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FIRST MEMOIR.

NOTES ON THE BACTERIOLOGICAL EXAMINATION OF THE SOIL OF PHILADELPHIA.

NOTES ON THE BACTERIOLOGICAL EXAMINATION OF THE SOIL OF PHILADELPHIA.

By Mazyck P. Ravenel, M. D.

Scott Fellow in Hygiene, 1893–94.

Presented by Dr. J. S. Billings.

This work was undertaken at the instance of Dr. John S. Billings, Director of the Laboratory of Hygiene, University of Pennsylvania, with the view of obtaining, if possible, some explanation, from a bacteriological standpoint, of the greater mortality among persons living in houses built on made ground over those living on virgin soil. In some cities, as Washington and New York, filled localities can be mapped out and the course of old runs followed by the higher death rate in these districts. No positive opinion can be based on the data so far obtained, and these notes are presented mainly as a small contribution to our knowledge of the bacteria of the soil.

In the prosecution of the work I have had the advice of Dr. Billings and of Dr. A. C. Abbott, first assistant, to both of whom I am much indebted.

SUMMARY.

The work has extended over a period of ten months, with considerable interruption during much of the time.

Virgin soil was examined to a depth of 12 feet, samples having been obtained from the walls of an excavation at intervals of a foot. Samples of made soil were obtained in the same way to a depth of 9 feet. Other samples of both made and virgin soil were obtained by Fränkel's earth borer to a depth of 5½ feet.

From these samples of earth 71 cultures were isolated and carefully studied. Wherever possible they were identified with already described species, and with each other, the final result being 36 varieties of organisms, of which 29 are believed to be new.

Morphology.—The bacillus forms predominate largely. Only two cocci were found, both new. No spirilla were found, and but one sarcina. Five varieties of cladothrix were found, only one of which has been identified with already described species—the *Cladothrix dichotoma* of Cohn. This species has been found repeatedly at different depths in both made and virgin soils, being apparently the most common and widely distributed form of the genus.

Depth.—The greatest depth at which bacteria have been found in virgin soil was 6 feet, at which depth the bacillus Megatherium and the bacillus ramosus were observed. All samples of virgin soil below this were found to be sterile.

This result agrees closely with the experiments of Koch and Fränkel. The former in 1881 found that few bacteria were to be found 1 meter below the surface in soil which had not been disturbed. Fränkel found that the number of organisms decreased greatly and suddenly at a depth of three-fourths of a meter to 1½ meters, while at the latter depth life was absent in many instances. He obtained, however, in other experiments, colonies from a depth of 3 and 4 meters, which took a long time to make their appearance (Sternberg). Only one of the varieties most commonly found by Fränkel in the deeper layers of the soil was encountered in these experiments, the bacillus ramosus. In two experiments a sterile layer was found at the depth of about 1 meter, below which a considerable number of bacteria were observed.

From made soil, although many years old and paved over, numerous colonies were obtained from a depth of 9 feet. No actual count was made, but the number of bacteria at this depth was apparently as great as at the surface.

Method of collecting samples.—Whenever possible, the samples were taken from the wall of a freshly made excavation, the wall being dug away to a depth of several inches just before taking the sample, and care was exercised that the pick should not touch the spot from which the earth was taken. A short tube of thick glass, previously plugged and sterilized, was bored into the fresh surface until a sufficient quantity was obtained. In all other instances the earth borer of Fränkel was used, but was not found satisfactory, besides being difficult to operate, the soil being a very stiff clay containing numerous pebbles.

Method of examination of samples.—Two methods of examination have been suggested. In one—that preferred by Fränkel in making counts—a portion of the earth to be examined is put into liquefied gelatin and thoroughly broken up with a sterile rod, after which it is mixed by tilting the tube up and down, revolving it at the same time, and lastly rolled. The second method consists in crushing the earth in a tube of sterile water and washing it well by agitation. A certain amount of the water is then introduced into the liquid medium and roll tubes made. Both methods were tried, the former being found to be more satisfactory. It was used exclusively, with the modification of pouring the gelatin into Petri dishes instead of making roll tubes; and in every instance dilutions were made from the original tube, in order to better isolate the colonies. To determine the temperature at which the cultures should be kept, duplicate plates on agar-agar and gelatin were made from several samples of earth, following the second method described. After washing the earth thoroughly in sterile water, equal quantities of the water were mixed into tubes of liquid agar-agar and gelatin and then poured into Petri dishes. All of the gelatin and a duplicate series of the agar-agar plates were kept at room temperature, the others being placed in the incubator at 35° to 36° C. At the end of thirty-six hours a count showed that those plates kept at room temperature contained the greater number of colonies. In all the subsequent experiments gelatin has been used and the plates kept at room temperature. The wisdom of this has been confirmed by the subsequent study of the individual organisms isolated, since quite a large proportion of them grow better at room temperature than at 35° to 36° C., and some will not grow at all at the latter temperature.

Study of organisms.—The bacteria isolated have each been studied as to their morphology, both in stained preparations and in the hanging drop; as to motility and cultural peculiarities; all have been stained for flagella after the method of Löffler, and all have been placed in an atmosphere of pure hydrogen and the growth noted. The culture media employed have been those given in the text-books, and the percentages have not been changed except in very hot weather, when it was found necessary to add gelatin in the proportion of 12 per cent instead of the 10 per cent used during most of the work.

CONCLUSIONS.

As stated at the outset, the data gained during this study are not sufficient to base any positive conclusions upon. The following propositions have been substantiated to a greater or less extent:

(1) Made soils, as commonly found, are rich in organic matter, and excessively damp through poor drainage.

(2) They furnish conditions more suited to the multiplication of bacteria than do virgin soils, unless the latter are contaminated by sewage or offal.

(3) Made soils contain a larger number of bacteria per gram, and the number of species is greater, while the deeper layers are as rich, both in numbers and varieties, as are the upper ones. After some years the number in the deeper layers probably becomes proportionately less.

(4) There is a greater probability that made soils may contain pathogenic bacteria.

THE CULTIVATION OF ANAËROBIC BACTERIA.

Among the organisms which find their habitat in the upper layers of the soil, several of the most interesting and important, from a pathological point of view, belong to the class of strict

anaërobes. Their study presents considerable technical difficulties. Of the various methods proposed for the cultivation of these bacteria, two appear to be of special value. These are the method of Buchner (Fig. 1), in which the oxygen is absorbed by means of pyrogallic acid, leaving a residual atmosphere of nitrogen; and, second, the employment of an atmosphere of hydrogen. Buchner's method has the objectionable feature of causing a negative pressure, which puts the bacteria under unnatural conditions. All things considered, the use of an atmosphere of hydrogen seems the most practical method we possess, and is favorable to the growth of the most important anaërobic organisms known to us.

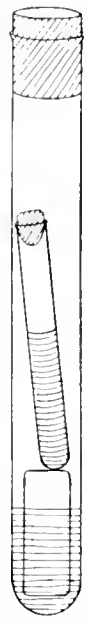


FIG. 1.

For plate cultivation, an apparatus similar to that described by Liborius in the Zeitschrift für Hygiene, Vol. I, page 128, is most useful. It consists of a bell jar having openings at the top and near the bottom, in which perforated rubber stoppers, bearing glass tubes with stopcocks, are inserted. The jar and plate on which it rests are put in a frame by which they can be firmly clamped together. A ring of soft rubber is put between the jar and plate, and it is well to supplement this by several coats of melted paraffin applied outside. The air is pumped out from the bottom and hydrogen introduced at the top, the process being repeated three times, at least, in order to insure the removal of all oxygen. It is well to put a vessel containing about 50 c. c. of an alkaline solution of pyrogallic acid under the jar also, as it shows whether the apparatus is leaking or not, and at the same time serves to absorb any oxygen which may have remained. (See Fig. 2.)

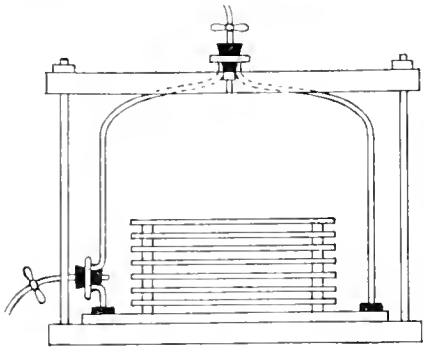


FIG. 2.

For test-tube cultures the method of Fränkel (Fig. 3), or, better, the method of Sternberg (Fig. 4) may be employed. In the former an ordinary tube is closed by a soft-rubber stopper, through which two glass tubes pass, one reaching nearly to the bottom of the test tube, for the introduction of the hydrogen; and the other, a short one, for the escape of the gas. The method of Sternberg is essentially a modification of this. After inoculating the tubes the cotton plug, or a part of it, is pushed down into the neck of the tube. Above this a section of a rubber stopper, carrying two glass tubes, both short, is inserted for about a half inch. The space above is coated with melted sealing wax, which does not contract on cooling. The tube is then attached to the hydrogen generator and inverted, the gelatin or agar being solidified. The hydrogen being light rises into the tube, displacing the air. After a sufficient time the outlet tube is sealed in the flame, then the inlet also. Both of these methods are useful mainly for the study of colonies in roll tubes, and the latter can be used only for solid cultures. The employment of the air pump attached to the outlet tube facilitates matters greatly and enables Sternberg's method to be applied to liquid cultures. Should Sternberg's method be used the tubes should be freshly sterilized and the top of the plug of cotton burned off, as otherwise the culture will soon be contaminated with moulds in abundance, many of which thrive in an atmosphere of hydrogen.

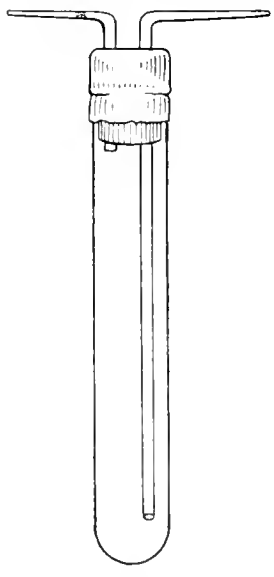


FIG. 3.

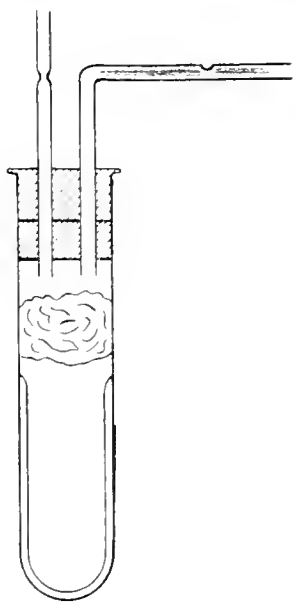


FIG. 4

The most simple method of test-tube culture is the employment of a jar or bottle, in which a number of tubes may be placed at the same time. The apparatus of Liborius above described

may be used for this purpose, or an ordinary wide-mouthed bottle, fitted with a rubber stopper carrying two tubes, one reaching to the bottom, the other extending only through the stopper, serves the purpose well. In the Centralblatt für Bakteriologie und Parasitenkunde, for November, 1893, Dr. F. G. Novy describes a jar devised by him which embodies this principle, and has been found very satisfactory by him (Fig. 5). Using the same principle, I have designed a jar for what may aptly be termed cultivation "en masse," which has advantages not possessed by any other apparatus for the same purpose with which I am acquainted. It fulfills every requirement perfectly, if well constructed, and is easy to operate. The general plan is modeled after the jar used for drying gases, known as "Fresenius's Improved" calcium chloride jar. It may be purchased of any dealer in laboratory supplies, and even without modification is very useful. The older forms may also be used by fitting rubber corks carrying glass tubes to the mouth and to the lower opening.

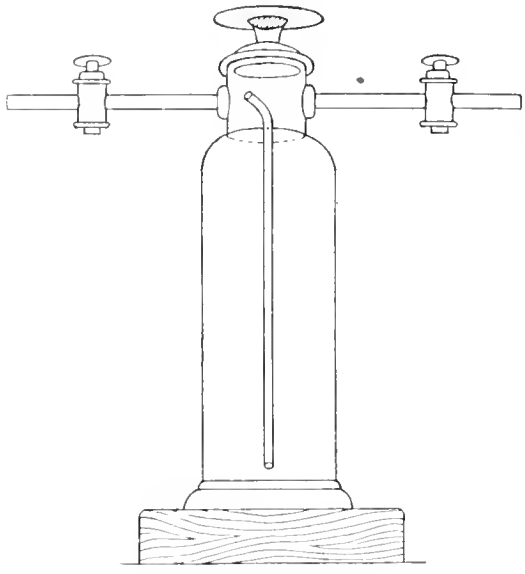


FIG. 5.

As adapted to the cultivation of anaërobic bacteria, the jar is as follows: It consists essentially of a glass cylinder, with a good base, and having some 2 inches from the bottom a constriction, dividing it into two chambers which communicate. Opening into the bottom chamber, at the shoulder, is a corrugated glass tube, fitted with a well-ground stopcock. The mouth of the jar is large, and fitted with a perforated glass stopper, the perforation opening into the cavity of the jar. A corrugated glass tube is attached to the neck of the jar, through which a hole has been made continuous with the perforation of the stopper. By turning the stopper this is closed, sealing the jar at the top. (See Fig. 6.) The jar may be made of different sizes, the following dimensions being most serviceable for general use: Diameter of upper chamber, 3 inches; of mouth (inside), 1.5 inches; height of upper chamber (inside, clear of shoulders), 7 inches; diameter of lower chamber, 3 inches; height of lower chamber, 2 inches.

A most essential feature is that the stopper and the stopcock shall be accurately ground, so as to be absolutely air-tight. The height of the upper chamber is adapted to the length of the test tubes one wishes to use, and the diameter to the number of cultures most convenient. The use of the apparatus is as follows: A piece of wire gauze is inserted, which rests on the shoulders of the constriction, and completes the floor of the upper chamber. On this a layer of cotton is placed. All the media to be used are steamed for fifteen to twenty minutes, and cooled rapidly in ice water. The tubes having been inoculated are then introduced and the jar closed. Into the lower chamber is introduced, through the lower tube, an alkaline solution of pyrogallic acid, enough being put in to fill the chamber up to the opening of the tube. The lower tube is then at once connected with the air pump, and the upper one with a hydrogen generator, the stopper being so turned as to close the jar. When the air has been exhausted, as indicated by the vacuum meter, the lower stopcock is closed and the jar filled with hydrogen. The hydrogen is then cut off and the jar again exhausted, and again filled with hydrogen, the process being repeated three times in order to make sure of all the oxygen being removed. The jar is then sealed above and below, and may be put in the incubator if no gelatin has been used.

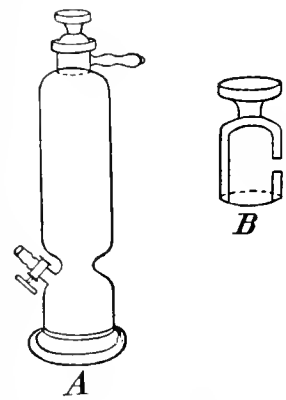


FIG. 6.—*A*, jar; *B*, sectional view of stopper.

The strength of the solution of pyrogallic acid used is one-half that recommended by Buchner for his method, viz, 1 gram of pyrogallic acid to 20 c. c. of a 10 per cent solution of caustic potash. The use of the pyrogallic acid is not necessary if the jars be well constructed, but is employed as a safeguard, and is useful as an indication of the efficiency of the apparatus.

The most convenient tube for use in this jar is 6 inches long by three-eighths of an inch in diameter.

