing; in this way these moths resemble the Trichoptera.

The wings are covered with scales or modified hairs, the common character of the order, and in addition to these scales there is a covering of fine hairs, which, according to Kellogg<sup>1</sup> are found in the *Jugatae* but not in the more specialized *Frenatae*. A similar coating of hairs is found in the Trichoptera, which indicates that it

<sup>1</sup> Kansas Univ. Quarterly, III, no. 1, 1894, p. 80; also Amer. Nat., XXIX, 1895, p. 250.

is a generalized feature and was probably possessed by the stem form of the Lepidoptera.

The mouth parts of *Eriocephala* are unique among Lepidoptera. The first pair of maxillae have an inner lobe, the galea (Pl. 1155, fig. 2, *g*) and an outer lobe, lacinia (fig. 2, *l*), besides the palpi (fig. 2, *mxp*). These lobes are homologous with the same parts in the mandibulate insects. *Eriocephala* is the only Lepidopteran known that possesses the lacinia, as it is usually the two galeae which unite to form the sucking tube.<sup>1</sup> According to Chapman<sup>2</sup> these moths use the great claw-like maxillary palpi with sharp knife-points to scrape and tear at both the pollen of the stamens and the surface of the petals, in the latter case perhaps collecting fallen pollen.

The second pair of maxillae are also provided with two lobes and a palpus. Besides the maxillae there is a pair of toothed mandibles (fig. 1) which are used as in the biting insects.

*Hepialus argenteomaculatus* is another moth belonging to the Jugatae. The caterpillar is naked and has the three pairs of thoracic legs and five pairs of prop-legs. It pupates in the earth like many beetles. The hind wings of the adult (No. 1156) are much longer than in most Lepidoptera, but the venation of the wings is simple (see Pl. 1157, figs. A, B, *H. gracilis*). As in *Eriocephala* the fore and hind wings are fastened by the jugum (fig. A, *j*).

The remaining moths and butterflies belong to the Frenatae, since instead of a jugum for fastening the wings together, many Frenatae have a frenulum which is a strong spine in the male and a bunch of bristles in the female borne on the front edge of the base of the hind wing (Pl. 1158, fig. B, *f*). In the male the frenulum fits into a hook on the lower surface of the fore wing (fig. A) but the female seldom has this hook.

<sup>1</sup> Packard, Amer. Nat., XXIX, 1895, p. 637.

<sup>2</sup> Trans. Ent. Soc. London, 1894, p. 338.

According to Comstock, whose natural classification of the Lepidoptera we have adopted essentially, the Frenatae which do not now possess a frenulum (some moths, all skippers, and butterflies) have gradually lost it, owing probably to the large development of the front edge of the basal portion of the hind wing which fits under the fore wings so closely that unity of action is made possible. The frenulum, not needed, would gradually tend to disappear.<sup>1</sup>

*Frenatae.* The larvae of the flannel moths of the family Megalopygidae have seven pairs of prop-legs besides the three pairs of thoracic legs (No. 1159, upper left hand specimen of *Megalopyge crispata*). They make a trap-door cocoon (No. 1159, lower left hand specimen). The adult (No. 1159, right hand specimen) is covered with crinkly hair and hence the popular name.

The Psychidae remind one of caddis-flies, since their caterpillars make a bag and cover it with sticks (No. 1160, *Psyche pulla*) which they carry about with them. The adult (No. 1161, ♂) is one of the small moths. The wingless female is specialized by reduction and is an illustration of suppressed development. This reduction is clearly shown in the evergreen bag-worm, *Thyridopteryx ephemeriformis* Haw. (Pl. 1162, figs. 1-6). If the larva (fig. 1; fig. 2, in case of "bag") is to become a male (according to Riley the caterpillars are all alike until the pupal stage is reached, when the sexes are differentiated), the development proceeds as in most Lepidopterous in-

<sup>1</sup>Dr. A. S. Packard (Mem. Nat. Acad. Sci., VII, Monograph 1, 1895, p. 57) objects to this division of the Lepidoptera into the Jugatae and Frenatae on the ground that the characters are too slight, considering that the structure of the mouth parts and more especially the characters of the pupa are of fundamental importance in working out the phylogeny of the group.

For our present purpose, however, the classification given by Comstock is more simple and more in harmony with that of the other orders of insects, while at the same time it is based on philosophical reasoning.

sects and the pupa (fig. 3) becomes a winged male (fig. 4); but if the larva is to be a female, it remains in the pupa-case (fig. 5, female with split pupa skin) and becomes little more than an egg-sac (fig. 6). Its legs and antennae are lost and the wings never develop; in fact, it has no external features that would place it in the order Lepidoptera.<sup>1</sup> When egg laying is accomplished, little is left of the body of the parent. The "weather-beaten bags," full of yellow eggs, are tightly fastened to the twigs of trees and in this secure situation usually pass the winter successfully.

Other moths belonging to the generalized Frenatae and affording illustrations of specialization by reduction are the Cossidae or carpenter moths, the larvae of which are borers. Like the young of the Cerambycidae or boring beetles these larvae are more or less grub-like in form, and, although thoracic legs and prop-legs are present, they are reduced in size and are not seen in a dorsal view (Pl. 1163, fig. 1, young caterpillar of *Cossus centerensis* Lintner, or the poplar goat moth; fig. 2, mature caterpillar, three years of age). The larvae excavate burrows in wood by means of their strong black mandibles, and one has been known to bore through a large leaden bullet which was embedded in an oak tree.<sup>2</sup>

At the end of three years a pupa cell or cocoon (fig. 3) is formed which is apparently an enlarged and more carefully finished burrow. Filling the exit end are coarse and fine wood-scrapings through which the pupa (fig. 4, ♀) passes to the exterior where it becomes the winged insect (fig. 5, ♀, showing ovipositor).

The reduced condition of the legs is carried still further in the Eucleidae or slug caterpillar moths. In these larvae neither legs nor prop-legs can be seen in a side view and the larva appears to be legless. The prop-legs, in

<sup>1</sup> Lintner, 1st Ann. Rep. Ins. N. Y., 1882, p. 82.

<sup>2</sup> U. S. Dep. Agric., Div. Ent., Bull. 10 (n. s.), 1898, p. 88.

fact, should hardly be called by the name, since they are mere swellings.

The more specialized Frenatae may be divided into two groups: one represented by the Orneodidae, Pyralidae, Tortricidae, Tineidae, and Sesiidae, and the other by the so called frenulum conservors and the frenulum losers.

The larvae of the plume moths or Orneodidae spin no cocoon but they often fasten themselves within a curved leaf, thereby showing a tendency towards cocoon making. The adults (No. 1164, *Orneodes hexadactyla* Linn.) of some species have each of the four wings divided into six parts, giving a feathery appearance to these organs of flight.

The Pyralidae are especially interesting since certain larvae of this family have become adapted for aquatic life. Tufts of respiratory filaments or gills which are supplied with special air-tubes occur on each side of the body (Pl. 1165, fig. 1, *Paraponyx obscuralis* Gr.; fig. 2, respiratory filament). The air contained in the water passes through the walls of the filament and supplies the tubes. These caterpillars, according to Hart,<sup>1</sup> are usually concealed by leaves which the insect has fastened together with silk; when these hiding places are broken up, the caterpillars swim about in the water. The larva spins a dense cocoon. The pupa (fig. 3) is without gills, but has conspicuous spiracles on either side. According to Miall<sup>2</sup> the cocoon of *Paraponyx stratiotata* though immersed in water, is filled with air, and the facts tend to prove that the spiracles of the pupa are used in respiration.

The larvae of the Tortricidae have the habit of rolling up leaves which serve both for a habitation and for food. Here they live together in companies. When ready to transform the pupae cling to the surface of the nest, while the winged insects fly away leaving the empty pupa skins as seen in No. 1166.

<sup>1</sup> Bull. Ill. State Lab. Nat. Hist., IV, 1895, p. 167.

<sup>2</sup> Nat. Hist. Aquatic Insects, 1895, p. 233.

The young *Tortrix testudinana* has no prop-legs, while the six thoracic legs are so small that they are difficult to perceive and are of little use. No. 1167 is an adult Tortricid, *Cacoecia rosaceana*.

One of the best known families of moths is the Tineidae, represented by the familiar clothes moth, *Tinea pellionella* Linn., and by *Coptodisca* (= *Aspidisca*) *splendoriferella* Clem.

*Tinea pellionella* Linn., produces at the north but one generation in a year. Under normal conditions the eggs are laid from May to August, but in furnace-heated houses the moths are often seen in April, and sometimes as early as March, so that the eggs in these cases are laid earlier. In about a week the eggs hatch and the larvae (Pl. 1168, fig. 1) begin to feed at once. They can live, if necessary, upon almost any dry animal matter, but since the earliest times they have preferred to infest our houses and feed upon woolen goods, fur, feathers, and even cotton cloth. The larvae do all the damage. As soon as hatched, the larva makes a protective case for itself from the material on which it feeds. This case (fig. 2) it seldom leaves but as the animal grows larger it increases the size of its protective covering by slitting the edge and setting in gores. By turning about in its case it is able to do this at each end.

The larva reaches its full size toward winter; it then finds a safe place where it fastens itself securely and in its closed case remains torpid till spring. The moth (No. 1169; Pl. 1168, fig. 3) is dull-colored and expands about one half inch. Its mouth parts are in such a vestigial condition it cannot obtain food and after egg-laying is completed it dies.

*Coptodisca* (= *Aspidisca*) *splendoriferella* Clem., when a larva (Pl. 1170, fig. 1), lives in apple tree leaves, mining the parenchyma between the two layers (fig. 2). In the autumn it makes a case for itself from the layers of the leaf and travels about (fig. 3), selecting a spot on the

trunk or branches where it can spend the winter. Several of these attached hibernating larvae are seen on the branch in fig. 2, and the larva with the case removed in fig. 4. In the spring the larva changes to a pupa (fig. 5) and finally becomes the winged adult (fig. 6).

The habit of leaf mining in the larval state has brought about a reduction of the locomotor organs of *Coptodisca*, so that, according to Clemens,<sup>1</sup> there are no thoracic legs but rather cup-like depressions on both the ventral and dorsal side which are capable of contraction and expansion. Neither are there prop-legs, but in their places are folds of the integument which act as substitutes for these organs.

This tendency towards reduction and loss of the legs is carried so far that in *Phyllocnistis*, according to the same author,<sup>2</sup> not only are there no legs nor prop-legs, but voluntary motion has almost wholly ceased.

The Sesiidae or clear-winged moths are represented by *Melittia satyriniformis* Hbn. (Pl. 1171, figs. 1-7). This genus is especially interesting since the newly hatched larva (fig. 1) is similar to the Thysanuriform stage of the more primitive insects. The shape of its body, the three pairs of legs which, though small, are plainly seen from above extending outward on either side of the thorax, the bristles at the posterior end of the body, are all characters suggestive of the Thysanura and the Thysanuriform stage of development. This stage, however, is quickly passed over, so that the half-grown larva (fig. 2) has the caterpillar form. The mature larva (fig. 3) is a borer in the hollow stems of the squash vine, and it shows adaptation to its habitat by the reduced condition of the legs.

Like many beetles, *Melittia* descends into the earth to

<sup>1</sup>U. S. Dep. Agric., Rep. of Entomologist, by Comstock, 1879, p. 213.

<sup>2</sup>*Tineina* of N. A., 1872, p. 25.

pupate. There it spins a silken cocoon (fig. 4) that is black inside and out, and changes to a pupa (fig. 5). The latter is provided with a horn-like process on its head (see fig. 5) for opening a way out of the cocoon and with abdominal hook-like spines for working its way to the surface where it transforms to the winged adult (fig. 6, ♂ ; fig. 7, ♀).

The adults of this family, Sesiidae, have the larger part of one or both pairs of wings free from scales (No. 1172, *Sesia thysbe* Fabr). The latter are found, however, on the veins and the edges of the wings. The bristles of the frenulum in the female are consolidated into one organ as in the male.

Among the frenulum conservors are the Geometrids whose larvae appear to measure the surface over which they walk. It is probable that the caterpillars of the ancient Geometrids had several pairs of prop-legs like the larvae of most living Lepidoptera, but when the Geometrids acquired the habit of walking by looping the body, there would be no need of any of the prop-legs excepting the last pair or two and disuse would tend to bring about reduction and loss of these organs.

The canker caterpillar, so disastrous to shade and fruit trees, is a Geometer. It occurs in the spring form, *Paleacrita vernata* Peck, and the fall form, *Anisopteryx pometaria* Harr. (No. 1173, ♂, ♀). The position that the quiet larva often takes causes it to resemble a twig and this is doubtless a means of protection. When walking it brings the posterior end of its body forward towards the head end and takes firm hold of the twig by its prop-legs, thereby looping its body; it then stretches out the forward end and takes hold by the thoracic legs when the posterior part is again brought forward.

The larvae of some of the Noctuidae or owlet moths do great damage to grass and crops. One well known species is the northern army caterpillar, *Leucania unipuncta* Haw. (No. 1174, larva and adult). It is probable



that at some remote time the food supply of these caterpillars failed and that gradually the habit was acquired of moving in companies toward fresh grass lands upon which to feed. Now the habit has become fixed in the organization and is inherited. In this way the army caterpillar has overcome conditions that would be adverse to its own preservation.

Suddenly a field that has been swarming with these caterpillars is wholly free from them. This is owing to the fact that they have descended into the ground where their pupal life is spent.

*Erebus strex* (No. 1175) is one of the largest and handsomest members of the Noctuidae.

The extremely interesting fact has been proved by Gentry<sup>1</sup> that a normal cocoon-builder under certain conditions may pass into the pupal stage as a chrysalis. While the majority of the larvae of the Noctuid *Acronycta obliquata* went through their transformations in the normal manner, at least three without the slightest attempt at cocoon-making lay upon the soil and after a period of five days entered the chrysalis state. Facts like this suggest the origin and the evolution of the chrysalis-producing butterflies from the cocoon-making moths.

The tussock moths or Lymantriidae have become well known of late years through their representative the gypsy moth, *Porthetria* (= *Ocneria*) *dispar* Linn. (No. 1176; Pl. 1177, figs. 1-6; Nos. 1178, 1179, large specimens of the male and female). A cluster of eggs covered by yellow hairs from the body of the female is seen at the left in No. 1176 and in Pl. 1177, fig. 1, and a few eggs, enlarged, in fig. 2. These eggs are laid in July, August, and September, on the bark of trees, and the moth hibernates in the egg stage. The following spring the caterpillars (No. 1176; Pl. 1177, fig. 3) are hatched and the length of larval life probably averages ten weeks. If the

<sup>1</sup> Proc. Acad. Nat. Sci. Phila., 1875, p. 25.

temperature is favorable, they will search for food before they are twenty-four hours old.<sup>1</sup> They feed chiefly at night, going up the trees and out on the branches after dark and returning to sheltered places before light. The necessity of fighting this insect intelligently and unceasingly is evident when we consider that it is known to destroy the foliage of nearly all trees and most plants of economic importance. This is most unusual, for though the newly hatched Lepidopterous larva is far less specialized in regard to its food plants than the mature larva, yet the latter as a rule feeds upon a very restricted diet.

The caterpillar when full grown becomes a pupa (No. 1176; Pl. 1177, fig. 4) usually in July or August, and in from eight to twelve days in Massachusetts the pupa changes to the moth (Nos. 1176, 1178, ♂; Pl. 1177, fig. 5; Nos. 1176, 1179, ♀; Pl. 1177, fig. 6). It is interesting to notice the difference in size between the well fed specimens (Nos. 1178, 1179) and those less fortunate (No. 1176, specimens on the right). Within a few hours after emerging from the pupa-case the female lays eggs. The male is a swift flier, but the locomotion of the female is limited to a few struggling flaps which result simply in lessening the force of her fall from a height.<sup>2</sup> She lays her eggs either before this fall or afterward and then dies.

One of the moths that winter in the larval stage is *Pyrrhactia isabella* Smith (No. 1180, larva, pupa, cocoon, imago), of the family Arctiidae. This is the black and reddish brown colored caterpillar sometimes seen crawling over snow. When the larva is ready to transform the body shortens and apparently a thin gray veil slowly covers it which grows thicker till the insect within is

<sup>1</sup> Rep. Mass. State Board Agric. on Work of Extermination of Gypsy Moth, 1893, p. 12 (Senate document, No. 6).