A word may be said about hydrogen generators. The apparatus of Kipp has a wide use, but has not proved altogether satisfactory where a considerable quantity of the gas is desired. The apparatus of Sternberg is an excellent one, and simple in construction (Fig. 7). (Manual of Bacteriology, p. 83.) I have found much satisfaction in the use of an apparatus constructed as follows (Fig. 8): Two bottles holding from 3 to 4 liters are fitted with perforated rubber stoppers, that of bottle *A* carrying two tubes, one reaching to the bottom of the bottle, while the other is short, bent at right angles, and fitted with a stopcock. The stopper of bottle *B* also carries a tube reaching to the bottom, and into the second hole a glass plug is placed, for which a safety tube may be substituted. By the use of the plug the gas can be stored in greater quantity under some pressure. Broken glass is put into bottle *A* for a depth of about an inch, and on this the zinc is placed. The long tubes are connected with stout rubber tubing, on which it is well to have a screw pinchcock. Bottle *B* is raised some 4 inches above *A*, and the dilute acid placed in it. To start the apparatus, slight suction is applied to the outlet tube of bottle *A*. As soon as the acid starts to flow it will go by the action of the siphon into bottle *A*. When enough has gone over, the pinchcock is closed to prevent the suction of air. On closing the stopcock of the outlet tube the acid is forced back into the upper bottle, and the zinc is left dry. By using a stopper in the upper bottle instead of a safety tube, there is always enough pressure to force the acid over into *A*, making the apparatus practically automatic. As it is almost always used in connection with an air pump, however, this is not a matter of importance. The stopcock of the outlet should never be turned off when the tube connecting the two bottles is closed, otherwise an explosion is apt to result. With this apparatus one has always at hand from 3 to 4 liters of hydrogen under pressure, and it is a simple matter to fill any vessel, from a test tube to a bell jar. In every case the air is first exhausted, and then the hydrogen let in, the process being repeated three or more times.[1]

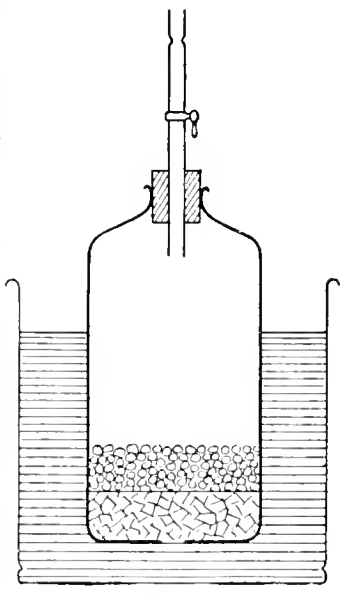


FIG. 7.

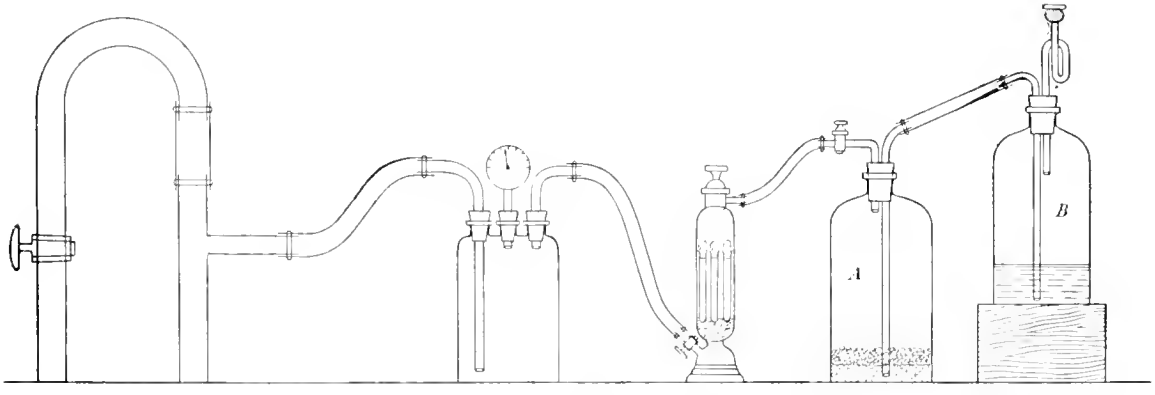


FIG. 8.

For the purpose of exhausting the air, the most convenient pump is the simple one constructed on the principle of Sprengel's mercurial pump, in which a stream of water does the work. It is attached to a spigot, and the suction tube is connected with a Woulf bottle to prevent any back flow of water.

The entire apparatus, including the anaërobic jar, is shown in Fig. 8.

[1] This apparatus was suggested to me by Dr. S. S. Kneass, a former student in Professor Roux's laboratory at the Pasteur Institute, where he saw a similar one in use.

DESCRIPTION OF ORGANISMS ISOLATED.

Micrococcus Orbicularis Flavus.

Found in virgin soil at the depth of 5 feet.

Character.—Shows slight growth in an atmosphere of hydrogen.

Morphology.—Large cocci, irregularly grouped.

Spore formation not observed.

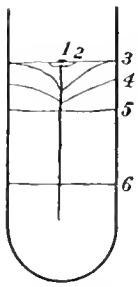
Motility.—Non-motile.

Flagella not demonstrated.

Colonies on gelatin plates.—The colonies first make their appearance about the third day, as minute, pale yellowish dots. ×80. No distinction can be made between the deep and surface colonies, except that the latter are larger. They appear as homogeneous, or, sometimes, slightly granular, disks, with even edges and a yellowish hue. The growth is very slow, and at the end of five days the surface colonies are less than 1 mm. in diameter, round, even edged, and only slightly elevated. ×80. They show a homogeneous center, with a finely granular margin. The edges are even and clean-cut. The deep colonies are rather irregular in shape, yellow in color, and finely granular. Here and there they appear to be folded. There is nothing distinctive about either the deep or the surface colonies. The colonies lie in a saucer of liquefied gelatin, which is circular and has smooth margins to the naked eye.

Agar slant.—A faint yellowish hue forms by the second day, which increases rather slowly. At the end of a week a canary-colored layer, some 2 mm. wide, has formed. It has a smooth, glistening surface and rather uneven margins.

Gelatin stab.—Growth occurs deep down the puncture, and a small yellow button forms on the surface, which is soon floating in a saucer of liquefaction. Liquefaction is rather slow, being complete in four to five weeks. The floor becomes level at the end of a week, and is covered with a yellowish flocculent deposit, while the liquefied gelatin is cloudy.



Gelatin stab.

Potato.—A moist, colorless, very thin layer forms over a large part of the surface by the third day. It becomes thicker and turns yellow about the fourth day. It then becomes somewhat granular looking, and is moist and shining, the color being somewhat deeper than on agar.

Bouillon.—Becomes diffusely cloudy by the second day. A white deposit forms on the bottom, which becomes a faint yellow after some time.

Rosolic acid.—Becomes slightly darker after two weeks.

Lituus milk.—No change of any kind can be seen. Reaction amphoteric.

Sugar gelatin, deep stab.—Growth quite deep along the puncture. Liquefaction is more rapid than in plain. No gas formed.

Indol.—Faint reaction with both sulphuric acid and sodium nitrite.

Relation to temperature.—Grows more rapidly at room temperature than in the incubator.

Bacillus Aurescens.

Found in virgin soil at the depth of 30 inches.

Character.—Strict aërobe. No growth in an atmosphere of hydrogen.

Morphology.—Short, straight rods with oval ends, making the cells spindle shaped. Length from two to three times as great as breadth. Found singly.

Spore formation not positively demonstrated. In some of the rods are seen oval, bright spots which resemble spores somewhat.

Motility very slight.

Flagella not demonstrated.

Colonies on gelatin plates.—Colonies seen at the end of thirty-six to forty hours as minute whitish points, which may easily escape observation. ×80. No distinction can be made out between the deep and surface colonies at this stage. They appear as coarsely granular disks of

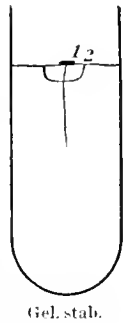
a brownish east, and have even edges. At the end of four days the surface colonies are one-half of a millimeter in diameter and yellow. They seldom attain a greater size than this. The deep colonies are punctiform and whitish. ×80. Both deep and surface colonies have much the same structure and neither show any distinctive features, even after ten days. They are yellowish-brown granular disks with even margins. The surface colonies became orange yellow after some days. The gelatin may be softened, but no liquefaction was observed.

Agar slant.—A thin faintly yellow line forms by the second day, which has spread irregularly near the bottom. It increases rather slowly and becomes viscous or tenacious. The color becomes a golden yellow.

Gelatin slant.—Forms a yellow band, with even edges, and not much elevated. If the inoculating needle contains but little of the culture, isolated circular colonies about 1 mm. in diameter are formed along the line of inoculation.

Gelatin stab.—Slight development occurs along the upper part of the puncture, while a yellow button of growth forms on the surface, reaching a diameter of 1 mm. by the fourth day. At the end of ten days the top growth has become somewhat sunken, and in eighteen to twenty days a cup-shaped depression about 5 mm. deep has formed, but no liquefaction can be detected evaporation keeping pace with it.

Potato.—A moist yellow band forms along the line of inoculation in twenty-four hours. It soon spreads over much of the plug in a thick moist layer, and the color deepens to an orange yellow.



Gel. stab.

Bouillon.—Slight cloudiness is observed on the fourth day, the growth being slow. This increases later, and dense flocculi which sink to the bottom are formed.

Rosolic acid.—Very slight growth. Color becomes slightly deeper after eight to ten days.

Litmus milk.—Becomes lighter after a week, and the color is slowly discharged without turning red. There is no coagulation of the casein.

Sugar gelatin, deep stab.—Growth confined to the surface. No gas is produced.

Indol.—Reaction negative.

Relation to temperature.—Grows somewhat more rapidly at 35° to 36° C. than at room temperature.

Note.—This resembles the bacillus Flavescens (Pohl) very closely, as far as the published descriptions go. The former is non-liquefying, while this is a very slow liquefier. In fact, no liquefaction could be detected, but was inferred from the depression of the surface growth on gelatin.

Bacillus Fluorescens Ovalis.

Found at a depth of 2 feet in a cultivated field.

Character.—Facultative anaërobe.

Morphology.—Short straight rods, with rounded ends, from two to three times as long as broad. Occurs singly. Many of the rods show irregular staining.

Spore formation not positively demonstrated.

Motility.—Actively motile.

Flagella are polar.

Colonies on gelatin plates.—Colonies are seen at the end of twelve hours as minute translucent grayish dots. × 80. The deep are pale gray, finely granular disks, with even margins. The surface colonies are irregularly circular, pale gray, and finely granular, with even edges. At the end of three days the surface colonies are 1 mm. in diameter and a bluish white color; the deep are still punctiform. ×80. They are yellowish and almost homogeneous, some faint markings being seen near the center. At the end of eight days the surface colonies are 1 mm. in diameter, circular, with well defined margins, and greenish white in color. Deep are punctiform. ×80. Deep show no change, except in density and in color, which is now yellowish. Those on the surface are also more dense, and show little or no structure. Near the margins darker lines can be faintly seen radiating from the center. There is no liquefaction nor discoloration of the gelatin.

Agar slant.—A thin greenish white band forms along the line of inoculation by the second day, and the agar has acquired a faint green tint. It soon spreads, reaching the tube wall for the lower third, and has leafy margins. The agar becomes a beautiful yellowish green.

Gelatin stab.—Growth occurs for some distance down the puncture, and a white button with irregular leafy margins forms on the surface. After several days fine spinous outgrowths form along the puncture, about 1 mm. long and whitish in color. The gelatin becomes faintly green near the surface. There is no liquefaction.

Gel. stab.

Potato.—By the second day a very thin moist layer about the color of honey has formed over a large part of the surface. After some time this becomes a pale yellowish brown. It remains very thin and has no distinctive features.

Bouillon.—Becomes diffusely cloudy and an incomplete flaky pellicle forms on the surface. After five days the bouillon becomes a faint greenish tint, and is opaque, while a white mass forms at the bottom of the tube.

Rosolic acid.—Becomes slightly darker after five days.

Litmus milk.—After a week the color becomes more blue, and at the end of four weeks is a slaty blue. A whitish deposit forms on the bottom of the tube, but there seems to be no change in the milk itself. The reaction is decidedly alkaline.

Sugar gelatin, deep stab.—Growth quite deep along the puncture, and a button on the surface. There is no liquefaction nor gas production.

Indol.—Reaction negative.

Gelatin slant.—A greenish white band with beaded edges forms along the line of inoculation. The gelatin acquires a green tint about the third day. No liquefaction occurs.

Relation to temperature.—Grows well at both room temperature and at 35° to 36° C.

Sarcina Subflava.

Found at the surface of a cultivated field.

Character.—No growth in an atmosphere of hydrogen.

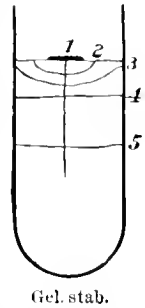
Morphology.—Packets square and longer than broad, showing 4, 8, 16, 32, or more elements on each face.

Spore formation not observed.

Motility.—Non-motile.

Flagella not demonstrated.

Colonies on gelatin plates.—Colonies become visible in thirty-six to forty hours as minute yellowish dots. ×80. They are finely granular, yellowish disks with even margins. By the fourth day the surface colonies are 1 mm. in diameter, a pale yellow, and are slightly sunken in the gelatin. ×80. They are a pale yellow, homogeneous, and have even margins. After some days the margins may become irregular and look more or less granular. The deep colonies increase very slowly and only change in appearance by becoming more dense. Liquefaction is rather slow. There is nothing distinctive about the colonies at all.



Gel. stab.

Agar slant.—A yellowish band, 3 mm. wide, forms by the fourth or fifth day. It is smooth, pale yellow, and has irregular beaded margins.

Gelatin stab.—Growth quite deep along the puncture, and a small almost white button forms on the surface, which has irregular margins. Slow liquefaction takes place under this in saucer shape. At the end of ten days the liquefaction is 1 cm. deep and has a level floor. The liquid is cloudy.

Potato.—No growth could be obtained after a number of trials.

Bouillon.—Whitish flocculi form at the bottom, and after several days a thin pellicle forms on the surface. The bouillon does not become clouded.

Rosolic acid.—No change observed.

Litmus milk.—No change either in color or in the milk itself after four weeks. Reaction faintly acid.

Sugar gelatin, deep stab.—Growth quite deep and on the surface, with slow liquefaction. No gas production.

Fig. 2

Fig. 3

Fig. 4

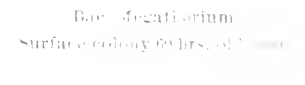


Fig. 5

Fig. 6

Fig. 7

Fig. 8

Fig. 9

Fig. 10

Fig. 11

Fig. 12

Fig. 13

Indol.—Reaction negative.

Relation to temperature.—Grows well at both room temperature and at 35° to 36° C.

Note.—This may be identical with the *Sarcina flava* (De Barry). The published descriptions are so meager that positive identification has not been possible. The chief difference noted has been in the growth on potato. I have not been able to obtain any growth, while the growth of the *Sarcina flava* is scanty and limited to the line of inoculation.

Bacillus Megatherium.

(Figs. 1, 2, 3, 4, and 5, Pl. 1.)

Very common in soil, both made and virgin, at all depths where bacteria are found at all. In the course of this work it was found as low as 7 feet in made soil which had been paved for a number of years.

Character.—It is a strict aërobe, no development occurring in an atmosphere of hydrogen.

Morphology.—Thick straight rods, with rounded ends, from three to five times as long as broad. It forms quite long chains, in which the rods are often bent on each other and are of unequal lengths. The rods show a peculiar granulation of their contents, said to be peculiar to this organism.

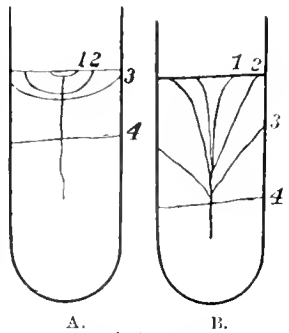
Spore formation is usually well advanced at the end of sixteen hours in a warm room. The rods appear to grow shorter and oval, while the center is occupied by a long oval spore almost as long as the rod itself. In cultures thirty six hours old chains of spores are seen, which are often pushed together, the ends overlapping each other.

Motility.—Slight movements are seen, which have been described as "amœboid."

Flagella not demonstrated.

Colonies on gelatin plates.—Colonies are seen at the end of twelve to sixteen hours as whitish dots, ×80. The deep appear brown and have regular margins. No structure can be made out. Those on the surface are lighter in color and have very irregular margins. The center is too dense to show much structure, but where any can be made out consists of a cloudy mass of interwoven and tangled filaments. By the third day the surface colonies are each in a saucer of liquefaction, 4 mm. in diameter, in which floats a whitish island with irregular margins, surrounded by a zone of opaque grayish liquefied gelatin, ×80. Deep are unchanged. The surface show the dense cloudy masses in the center, merging into the lighter masses made up of broken and tangled filaments floating in the liquefied gelatin. The margins of the saucer of liquefaction are even. When a colony has begun beneath the surface and broken through there is a well-defined darker center, surrounded by a ragged fringe of coarse filaments. In some colonies this fringe is much more regular, and assumes a festoon-like arrangement, going out in bundles at tolerably regular intervals, which divide to the right and left, joining those next them, thus forming a series of loops or festoons around the colony. This arrangement is lost in twenty-four hours by the liquefaction of the gelatin, and only broken filaments can be seen around the colony.

Agar slant.—The growth is at first a creamy white color, and forms abundantly, sometimes being piled up 1 mm. in height. The surface is moist, smooth, and glistening. It often becomes yellowish in color, and forms a thick pasty mass, with a strong smell of stale milk. After several generations on agar it changes its character, apparently, and forms a thin dirty gray layer, the agar becoming brownish after a time.



Gelatin stab.