<sup>2</sup> Howard, U. S. Dep. Agric., Div. Ent., Bull. no. 11 (n. s.), 1897, p. 7.

invisible. This covering or pupa-case is really formed of the hairs thrown off by the caterpillar and these are fastened together by silk.

There are scarcely any Lepidopterous insects that are parasites, but *Epipyrops anomala* Westw., is an exception, since its caterpillar (Pl. 1181, fig. 1, cast skin of a young larva; fig. 2 fully grown larva, dorsal view; fig. 3, ventral view) is found attached to the back of the Chinese lantern fly, *Hotinus candelarius* Linn.

The body is flattened and broadened out while the legs are greatly reduced in size. When young the larvae are free from the wax secreted by the *Hotinus*, but as they develop they become entirely covered with it.

According to Westwood these parasites probably feed upon the waxy secretions of the *Hotinus*. When full grown they drop off their host and secrete "a cottony substance" doubtless made from their waxy food, which serves as a cocoon (fig. 4) for the pupa (fig. 5). After a variable time (from nine days to upwards of twelve months) the moth (fig. 6) escapes.

Since *Epipyrops* is an external parasite it has not undergone marked structural changes but its life history is unique among Lepidoptera.

The green larvae of the hawk moths or Sphingidae have the habit of raising the forward end of the body and holding it motionless for a long time; hence the name of the family. They feed on the tomato, potato, and tobacco plants. The common species is *Phlegethonius celeus* (= *Macrosila quinquemaculata* Haw.) (No. 1182, larva, pupa, and moth). The pupa is not protected by a cocoon, but is a chrysalis with a long handle-like appendage which is the case of the sucking tube.

The adult (No. 1182) is a swifter flier than most Lepidoptera, and this habit is correlated with the structure of the mesothorax and metathorax, these two segments being more closely consolidated in the hawk moths than in other members of the order.

The mesothorax bears a pair of shoulder lappets or patagia which protect the basal portion of the front wings. Kellogg<sup>1</sup> has pointed out that these organs are small and inconspicuous in the generalized moths but are remarkably developed in these swift-flying Sphingidae.

The Bombycidae are well known through the silk made by *Bombyx mori* Linn. Its cocoon (No. 1183) yields the greater part of the silk of commerce. This moth (No. 1184) has been domesticated since early times and in consequence has almost wholly lost the power of flight. The wings (Pl. 1185, fig. 1, fore wing; fig. 2, hind wing) of the Bombycidae are interesting, since the frenulum is in a vestigial condition, as seen in *Bombyx mori* Linn. (fig. 2, *f*), while the humeral angle of the wing (fig. 2, *h*) is becoming extended as in the group of frenulum losers soon to be described.

Dr. A. S. Packard has pointed out in his valuable memoir on Bombycine moths<sup>2</sup> that the larvae of the more generalized moths, the Noctuidae, for example, are low-feeders; that is, they live on grasses and low-growing plants, and that as a rule they are without spines, horns, tufts, or other ornamentation; their color is green or some quiet shade. On the other hand, the larvae of the more specialized moths, like the Bombyces, have taken to tall blossoming plants or to trees. They have become adapted to their environment by developing brilliant colors or varied ornamentation.

The resemblance often existing between a caterpillar and its surroundings is illustrated by *Nerice bidentata* Walk. (Pl. 1186). The saw like back of this larva and its green color dashed with white are in harmony with the serrated margin and color markings of the elm leaves upon which it feeds.

One species of the genus *Heterocampa*, (*H. obliqua*

<sup>1</sup>Amer. Nat., XXIX, March, 1895, p. 255.

<sup>2</sup>Mem. Nat. Acad. Sci., VII, Monograph 1, 1895.

Pack.), possesses in the young larval state a pair of antler-like horns (Pl. 1187, fig. 1, side view; fig. 2, front view of head and prothoracic horns, greatly magnified), the use of which is unknown. When older the larva loses these organs, as seen in fig. 3.

Among the more specialized of the Bombycine moths is *Cerura cinerea* Walk., in which the anal prop-legs have become two long tubes (Pl. 1188, fig. 1), each containing a highly colored tentacle or whip with which *Cerura* lashes its body to drive away its enemies.<sup>1</sup> The dull-colored moth is seen in fig. 2.

The American silk moth, *Telea polyphemus* Linn., of the family Saturniidae, is a good type form of the group of moths. The thoracic and abdominal regions of the larva (No. 1189, larva, pupa, cocoon, and imago) are large, while the head is small. The mouth parts are efficient biting organs. The thoracic legs are weak but the four pairs of prop-legs are strong. The caterpillar spins a cocoon within which the pupa remains motionless for a longer or shorter time, according to temperature. During this time its appendages are encased in sheaths and are fastened closely to the body. When ready to transform, the pupa secretes a liquid which dissolves the gluey substance holding the silken threads together, so that the pupa emerges without doing great damage.<sup>2</sup>

The moth (No. 1189) has a robust body, the thorax being the largest part. The three regions are not closely connected, and the junction of the thorax with the abdomen is broad.

The antennae are either thread-like or feather-like, and as a rule these organs in the male are much broader than in the female. The mouth parts are vestiges and the

<sup>1</sup> Scudder. Trans. Amer. Ent. Soc. Phila., 1877, p. 77.

<sup>2</sup> Trouvelot states the adult escapes without breaking a fiber. Comstock says, "and breaking the threads," the adult escapes through the large round hole.

food is obtained by lapping. The fore wings are large, while the hind wings are reduced in size, and there is a corresponding reduction in the metathoracic segment. The frenulum is now wholly lost, and the humeral angle is large. Both pairs of wings are held in a drooping position when the insect is resting.

The remaining families of moths, skippers, and butterflies are grouped together as frenulum losers. In place of the frenulum they have a greatly extended humeral angle of the hind wings which passes under the fore wing, as already stated, and ensures unity of action in the two wings.

The Saturniidae include some of our largest and most beautiful moths, such as the Luna, *Actias luna* Linn., (No. 1190). The great Cecropia, *Samia cecropia* Linn., (Nos. 1191, 1192) suspends her cocoon (No. 1191) like a cradle, while the Promethea moth, *Callosamia promethea* Drury (Nos. 1193, 1194), hangs hers from a twig.

Among the varied habits of larvae that of the apple-tree tent caterpillar, *Clisiocampa americana* Harr. (No. 1195, eggs, larva, cocoon, pupa, moth) is interesting. These social larvae spin a tent and live together in great numbers. They leave the tent to feed but return to it when satisfied.

*Urbiculae.* The skippers resemble moths in certain features, while in other respects they are like butterflies. The larvae have the general characters common to both moths and butterflies, while they differ from those of both groups by having a large prominent head and a well developed prothorax (Pl. 1196, fig. 1, *Epargyreus tityrus* Fabr.). On the dorsal side of this segment there is a horny shield. The pupae (fig. 2) are rounded like those of moths and the pupal stage is passed in a frail cocoon made of leaves lined thinly with silk (fig. 2). This pupa, however, is not free within its cocoon but is fastened by means of a hook or cremaster at the posterior end of its body to a Y-shaped thread

while the opposite end of the body is held in the loop of a second Y-shaped thread (fig. 2).

The adults (No. 1197) have the robust body of moths. The head is broad and the antennae are usually thread-like but are enlarged near the end, though the tip curves backward like a hook. The sucking tube in these insects is remarkably long.

Skippers fly by day; a few hold their wings when at rest in a horizontal position, while some hold the hind wings in this way and the fore wings erect; most, however, hold their wings erect like the butterflies next to be described.

*Papilionidae or swallow-tails.* This family includes the more generalized butterflies. The caterpillars of the swallow-tails (No. 1198, *Papilio asterias*, dorsal view; No. 1199, side view) are naked, being without spines or conspicuous hairs. They have two processes on the prothorax called osmateria which can be thrown out and withdrawn, and since they give out a disagreeable odor are supposed to be organs of defence.

The pupa (No. 1198), now called the chrysalis, is angular and not rounded like that of the moth. It is without a cocoon but is covered by the dry, hardened skin of the larva; it hangs suspended by the tail and a loose girt around the middle.