Gelatin stab.—Liquefaction occurs in two different ways, according to the vigor of the growth apparently. In the first a saucer of liquefaction is formed, which increases, reaching the tube wall and becoming deeper. Whitish flocculi float in the liquid and gradually settle to the floor, which becomes level. In other cultures growth takes place deep down the stab, and liquefaction occurs in funnel form by the second day. The floor becomes level after ten to twelve days.

Potato.—A thick band, whitish and looking like melted candy, is formed by the second day. It is smooth and glistening. It increases rapidly, and is thrown into large folds and wrinkles by

the third or fourth day, and becomes cream colored. The folds soften down, or are overgrown in a few days, and the layer becomes a shiny looking dirty cream or putty color. It has a strong musty odor, like stale milk.

Bouillon.—Becomes diffusely clouded in thirty-six hours, and has large white flocculi floating in it. These settle to the bottom, forming a dense whitish deposit, while the bouillon remains almost entirely clear.

Litmus milk.—The milk becomes stratified, being lightest at the bottom, and somewhat reddish at the top, where it is watery and translucent. The color is discharged slowly and the casein apparently dissolved. Reaction neutral. In some cultures the milk becomes more blue, and after a time, a beautiful violet color by transmitted light, with a decidedly alkaline reaction, the casein being dissolved.

Sugar gelatin, deep stab.—Growth the same as in plain, but liquefaction takes place much more rapidly. No gas is produced.

Rosolic acid.—No change in color is noticed.

Indol.—Reaction negative.

Relation to temperature.—Grows somewhat more rapidly at 35° to 36° C.

Note.—The above description differs from those found in most books in some respects. I have found considerable differences in different cultures of *Megatherium*, and cultures recently obtained from the earth behave differently than when kept on artificial culture media for some time. As Fränkel says, "It seems almost as if a continued nutrition with our usual food media did not agree with this micro-organism." And speaking of the appearance of the rods he says, * * * "and one might be tempted to suppose that a new variety had arisen, were it not always easy to breed normal cells again from these monstrous and crippled forms by employing a more suitable culture medium." (Text-book of Bacteriology, American edition.)

I have found this true as regards the cells themselves, but the growth in the different media is never quite the same as when the cultures are fresh from the soil, so much so that it is often hard to believe that one has the same organism.

Bacillus Formosus.

(Figs. 6 and 7, Pl. I.)

Found in made soil a number of years old.

Character.—Requires oxygen for good development, but shows some growth in an atmosphere of hydrogen.

Morphology.—Slender, straight rods, with rounded ends, from seven to eleven times as long as broad. Occurs singly and in twos and threes.

Motility.—Slight independent movements noticed.

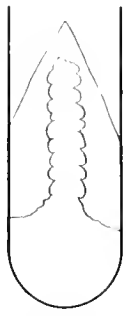
Flagella not demonstrated.

Spore formation doubtful. Probably does not form spores.

Colonies on gelatin plates.—Colonies are seen in twenty-four to twenty-eight hours as minute greenish-white dots. At the end of thirty-six hours the deep are still punctiform, while those on the surface are one-fourth of a millimeter in diameter. × 80. The deep are yellowish disks, with even edges and finely granular contents. The surfaces are circular, have even edges, and are yellowish in the center, fading to gray at the edges. They are finely granular, with no distinctive features. At the end of sixty hours the deep colonies are yellowish dots, while on the surface they are white, and one-half of a millimeter in diameter. × 80. Deep show no change. On the surface the colonies are made up of a nucleus, more or less distinct in the different colonies and yellowish brown in color. Around this is a zone of lighter yellowish hue, traversed by brownish wavy lines. Beyond is a zone of much darker color, and fading into pale yellow at the margins. It is made up of lines radially disposed, with here and there cloudy masses of brownish granules. The edges are regular and smooth. At the end of a week the surface colonies are about 1 mm. in diameter. × 80. Many still show a nucleus, and the zones above described. In the majority the nucleus and zone next to it have become of the same color, and merge into a dark-brown zone, which fades into a lighter marginal zone. In all the colonies, numbers of amorphous

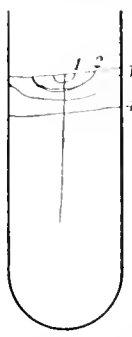
granules are seen scattered through the colony without any attempt at arrangement. The edges have lost their distinct outline, and the granules are seen invading the gelatin beyond. Rather slow liquefaction takes place.

Agar slant.—A whitish band, 1 mm. wide, with notched edges forms in twenty-four hours. By the third day this has become 4 mm. wide and spread to the tube wall near the bottom. It is a smooth, white, glistening band with notched edges, and not very thick.



Agar slant.

Gelatin stab.—By the third day a small saucer of liquefaction has formed, 2 mm. in diameter, while the growth along the puncture is very scanty. Liquefaction is slow, and by the end of two weeks has reached a depth of 1 cm. The floor becomes level and is covered with white flocculi, while the liquefied gelatin is almost perfectly clear.



Gel. stab.

Potato.—A moist white band is formed along the line of inoculation. It spreads widely where moist, and becomes a cream color by the fourth day. Later it spreads all around the plug and changes to a dirty cream color, and is brownish at the edges where it is thin.

Bouillon.—Diffuse cloudiness is caused in twenty-four hours; a dirty white deposit forms on the bottom of the tube.

Rosolic acid.—Becomes slightly darker.

Litmus milk.—Becomes more blue by the third day, after which the color is rapidly discharged, being gone by the tenth day. There is no coagulation of the casein. A white deposit collects on the bottom of the tube.

Sugar gelatin, deep stab.—Growth confined to upper part of puncture, with liquefaction in saucer shape. No gas is produced.

Indol.—Reaction negative.

Relation to temperature.—Grows better at room temperature than at 35° to 36° C.

Bacillus Verticillatus.

(Figs. 8 and 9, Pl. I.)

Found at a depth of 7 feet in made soil which had been paved over for a number of years.

Character.—Good growth in an atmosphere of hydrogen, with extensive liquefaction.

Morphology.—Thick, straight rods, with rounded ends, from three to five times as long as broad. Forms chains of ten to twelve elements.

Spore formation observed only in potato cultures after two weeks. They are oval and formed in the center of the rod.

Motility.—Doubtful; slight, if at all.

Flagella not demonstrated.

Colonies on gelatin plates.—Colonies appear in twelve hours, and in fourteen hours those on the surface have attained a diameter of 1 mm., while the deep are one-fourth of a millimeter, and whitish. The surface colonies are each in a small saucer of liquefaction, with even circular margins. They are grayish in color and translucent. ×80. Deep are grayish looking, and consist of a tangled mass of fine filaments, surrounded by quite a deep fringe of fine lines arranged in a whorl from right to left. The surface colonies are filled with slightly opaque liquefied gelatin, in which fine tangled lines like a ball of thread are seen. At this stage the colonies are indistinguishable from those of the potato bacillus. The edge is fringed with a corona of fine wavy spear points. Liquefaction is rapid, and at the end of twenty hours many of the colonies are 8 mm. in diameter. Each colony soon becomes covered with a thick pellicle, which is a cloudy white, and has irregular ragged edges.

Agar slant.—A scanty granular looking white band forms along the line of inoculation. At the end of four days it has spread to a width of 6 mm., and become white and smooth in the middle, with irregular, granular edges, looking frosted, as it were. After some time it becomes dirty white, and the agar is colored a faint brown.

Gelatin stab.—A small saucer of liquefaction has formed in twenty-four hours, and slight whitish growth is seen along the puncture. The liquefaction assumes the funnel form. The

liquified gelatin has dense white flocculi floating in it, which finally settle to the bottom, leaving the fluid portion almost perfectly clear. The floor becomes level after a time. In cultures kept in an atmosphere of hydrogen, long hair-like outgrowths from the puncture are formed. Smaller ones are sometimes seen in the ordinary cultures also.

Potato.—A dry white layer forms over much of the surface by the third day, which soon becomes a dirty white, smooth, and shining. After two weeks a faint pink color is noticed. The growth does not become folded nor wrinkled.

Bouillon.—Becomes diffusely cloudy by the third day, and a thin pellicle forms on the surface by the fifth day. This becomes thicker, acquires a metallic sheen, and is thrown into large folds.

Rosolic acid.—Becomes lighter about the fifth day. A thin pellicle forms on the surface, and the color is entirely discharged after ten days. The reaction is alkaline.

Litmus milk.—Color becomes lighter and the casein is coagulated in fine flocculi by the fourth day. The color is discharged at the end of a week, and there is a dense shiny deposit at the bottom, apparently casein, that has been changed in some way. Reaction alkaline.

Sugar gelatin, deep stab.—Growth quite deep, with liquefaction as in plain gelatin. No gas formed.

Indol.—Reaction negative.

Relation to temperature.—Grows more rapidly at 35° to 36° C. than at room temperature.

Note.—This bacillus seems to belong to the potato group, and also resembles the *subtilis* in many respects. It is to be distinguished by the formation of its colonies, especially the deep ones, by its lack of motility and the tardy spore formation. From the potato bacillus especially, it may be distinguished by the good growth in hydrogen and its effect on rosolic acid.

Bacillus Viridescens Non-liquefaciens.

Found in made soil, a number of years old, at the depth of 54 inches.

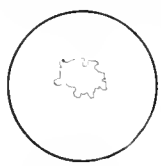
Character.—Good growth in an atmosphere of hydrogen.

Morphology.—Short, straight rods with rounded ends, from two to three times as long as broad. Many of the rods are so short as to be oval. Occurs singly mostly, but also in twos and threes. It stains more deeply at the ends.

Spore formation not observed.

Motility.—Actively motile.

Colonies on gelatin plates.—Colonies appear in thirty-six to forty hours as minute dots, having a faintly greenish tint. At the end of forty-eight hours, the deep colonies are about one-tenth of a millimeter in diameter, while those on the surface are 1 mm. in diameter. × 80. The deep are finely granular, circular in shape, and with even edges. Near the margins fine striæ may be indistinctly seen. The surface colonies have a circular shape, with clean cut margins, and a faintly green color. × 80. A dense yellowish disk with even margins, in which not much structure can be made out, except near the edges, where it is finely striated. A nucleus, usually eccentric, can generally be made out, and the colony is more dense just around it. Later, the nucleus becomes lost by the increased density, and the edges become finely notched. There is no liquefaction of the gelatin.

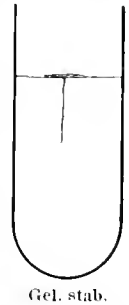


Gel. stab.
Surface growth

Agar slant.—A very thin greenish white band forms along the line of inoculation by the second day. This spreads near the bottom to the tube walls. It is never thick, and is smooth and glistening, and a very faint greenish white.

Gelatin slant.—A smooth, translucent, greenish white band is formed by the second day with even margins. It becomes more white, is thin and lacks tenacity, so that it flows down to the bottom, collecting in a white mass. It never spreads more than 2 mm., and does not liquefy the gelatin.

Gelatin stab.—The growth down the puncture is scanty, being confined mainly to the surface, where a button 1 mm. in diameter has formed by the second day. This increases until by the end of a week it is 5 mm. in diameter, is white, not very thick, and has irregular leafy edges. There is no liquefaction at the end of four weeks.



Gel. stab.

Potato.—A faintly yellowish, thin layer forms by the second day, and where the potato is moist has spread to the tube wall. It is smooth, moist, and shining. By the fourth day

it has passed all around the plug and become a chocolate brown. Later it becomes dry looking, but is still glistening, and never becomes wrinkled.

Bouillon.—Becomes diffusely cloudy by the third day, and flocculi form on the surface. After two weeks the bouillon becomes a pale green, and a whitish deposit forms at the bottom.

Rosolic acid.—Color becomes darker in four to six days.

Litmus milk.—Becomes more blue by the third day and is a pure blue by the fifth day. Later, a whitish deposit forms at the bottom. There is apparantly no change in the milk itself. Reaction alkaline.

Sugar gelatin, deep stab.—Growth confined mainly to the surface as in plain gelatin. After some time the surface growth become concave, though no softening can be detected. There is no formation of gas.

Indol.—Faint reaction on addition of both sulphuric acid and sodium nitrite.

Relation to temperature.—Grows better at room temperature than at 35° to 36° C.

Cladothrix Dichotoma (Cohn).

(Fig 10, Pl. I.)

Synonym: Brown Cladothrix (Bolton).

Found often in the upper layers of made and virgin soil. Widely distributed. It is also often found in the water of the Schuylkill and other rivers.

Character.—No growth in an atmosphere of hydrogen.

Morphology.—Forms long chains and filaments, with the characteristic false branching which distinguishes the genus. The rods are of very variable length, many of them being club-shaped. Spiral forms are also observed.

Spores have not been demonstrated.

Motility.—Non-motile.

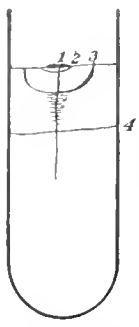
Flagella not demonstrated.

Colonies on gelatin plates.—Colonies appear on the second day as minute white dots. × 80. They are seen to be made up of a tangle of fine lines, the center being so dense that no structure can be positively made out. Toward the edge the lines are wavy and project some distance into the gelatin. At the end of forty-eight hours the deep colonies are one-sixth of a milimeter in diameter, while those on the surface are one-half of a milimeter. Both have acquired a brown color, which extends some distance into the surrounding gelatin. × 80. The deep and surface colonies look much alike, the general structure being the same. The deep colonies grow gradually less dense from the center to the edge, while on the surface there is a tolerably well-defined line of division between the dense central portion and the surrounding corona, marking no doubt the outline of the original growth as it broke through to the surface. Each colony lies in a saucer-shaped depression, and after three to four days a thick brown skin has formed on the liquefied gelatin. At the end of five days the largest colonies are about 3 mm. in diameter, and the brown discoloration extends about 3 mm. into the gelatin, the center being lighter than the surrounding gelatin. × 80. The center is two dense for the structure to be made out, and is brownish in color. The corona is made up of fine wavy lines piercing the gelatin, but they are much shorter in proportion than in the younger colonies.

Agar slant.—At the end of twenty-four hours a whitish line has formed along the inoculation, and the agar has already become a brown tint for 2 or 3 mm. on each side of the growth. The band soon becomes wider and bends across its long axis, sometimes being thrown into wrinkles. It takes firm hold on the agar, and has a dense gristly feel to the needle. It is hard to take up any portion of the growth or to spread it on a cover glass. It has to be broken up by long rubbing and even then many dense masses are left. The agar becomes a beautiful clear brown throughout.

Gelatin stab.—Very slight growth occurs down the line of puncture, and a button forms on the surface, which has begun to sink by the end of twenty-four hours. The gelatin becomes a clear brown. At the end of a week the saucer of liquefaction is about 6 mm. deep, and from the

puncture fine spinous outgrowths may be seen piercing the gelatin. At the end of three weeks, the liquefaction has reached a depth of 1 cm., and apparently the action has ceased. The floor is level, and covered with a whitish flocculent deposit, while the liquefied gelatin is a clear dark brown, the color extending into the solid gelatin for some distance.



Gel. stab.

Potato.—At the end of the third day an elevated, rough, wrinkled band has formed along the line of inoculation. It is of a grayish color, and the potato has turned a deep brown for 2 mm. on both sides of the growth. At the end of four days the growth is 1 mm. high, and the wrinkles have increased. It looks now exactly like a mass of small intestines, closely packed together. Where it has become dry it has turned white on the surface. The potato is colored a dark brown through and through, and the growth can be found in any part of it.

Bouillon.—Growth occurs almost entirely at the bottom in the form of dirty whitish flocculi, while the liquid becomes the color of brandy after some days.

Rosolic acid.—No growth observed.

Litmus milk.—Becomes more blue after two or three days and then grows gradually lighter, and the casein appears to be digested. At the end of three weeks it has become a beautiful violet hue by transmitted light, and in six weeks is a cherry red, a dark brown ring having formed around the tube at the surface.

Sugar gelatin, deep stab.—Growth confined mainly to the surface. Slow liquefaction is caused, and the gelatin becomes brown. No gas is produced.

Indol.—On the addition of both sulphuric acid and sodium nitrite, a reddish color is produced, probably indol.

Relation to temperature.—Growth is more rapid at 35° to 36° C. than at room temperature.

Cladothrix Non-liquefaciens.

(Figs. 11, 12, 13, and 14, Pl. II.)

Found at the depth of 9 feet in made soil, which had been paved for a number of years.

Character.—Requires oxygen. Shows very slight growth in an atmosphere of hydrogen.

Morphology.—Forms long chains and filaments, which show false branching. No spiral nor coccus forms observed. The filaments break up into rods of various lengths, which have square ends.

Spore formation not observed, though in old cultures some of the rods show unstained areas.

Motility.—Non-motile.

Flagella not demonstrated.

Colonies on gelatin plates.—Colonies appear in thirty-six to forty hours as minute white dots, those on the surface being somewhat larger and yellowish. × 80. The deep have a structure like the branching of a tree, the branches apparently arising from a common center and running outward in every direction to form a circular growth. On the surface the colonies have a central portion of grayish color, made up of fine densely interwoven lines. Toward the edge the lines can be clearly seen in tangled masses, growing thinner and finally breaking out to form a corona of coarse spear points, which are almost straight, and seem to be as large at the ends as when they leave the colony.

The deep colonies grow almost as fast as those on the surface, but after a week become very different in appearance. They are yellowish in color, circular, and not as large as the surface colonies. × 80. They show an opaque center of reddish-yellow hue, surrounded by a beautiful corona of fine wavy and branched lines, which push into the gelatin for a distance nearly equal to the diameter of the colony. The surface colonies at the end of a week are 1 mm. in diameter, are elevated, and nearly hemispherical with white moldy looking surfaces. × 80. They show a dense opaque yellowish center, growing brown toward the edges, where it breaks up into a corona of short, coarse spear points. These bore into the gelatin at tangents crossing each other, forming a coarse basket work which resembles a swallow's nest. After a few days more a second set of finer wavy lines are seen outside of these, and apparently beneath them. At this time

Fig. 11

Fig. 13

Fig. 14

Cladothrix non liquefaciens
A. Deep colony 44 hrs. old. x 80

Fig. 12.

Surface colony 44 hrs. old. x 80

A

Cladothrix non liquefaciens

B

A. Deep colony 8 days old. x 80.
B. Surface colony 8 days old. x 80.

Fig. 15

Fig. 16

Fig. 17.

A

Cladothrix Profundus.
A. Deep colony 36 hrs. old. x 80.
B. Surface colony 36 hrs. old. x 80.

B

Bac. Fluorescens Liquifaciens
Deep colony 36 hrs. old. x 80

Fig. 18

Fig. 19

Surface colony 36 hrs. old. x 80

B. Serratus Viridis
3rd day. x 80

Fig. 20

Fig. 21

B. [illegible]

Bac. [illegible]
Deep colony 36 hrs. old. x 80

Fig. 22

Fig. 23

B. [illegible]
36 hrs. old. x 80

the corona of the deep colonies is almost twice the diameter of the central portion. There is no liquefaction of the gelatin.

Agar slant.—A thin whitish layer forms in the course of thirty-six hours. It has smooth edges and is marked by yellowish points. After a few days the yellow growth predominates, and an elevated band 1 mm. high is formed, about salmon color. On the surface it is almost covered with a white mouldy looking growth, which is dry and thin and easily scooped off. Under the microscope it is seen to be made up of short rods and filaments, many of which show false branching. A fine whitish mossy-looking growth is seen pushing into the agar from the under surface of the layer, which appears to be made up of numberless filaments closely packed. In some cultures the salmon-colored layer is absent, the growth being limited to beneath the surface of the agar, with a white, dry, very thin layer on the surface. This is easily scraped off, leaving the surface of the agar perfectly smooth. The conditions which cause this difference of growth have not been clearly made out.

Gelatin stab.—Growth occurs along the puncture and is seen in twenty-four hours, and a white dry looking button forms on the surface, which attains a diameter of 5 mm. by the end of a week. At the same time fine feathery looking offshoots are seen passing out from the puncture. No liquefaction takes place. A very slight brownish discoloration of the gelatin is caused near the surface.

Gel. stab.

Potato.—A yellowish growth, marked with whitish points, is formed along the line of inoculation. It is rough and dry looking, and soon becomes thrown into numberless fine folds and wrinkles. It acquires a pinkish tinge. Is never very abundant.

Bouillon.—A thin film with white powdery looking matter on it is formed in thirty-six hours. The liquid remains almost perfectly clear, while whitish flocculi collect at the bottom.

Rosolic acid.—Growth very scanty. No change in color.

Litmus milk.—The milk becomes more blue by the third day. A thick yellowish ring forms around the tube at the surface. There is no change apparently in the milk itself. Reaction alkaline.

Sugar gelatin, deep stab.—Growth down stab and on surface, as in plain gelatin.

Indol.—Reaction negative.

Relation to temperature.—More rapid growth at 35° to 36° C. than at room temperature.

Cladothrix Profundus.

(Figs. 15 and 16, Pl. II.)

Found at the depth of 9 feet in made soil, which had been paved over for a number of years.

Character.—Requires oxygen. No growth in an atmosphere of hydrogen.

Morphology.—Forms long chains and filaments, which show the characteristic false branching.

Spore formation not observed.

Motility.—Non-motile.

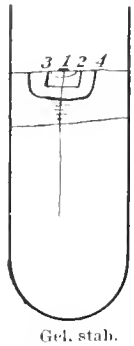
Flagella not demonstrated.

Colonies on gelatin plates.—Colonies become visible in from twenty-four to twenty-eight hours as minute circular white dots. At the end of thirty-six hours the surface colonies are one fourth of a millimeter in diameter; the deep still punctiform. ×80. The deep are made up of very fine wavy lines running radially from the center into the gelatin. The surface colonies are of the same general structure, but the center is too dense to be made out clearly. It is brownish in color, surrounded by a beautiful corona of long, wavy, fine lines, quite regularly disposed. At the end of forty-eight hours the gelatin has taken on a clear brownish hue, and each colony is in a small saucer of liquefaction. As the surface colonies grow older, the center becomes a mottled brown, but no structure can be made out. Surrounding this is a darker zone, made up of densely matted fibers, from which the corona is given off. It is much narrower in proportion than in the younger colonies. A whitish skin, folded in a radial direction, forms after some days on the liquefied gelatin. At the end of five or six days the entire plate becomes liquefied, if it contains

many colonies, and the colonies float in it as small circular islands. Where the plate contains only a few colonies, each may attain a diameter of 3 mm. The liquefied gelatin is brown in color, and the color penetrates the unliquefied portion for about 2 mm.

Agar slant.—A rough, grayish, glistening band, with irregular beaded edges, is formed in the course of thirty-six hours. As it increases it bends in a transverse direction, and along the line of inoculation becomes finely wrinkled, the edges being thinner and undulating. The surface is a bluish gray and has a metallic luster. The growth takes firm hold on the agar, and forms a tenacious leathery membrane. The agar becomes a clear brown.

Gelatin stab.—Growth occurs only in the upper part of the puncture, and on the surface a small button forms. By the third day this has begun to sink and from the puncture fine outgrowths are seen. The growth on the surface becomes white, while the gelatin grows brown for some distance down. The depression in the gelatin has vertical walls, as if punched out. The liquefaction is slow and apparently ceases when a depth of about 2 cm. has been reached. The floor becomes level and has some grayish deposit on it. The liquefied gelatin is a clear brown and the color extends some distance into the solid portion below.



Gel. stab.

Potato.—No growth is seen until the third day, when a yellowish discoloration is noticed. By the next day a finely wrinkled, almost colorless band has formed, and the potato shows a brown discoloration for some distance from each border. It spreads over much of the surface, acquires a grayish hue, and resembles a coil of small intestines very closely. It dries after a time into a thin brownish layer, showing many fine wrinkles, having lost the resemblance to intestines. The potato is never much discolored.

Bouillon.—Growth is confined to the bottom, and around the edges at the surface, while a few flakes of grayish color form on the surface. The bouillon becomes a dark sherry-wine color.

Rosolic acid.—No growth apparently.

Litmus milk.—No change is noticed for some days, when it becomes violet colo . This is slowly changed, and at the end of six weeks has become a plum color. The casein seems to be dissolved, and a whitish deposit forms on the bottom of the tube. Reaction strongly alkaline.

Sugar gelatin, deep stab.—Growth is confined to the upper third of puncture and to the surface. Liquefaction is much more rapid than in plain gelatin, and there is not nearly so much discoloration. A wrinkled yellowish membrane forms on the walls of the depression caused by the liquefaction. There is no gas produced.

Indol.—Reaction negative.

Relation to temperature.—Grows more rapidly at 35° to 36° C. than at room temperature.

Cladothrix Intestinalis.

Found in virgin soil at a depth of 6 feet.

Character.—No growth in an atmosphere of hydrogen

Morphology.—Forms long filaments, which break up into rods of different lengths. The false branching is seen, characteristic of the genus. The filaments have "buds" on them here and there, which are almost spherical.

Spore formation not observed.

Motility.—Non-motile.

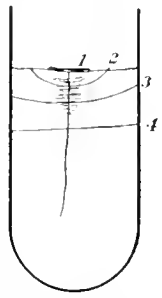
Flagella not demonstrated

Colonies on gelatin plates.—Colonies appear in from thirty-six to forty hours as minute white dots, those on the surface being somewhat larger. ×80. Deep are made up of branching filaments, running from a common center in every direction. On the surface the colonies show a central portion made up of densely packed filaments, the growth being too dense to show the structure clearly. Toward the edge the filaments are well seen, lying in tangled masses, which break up to form a corona of coarse and somewhat wavy spear points. The color is gray. As the colonies grow older, they become more dense in the center, while the corona of the deep colonies becomes much longer in proportion to the diameter. The filaments are seen to branch distinctly. The surface colonies become white and somewhat mouldy looking, and the gelatin is

slowly liquefied and takes on a brown color. ×80. They do not show much change. The center becomes more dense, and the corona is not so deep in proportion to the diameter of the colony.

Agar slant.—A whitish or grayish beaded growth is seen on the second day. After four days it has become 2 mm. wide, is rough and wrinkled, and the color of dead skin after maceration in water. The wrinkles increase, and after some days the growth resembles a coil of intestines. It does not take firm hold on the agar, and is rather friable. It can not, however, be spread, holding together in small tough masses. The agar is but little discolored.

Gelatin stab.—Growth occurs along the puncture, and on the surface a white mouldy-looking button forms. After five or six days this folds in a radial direction and the edges become somewhat wavy in outline. From the line of puncture beautifully fine feathery outgrowths are seen at the end of a week. Liquefaction occurs slowly, and after six weeks the floor has become level some 2 cm. below the surface. There is some brownish discoloration of the liquefied gelatin, but not much. The button floats on the surface.



Gel. stab.

Potato.—At the end of twenty-four hours only a slight brownish discoloration of the potato is noticed. By the next day a thin layer about the color of the potato has formed, and is much folded and wrinkled. It increases in thickness and the folds become more closely packed together, so at the end of four or five days it resembles a lot of very small intestines very closely—more so than the culture on agar. The potato is only slightly discolored. It soon becomes dry and turns white, as if covered with a fine mould.

Bouillon.—White flocculi settle to the bottom, and the bouillon becomes the color of dark sherry wine at the end of a week.

Rosolic acid.—No growth.

Litmus milk.—Becomes lighter blue in three or four days, a thick pellicle forms on the surface, and a dirty brown ring around the tube. At the end of a week it has become a beautiful violet hue by transmitted light. The color is slowly discharged, but is still present at the end of eight weeks. The casein seems to be dissolved without previous coagulation. Reaction decidedly alkaline.

Sugar gelatin, deep stab.—A fine feathery growth along the puncture and button on surface, as in plain gelatin, with slow liquefaction. There is no discoloration, and no gas produced.

Indol.—The peptone solution becomes the color of pale sherry wine, which interferes with the observation of the reaction. On the addition of both sulphuric acid and sodium nitrite a reddish color is produced, probably due to indol.

Relation to temperature.—More rapid and abundant growth at 35° to 36° C. than at room temperature.

Cladothrix Fungiformis.

Found at the depth of 5 feet in virgin soil.

Character.—Requires oxygen. No growth in an atmosphere of hydrogen.

Morphology.—Forms quite long chains and filaments, which show false branching, not always easily made out.

Spore formation not observed.

Motility.—Non-motile.

Flagella not demonstrated.

Colonies on gelatin plates.—Colonies become visible in about forty hours as minute white dots. × 80. Deep colonies are made up of branching filaments running out in every direction from a common center. The surface colonies have a central portion, made up of densely packed and interwoven filaments, which is bordered by a corona of fine branching filaments. Both deep and surface colonies are gray. At the end of a week the surface colonies are about 1 mm. in diameter, while the deep are somewhat larger. Those on the surface are white and mouldy looking, and have sunk into the gelatin, the depressions looking punched out. Not much structure can be made out under the microscope. The deep colonies show the same general structure, a yellowish center, which has become too dense to show the network of lines of which it is made up, surrounded by a corona of fine filaments, often interwoven and tangled. The gelatin does not become discolored

Agar slant.—A whitish, elevated growth, which soon becomes almost pure white and mouldy looking, is formed in the course of three or four days, and takes firm hold on the agar. After some time it splits here and there, and shows a dark-brown underlayer, the edges of the fissured crusts curling back a little. It has a strong smell of rotten wood. At the end of three or four weeks the agar turns slightly darker.

Gelatin stab.—By the third day there is good growth down the puncture, fine outgrowths having formed for some distance. A white button forms on the surface, and under this slow liquefaction goes on. The depression has at first a punched out look, with perpendicular walls. It finally reaches the tube wall in about eight days, leaving a ring of gelatin attached to the tube at the surface. The liquefied gelatin is almost clear, and the floor has whitish masses on it. There is no discoloration of the gelatin observed.

Potato.—At the end of three days a scanty almost colorless growth has formed along the line of inoculation, and the potato is distinctly whiter for a distance of 1.5 mm. along each border. The growth becomes a faint yellow, but is always very scanty and thin.

Bouillon.—The liquid remains clear, but becomes slightly darker. A mass of whitish ball-like flocculi collects at the bottom, and colonies about 1 mm. in diameter form around the tube at the surface.

Rosolic acid.—No growth.

Litmus milk.—Becomes more blue by the third day, and a mass of growth floats on the surface. It slowly acquired a beautiful violet tint by transmitted light, and at the end of four weeks has changed to a cherry color. The casein seems to be dissolved without previous coagulation. The reaction is strongly alkaline.

Sugar gelatin, deep stab.—Growth as in plain gelatin. No gas production.

Indol.—Slight color after standing several hours with both sulphuric acid and sodium nitrite.

Relation to temperature.—Grows more rapidly at 35° to 36° C. than at room temperature.

Bacillus Fluorescens Undulatus.

(Figs. 17 and 18, Pl. II.)

Found at a depth of 14 inches in made soil a number of years old.

Character.—Requires oxygen for its full development, though there is some growth in an atmosphere of hydrogen.

Morphology.—Slender, straight rods with rounded ends, from seven to eleven times as long as broad. Forms long chains.

Spores are small and oval in form.

Motility.—Actively motile.

Flagella are situated at the poles.

Colonies on gelatin plates.—The colonies appear in about thirty hours as greenish dots. × 80. Deep colonies are dense-looking brown or gray disks, darker in the center than at the edges, where masses of fine wavy lines can be made out. The surface colonies look much like drops of moisture at the end of thirty-six hours, and have a greenish line. × 80. They are gray disks, with a well defined nucleus, eccentrically placed and somewhat granular looking. Around the nucleus, and apparently coming out of it, is a zone composed of the most exquisitely fine hair lines, wavy and packed closely together. At the end of three days the surface colonies are 1 mm. in diameter and do not increase in size, but become more dense and elevated. The surface is convex, white in color, with a greenish, iridescent line. The deep never become larger than one-fourth of a millimeter. × 80. The deep, after a week, are much the same as described above, but more dense and granular. The edges are well defined and even. Those on the surface have become so dense that the structure can not be made out except near the margins, where fine striæ are seen. The nucleus remains visible. There is no liquefaction of the gelatin, and it acquires a faint green color around the colonies.

Agar slant.—In twenty-four hours a thin, translucent, greenish band 2 mm. long has formed along the line of inoculation. It never becomes thick, and after four or five days has spread to the tube wall in a very thin layer for the lower third. It has dentate margins. The color is imparted to the agar—a faint clear green.

Gelatin slant.—An elevated band with even margins forms in thirty-six hours. It becomes elevated, white, and has a greenish, iridescent surface. There is no liquefaction.

Gelatin stab.—Very slight growth along the puncture. A button forms on the surface, which attains a diameter of 4 mm. It is white, shining, and has irregular, leafy margins. There is no liquefaction, and the gelatin may become faintly tinged with green near the surface.

Potato.—A yellowish, moist layer spreads over much of the surface by the third day, and all around the plug at the bottom. It soon becomes a dirty, yellowish brown, is always thin, and has a glossy moist surface.

Bouillon.—Diffuse, but slight cloudiness is seen by the second day, which increases to some extent, but the growth settles largely to the bottom. After some days the bouillon acquires a faint green tint, and at the end of two weeks is a pale clear green.

Rosolic acid.—Very slight growth. After three weeks the color has become darker.