The adult (No. 1198) has a slender body very different from that of the moth. The antennae are knobbed at their ends without a recurved hook. The three pairs of thoracic legs are well developed. These insects fly by day and when at rest hold their wings erect. The Papilionidae can be easily distinguished from other butterflies by the prolongation of the hind wings.

*Pieridae.* Our most common white and yellow butterflies belong to the Pieridae. The larva of the cabbage butterfly, *Pieris rapae* Schrank (No. 1200 larva, chrysalis, ♂; No. 1201, ♀) is a naked green caterpillar. The chrysalis is suspended in the same way as that of

the Papilionidae. The sexes of the adult can be distinguished by the black rounded spots on the fore wing, the male (No. 1200) having one spot and the female (No. 1201) two. Pl. 1202 will be referred to farther on when speaking of the development of the wings.

*Lycaenidae or gossamer-winged butterflies.* The caterpillars of this family remind one of the Eucleidae among the moths. The body is slug-like and the thoracic legs and prop-legs are not seen from above. In fact, the prop-legs are so small in some species, as in the American copper, *Heodes hypophlaeas* Scudd. (No. 1203), that, according to Scudder<sup>1</sup> they can be readily detected only when the skin of the caterpillar is prepared by inflation. The chrysalis of *Heodes hypophlaeas* Scudd., is suspended by the tail and the loop around the middle, but the latter is drawn much tighter than in the Papilionidae. The adult shows a tendency in the male towards a reduction of the fore legs, but in the female the three pairs are useful and similar in structure as in the Papilionidae, skippers, and moths.

Most caterpillars feed upon vegetable food, as we have already seen, but the wanderer, *Feniseca tarquinius* Grote, belonging to the Lycaenidae, is an exception to the rule, since it is carnivorous, living wholly upon Aphides.

The larva of the spring azure, *Cyaniris pseudargiolus* Bd. and Lec. (No. 1204) is provided with tubes on the seventh and eighth abdominal segments which secrete honey that is keenly relished by ants, so that these latter insects usually attend the caterpillars.

According to Comstock, *Cyaniris* exhibits polymorphism to the greatest degree of any known species, as many as nine or ten forms having been discovered.

Thecla (No. 1205) is one of the hair-streaks which with the blues and coppers make up the Lycaenidae. These are all small in size and delicate in organization.

<sup>1</sup> Butterflies, 1881, p. 19.



*Nymphalidae* or brush-footed butterflies. A typical form of each of the large orders of insects so far described has been given, and now one of the *Nymphalidae* is chosen to represent the order of Lepidoptera. The milkweed butterfly, *Danais plexippus* Linn. (Nos. 1206–1208) combines many of the essential characters of the order. Its egg (Pl. 1206, fig. 1), like that of many Lepidoptera, is symmetrical and highly ornamented. The caterpillar (No. 1207; Pl. 1206, fig. 2) has the cylindrical segmented body of most young Lepidoptera. Even in its earliest stage it has this secondary or caterpillar form, the primitive Thysanuriform larval stage being wholly skipped. In its biting mouth parts, however, the caterpillar resembles the generalized insects. The three pairs are present, the mandibles (Pl. 1206, fig. 3, *md*) being strong and well developed. Attached to the second pair of maxillae is the horny tube, the spinneret (fig. 3, *s*), by means of which the insect spins the silken attachment that suspends the chrysalis.

The thorax bears the three pairs of jointed legs, each ending in a hook. It has also been found that the mesothorax and metathorax of the caterpillar bear the rudiments of wings beneath the outer skin. These are indicated, according to Gonin,<sup>1</sup> by a bagging inward of the hypodermis (Pl. 1202, fig. 1, *Pieris brassicae*, before the first moult). These rudiments develop as shown by fig. 2, which is the wing-rudiment of the full-grown larva with its trachea and branches. By dissecting away the body wall just before pupation, the crumpled wings may be seen as in fig. 3. The existence of these appendages in the larva demonstrates more forcibly than almost any other discovery possibly could, a fact difficult for most people to grasp fully; namely, that the caterpillar is a young butterfly.

It is seen that the time for acquiring these rudiments

<sup>1</sup> See also Mayer, Bull. Mus. Comp. Zool., XXIX, no. 5, 1896.

has been carried back from the pupal stage to the early life of the larva which is what we should naturally expect to find in the specialized orders of insects.

The abdomen is provided with five pairs of fleshy prolegs, each supplied with many hooks.

According to Scudder the bright colors of the young Danais may be considered as warning colors indicating the unpalatable nature of the animal. While this caterpillar is without tubercles, it has a pair of fleshy filaments extending from the anterior and posterior parts of the body that are not present in the young larva but which develop in the process of growth.

The mature larva fastens itself by the tail only, the girt around the middle being no longer necessary, and transforms to the beautiful bright green chrysalis (No. 1207; Pl. 1206, fig. 4) marked by brilliant golden spots. The appendages are encased in sheaths and fastened to the body.

The adult (No. 1207, ♀) has a cylindrical body covered with a coating of hairs and scales. When this coating is removed, the three regions are found to be somewhat loosely connected and the mesothorax and metathorax (Pl. 1206, fig. 5), although more complex than in most of the generalized insects, are still capable of considerable motion.

The head is freely movable, although in a lesser degree than that of dragon-flies. This freedom is partly due to the free prothorax which in the Lepidoptera is reduced, as we have already seen, to a mere collar-like segment (fig. 7, *p*; see also fig. 5). The deep groove between the mesothorax (fig. 7, *ms*) and metathorax (fig. 7, *mt*; shaded in fig. 5), and the power possessed by these two segments of moving upon each other are probably due to the peculiar wave-like motion of the insect which is in striking contrast to the swift, arrow-like flight of the dragon-fly.

The compound eyes constitute about two thirds of the

head; there are no ocelli, though each compound eye is made up of an immense number of single eyes.

The antennae (No. 1207; Pl. 1206, fig. 7) are knobbed, the typical character of butterflies, as already stated.

Remarkable modifications in structure have taken place in the mouth parts, suggestive of equally great changes in the habits of these insects in some remote past.

The mandibles described in the young butterfly have become obsolete, consisting only of tiny plates (Pl. 1206, fig. 6, *md*) immovably fastened to the head. The first pair of maxillae has taken upon itself the function of sucking nectar from the corollas of flowers, and has become a long spiral organ (fig. 7, *mx'*). The palpi (fig. 7, *p''*) of the second pair of maxillae have become brushes for aiding the insect in obtaining nectar.

The reduction of the prothorax indicates that the first pair of legs are of little or no use, and this is the case, since they do not even support the insect when it alights but are folded across the breast. The first section is supplied thickly with hairs, hence the name of Nymphalidae or brush-footed butterflies. The remaining legs are weak and are of no service in locomotion but simply in supporting the insect.

The chief character of the wings is the coating of scales which are modified hairs. This peculiarity has given the order the name of Lepidoptera, meaning scale and wing. These scales are striated and of different colors; each is attached by a stem or pedicel and their arrangement on the wing is like that of shingles on a house.

According to Mayer<sup>1</sup> the wings of *Danais plexippus* Linn., during early pupal life, are transparent as glass, and this condition corresponds to the period before the scales are formed. From five to ten days before emergence the wings become opaque and white. This condition is caused by the withdrawal of the protoplasm from

<sup>1</sup> Bull. Mus. Comp. Zool., XXIX, no. 5, 1896, p. 209.

the scales, leaving them as little hollow bags filled with air. After this a dull ochre yellow or drab color suffuses the wing excepting where the white spots of the mature wing are to be (see Pl. 1208, fig. 1). This color is due to the fact that after the protoplasm has left the scales the "blood" or haemolymph enters them and changes to an ochre yellow and finally to a drab. About twenty-four hours later the mature colors gradually develop, appearing first *between* the nervures or veins (figs. 2, 3) and finally on the nervures and anterior margin (fig. 4). These colors are due to chemical changes taking place in the haemolymph itself.

It is interesting to note that ochre yellow and drab tints which appear first after the white are the shades peculiar to the more generalized nocturnal moths, while the brilliant colors which are the result of more complex chemical processes are found in the specialized diurnal butterflies.

When the insect is resting, the wings are held in an erect position over the back.