Litmus milk.—Becomes more blue after three or four days. At the end of three weeks it is a deep pure blue. There is no coagulation of the casein or any apparent change in the milk itself.

Sugar gelatin, deep stab.—A button forms on the surface; no growth along the puncture. There is no gas produced.

Indol.—Reaction negative.

Relation to temperature.—Grows better at room temperature than at 35° to 36° C.

Micrococcus Putatus.

Found in made soil at a depth of 38 inches.

Character.—Strict aërobe.

Morphology.—Large coccus forming irregular groups.

Spore formation not observed.

Motility.—Non-motile.

Flagella not demonstrated.

Colonies on gelatin plates.—Colonies appear in from forty to forty-eight hours as minute yellowish dots, which easily escape observation, being translucent. On the surface they are only one-tenth of a millimeter in diamater. × 80. Deep are round, finely granular, and have even edges. Those on the surface are round, with regular edges, and have a yellowish cast. They are finely granular, and have an eccentric nucleus, of slightly darker hue. After five days, the deep colonies are still punctiform, while those on the surface are one-half of a millimeter in diameter, and have a greenish yellow color. × 80. Deep have become more dense, but otherwise are unchanged. The surface are yellowish disks, with even distinct edges. No structure can be made out except near the edges, where fine wavy lines radially disposed are seen. The nucleus still remains visible. At the end of a week the colonies are distinctly yellow, but never become larger than 1 mm. Slow liquefaction occurs after two weeks.

Agar slant.—A beaded line forms along the needle stroke in twenty-four hours, of a faint yellowish color. It increases rather slowly, and becomes a canary yellow after ten or twelve days. The surface becomes smooth and glistening, and the edges of the band are notched.

Gelatin slant.—A band 1 mm. wide forms along the line of inoculation, of a yellowish hue. At the end of four days the canary yellow color is well developed. After two or three weeks the gelatin is slowly liquefied, and the growth slips slowly down the shallow groove which is formed.

Gelatin stab.—Growth is confined to the upper part of the puncture, and by the fourth day a button has formed on the surface, which reaches a diameter of 4 mm. at the end of ten days. It is quite thin, yellow in color, and has even margins. Liquefaction begins about the twelfth day, and the surface growth becomes concave, then slowly sinks.

Potato.—A yellow layer is formed by the third day, spreading at the bottom. After ten days a dense, abundant growth has formed, reaching the walls of the tube for the lower half. It is smooth, moist, and shining, and lemon yellow in color.

Bouillon.—The liquid becomes slightly cloudy by the third day, but the growth is confined almost entirely to the bottom, where it forms granular-looking yellowish masses, not abundant.

Rosolic acid.—Growth is scanty. Color is somewhat darker after a week.

Litmus milk.—Becomes more blue by the third day. After a week is a pure blue. There is no coagulation or any change apparent in the milk itself. A yellowish deposit forms at the bottom of the tube.

Sugar gelatin, deep stab.—Very scanty growth, and confined to the surface mainly. No gas is produced.

Indol.—Reaction negative.

Relation to temperature.—Almost no growth at 35° to 36° C.

Bacillus Striatus Viridis.

(Figs. 19 and 20, Pl. II.)

Found at a depth of 18 inches in made soil a number of years old.

Character.—No growth at all in an atmosphere of hydrogen.

Morphology.—Straight, rather slender rods, of variable length, with rounded ends. Each rod is marked by transverse bands which do not take the stain, giving it a striated appearance, not unlike the bacillus *Diphtheriæ*. Occurs singly for the most part, though pairs are seen also.

Spores.—Formation of spores is doubtful.

Motility.—Actively motile. Occasionally one or more rods will dart across the field with a rapidity which makes it hard to follow them.

Flagella are situated at the poles.

Colonies on gelatin plates.—Colonies appear at the end of thirty hours as minute bluish-white, translucent dots, about one-sixth of a millimeter in diameter. Deep colonies are punctiform, × 80. Deep are yellowish, finely granular, with circular even edges. Those on the surface have a yellow hue, and three distinct zones can be made out, the color growing paler from the center outward. Growth is slow, and at the end of five days the surface colonies are only 1 mm. in diameter, the deep remaining whitish dots. × 80. Deep appear as dense brown disks with even edges. The surface colonies still show the zones. Just outside of the zone surrounding the nucleus have appeared brownish masses, with clearly defined edges, heaped irregularly on each other, resembling amorphous crystals. The nucleus is usually eccentric. In some colonies these amorphous granules are almost all grouped at one side of the colony, but usually they form a more or less regular circle. (See drawing.) After a few days the colonies become grayish and lose their even margin, a fringe of fine wavy lines having formed. The granules have become more numerous and are more regularly disposed.

Agar slant.—By the second day a smooth, shining band, with irregular margins has formed, which spreads near the bottom in a very thin almost invisible layer, which has leafy margins. The agar acquires a faint green tint by the third day, which later becomes a yellowish green. The growth soon covers much of the surface of the agar, but is never very thick, and becomes somewhat shiny.

Gelatin stab.—Growth is quite slow, and confined mainly to the surface, where a whitish button, some 2 mm. in diameter, is formed by the end of a week, and later becomes double that size. It has even, elevated margins and is white. There is no liquefaction of the gelatin.

Potato.—By the second day there is an abundant growth, spreading widely over the plug where it is moist. It becomes a chocolate brown after two weeks, and is moist and shining.

Bouillon.—Diffusely cloudy at the end of twenty-four hours. Becomes a faint green at the end of a week and the growth settles to the bottom as a white mass.

Rosolic acid.—No change in color is produced.

Litmus milk.—No change is seen until about the tenth day, when it becomes more blue, without any coagulation. After five weeks, the color has been entirely discharged.

Sugar gelatin, deep stab.—Growth very scanty and mostly on the surface, where a button forms. There is no liquefaction and no production of gas.

Indol.—Reaction negative.

Relation to temperature.—Grows well at both room temperature and at 35° to 36° C.

Bacillus Viscosus (Frankland).

(Fig. 21, Pl. II.)

Found in meadow soil at the depth of 30 inches.

Character.—Very slight growth in an atmosphere of hydrogen.

Morphology.—Small, straight rods with rounded ends, from three to five times as long as broad. Occurs singly and in pairs.

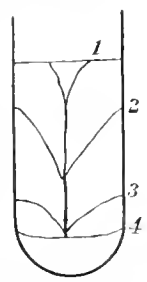
Motility.—Actively motile.

Flagella situated at the poles.

Spores not observed.

Colonies on gelatin plates.—Colonies appear in twelve to fourteen hours as minute whitish dots, barely visible to the naked eye. × 80. They are finely granular, grayish disks, with even margins. At the end of eighteen hours the surface colonies are one-half of a millimeter in diameter, circular and whitish, each lying in a small saucer of liquefaction. × 80. They are made up of masses of fine wavy lines, giving a fringed appearance to the margins which are uneven, though generally circular in shape. Liquefaction is rapid, and at the end of thirty-six hours the surface colonies are 6 to 8 mm. in diameter, the liquefied gelatin containing grayish flocculi. The edges are clear cut and circular. × 80. The flocculi are made up of fine threads in tangled masses. At the edge these lines assume an outward direction, forming a corona of fine spear points, the colonies at this stage resembling those of the subtilis very closely. The deep colonies are one-sixth of a millimeter in diameter, and whitish in color. × 80. The central portion is yellowish brown and granular, and is surrounded by a corona of fine wavy lines, whose length is about equal to the diameter of the central part of the colony. Liquefaction is rapid on the surface, and further observation is impracticable.

Agar slant.—A thin, smooth, glistening, greenish line is formed along the needle mark at the end of twenty-four hours. This soon spreads over a large part of the surface, and the agar acquires a green tint.



Gel. stab.

Gelatin stab.—Growth occurs down the puncture, and a funnel of liquefaction is formed by the second day, in which whitish flocculi are floating. By the third day the gelatin is liquefied to a depth of 1 cm., measured along the tube wall, and the floor is becoming less funnel shaped. A tenacious layer forms on the surface about the fifth day, and the whitish deposit at the bottom is also tenacious. The liquefaction proceeds nearly to the bottom, and the floor becomes level, after which the action seems to cease.

Potato.—A smooth, moist layer of yellowish hue forms in twenty-four hours. This soon spreads over the entire surface of the plug in a thin layer, and becomes a chocolate brown about the tenth day. It is smooth, moist, and shining.

Bouillon.—Diffuse cloudiness, not very intense, is caused by the third day. The bouillon becomes green at the surface about the same time, the color extending downward, so that about the tenth day it is green all through. A whitish deposit forms at the bottom.

Rosolic acid.—A slight film forms on the surface, but no change occurs in the color.

Litmus milk.—Becomes reddish about the fifth day, but no coagulation can be detected. Later the milk becomes watery, apparently from digestion of the casein, and a white deposit collects at the bottom.

Sugar gelatin, deep stab.—Growth occurs deep along the puncture, with rapid liquefaction, and a layer forms on the surface. No gas is produced.

Indol.—Reaction negative. An odor like skatol is produced by boiling with sulphuric acid and sodium nitrite.

Relation to temperature.—More rapid at 35° to 36° C.

Note.—This bacillus was first described by Grace and Percy Frankland in the Zeitschrift für Hygiene, Vol. VI, 1889.

Bacillus Viridescens Liquefaciens.

Found in meadow soil at a depth of 30 inches.

Character.—Requires oxygen for its full development, though some growth occurs in an atmosphere of hydrogen.

Morphology.—Small, straight rods, with rounded ends, from three to five times as long as broad. Occurs singly.

Spores are not formed until about the tenth day. They are small ovals and formed in the center of the rods.

Motility.—Active movements.

Flagella situated at the poles.

Colonies on gelatin plates.—Colonies seen at the end of twelve hours as minute whitish dots, with a bluish cast. × 80. They are translucent disks, looking like drops of moisture, with even edges. At twenty hours they are more white and the largest one-half of a millimeter in diameter, and each one is already beginning to form a saucer of liquefaction. × 80. Both deep and surface colonies appear as grayish, granular disks, with well-defined but irregular margins. On the surface the margins are soon lost, and the colony appears as a mass of fine wavy lines, twisted and curled. The central portion is made up of cloudy masses of a grayish hue. Some of the deep colonies have a lobed appearance, the center appearing as if higher than the edges, which have a fissured look. Liquefaction proceeds very rapidly, and the colonies lose any characteristic form very soon.

Agar slant.—A smooth, elevated, greenish-white band, spreading widely at the bottom, is formed by the second day. At 35° to 36° C. the agar is largely covered in twenty hours, and has already acquired a green tint, which only comes at room temperature about the third day. The growth spreads from the edges in a very thin layer with uneven margins, and becomes a beautiful yellowish green. It is white in the water at the bottom.

Gelatin stab.—Good growth is seen down the puncture in twenty-four hours, and at the surface a funnel of liquefaction has formed, whitish flocculi sinking to the bottom. By the third day the liquefaction has reached a depth of 1 cm., measured at the tube wall, the floor becoming less funnel shaped. By the fourth day more than two-thirds of the gelatin has been liquefied. The floor becomes level after a few days more and covered with white flocculi. The process seems to stop, or else proceeds very slowly. The liquefied gelatin does not become green.

Potato.—An abundant yellowish growth, spreading to the walls of the tube where moist, is seen on the second day. It is moist and shining, not very thick. After five or six days it becomes a brownish color.

Bouillon.—Diffuse cloudiness on second day. Green tint is caused near the surface by the end of the third day, and soon the whole of the liquid becomes green. On the bottom of the tube an abundant white deposit collects.

Rosolic acid.—A thin film forms on the surface, but no change in color is caused.

Litmus milk.—Reddish tinge appears in forty-eight hours, but no coagulation of the casein is observed. A scum forms on the surface and a whitish deposit at the bottom. After some days the milk becomes watery, apparently from digestion of the casein.

Sugar gelatin, deep stab.—Grows to bottom of puncture and causes rapid liquefaction. No gas produced.

Indol.—Reaction negative. On boiling after the addition of sulphuric acid and sodium nitrite an odor like skatol is produced.

Relation to temperature.—More rapid at 35° to 36° C.

Note.—This bacillus resembles the *Fluorescens liquefaciens* very closely, and may be identical with it. The chief difference noted, as far as the published descriptions go, is in the production of spores. No culture of the bacillus *F. liquefaciens* was at hand with which it could be compared.

Bacillus Ramosus.

Synonyms: Bacillus Mycoides (Flügge). Root form bacillus (Fränkel); Wurtzel bacillus.

Character.—Aërobe. Found constantly in both made and virgin soils, both near the surface and at a considerable depth.

Morphology.—Thick, straight rods with rounded ends, from two to three times as long as broad. Forms chains of considerable length.

Spores are large ovals, formed about the center of the rods.

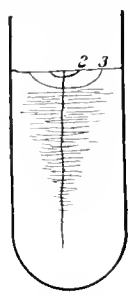
Motility.—Movements are sluggish.

Flagella not demonstrated.

Colonies on gelatin plates.—Colonies are well advanced in sixteen hours. They are indistinct cloudy masses, with ill-defined margins, resembling the mycelium of a fungus somewhat. × 80. The center is composed of fine tangled lines, which send out long filaments in every direction, forming a circular mass. They are much tangled and twisted. At the end of twenty-four hours the colonies are more distinct, and 4 mm. in diameter. The gelatin has become softer, and has an iridescent gleam when viewed slantingly. By the third day the colonies are more than 1 cm. in diameter if there be but few on the plate. The gelatin does not pour as when liquefied by the *Subtilis*, for example, being held in the interstices of the dense network of fibers. × 80. But little more is seen than on the first day. The fibers have multiplied immensely and are closely matted together, giving a grayish appearance.

Agar slant.—A moist looking, grayish growth forms in twenty-four hours along the line of inoculation, which has a somewhat felted look. From the edges fine fibers run out and soon reach the tube wall. The whole mass thickens, forming a grayish layer, which often wrinkles in the middle. The folds are best seen by looking at the under surface.

Gelatin stab.—A small saucer of liquefaction is formed on the surface by the second day, and very soon fine filaments are seen boring into the gelatin in every direction, giving the appearance of "an inverted fir tree." A moist, shining skin is formed on the surface, which becomes folded and slowly sinks, a second one forming. The liquefaction becomes complete after some days, and the cloudy masses which floated in the liquid sink to the bottom.



Gel. stab.

Potato.—A white granular-looking layer, which covers much of the plug is formed in the course of four days. This becomes much folded and wrinkled if the potato has been freshly prepared.

Bouillon.—Good growth in the form of veil-like masses, which resemble closely bits of Japanese tissue paper sunk in the liquid. The bouillon does not become cloudy.

Rosolic acid.—Color is deepened in thirty hours, and becomes decidedly deeper in ten days.

Litmus milk.—Casein is precipitated as a jelly-like mass in twenty-four hours, and the color is slightly darker. The blue color is lost from above downward, the clot becoming the color of milk. It is digested from above downward also, the process being complete in about two weeks. It is then the color of whey, and a blue ring is seen around the tube at the surface. The reaction is decidedly alkaline.

Sugar gelatin, deep stab.—Growth quite deep down the puncture, with formation of fine outgrowths, as in plain gelatin. No gas is produced.

Indol.—Reaction negative.

Relation to temperature.—Grows well at room temperature, and also at 35° to 36° C.

Bacillus Antenniformis.

(Figs. 22 and 23, Pl. II.)

Found at the depth of 5 feet, in virgin soil used as a meadow.

Character.—No growth in an atmosphere of hydrogen.

Morphology.—Large, straight rods, with rounded ends, from eight to ten times as long as broad. Occurs singly for most part.

Motility.—Actively motile.

Flagella not demonstrated.

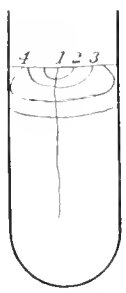
Spore formation not observed.

Colonies on gelatin plates.—Colonies are seen in from twelve to fourteen hours as minute colorless dots. × 80. They are slightly oval, yellowish, and granular. From various portions of the periphery, mainly near the poles of the oval, short fine projections are seen, resembling

the antennæ of insects. At the end of thirty-six hours these can not be seen and the resemblance is lost. At this time the surface colonies are one-fourth of a millimeter in diameter, and are grayish. × 80. They have an orange-brown center, which sometimes shows a granular nucleus. Around it is a coarsely granular zone of the same color, which passes into a fringe of wavy lines, beyond which is a border of colorless markings apparently made up of parallel lines closely packed and folding in and out. It is deeply dentate, and so faint as to be easily overlooked. As the colonies grow older, the granular center encroaches on the zone of the wavy lines and they in turn on the border, which becomes more regular in outline and narrower in proportion to the size of the colony. Each colony causes a saucer of liquefaction on which a pellicle forms, which soon becomes folded. Liquefaction is not very rapid. At the end of a week the colonies are about 6 millimeters in diameter. Under 80 not much can be made out except near the edges, where they have a reticular appearance. They are circular and have well-defined edges.