The power for sustained flight possessed by *Danais* is exceptional. It migrates southward, flying long distances in flocks numbering hundreds of thousands. It has also been seen at sea five hundred miles from land (Scudder).

Besides the legs and wings there are a pair of shoulder lappets or patagia attached to the mesothorax which protect the hinge of the anterior wing from injuries. These we have already seen in the hawk moths.

The male is distinguished from the female by the black patch next one of the veins near the middle of the hind wings. This patch is really a little pocket containing specialized scent scales or androconia.

The family Nymphalidae includes many genera. *Libythea carinenta* Cram. (No. 1209) is remarkable for having long palpi which extend forward in the form of a beak. *Heliconius charitonius* Linn. (No. 1210) is conspicuously colored, while the mourning cloak, *Vanessa antiopa* (No.

1211) has deep, rich hues and is one of our common New England butterflies.

One of the most magnificent genera is *Morpho*, some of whose species are regal in their coloring. *Morpho epistrophis* Hübn. (No. 1212) is an exquisite light blue species.

### Order 15. — HYMENOPTERA.

The Hymenoptera and the following order, the Diptera, are extremely interesting, since the former illustrate better than any other order of insects specialization by addition, and the latter specialization by reduction.

Partly because of the many adaptive organs possessed by Hymenoptera and partly on account of their remarkable physiological development, reaching in the case of ants an intelligence which differs from that of man only in degree and not in kind (Lubbock), the order Hymenoptera has been placed by many entomologists at the head of the insect group. In a natural classification, however, it is evident that that order of insects which is farthest removed, both in its larval and adult structural features, from the primitive ancestral stock-form is the one entitled to the position of the most specialized of its kind. It will be seen (p. 493) that the young and full grown Diptera are unquestionably farther removed from the Thysanuriform type of insect than these stages of other orders and for this reason the Diptera are placed last in our Synoptic Collection of insects as representing the acme of specialization.

*Terebrantia, or boring Hymenoptera.* The larvae of the Hymenopterous family of saw-flies, Tenthredinidae, are caterpillar-like in form and general characters, as seen in the violet sawfly, *Emphytus canadensis* Kby. (Pl. 1213, fig. 1, × 4). The active larva is provided with biting mouth parts, jointed thoracic legs, and eight pairs of prop

legs. The cocoon (fig. 2) is spun by the larva for the protection of the pupa (fig. 3). In these ways the generalized Hymenoptera prove their kinship with the Lepidoptera.

The adult Emphytus (fig. 4) has a robust body and the junction of the thorax and abdomen is broad, as in the generalized Lepidoptera. The mouth parts are specialized by addition, being adapted for biting and sucking. The two pairs of wings are membranous with few veins, and the posterior pair is much smaller than the forward pair. The ovipositor has become modified into a pair of saws by means of which the insect makes holes in leaves wherein its eggs are deposited.

Many of these characters are more plainly seen in one of our largest sawflies, *Cimbex americana* Leach (No. 1214), and the saws of *Cimbex sylvanum* are figured in Pl. 1215. Here they are spread out horizontally and the toothed edges of the saws are seen on the outer side.

Another generalized family of the Hymenoptera is the Siricidae or horntails. The larvae of these insects, however, show marked adaptation of structure to habit. For instance, the larva of *Tremex columba* Linn. lives in wood and this habitat has brought about a reduction in the size of the legs and a loss of the prop-legs, causing the insect to resemble the wood-inhabiting larvae of the Coleoptera. The pupa is protected by a cocoon of silk and wood chips.

The adult (No. 1216) has a sessile abdomen like the sawflies. The ovipositor, in this case, is a boring implement instead of a saw, and it is used for boring holes in trees in each of which an egg is deposited.

*Cynipidae*. It has been pointed out by Dr. Adler<sup>1</sup> that the galls of Cynipidae may be arranged in groups of constantly increasing complexity, beginning with those like

<sup>1</sup> Oak Galls and Gall Flies, 1894; English transl. by Straton, p. xxxiii.

*Spathogaster baccarum* Linn. (Pl. 1217, figs. 1, 2), and leading up to the complicated structure of *Cynips kollari* Hartig (No. 1218, complex gall of *Cynips*; No. 1219, young and adult *Cynips quercus spongifica* O. S.). In *Spathogaster* the simple gall (Pl. 1217, on oak leaf and the peduncle of the flowering catkin of the oak) consists of nutritive tissue enclosed in thin-walled parenchyma, while in *Cynips* the gall has an inner gall enclosed in thick-walled parenchyma, surrounded by spongy tissue and covered by a differentiated epidermis. The gall is an abnormal growth of the plant caused by animal agency working from within (Adler).

The female punctures the oak leaf and deposits her egg, but the gall does not begin to develop until the larva is hatched. It is therefore through the agency of the young gall-fly that the plant is excited into active gall-growth. "The moment the larva has for the first time wounded the surrounding cells with its delicate mandibles, a rapid cell growth begins."<sup>1</sup>

The larva spends its whole life within the narrow confines of the gall. Having little need of antennae and legs, these organs exist as vestiges. The pupal stage is also passed in the home of the larva, and the adult fly (No. 1219) makes a hole in the outer wall in order to escape.

These insects illustrate alternation of generations, since the brood of the first generation (the spring gall flies, *Cynips quercus spongifica* O. S.) is made up of males and females, while that of the second generation (the fall gall flies, *Cynips quercus aciculata* O. S.) is composed wholly of agamous females.

The parasitic Hymenoptera seem to be more nearly related to the Terebrantia already described than to the next division of Hymenoptera, the Aculeata, and for this reason they are now considered. All the species of the immense family of Ichneumonidae are parasites, destroy-

<sup>1</sup> Adler, *loc. cit.*, p. 101.

ing either the eggs, larvae, pupae, or adults of other insects, and in this way proving more beneficial to man than almost any other group. It is indeed singular that a whole family should take upon itself so completely the parasitic habit; and since this habit is far removed from the primitive habits of primitive insects, so the structure of these parasites is very different from that of their Thysanuran ancestors.

*Thalessa lunator* Fabr. (No. 1220, ♀; No. 1221, ♂) is one of our largest species. The extremely long ovipositor of the female (No. 1220), measuring from three to five inches, consists of three parts and is encased in a sheath made of two parts. By means of this awl-like organ *Thalessa* reaches the burrow of the horntail, *Tremex columba* Linn. and deposits its egg. The footless larva on hatching attaches itself to the *Tremex* larva and sucks its blood. According to one observer quoted by Lintner<sup>1</sup> *Thalessa* has been seen "sitting upon the bark where perforations mark the exits of previous occupants and also running around until she finds a promising spot, as, for instance, the hole made by a *Tremex* in depositing her eggs." This hole she sometimes takes advantage of, probing it with her ovipositor until the burrow is reached. Riley has shown that the instinct which guides *Thalessa* to a *Tremex* burrow is not unerring, but more or less experimental work is done and often mistakes are made.

Those ichneumons that lay their eggs in caterpillars and the like do not need long ovipositors and therefore this organ is shortened (No. 1222, *Ichneumon grandis* Brullé).

The social Hymenoptera or the wasps, bees, and ants, are remarkable animals when considered from a physiological point of view. Their skill, intelligence, and their power to improvise implements and use them, challenge the profoundest thought of the biologist. Among all the

<sup>1</sup>4th Rep. Ins. N. Y., 1888, p. 38.



animals so far described, the social instinct reaches its most complete development in the ants. This communitistic life of the social Hymenoptera has been brought about by the specialization of certain individuals which started as solitary insects of either the male or female sex. It has doubtless required a long period of time and a vast number of generations to bring this social organization to such a state of efficiency as we find it to-day. If mental qualities were made the basis of our classification, ants would not only be the most specialized of insects but would come nearer to man than the ape (Lubbock). It is obvious, however, that such a classification would not represent the genealogical succession of animals upon our earth; such a succession, it must be borne in mind, can be determined only by a knowledge of the structure and the development of animals.

The species of solitary wasps far outnumber the social species in the United States. The fossorial or digger wasps are solitary in their habits and are either male or female. Like most insects, also, their life is so short that as a rule they neither see nor care for their young, although the preparation they make for them is exceptional in its character.