Agar slant.—On the second day a very thin, barely visible band with irregular margins is seen, which near the bottom has spread considerably in leafy shapes. It soon spreads over the entire surface of the agar, except near the top. It is very thin, smooth, translucent, and grayish.

Gelatin stab.—Slight development down the stab near the surface. On the third day a saucer of liquefaction 2 mm. in diameter has formed, which soon has a pellicle on its surface. The liquefaction reaches the wall of the tube under the surface of the gelatin, leaving a ring attached to the tube. The floor becomes level by the tenth day, 1 cm. from surface, and has a light deposit of whitish flocculi on it. The liquid is cloudy. Further liquefaction is very slow.



Gel. stab.

Potato.—"Invisible" on the second day. A moisture only is seen along the line of inoculation, spreading near the bottom to the tube wall. By the third day much of the surface is covered and the layer is thrown into fine folds, which resemble herpetic vesicles at some points. It becomes putty-colored and drier looking, and the folds more numerous. It is always very thin.

Bouillon.—Growth is never abundant, and soon settles to the bottom, a few flakes floating on the surface.

Rosolic acid.—Very slight growth and barely perceptible deepening of the color.

Litmus milk.—No change until fifth day, when the color becomes lighter without redness. It is discharged in ten to twelve days, and the milk becomes watery. No coagulation of the casein observed. Reaction faintly acid.

Sugar gelatin, deep stab.—Growth is scant deep down, and not seen until three or four days. Liquefaction takes place at the surface. No gas produced.

Indol.—Reaction negative.

Relation to temperature.—Grows well at room temperature, but somewhat faster at 35° to 36° C.

Bacillus Trommelschlägel.

Found at the depth of 4 feet in made soil, which had been paved over for several years.

Character.—Grows fairly well in an atmosphere of hydrogen.

Morphology.—Slender, straight rods with rounded ends, from five to seven times as long as broad. Occurs singly and also forms short chains. In the separate rods, as in the chains, are seen deeply stained dots, from one to three in each rod. In the chains the line of division between the separate elements is often impossible to make out.

Spores are formed in eighteen to twenty hours at 35° to 36° C. They are round or slightly oval and formed at the ends, giving the most perfect form of the drumstick. The spore is not exactly at the end, as a small part of the rod, which is usually pointed, projects beyond it. The best specimens are obtained from agar cultures, at room temperature, on the third day.

Motility.—Movements are active and progressive. Spore-bearing rods are non-motile.

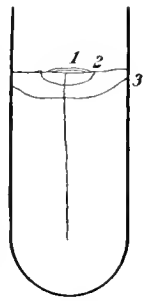
Flagella are attached at the poles.

Colonies on gelatin.—Colonies seen at the end of twenty to twenty-four hours. Deep are whitish and punctiform, and those on the surface but little larger. × 80. Deep are irregularly circular, yellowish, granular disks, with even edges. The surface colonies show a nucleus, usually

placed to one side of the center. Around the nucleus is a yellowish, granular zone, which in turn is surrounded by a grayish zone, also granular, and which has very irregular edges. Both are finely veined. After several days the surface colonies attain a diameter of 1 mm., and become porcelain white and elevated, with even edges. The deep do not get much larger, but become more dense and whiter. × 80. There is no change seen in the deep colonies. Those on the surface become too dense to show much structure. They appear as gray disks with regular margins, and near the margins have a finely granular and veined appearance. There is nothing at all distinctive about the colonies. No liquefaction takes place.

Agar slant.—On the second day a very thin, translucent layer has formed, which extends to the tube wall for the lower half. It is smooth, shining, and has a greenish tint. After some days it is somewhat thicker, but always very thin and translucent. After ten days the agar acquires a faint yellowish-green tint, which becomes brownish after three or four weeks.

Gelatin stab.—Growth occurs along the puncture in twenty-four hours. By the third day there has formed a thin white layer on the surface, which has become 4 mm. in diameter by the end of a week. It is white in color, and has irregular, leafy margins. The growth along the puncture has not increased to any extent. Slow liquefaction is observed about this time, and the surface growth sinks slowly. The gelatin below the liquefied portion becomes cloudy after two weeks. At the end of two weeks the liquefaction is only about 2 mm. deep, and reaches the tube wall.



Gel. stab.

Potato.—At the end of twenty-four hours only a widespread moisture can be seen. By the next day it has become like a thin layer of honey. By the fifth day it is brown and dry, and has a metallic luster. No further change takes place.

Bouillon.—A slight, diffuse cloudiness is caused by the second day. At the end of a week most of the growth has settled to the bottom, leaving the liquid tolerably clear.

Rosolic acid.—Becomes slightly darker after two or three days.

Litmus milk.—Becomes darker by the third day, after which the color is gradually discharged. The reaction is alkaline. At the end of two weeks the milk is a dirty white, while a blue zone is formed on the tube wall at the surface. After four weeks the casein seems to be dissolved, the milk becoming watery and translucent.

Sugar gelatin, deep stab.—Growth occurs quite deep along the puncture, and a button forms on the surface, with slow liquefaction. No gas is produced.

Indol.—Reaction negative.

Relation to temperature.—More rapid and abundant at 35° to 36° C.

Bacillus Geminus Major.

Found at a depth of 4 feet in made soil, which had been paved for several years.

Character.—Strict aërobe. No growth in atmosphere of hydrogen.

Morphology.—Straight, thick rods of irregular length, with rounded ends. Occurs singly, though short chains are occasionally found. The rods show deeply stained points, usually situated near the ends, from one to three in each rod.

Spores not observed.

Motility.—Very slight movement.

Flagella not demonstrated.

Colonies on gelatin plates.—Colonies appear in twenty hours as minute whitish dots. × 100. Deep are brownish, granular disks, with even edges. Surface are grayish and wavy looking, and have a wavy outline. Many show nuclei. At the end of forty-two hours the deep are still punctiform. Those on the surface are 1 mm. in diameter and have a greenish cast. × 100. Deep unchanged, except that they have become more dense. The surface are grayish, and have an eccentric nucleus and a wavy outline. They are marked by darker lines irregularly distributed, and joining each other, giving the colony a marbled appearance. The colonies are not unlike those of the typhoid bacillus, but are more granular and coarser. The gelatin becomes somewhat softened after a time, but no distinct liquefaction can be detected.

Agar slant.—A faint band with leafy margins is formed by the second day. It spreads to the tube at the bottom and becomes somewhat thicker, but is always a very thin, translucent layer without color. The deposit in the water at the bottom is white.

Gelatin stab.—Growth occurs quite deep down, and a whitish layer forms on the surface, which is only about 1 mm. in diameter, and has irregular margins. By the third day from the upper part of the stab delicate offshoots pierce the gelatin, which soon reach nearly to the tube wall and resemble the leaves of asparagus. The growth on the surface extends in a barely perceptible layer until, after two weeks, the surface is largely covered. There seems to be some softening at the surface after eighteen or twenty days, but no liquefaction can be made out.

Gel. stab.

Potato.—A thin layer of moisture, very faintly yellowish, is seen on the second day. It becomes thicker, and about the color of honey on the third or fourth day, and is moist, smooth, and shiny. After a week it becomes a chocolate brown, but does not increase in thickness.

Bouillon.—Becomes diffusely cloudy on the third day. After a week the growth begins to settle to the bottom, and the liquid is left tolerably clear.

Rosolic acid.—Becomes slightly darker after ten days.

Litmus milk.—Becomes more blue after a week. At the end of two weeks it is a sky-blue. There is no coagulation of the casein, but a white precipitate collects at the bottom of the tube. After five weeks the color is somewhat lighter, but a pure blue. Reaction is amphoteric.

Sugar gelatin, deep stab.—Growth quite deep down and on the surface. There is more liquefaction than in plain gelatin. No gas is formed.

Indol.—Negative reaction.

Relation to temperature.—More rapid and abundant at 35° to 36° C.

Note.—This bacillus does not form glutinous masses on any culture medium, but seems to have the power of holding other growths to it. The bacillus *Geminus minor* was found with it, and it was with much difficulty that the two were separated. A portion of the growth was placed in Dunham's solution, and repeatedly shaken at intervals for two or three hours, and from this plates were made. It was only after repeated trials that the two were gotten out in pure culture.

Bacillus Geminus Minor.

Found at a depth of 4 feet in made soil, which had been paved for several years, in close union with the bacillus *Geminus major*.

Character.—Requires oxygen for its development.

Morphology.—Very short straight rods, with rounded ends, from two to four times as long as broad. Occurs singly.

Spore formation not observed.

Motility.—Very active movements, like fighting or playing.

Flagella not demonstrated.

Colonies on gelatin plates.—Colonies become visible in twenty-four to thirty hours. At the end of thirty-six hours the deep are whitish punctiform dots, while those on the surface are white also and one-sixth of a millimeter in diameter. × 80. Deep are yellowish in color, coarsely granular, with even margins. The surface colonies are much the same, only showing a nucleus. By the third day the surface colonies have become pearly white, are evenly circular, and have rounded surfaces. They are so dense that little can be seen under the microscope. Near the edges they have a wavy appearance, as if made up of serpentine parallel lines closely packed. After ten days they have become 1.5 mm. in diameter, are more elevated, and are a pearly white. They retain their circular outline and have well-defined edges. They become too dense to show any structure under the microscope. The deep colonies remain unchanged, except to increase in density. There is no liquefaction of the gelatin.

Agar slant.—A thin greenish-white line is formed by the second day. It spreads rather slowly, grows more white, and in eight or ten days has covered much of the surface of the agar in a thin shiny-looking layer, which runs to the bottom.

Gelatin slant.—An elevated porcelain-white band 1 mm. wide, which has a smooth surface and even margins, is formed by the third day. It is raised one-half of a millimeter. After about ten days indistinct striations may be seen on the surface of the gelatin running at right angles to the band of growth, but no growth can be made out positively.

7 days. Gel. stab.

Gelatin stab.—Good growth occurs quite deep, and on the surface a button forms by the second day. It is 1 mm. in diameter and half as high. After a time the edges, which are thinner, become corrugated, while the center remains smooth and a glistening pearl white. For some distance down puncture delicate, spinous offshoots are seen, not more than one-fourth of a millimeter long. There is no liquefaction.

Potato.—A faintly yellowish line forms along the needle mark by the second day, which has spread widely, where the potato is moist, in a very thin colorless layer. It increases slowly and becomes by the tenth day a dirty white, smooth, moist, and shining layer.

20 days. Gel. stab.

Bouillon.—Becomes diffusely clouded by the third day, and a thin film forms on the surface. Later, the growth collects at the bottom of the tube.

Rosolic acid.—Becomes cloudy, and by the tenth day is a cherry-red color.

Litmus milk.—More blue by fourth day. After two weeks changes to a slate-blue, and a whitish deposit forms at the bottom. There is no coagulation or any change apparently in the milk itself. The reaction is strongly alkaline.

Sugar gelatin, deep stab.—Growth quite deep down the stab and on the surface. No gas is produced.

Indol.—Good reaction with both acid and sodium nitrite.

Relation to temperature.—Grows more rapidly at 35° to 36° C.

Bacillus Solitarius.

Found at the depth of 4 feet in made soil, which had been paved for several years.

Character.—Strict aërobe. No growth in an atmosphere of hydrogen.

Morphology.—Slender, straight rods, with rounded ends, from three to seven times as long as broad. Occurs singly.

Spore formation not observed.

Motility.—Some rotatory non-progressive movements.

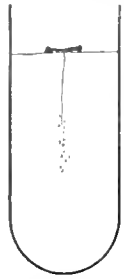
Flagella not demonstrated.

Colonies on gelatin plates.—Colonies become visible in from thirty-six to forty hours, as grayish dots. × 80. Deep are grayish, smooth-looking disks, with finely notched margins, the contents being homogeneous or sometimes finely granular toward the center. Surface colonies present much the same appearance, but are larger, and some irregular bundles of fine lines can be seen. At the end of forty-eight hours the deep colonies show a nucleus, around which are tolerably well-defined rings or zones, growing lighter toward the edge. Fine wavy lines can be seen running in various directions, giving the colony a somewhat marbled appearance. At the end of seventy hours the surface colonies are 1 mm. in diameter, and of a greenish-white color, with even edges. × 80. A granular nucleus is seen, surrounded by an orange-colored zone, made up of fine lines closely packed. Some are so dense that the lines can not be made out. The edges of this zone are not well defined, and are irregular, sending ragged offshoots into the surrounding zone, which is a lighter shade, and in which wavy lines running toward the edge can be seen. At the end of a week the surface colonies are milk white, round, elevated, and have smooth surfaces and even edges. They are too dense to show any structure under the microscope, except near the margins, where wavy lines are seen. Deep have not changed, except to grow more dense. There is no liquefaction of the gelatin.

Agar slant.—By the second day a greenish-white line 1 mm. wide has formed. It grows thicker, spreads almost to the tube wall for the lower third, and becomes much whiter, so that by the fourth day it is porcelain white, has irregular margins, and is smooth, moist, and shining. The growth which collects at the bottom becomes cream colored after some days.

Gelatin slant.—Resembles the growth of the typhoid bacillus very closely. A dry, white line, thin and with iridescent gleam, and later cracks across the surface transverse to the long axis.

Gelatin stab.—Growth is confined to the surface mostly for the first three or four days, forming a button like a drop of milk. By the fourth day there is good development to the bottom of the puncture, being in separate colonies low down, as minute white spheres. The growth on the surface attains a diameter of 4 mm. by the eighth day, and is elevated 1 mm., with a slight central depression. It is porcelain white and has even edges. The gelatin becomes opaque around it, but no growth can be detected with the needle. The button later becomes cream colored. There is no liquefaction.



Gel. stab.

Potato.—At the end of twenty-four hours a line of moisture is seen along the needle mark. By the next day it has spread widely in a thin whitish layer. It increases in thickness, and has a curdled appearance. At the end of two weeks it becomes thick and pasty looking, and the color of putty.

Bouillon.—Becomes diffusely clouded by the third day, and later a dirty-white deposit is seen on the bottom.

Rosolic acid.—Becomes lighter by the third day, and the color is almost entirely discharged at the end of a week. Reaction alkaline.

Litmus milk.—The color becomes a pure blue in three days and then grows darker, until at the end of three weeks it is slate colored. There is no change apparently in the milk itself. A white deposit collects at the bottom.

Sugar gelatin, deep stab.—Growth in separate colonies deep down, with button on the surface. There is no gas produced.

Indol.—Reaction negative.

Relation to temperature.—More rapid at 35° to 36° C.

Note.—This bacillus resembles the *Geminus minor* very closely in many ways. The chief points of diagnosis are the discharging of the color of rosolic acid, while the former changes it to cherry red, and the formation of single colonies in the bottom of gelatin stab cultures.

Bacillus Cinctus.

(Figs. 24, 25, and 26, Pl. III.)

Found at the depth of 4 feet in made soil, which had been paved over for several years.

Character.—Very slight growth in an atmosphere of hydrogen.

Morphology.—Straight rods which vary considerably in size. Involution forms are found in eighteen to twenty hours in agar cultures kept in the incubator. It occurs singly mostly, but chains of several elements are found also, the line of division not being well marked. Each rod has from one to three deeply stained dots in it, placed irregularly, though a majority are at, or near, the poles. These do not seem to have anything to do with spore formation, as they are seen in spore-bearing rods.

Spores are formed in three days at room temperature. They are large ovals, and distend the walls of the cells. Formed near the ends.

Motility.—It is actively and progressively motile.

Flagella not demonstrated.

Colonies on gelatin plates.—Colonies seen in twenty to twenty-four hours as indistinct translucent points, which, under a low power, are yellowish, granular disks, with even margins. Growth is slow, and at the end of seventy hours the deep colonies are still punctiform, while those on the surface are one-half of a millimeter in diameter. The latter are greenish white, with irregular margins. × 80. The surface colonies show a nucleus, eccentrically placed, around which is a zone, yellowish in color, which appears granular at first. A close study shows fine lines so closely laid as to produce this appearance. Outside of this is a zone of gray, which is irregularly veined, and has very irregular margins. There is but little change from day to day. At the end of eight days the surface colonies are only 1 mm. in diameter, greenish white, round, and elevated, with even margins. The deep are about one-sixth of a millimeter in diameter, and grayish. × 80. Deep are a bright yellow with reddish tinge, fading gradually to a grayish color at the margins,

Fig. 24

Bac. Cuneatus
One form of surface colony 36 hrs. old. X 80

Fig. 25

Fig. 26

A

Bac. Cuneatus
A. Deep colony 70 hrs. old. X 80. B.
B. Surface colony 72 hrs. old X 80

Fig. 27.

Fig. 28

Fig. 29

A

Bac. Viridans
Deep colony 48 hrs. old. X 80
B

Fig. 30

Fig. 31

Bac. Viridans
Deep colony 14 hrs. old. X 80

Fig. 32.

Bac. Erodens
Deep colony 36 hrs. old. X 80

Fig. 33

Fig. 34.

Fig. 35.

Fig. 36

Bac. Ganglyanus
Surface colony 5 days old. X 80

Fig. 37

Fig. 38

Fig. 39

B

A

Bac. Fissuratus
A. Deep colony 36 hrs. old. X 80.
B. Deep colony 70 hrs. old. X 80

Fig. 40

Fig. 41

A. HOEN & CO. LITH., BALTIMORE

showing several zones or concentric circles. The center is indistinctly veined and granular, the edges smooth and clear cut. The cause of the zones is not apparent, as there is no abrupt change in color or density. The surface colonies still show a nucleus, surrounded by a reddish-yellow zone, which has smooth edges and fades evenly from center to margin. It is finely veined and sometimes mottled. Some colonies have a striking resemblance to the shell of an oyster. When there are very few on the plate, grotesque forms are produced after a time, ferny outgrowths going from the margins. These spread in most irregular shapes, later inclosing islands of gelatin, by the projections meeting each other. They attain a diameter of 4 mm.

Agar slant.—A thin, glistening, pale green layer forms along the line of inoculation which has spread to the tube wall for the lower half by the second day. It increases somewhat, but is always thin and translucent, with smooth surface. The agar becomes a faint yellow.

Gelatin slant.—A white band is formed, 1 mm. wide, with rather uneven edges. After a time it cracks across the long axis, and the gelatin seems somewhat softened at the end of five weeks, but no liquefaction occurs.

Gelatin stab.—Growth occurs along puncture, and a white layer forms on the surface, which has very irregular leafy margins, and attains a diameter of 2 mm. No liquefaction is caused.

Surface growth. Gel. stab.

Potato.—Only a widespread moisture is seen at first, which by the third day has become like a thin layer of honey in appearance. It is moist and shining and very thin. After a time it becomes slightly darker.

Bouillon.—Diffuse cloudiness in twenty-four hours. The growth settles to bottom after two weeks, leaving the liquid tolerably clear. The bouillon acquires a faint greenish color.

Gel. stab.

Rosolic acid.—Becomes very slightly darker after three or four days.

Litmus milk.—Becomes darker blue on third day, but soon begins to lose its color. There is no coagulation. Reaction alkaline.

Sugar gelatin, deep stab.—Growth some distance down puncture, and on the surface similar to plain gelatin. No gas produced.

Indol.—Reaction negative.

Relation to temperature.—More rapid and abundant at 35° to 36° C.

Note.—In the Zeitschrift für Hygiene, Vol. IV, page 25, is an article on the "*Xerosis Bacillus* and its spore formation." The drawings correspond exactly with the organism just described, but the description, as far as it goes, is different.

Bacillus Vacuolatus.

(Fig. 27, Pl. III.)

Found at the depth of 7 feet in made soil, which had been paved for several years.

Character.—Strict aërobe; no development in an atmosphere of hydrogen.

Morphology.—Resembles the Klebs-Löffler bacillus very closely in its manner of staining, though it is much longer and more regular in shape. The rods are single, straight, and have rounded ends. Potato cultures form chains of several elements. The transverse bands which remain unstained give the rods a ringed appearance. It is best seen when the culture is about a week old.

Spores are large and oval, and may be seen at the end of twenty-four hours.

Motility.—Shows movements which are not very active.

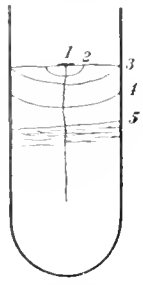
Flagella not demonstrated.

Colonies on gelatin plates.—Colonies appear in thirty-six to forty hours. Those on the surface grow rapidly, and in forty eight hours have become one-half of a millimeter in diameter. They have a circular outline and are whitish, looking like drops of thin milk. By transmitted light they are bluish. The deep colonies are punctiform. × 80. Deep are yellowish, finely granular disks, with even edges. Surface are yellowish in color, have an irregular, though clean-cut outline, and are granular or mottled in appearance. A nucleus, usually eccentric, is present in most of them.

Liquefaction takes place in saucer shape; not extensive. The colonies become more dense, and after five days a finely patterned edge with leafy outlines is seen around them. The mottled or marbled appearance is lost, and dark wavy lines running a long distance are seen. After this time the liquefaction is too extensive to make further observation.

Agar slant.—A thin translucent layer, almost without color, with irregular margins, is formed, and reaches the tube wall near the bottom after several days. It is smooth and shining, a faint greenish tint by transmitted light. The smooth surface is lost after some time by the growth of small rounded elevations, like colonies. The agar acquires a faint greenish tint.

Gelatin stab.—Good growth deep down, with a button on the surface. By the third day a small saucer of liquefaction has formed, which soon reaches the tube wall. At the end of a week the liquefaction is 1 cm. deep and the floor almost level, and covered with a whitish flocculent precipitate, the liquefied gelatin being clear. A mycoderma floats on the surface. The gelatin below the floor acquires a hazy look and liquefaction progresses slowly, being complete in about six weeks.



Gel. stab.

Potato.—Growth is seen on the second day along the line of inoculation. It soon becomes a slimy-looking, dirty light-brown layer, which covers most of the plug at the end of a week, passing around behind it. It is thick and moist and has a smooth surface. The color changes to yellowish brown as it grows older.

Bouillon.—Diffuse cloudiness by the second day. A thin pellicle which sinks easily is formed on the surface after ten days. The growth settles to the bottom, leaving the liquid quite clear.

Rosolic acid.—Becomes a cherry red in twelve to fourteen days, and a pellicle forms on the surface.

Litmus milk.—Becomes more blue after five or six days, then becomes watery and translucent. The color is almost all gone in twelve days, while a blue zone forms at the surface on the tube wall. The casein becomes dissolved without previous coagulation. Reaction alkaline.

Sugar gelatin, deep stab.—Grows only near surface. Same appearance as in plain gelatin.

Indol.—Good reaction with both sulphuric acid and sodium nitrite.

Relation to temperature.—More rapid and abundant at 35° to 36° C.

Bacillus Pinnatus.

(Figs. 28 and 29, Pl. III.)

Found at the depth of 6 feet in made soil, which had been paved for several years.

Character.—Grows well in an atmosphere of hydrogen.

Morphology.—Slender, short, straight rods with rounded ends, three to five times as long as broad. Occurs singly or in chains of two and three elements. In old cultures the rods are so short as to be oval.

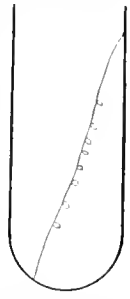
Spores have not been observed.

Motility.—The movements are slow and mostly rotatory, but now and then a rod will move some distance across the field.

Flagella not demonstrated.

Colonies on gelatin plates.—Colonies become visible in thirty to thirty-six hours as bluish dots, which appear as finely granular disks with smooth edges under a low power. At the end of sixty hours the surface colonies are one-half of a millimeter in diameter, and stand up from the surface like minute drops of milk. The deep colonies are punctiform. × 80. Deep are finely granular, yellowish, and have smooth edges. The surface colonies are made up of a central portion of yellowish-brown color, finely granular, and growing uniformly lighter from center to edge. Outside of this is a zone of pale gray in which no structure can be made out. The division between the two is sharply defined by a line of light. The edges are clear-cut and even. Some colonies are oval, but most of them are circular, and all have the same general structure. The colonies grow more dense as they get older, the center becomes brownish, and the line of demarkation between the zones less distinct. The colonies never grow larger than 1 mm. in diameter, and no liquefaction is caused.

Agar slant.—A whitish translucent band forms along the line of inoculation, and by the third day is 3 mm. wide. It is very thin, moist, and has uneven edges. It seems to be watery, and flows down to the bottom, having a shiny look. It is not tenacious, and but little clings to the needle. About the tenth day whitish masses are seen, much more dense than the growth. On holding the tube to the light these are seen to be projections into the agar. They are oval in shape and extend about 1 mm. down. The surface of the agar has a roughened feel to the needle. Quite a quantity of the growth collects in the water at the bottom, and is milk white in color.


Agar slant.


Gel. stab.

Gelatin stab.—Growth occurs all along the line of puncture, and a button forms on the surface. In three days this button is one fourth of a millimeter in height and 2 mm. in diameter, and is a porcelain white, smooth and glistening. It does not spread further, but the edges become elevated, forming a shallow basin. The gelatin after a time becomes cloudy on the surface, though no growth can be detected. No liquefaction occurs.

Potato.—Only a moisture along line of inoculation is seen at first. It soon spreads in a very thin, colorless layer over much of the surface. After four or five days it becomes a light, dirty brown, smooth, moist, and shining.

Bouillon.—Growth occurs first at bottom of the tube, but by the third day the liquid is diffusely cloudy. Dirty-looking whitish flakes form on the surface, but do not form a pellicle, and sink to the bottom on shaking the tube. The bulk of the growth settles to the bottom as a white mass.

Rosolic acid.—Becomes much lighter by the fourth day, and is completely decolorized in two weeks. The reaction is alkaline.

Litmus milk.—Shows no change until a week has passed, when it becomes darker, and finally changes to an indigo blue, almost. There is no coagulation and no further change seen at end of six weeks.

Sugar gelatin, deep stab.—Growth quite deep down puncture and on the surface. No liquefaction and no gas production.

Gelatin slant.—A porcelain white line 2 mm. wide is formed, which has even, elevated edges and a smooth, glossy surface. The whole surface of the gelatin becomes a cloudy white after some days, but no growth can be detected.

Indol.—Good reaction takes place with both sulphuric acid and sodium nitrite.

Relation to temperature.—Grows well at room temperature, but somewhat faster at 35° to 36° C.

Bacillus Diffusus (Frankland).

Found at the depth of 6 feet in made soil, which had been paved for several years.

Character.—Shows very slight growth in an atmosphere of hydrogen.

Morphology.—Slender straight rods, from five to seven times as long as broad. Occurs singly mostly, and in short chains.

Motility.—Some movement of an oscillatory character, but no progression.

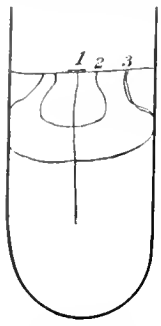
Flagella not demonstrated.

Spore formation not observed.

Colonies on gelatin plates.—Colonies do not become visible until the third day, when they appear as whitish dots. × 80. The deep colonies resemble those of the *Comma bacillus*, being coarsely granular with irregular margins. Near the edge wavy lines can be made out. The surface colonies have very little color at this stage, being faint bluish green. × 80. They show an indistinct nucleus, are irregularly circular, and have granular contents. As the colonies get older the deep ones reach the surface, and their margins become less distinct, a fringe-like border growing out over the surface of the gelatin. This border has leafy or deeply dentate margins, and is finely granular in structure, while the original colony is darker and very coarsely granular. Liquefaction takes place rather slowly, and each colony is in a saucer-shaped depression.

Agar slant.—A thin greenish-white layer is developed, which has smooth edges, and is moist and shining. As it increases in thickness it becomes a very pale-yellow color.

Gelatin stab.—Growth occurs along the puncture for some distance down, while a thin yellowish layer forms on the surface. This becomes concave after a few days and slowly sinks, liquefaction progressing slowly. Liquefaction causes a globe-shaped cavity, the tube wall being reached below the surface, leaving a ring of gelatin attached to the tube at the surface. On the liquid gelatin the original surface growth floats. After three weeks the floor becomes level, and has a slight whitish deposit on it. The process seems to stop here, further liquefaction not being observed. The liquefied gelatin is only slightly turbid.



Gel. stab.

Potato.—A greenish-yellow layer covers much of the surface in five or six days. It is quite thin, smooth, moist, and shining, and later acquires a transparent look and becomes more yellow.

Bouillon.—Diffuse cloudiness, not very intense. No pellicle forms on surface.

Rosolic acid.—Becomes slightly darker after four or five days.

Litmus milk.—Becomes a purer blue at end of six days, but the color is discharged soon after, being gone at end of the next week. No coagulation occurs. Reaction alkaline.

Sugar gelatin, deep stab.—Growth quite deep with button on surface, which slowly sinks. No gas production.

Indol.—Reaction negative.

Relation to temperature.—Grows more rapidly at 35° to 36° C.

Note.—This bacillus was first described by Grace and Percy Frankland in the Zeitschrift für Hygiene, Vol. VI, page 396. They give its growth on only four culture media, however, and its action on nitrates. The organism described above corresponds with their description quite closely, convincing me of their identity, though there are some slight differences.

Bacillus Gangliformis.

(Fig. 30, Pl. III.)

Found at a depth of 6 feet in made soil, which had been paved for a number of years.

Character.—Grows well in an atmosphere of hydrogen.

Morphology.—Large straight rods with rounded ends, five to seven times as long as broad. Forms chains of considerable length.

Motility.—Non motile.

Flagella not demonstrated.

Spores are large, oval, and formed in center of rod. They were found only in cultures on potato.

Colonies on gelatin plate.—Colonies are seen at the end of twelve hours. The deep resemble bits of asbestos fiber embedded in the gelatin. Those on the surface are circular saucers of liquefaction, with whitish masses in the center. × 80. The deep colonies are made up of coarse lines, irregularly disposed, and running from centers here and there, which are made up of more compact masses of lines. On the surface the colonies have a well-defined margin, which is bordered by a corona of fine spear points. In the liquefied gelatin are tangled masses of the thread-like lines, resembling the colonies of the potato bacillus. Here and there a bunch of lines will pass far out into the gelatin beyond the border. Liquefaction is rapid, and the deep colonies soon reach the surface, where they become like those which began there. At the end of twenty hours some of the colonies have attained a diameter of 6 mm. On the second day a thick mycoderma has formed on each colony. This is somewhat peculiar in its character. In the center is an island, then comes a space uncovered by growth, or very thinly covered; beyond this is a lace-work, the bars running in a radial direction. The edges are somewhat uneven.

Agar slant.—In twenty-four hours a bluish-white line 2 mm. wide has formed along the line of inoculation, spreading to the tube wall near the bottom. By the second day it has become twice as wide, is a dirty-white, dry-looking band, with irregular, ferny edges. It soon becomes thrown into large wrinkles, which have an elevation of 1 mm. The usual arrangement of the folds is a large one in the middle from top to bottom, with numerous smaller ones at right angles to this. The folding, however, is dependent on the vigor of growth and is different in each culture.

Gelatin stab.—By the end of twenty-four hours a saucer of liquefaction 3 mm. in diameter has formed, and growth is seen deep down the puncture. By next day the liquefaction has nearly reached the tube wall, but is shallow, and a pellicle has formed on the surface, which soon becomes wrinkled, and climbs up the tube wall 2 to 3 mm. The liquefaction becomes funnel shaped by the fourth day and by the tenth is almost complete. The growth settles to the bottom in whitish flakes, leaving the liquid clear, but few flocculi floating in it.

Potato.—A dry-looking white growth soon covers a large part of the surface, and by the third day is thrown into large folds. These soften down after some days, and at the end of two weeks the growth is a putty-colored, moist, slimy-looking layer. It is not tenacious, however, and does not cling to the needle.

Bouillon.—Becomes diffusely cloudy, a mycoderma forms on the surface in four or five days, and the bottom of the tube is covered with a dense whitish deposit, while cotton-like flocculi float in the liquid.

Rosolic acid.—No growth.

Litmus milk.—Reddish tint is seen about the third day, and coagulation in flocculi takes place in four to five days. The color is rapidly discharged and the casein is dissolved by the end of ten days. A white mass floats on the surface, and there is a whitish deposit at the bottom. The reaction is alkaline at end of two weeks.

Sugar gelatin, deep stab.—Good growth deep down, with rapid liquefaction. No gas produced.

Indol.—Faint color is produced by the addition of both sulphuric acid and sodium nitrite. It does not come at once.

Relation to temperature.—More rapid growth at 35° to 36° C.

Note.—This bacillus is much like the potato bacillus, and belongs to that group without doubt. The chief points of difference are its effect on milk, the appearance of the deep colonies, and the production of indol.

Bacillus Erodens.

(Fig. 31, Pl. III.)

Found at the depth of 6 feet in made soil, which had been paved for a number of years.

Character.—Requires oxygen for good development, though it shows some growth in an atmosphere of hydrogen.

Morphology.—Straight, thick rods, with rounded ends, from three to seven times as long as broad. Occurs singly for the most part.