*Pepsis caerulea* Linn. (No. 1223), one of the Pompilidae, is a robust insect with the thorax attached to the abdomen by so short a peduncle that it is sometimes described as having none. Its mandibles are large, strong organs, and these together with the fore and hind pairs of legs are adapted for digging burrows in the ground, in each one of which an egg is placed. This habit is no new feature of insect economy, but what is unique is the knowledge the parent possesses of paralyzing insects without killing them. She must provide sufficient animal food for the entire life of her young; if the spiders, caterpillars, and the like were killed they would soon be unfit for food; therefore she thrusts her powerful sting and poison into the nerve centers of the particular animal her larva feeds

upon and renders it motionless. With these paralyzed animals she stocks the burrow; she then deposits an egg and closes it. When every egg is laid her life work is accomplished. No one can read the admirable observations and experiments of the Peckhams<sup>1</sup> without feeling that the solitary wasps offer remarkable instances of inherited instinct and of reasoning intelligence. It is interesting to note that the inherited instinct is much more flexible than has been generally supposed, and is often modified by individual judgment and experience.

*Sphex ichneumonea* Linn. (No. 1224 ♀; No. 1225, ♂), another fossorial and solitary wasp has the thorax fastened to the abdomen by a slender peduncle, the length of which varies in different species. The female stocks her burrow with the green grasshopper, *Orchelimum vulgare* (No. 1027).

The solitary wasp, *Odynerus*, makes its nest (No. 1226) of clay while other species of this genus fill up key holes and the like.

The most specialized of the solitary wasps are the Mutillidae. The thorax in the winged males (No. 1227, *Mutilla occidentalis*) exhibits the suture between the three segments as in most insects, but in the wingless females these sutures have become obliterated. This consolidated and sutureless condition is evidence of specialization by reduction and is suggestive of the evolutionary history through which this species has passed.

The most simple social conditions are found in the beginnings of a colony where the female makes a nest, lays her eggs, and instead of dying, lives on and works, taking upon herself the entire care of the young, doing all the tasks incident to family life, until the first brood of young (which are all females specialized by reduc-

<sup>1</sup> Instincts and Habits of the Solitary Wasps, by George W. and Elizabeth G. Peckham, Wisconsin Geol. and Nat. Hist. Survey, Bull. no. 2 (Sci. Ser., no. 1), 1898.

tion and called workers) are old enough to assume the responsibility of carrying on the industrial work of the nest and of providing in their turn for their mother. She then gives up the many activities in which she has been engaged and devotes herself wholly to one object, that of increasing the size of the family which now may be called a colony. In this colony there are, besides herself who is now the queen, males and workers. The males take no part whatever in the industrial employments of the nest and are apparently unaware of them (Sharp). There is no distinct line of demarcation between the worker and queen, such as we shall find farther on in the social bees, although the development of the reproductive organs of the worker has been in a measure suppressed.

The larva of most of the social wasps is a colorless, legless grub which lies head downward in the cell of the nest. It is held in this position when young by a sticky secretion; later the enlarged anterior end of the body just fits the opening and holds the insect in place. It is fed on prepared food, but the pupa stage is quickly reached and soon passed, and the adult (No. 1228, *Polistes metricus* Say) comes forth armed and equipped for work. It makes its nest (No. 1229) which consists of a single layer of cells without an external covering. The material of the nest is obtained by scraping weather-beaten wood with the mandibles, chewing it, and mixing it with the saliva. In each cell an egg is laid and when the young are hatched they are fed by the females and workers on the sweet juices of flowers and fruits besides some well masticated solid food.

One of the most social wasps is *Vespa maculata* Linn. (No. 1230, larva; No. 1231, ♂; No. 1232, ♀; No. 1233, ♀). Its papery nest (No. 1234) is made of rows of cells, one placed below the other, and protected by a thick outer covering. These nests vary in size, a large one in my possession measuring forty-two by fifty-one inches in circumference. These nests are used only one

season. In the autumn the males and workers die, while the females leave the nest and hibernate in sheltered places till spring comes, when they found new colonies.

*Apidae.* There are solitary bees like *Prosopis* (Pl. 1235, *P. signatus*) which are much less specialized than the social bees. The body is nearly naked. The proboscis is short and the hind pair of legs are not modified but are similar to the other two pairs. These bees are either male or female, like most other insects, and like the solitary wasps they do not live to care for their young.

There are also semi-social bees like the humble bee, *Bombus americana* (No. 1236). The female of this genus, like that of the generalized wasps, makes and provisions the nest, consisting of a few cells, lays the eggs, and cares for the young until enough workers have grown to perform the necessary industrial labor of the little colony; then she, as queen, devotes herself to one special occupation, that of egg-laying. It is interesting to note that the workers of this genus are slightly differentiated from the females, and it would seem as if here we had an evolutionary stage between the wholly undifferentiated female of the most generalized bees and the extremely modified worker of the specialized genera. The colony of *Bombus* survives only one season; a few females hibernate and start new colonies in the spring.

The most social of all bees is the domesticated honey bee, *Apis mellifica* Linn. (Nos. 1237-1248). The larva (No. 1237) is a soft colorless and footless grub. While this is true of the larva, as one sees it, it has been found that legs arise very early in larval life and grow in the interior of the body, but their development is suppressed so that the young bee has no functional legs.

The mouth parts are small and weak, since the food is of a pasty nature and the larva is supplied with it by certain adults specialized for the purpose. It is extremely nutritious, consisting of pollen, the vitalizing male element of plants, and of honey, the nectar of flowers that

has undergone a chemical change in the honey bags within the body of the bee. This helplessness of the larva is in striking contrast to the independence of the larvae of the Lepidoptera and of most generalized insects.

The larva spins a thin cocoon for the protection of the pupa (No. 1238). The appendages of the pupa are nearly free, although each one is covered by a delicate skin. The metamorphosis is rapid, twenty-four days being required for the male, twenty-one for the female, and only fifteen or sixteen for the queen.

The body of the adult bee (No. 1239; Pl. 1240; fig. 1, ♂, fig. 2, ♀, fig. 3, ♀) is shortened, compact, and hairy. The three regions are clearly differentiated, the junction between the head and thorax and the thorax and abdomen being a marked feature.

The thorax is complex and its three segments are closely consolidated on the dorsal side. The prothorax (Pl. 1241, fig. 1, ♀, *p*) is reduced in size. Its side pieces are detached from the dorsal portion causing the fore legs to work in connection with the head.

The mesothorax (Pl. 1241, fig. 1, *ms*) forms the greater part of the thorax, while the metathorax (fig. 1, *mt*) is narrow. The unique character of the Hymenoptera is the close union of the first abdominal segment (fig. 1, *ab'*), usually called the median segment or propodeum, with the metathorax. The tendency of this segment to press forward is seen in the more generalized orders, like the Orthoptera and Hemiptera, but nowhere is it carried to such an extreme as in the Hymenoptera and Diptera.

The narrow junction of the thorax with the abdomen is effected by the short, slender peduncle (fig. 1, *ab''*) which is in reality the second abdominal segment, although usually described as the first.

This articulation is doubtless produced by the habit of stinging, and it is an extremely perfect mechanical contrivance.

The appendages of the head are the antennae and

mouth parts, as in most insects, but the antennae differ from those of other orders in being elbowed and bent upon the face. The mouth parts offer one of the best illustrations of specialization by addition. Not only are these strong, chitinous mandibles (Pl. 1241, fig. 1, *md*) adapted for biting, cutting, kneading wax, crushing, and chewing, but the two pairs of united maxillae (fig. 1, *mx'*, *mx''*) are fitted for piercing, sucking, and lapping. The ligula (fig. 1, *mx''*, *l*) of the second pair of maxillae is the part usually described as the proboscis and its length varies in different species of bees in accordance with the varying length of the corollas of flowers frequented by these insects.

The legs are long, hairy organs, and the tibia of the third pair in the worker bee is provided with little cavities or baskets for holding pollen. Thus it is seen that the function of walking is combined with that of carrying food.

The tarsus or foot, a part of which is represented in fig. 2, side view, illustrates the correlation of structure and habit. By means of the hooks the bee walks on the edges of its comb, and hangs from other bees, while the soft cushion or pulvillus seen at the end secretes a sticky substance which enables the insect to walk on the polished surfaces of leaves and glass.

The wings of the second pair are reduced in size like the metathorax, which bears them. They are membranous — hence the name of Hymenoptera, meaning membrane and wing — and have few veins. The two pairs (Pl. 1242, figs. 1, 2) are fastened together by hooks. A portion of the posterior edge of the fore wing turns under in a plait (fig. 1; fig. 3, the plait enlarged) and a part of the anterior edge of the hind wing is provided with hooks (fig. 2; fig. 4, hooks enlarged); the two hook together as seen in fig. 5. This specialized condition enables the two wings to strike the air as one organ and long sustained flight to become possible.

There are among bees no wingless forms, and this is another proof that these insects are examples of specialization by addition.

The abdomen bears a sting which, however, is within the body. The origin of this organ is similar to that of the ovipositor of locusts. Connected with the sting are two poison glands. The abdomen of the worker is provided with glands for secreting wax. These are on the lower side and the wax is secreted in the form of scales which are worked over by the bees.

A prosperous colony of *Apis* consists of from 80,000 to 90,000 bees. Of these a few hundred are males, one is a female or queen, and the remainder are workers. Through the partial or complete suppression of the genital organs, and also through the acquisition of adaptive features, the workers of *Apis* have become differentiated to a greater degree than those of any other colony of bees. They secrete the wax for the comb (No. 1243), the hexagonal cells of which are cradles for the young and storehouses for honey. They, in brief, carry on all the industrial work of the hive and are equipped, as we have seen, with pollen baskets, wax-secreting glands and honey bags, none of which the male or female possesses.

There seems to be a superabundance of males, many of whom do little or nothing; a few only of the number aid in perpetuating the race. In the early spring the queen begins to lay eggs and is capable of laying 4,000 in twenty-four hours. So prolific is she that in time the nest or hive becomes overcrowded. Then it is that the old queen with from 60,000 to 70,000 workers emigrates and founds a new home, leaving in the old nest some 20,000 or 30,000 workers, many developing larvae and pupae (from one of which the new queen will eventually be born), and thousands of cells filled with honey. This is called the primary swarm; the second swarm, that often takes place later, is led by the new queen. After this second swarm has settled in its home, the new queen

with many males takes the nuptial flight, after which egg-laying begins and continues for several seasons, the queen often living for four or five years.

*Formicidae.* Specialization has gone on in ants till there are no solitary forms, all the species living together in colonies. There are, however, simple colonies, like those we have already found in wasps and bees. It has been observed and the observation proven by experiment that a colony of *Camponotus ligniperdus* is started by a single female who carries on the industrial work of the nest until her worker-children are old enough to assume the burden.

In the ant the body is less consolidated than in the bee, but in this case this lack of concentration is evidently a specialized condition and must not be confused with the unconsolidated state of primitive forms. That this laxity is an evidence of specialization is shown by the fact that there is less concentration in the specialized wingless workers than in the winged males and females. The habits of these insects are such that great mobility of body is necessary and therefore lack of concentration has become a secondary and adaptive character. The peculiar junction of the thorax and abdomen has probably been produced by the habit of stinging. The peduncle is formed of either the second abdominal segment or the second and third segments (counting the propodeum attached to the thorax as the first). These segments are extremely slender and are called nodes; by means of these the power of stinging is greatly increased. It is noticeable that there is but one of these nodes in most of the stingless species, as for instance in *Camponotus*. An extreme modification of the abdomen is seen in *Cremastogaster* (Pl. 1244, figs. 1, 2) where this part of the body can be thrown forward over the thorax and head.

Specialization among the ants has brought about division of labor, and correlatively the peculiar structures



which fit the laborers for their special duties. Not only are there males (Pl. 1245, fig. 1, *Formica pennsylvanica* De Geer), females (fig. 2), and workers (fig. 3), as in the bee, but there are soldiers (fig. 4) and the workers and soldiers are differentiated still further so that other forms appear, each one with its particular work to perform.

The males and females are provided with wings until after the nuptial flight, when the males are killed and the female sheds these organs. The workers, however, are always wingless, and are therefore examples of specialization by reduction. Even the sutures between the segments on the dorsal side are often obliterated, while they may be clearly seen in the winged male and female.

A colony of ants consists of males, many queens instead of one as in the bees, and thousands of workers and soldiers. The workers do all the industrial work of the nest, while the soldiers with their great heads and strong mandibles defend the colony. The winged individuals and the workers and soldiers of some species, *Atta* for instance (No. 1246, *A. fervens* Say, ♂; No. 1247, the same, ♀), are differentiated so that the subject of polymorphism is admirably illustrated.

The organization of the colony continues for years and the mother ant lives to see her children grow to maturity. It seems that the young are more helpless and also more tenderly cared for than in any other group of insects. They have the advantage of living with the old ants and of profiting by their experience. These conditions existing for unnumbered years and countless generations have led to the present efficient and intelligent social order.

#### Order 16.— DIPTERA.

The Diptera illustrate pre-eminently the efficiency which may be attained through specialization by reduction. These specializations will be brought out more clearly when considering a typical form of the order,

*Tabanus lineola* Fabr., but first the characters of the more generalized Diptera, the Orthorhapha, must become familiar.

The Tipulidae, represented by the crane-flies, have cylindrical, colorless, footless larvae (Pl. 1248, fig. 1, *Tipula eluta* Loew), proving that even in these most generalized members of the order the Thysanuriform larval stage is wholly skipped. The larvae, however, have horny mandibles for biting; they also have tubercles in place of feet.

The pupa (fig. 2) is free; that is, it is not enclosed in the hardened larval skin, the puparium, but is naked and the thoracic appendages are clearly seen. In this stage the respiratory tubes extend from the prothorax.

The adult *Tipula* (No. 1249) has a long body with the thoracic segments extended, and plainly visible (Pl. 1250, fig. 1, dorsal view of thorax of *Tipula*; fig. 2, side view of same).

The feeble legs are extremely long. The wings are reduced to one pair, the second pair of most insects acting as balancers or poisers. Proof that the balancers were originally wings is found in the fact that in the pupal stage of several species of Diptera these organs are large and broad.

The Tipulidae, like all Diptera, are without a sting, and, as one might expect, the abdomen is not pedunculated. *Tipula*, however, like the more generalized insects, has an external ovipositor with which it makes holes in earth, fungi, and the like for its eggs.

One species of this family, *Tipula agarici seticornis* De Geer, according to De Geer, has two spinnerets for spinning silk.<sup>1</sup>

The Culicidae or mosquitoes resemble the Tipulidae in certain adult characters, but the larvae are aquatic. The eggs (Pl. 1251, fig. 1, *Culex pungens* Wied) are laid

<sup>1</sup> Kirby and Spence, *Introd. to Ent.*, III, 1826, p. 125.

in masses of various shapes and the young larvae (fig. 2) are extremely active. They breathe by means of a respiratory tube which extends to the surface of the water, as seen in fig. 2. According to Howard the organs at the end of the abdomen called gill flaps (see No. 1252, species unknown) may be respiratory in the young larva but later are probably locomotor organs. These are seen more plainly in the full grown larva (Pl. 1251, fig. 3). The development is accelerated and when seven days have passed the larva becomes a pupa (fig. 4). In this stage it remains quiet at the surface unless disturbed when it moves by means of the muscles of the abdomen. It is a most peculiar looking insect on account of the swollen thoracic region. It breathes now by means of two tubes on the thorax seen in No. 1252. The pupal stage is only two days long when the adults (No. 1253; Pl. 1251, fig. 5, ♂; fig. 6, ♀) emerge.

The genus *Anopheles* is of especial interest on account of the part it plays in the transmission of disease. It has been discovered that the malaria germ is a Protozoan which lives as a parasite in human blood. When *Anopheles maculipennis* bites a person infected by this parasite it sucks up into its own body the malarial germ which in a short time undergoes a true sexual development. The fertilized parasite ultimately passes into the proboscis of the mosquito and is injected with the poison into the next person the insect bites, who thereby becomes a victim to malaria. While the larva of *Culex* is usually seen in the position represented in Pl. 1251, fig. 2, the larva of *Anopheles* rests in a nearly horizontal position just beneath the surface of the water. The head of the latter rotates and, according to Howard, can be turned completely round with the utmost ease, so that the insect has the habit of lying with its head upside down. The adults (No. 1254) are strong and bloodthirsty. The female *Anopheles* can be distinguished from the female of *Culex* by its long palpi. When resting, the body of *Anopheles*

is straight; that is, the head, thorax, and abdomen are in a horizontal line, while the body of *Culex* is hump-backed.

Among the most carnivorous Diptera, both in the larval and adult stages, is the robber-fly, *Asilus sericeus* Say (No. 1255). It is well adapted for the life which it leads, by having a robust body, bristling with stiff hairs, a strong, black proboscis able to inflict severe wounds, legs armed with spines and fitted for running, seizing prey, climbing, and digging, and wings with muscles capable of rapid flight.

Many of the specializations of the Diptera are well shown in the type form, *Tabanus*. The larva (Pl. 1256, fig. 1, *Tabanus atratus* Fabr.) tapers at both ends and in this way differs from the larvae of the Tipulidae. It is a footless animal with a head provided with curved dark brown mandibles.

The pupae (fig. 2, *Tabanus lineola* Fabr.) are free and may be distinguished by the large, ear-shaped spiracles on the thorax. In the Orthorhapha the winged insect emerges through a slit on the back of the pupa. The short, compact body of the adult (No. 1257; Pl. 1256, fig. 3; No. 1258, a larger species of *Tabanus*) exhibits extreme concentration of parts, while at the same time the three regions are sharply differentiated from one another.

The broad head with its great compound eyes is on a pivot-like neck. The thorax is complex in structure, differing from the more generalized thorax of the Tipulidae. The reduced collar-like prothorax (Pl. 1256, fig. 4, *p*) is firmly soldered to the large mesothorax (fig. 4, *ms*). The metathorax (fig. 4, *mt*) is only partly seen from above, the basal portion of the abdomen having crowded forward and covered up its posterior, dark-colored bulbous portion or scutellum (fig. 4, *sc'''*). This part is still better seen in fig. 5, which is a drawing of the head and thorax seen from the side. This peculiar

structure gives rise apparently to a sessile abdomen, but this condition must not be confused with the true sessile abdomen of the generalized insects, like that of the Orthoptera and Hemiptera. It may be called a pseudo-sessile abdomen which may have arisen from a pedunculated abdomen by the reduction of the peduncle and the complete concealment of the posterior part of the metathorax by the basal abdominal segment.

The antennae for some unknown reason have the third joint enlarged. The mouth parts are complex organs and are fitted for piercing, sucking, and lapping. The mandibles (fig. 4, *md*) and the first pair of maxillae (fig. 4, *mx'*) with their large palpi are modified into sharp piercing organs. The second pair of maxillae (fig. 4, *mx''*) are composed of leaf-like parts that spread out and are used for lapping sweet fluids.

The phylogenetic studies of Kellogg<sup>1</sup> have thrown much light on the Dipterous mouth parts. He shows the necessity of first becoming familiar with the mouth organs of generalized Diptera in order to interpret rightly the complex structure of these organs in specialized forms such as the Muscidae (see p. 493).

The legs of *Tabanus* are long and the hairs of the cushions of the feet secrete a sticky substance which enables the fly to walk on a ceiling. The process of specialization by reduction has reduced the number of wings from four to two; hence the name of Diptera, meaning two and wing. These wings are strong and the flight is exceedingly swift. We have already seen that a pair of balancers, also called halteres (fig. 4, *w''*) represent the second pair of wings. The function of these organs is not known with certainty. They may be sense organs (Sharp) assisting in the perception of sound. They also seem to aid in preserving the equilibrium of the body, and they may be useful in directing the flight of the insect.

<sup>1</sup> Psyche, VIII, no. 273, 1899; Biol. Bull., I, no. 2, 1900.

The Cecidomyiidae or gall gnats are among the more specialized forms of the Orthorhapha. The larva of one species of *Cecidomyia* (*C. strobiloides*) makes the pine-cone willow gall (No. 1259) which resembles strikingly a pine cone. The gall is really a deformed bud produced by the larva which lives within the gall until ready to transform.

The Hessian fly, *Cecidomyia destructor* Say, (Pl. 1260, figs. 1-4) differs from *Cecidomyia strobiloides*, since its larva does not make a true gall. This larva (fig. 1) has the head and mouth parts in such a vestigial condition that it absorbs its food, which is the sap of the wheat. When ready to transform, its skin becomes hard, brown, and unsegmented. The pupa (fig. 2, ventral view) within this hardened case or puparium (fig. 3) remains absolutely motionless. On account of the resemblance of the puparium to a flax seed this is known as the "flax seed state" of the insect. The presence of these "flaxseeds" between the leaf and the stalk of the wheat causes the stem to swell and the leaves to die (Packard) and thus in both the larval and the pupal stage the insect does great damage to the wheat crop.

It is interesting to note that in this Dipterous family, the Cecidomyiidae, there is an extremely interesting form, *Miastor*, whose larvae are capable of laying eggs. Here is a case where it would seem that the law of acceleration in development has acted so that the egg-laying habit peculiar to the adult stage in most animals has been carried back to the larval stage.

The next division of flies, the Cyclorhapha, are more specialized than the Orthorhapha, both in the larval and adult condition. The group is represented by the flesh-fly, *Sarcophaga* (No. 1261); and the house-fly, *Musca domestica* Linn. (No. 1262). The larva or "maggot" of *Musca* is more reduced than that of *Tabanus*. The head has nearly disappeared, and the mouth parts exist as mere vestiges.

In the transformation from larva to pupa most of the larval organs are destroyed, while from the so called "imaginal buds" that persist the parts of the pupa and imago arise. The pupa transforms in a puparium, and emerges in this entire group (Cyclorhapha) through an opening at the anterior end which is provided with a lid. The development is accelerated requiring from ten to fourteen days only, and according to Weismann this metamorphosis of the Muscidae is far more complex than in other insects.

The adult *Musca* (No. 1262) is also more reduced than the adult *Tabanus*. The mandibles and first pair of maxillae have become useless and the mouth parts have only one function,—that of lapping. That this function is performed with admirable perfection is demonstrated whenever *Musca* is watched sipping its meal of sweetened water.

The parasitic Diptera — the Pupipara — are reduced to the extremest degree. The wings have not only become tiny scales as in the semi-parasitic flea, *Pulex*, but in the Pupipara both wings and balancers are wanting altogether, as seen in *Melophagus ovinus* Linn. (Pl. 1263, fig. 1) and *Braula coeca* Nitzsch (fig. 2). With this reduction of the wings the thoracic segments have lost their typical features and in *Braula* have become like those of the abdomen (see fig. 2). But this is not all. The remarkable discovery by Adensamer of the bee parasite, *Ascodipteron* (Pl. 1264, *A. phyllorhinae*, dorsal view), proves that among insects the law of specialization by reduction may obliterate all trace of segmentation. In this parasite there is no external head and only the structure of the internal organs places it near *Melophagus*.

The Pupipara develop by a process that is remotely comparable to that of vertebrates. The young are retained in an enlargement of the oviduct and are nourished by a milk-like secretion. The larval stage is nearly or wholly passed within the body of the parent so that the young are born as pupae—a unique illustration of the law of acceleration in development.

The great class of Insecta may be considered as the most specialized of invertebrates. We have briefly traced the evolution of this class from the ancestral type as expressed by the Thysanura to the extremely differentiated forms of the Hymenoptera and Diptera. The primitive development of the simplest, wingless species and the straightforward, direct development of the more generalized winged forms are seen to be processes which, if understood, throw strong light on those complex metamorphoses that characterize the method of indirect development, and that make the study of insects at once most attractive and most difficult.

In no class of invertebrates are there such varied adaptations of structure to the favorable and adverse conditions of environment with the correlative increase or decrease in organs as in the Insecta. The Hymenoptera and Diptera challenge each other as demonstrators of the law of specialization,—the one of specialization by addition and the other of specialization by reduction. These forces we have found operative in most of the subkingdoms of invertebrates, but nowhere to such an extreme degree as in these two remarkable and intensely interesting orders of insects—the intelligent, progressive Hymenoptera, and the adaptive, reduced Diptera.



ALPHABETICAL LIST OF GENERA MENTIONED IN  
THIS GUIDE.

(Synonyms are in italics.)

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