Spores are formed rapidly at incubator temperature, the process being well advanced in sixteen hours. They are oval and formed near the center of the rods, often causing bulging of the wall of the cell. After a time the rods seem to shorten around the spore, and separated spores have not been demonstrated.

Motility.—Actively motile.

Flagella not demonstrated.

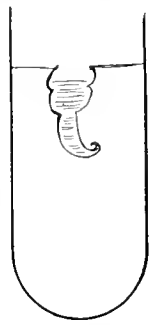
Colonies on gelatin plates.—Colonies are seen in twenty to twenty-four hours as minute whitish dots. ×80. Some resemble a small raspberry, while others show more of a nest-like arrangement, the granules not being so well marked. At the end of thirty-six hours the colonies are about one-tenth of a millimeter in diameter, and look white. ×80. They are round, with even edges, and dark gray in color. The distinctive feature about them is the movement of the contents, which is active and incessant. It is usually in the general direction of the hands of a watch, with many smaller eddies. On the third day the surface colonies may be 2 mm. in diameter, have well defined edges, and look as if they had been punched out. The even contour is usually kept at the surface, while the growth eats away the gelatin below. In some the action is uniform all around, so that the opening at the surface may be 2 mm. in diameter, while at the bottom it is 3 or 4 mm. The most constant feature, however, is the putting out of tunnels from the sides of the colony, some colonies having as many as five radiating from them. These extend 2 or 3 mm. and tend to curl up near the ends. A scant whitish growth is seen on the floor of each. The active movement in the colonies stops about the third day, probably from drying up, but is seen in the ends of these tunnels for five or six days. Occasionally a tunnel is sent

out from the deep colonies also. These tunnels with their curled ends are so striking and distinctive that they form an infallible guide to the diagnosis of this bacillus.

Agar slant.—Rapid growth takes place, and in twenty hours the surface is largely covered with a very thin, translucent, faintly greenish layer, which has leafy margins. After several days whitish specks, raised above the surface of the growth, appear, and the deposit in the water at the bottom takes on a faint salmon color.

Gelatin stab.—Growth occurs along the line of puncture, and by the third day a small funnel of liquefaction has formed at top. The deposit is very dense looking and almost white, resembling the pith of plants. After several days it begins to curl round at the bottom in the way the tunnels from the colonies do. The walls of the funnel often have an eroded look and little tunnels are sent out into the gelatin, each one curling up at the end after a few days. The top of the funnel is usually circular, but sometimes is eaten out into a very irregular shape. The growth is very striking and characteristic.

Gel. stab.


Gel. stab.

Potato.—Growth not visible until third day, when it has spread widely over the surface in a very thin layer, moist and shining, about the color of honey. After some time it becomes dryer looking, and minute whitish dots appear in it.

Bouillon.—Becomes diffusely cloudy in twenty-four hours. After three weeks the growth has mostly settled to the bottom, leaving the liquid tolerably clear. No skin forms on the surface.

Rosolic acid.—Very slight growth. After five or six weeks the color is slightly deeper.

Litmus milk.—After six days becomes lighter but a purer blue. The color is discharged entirely by the twelfth day. Reaction decidedly alkaline. No coagulation of the casein is seen.

Sugar gelatin, deep stab.—Growth quite deep, with liquefaction. Same appearance as in plain gelatin. No gas production.

Indol.—Reaction negative.

Relation to temperature.—More rapid and abundant growth at 35° to 36° C.

Note.—In the report of the State board of health of Massachusetts for 1890, Jordan describes a bacillus resembling the above in many respects under the name "*Circulans.*" He mentions also having observed movement in the colonies of several other species, though not so marked or constant. The bacillus *Erodens* differs in its action on milk and in its way of boring into the gelatin. He speaks, though, of the funnel having a "ringed" appearance, which is seen in the *Erodens* also.

Bacillus Mesentericus Vulgatus.

Synonym: *Potato bacillus* (Flügge).

(Figs. 32, 33, and 34, Pl. III.)

Found at the depth of 6 feet in made soil, which had been paved for a number of years.

Character.—Strict aërobe; no development in atmosphere of hydrogen.

Morphology.—Rather slender rods, straight, with rounded ends, from five to seven times as long as broad. It occurs singly in short chains and in irregular groups, the rods lying side by side.

Spores are oval and formed near center of rod. At 35° to 36° C. spore formation is well advanced in sixteen hours. The spores are usually large in proportion to size of rod, many of them occupying two-thirds of the cell, and causing slight bulging of the walls.

Motility.—Feebly motile.

Flagella not demonstrated.

Colonies on gelatin plates.—Colonies appear within twenty hours as minute whitish dots. Those on the surface are almost without color, being faint bluish white. × 80. The deep colonies appear as gray or brownish dots with regular margins, while near the edges fine lines can be seen. The center is granular. On reaching the surface liquefaction goes on very rapidly, so

that in a few hours, if the weather be warm, the colony will attain a diameter of about 1 cm. Each colony is saucer shaped, the liquefied gelatin almost perfectly clear, being a faint grayish hue, and the edges smooth and regular, forming a perfect circle. × 80. Fine threads in tangled masses are seen in the liquefied gelatin resembling, especially near the center, "a ball of string," as Fränkel so aptly describes it. The edge of the colony is made up of a corona of fine spear points boring vertically into the gelatin, but somewhat wavy. These are much longer in a colony which has just reached the surface.

Agar slant.—An indistinct line along the inoculation soon appears, thin and spreading irregularly at the margins. By the third day the growth has covered almost the entire surface of agar, and the water at the bottom, and climbed up the tube 4 mm. from the surface of the water. It soon becomes thrown into fine wrinkles, becomes gray and then brownish, and looks as if fine powder had been sprinkled over it.

Gelatin stab.—Growth is mostly in upper part of stab, with a funnel of liquefaction at top. The liquefaction reaches the tube wall in thirty-six to forty hours, but is not very deep. At the end of ten days the floor has become level, about 1.5 cm. below the surface. It is covered with whitish flocculi, while the liquefied gelatin is almost clear. A thin skin may form on the surface, which becomes wrinkled.

Potato.—Growth occurs first along needle stroke, and looks much as if the potato had been scraped up from side to side. The surface of the plug is nearly covered on the third day, and the growth has passed entirely around it where moist. It is thrown into large folds, and looks as if dusted with fine powder. It soon becomes dry looking, and dark gray, and is piled up 2 mm. high. When touched with the needle it will draw out into quite long strings, being glutinous.

Bouillon.—Diffuse cloudiness on second day. A thin pellicle soon forms on surface. The growth settles to the bottom, leaving the liquid tolerably clear.

Rosolic acid.—No change observed.

Litmus milk.—Reddish tinge seen on third day, but no coagulation. The milk soon becomes watery and translucent from digestion of the casein, and the color is entirely discharged by the sixth day. A whitish mass floats on the surface, and in the bottom of the tube is a dense, viscous mass. The reaction is alkaline.

Sugar gelatin, deep stab.—Growth quite deep, with rapid liquefaction. No gas production.

Indol.—Reaction negative.

Relation to temperature.—Growth more rapid at 35° to 36° C., the entire surface of the agar being covered in twelve hours.

Bacillus Ginglymus.

(Fig. 35, Pl. III.)

Found at the depth of 1 foot in made soil, which had been paved for several years.

Character.—Very little growth in atmosphere of hydrogen.

Morphology.—Slender straight rods with rounded ends, from three to seven times as long as broad. Occurs singly and in short chains of two and three elements.

Spores are small, oval, and formed in center of rod.

Motility.—Peculiar in character. One end of a rod will appear to be fixed, and the rod moves on this as on a pivot. In others the center of rod acts as pivot on which the rod moves backward and forward. Some of the chains are motile also, the end rod waving from side to side, drawing the others after it, they showing no movement. It seems as though there was a hinge joint between them.

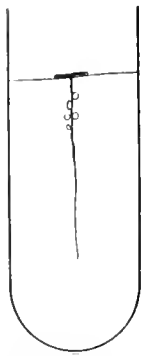
Flagella not demonstrated.

Colonies on gelatin plates.—Colonies seen in twenty to twenty-four hours as minute whitish dots. × 80. Gray granular disks with irregular edges. At end of thirty-six hours the surface colonies have reached a diameter of one-fourth of a millimeter, and are white. The deep are still punctiform. × 80. Surface colonies show central portion of orange brown color, made up of finely interwoven lines, giving a somewhat wavy appearance. Around this is an outer zone of gray with well-defined edges, but showing no particular structure. The deep colonies

are yellowish granular disks. The colonies slowly increase in size, but seldom get larger than one-half of a millimeter in diameter. At end of a week a colorless, fringe-like border has formed around the edge of the surface colonies, which has a leafy outline and is finely veined. The center of the colonies becomes so dense that no structure can be seen. At this time each colony shows a dense center, next a wavy looking zone of lighter brown which fades into a lighter colored and coarsely granular zone with a well-defined border, and lastly the colorless fringe. There is no liquefaction at end of ten days.

Agar slant.—A greenish-white line about 1 mm. wide forms along the line of inoculation in the course of thirty-six hours. It is slightly elevated, moist, and shining, and in a few days sends out a very thin, colorless layer from the edges, whose margins become very indistinct and almost impossible to locate positively.

Gelatin stab.—Growth along puncture occurs quite deep, and on the surface a grayish button is formed which attains a diameter of 2.5 mm., and has well-defined margins. After ten days indistinct outgrowths are seen along the puncture quite a distance below the surface. They are globular in shape. No liquefaction of the gelatin was seen at the end of twenty-eight days.



Gel. stab.

Gelatin slant.—A white line about 1 mm. is formed, not much elevated, smooth and shining, and with regular margins. No liquefaction took place, though at the end of a month the gelatin felt somewhat soft when touched with a needle.

Potato.—On second day a faint bluish discoloration is seen along line of inoculation. On third day the growth has spread over a large part of the surface of the plug in a thin yellowish layer, about the color of honey. It is moist and shining, and after two weeks becomes somewhat brown.

Bouillon.—Diffuse cloudiness is caused, the bulk of the growth finally settling to the bottom in gray masses.

Rosolic acid.—Becomes much lighter, so that at end of two weeks the color is entirely discharged.

Litmus milk.—Becomes a purer blue in twenty-four hours. No coagulation occurs. The milk gradually becomes translucent, and at end of two weeks is a beautiful violet color by transmitted light. This color fades slowly, but is still quite deep at end of six weeks.

Sugar gelatin, deep stab.—Growth quite deep along stab, with button on surface. No gas production.

Indol.—Reaction negative.

Relation to temperature.—Grows well at room temperature, more rapidly at 35° to 36° C.

Note.—This bacillus resembles the bacillus *Fissuratus* in many ways, and seems to be a variety of it. The chief differences are seen in the colonies on gelatin and in its non-liquefaction of gelatin. As the bacillus *Fissuratus* is a very slow liquefier, a hasty examination would make the two appear identical.

Bacillus Fissuratus.

(Figs. 36 and 37, Pl. III.)

Found at the depth of 1 foot in made earth, which had been paved for a number of years.

Character.—Shows very slight growth in atmosphere of hydrogen.

Morphology.—Small straight rods, two to three times as long as broad, with rounded ends Occurs singly for most part.

Spores are small, oval, and formed in center of rods.

Motility.—Only rotatory and oscillatory movements noted, which were active

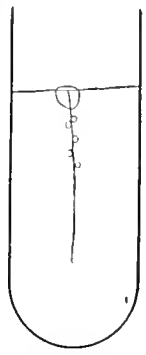
Flagella not demonstrated.

Colonies on gelatin plates.—Colonies may be seen at end of fourteen hours as minute whitish dots. × 80. No difference can be made out between the deep and superficial colonies at this stage. They are pale yellow, with irregular outline, darker at center, and give one the idea of flakes of mineral matter, or bits of shell. At the end of two days the surface colonies are 1 mm. in diameter and white, while the deep are still punctiform. × 80. Deep are orange brown and resemble a rosette somewhat. The surface colonies are circular in outline, but somewhat irregular.

The center is brown in color, and appears broken and fissured in every direction. Next is a zone much darker, but also brown in color, and fissured even more than the center. It begins quite abruptly and fades toward the edge gradually until it becomes gray. The gelatin is slowly softened rather than liquefied, and the colonies attain a diameter of 2 to 3 mm. Around the white central portion can be seen a faint halo, which under the microscope shows the same fissured character as the body of the colony, but is without color. As the growth gets older the zones become less distinctly defined, while the fissures get plainer.

Agar slant.—Very thin layer, 3 to 4 mm. wide, with indistinct edges, which finally look so much like agar that it is impossible to tell just where the growth begins. It is greenish white and translucent.

Gelatin stab.—Slight growth down puncture, and on the surface a button forms. After eight or nine days this button has sunk into the gelatin, but no liquid can be detected, evaporation going on as rapidly as liquefaction. At some distance below the surface may be seen globular outgrowths ranged along the stab. They are white and indistinct. After two weeks the cup of liquefaction is only 6 mm. deep.



Gel stab

Gelatin slant.—Band 4 mm. wide forms, which is not elevated, and has even edges. Surface of the growth is iridescent, and pale green by transmitted light. From the lower surface of growth rounded projections pierce the gelatin. The gelatin liquefies slowly and the growth slips to the bottom.

Potato.—Growth is scarcely visible until third day, though a bluish discoloration is seen along needle mark. It becomes abundant, of yellowish color, smooth, moist, and shining, resembling a thin layer of honey.

Bouillon.—Slight cloudiness at first. Growth settles to bottom later, leaving liquid tolerably clear.

Rosolic acid.—Color is almost entirely lost by the third day.

Litmus milk.—Becomes bluer without coagulation. After two weeks it becomes translucent, and is a beautiful violet color by transmitted light.

Sugar gelatin, deep stab.—Growth quite deep and on surface, same as plain. No gas production.

Indol.—Reaction negative.

Relation to temperature.—Grows more rapidly at 35° to 36° C.

Bacillus Arborescens Non liquefaciens.

(Fig. 38, Pl. III, and Figs. 39 and 40, Pl. IV.)

Isolated from made earth at depth of 2 feet.

Character.—Strict aërobe. No growth in an atmosphere of hydrogen.

Morphology.—Straight, slender rods, with rounded ends, from seven to thirteen times as long as broad. Occurs singly and in chains of several elements.

Spores not demonstrated.

Motility.—Rods turn almost end for end, and back again. No progression noticed.

Flagella not demonstrated.

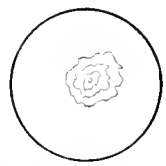
Colonies on gelatin plates.—Visible at end of forty-eight hours, as bluish, indistinct, cloudy dots, easily overlooked. The deep colonies can not be distinguished from those on surface. They resemble the colonies of the *Ramosus*, but are less distinct, smaller and not so white, nor do they grow so rapidly. Each colony consists of an axial trunk, both ends of which split up into numberless fine lines, somewhat interlaced, but on the whole radially disposed. These terminal branches are six to seven times as long as the trunk itself. In some colonies the trunk splits into several large branches, each of which gives rise to many fine ones, the whole giving a star-shaped figure. Others are made up of several sticks loosely laid together, each one of which splits up into fine branches at both ends; while others again are like the branch of a tree, one end breaking into smaller branches, which then break up into finer lines, while the other end is larger, and breaks up directly into the fine brush like filaments. After four days the colonies become more plainly visible, like bluish clouds. Under the low power (80 diameters) the fine terminal lines

have increased very much, so that the entire mass assumes a round shape. In many there are two foci, as it were, formed by the ends of the trunk where the branching first began. The lines increase for some time, growing longer and becoming more tangled, making the colony more dense in appearance, but even after two weeks they look only like bluish, cottony masses, none more than 1 mm. in diameter, and to the naked eye showing the bi-polar arrangement. There is never any liquefaction perceptible.

Agar slant.—Growth is barely perceptible until the third day, when it is found to have spread quite widely over the surface. It resembles the growth of the bacillus of influenza very closely. Along the needle stroke is a faint colorless line, and on either side may be seen, by close inspection, colonies which resemble drops of moisture. They are 0.5 mm. in diameter, colorless, and always discrete. The water at bottom shows a whitish growth. After three weeks the growth becomes somewhat more opaque, but never takes on color, and is always hard to see. It is best seen by transmitted light.

Gelatin stab.—On second day a faint whitish growth is seen on surface and along the stab. The surface growth spreads until about the sixth day, when it is 3 mm. in diameter, and is irregular in outline and thickness, piling up at the center. It looks as though layer after layer had grown from the center on the surface of the one preceding, each being of irregular outline, and extending a lesser distance from the common center. It acquires a white metallic luster about the same time. Along the stab fine outgrowths appear about the fifth day, while deeper the colonies appear as separate, minute, white dots, which extend to bottom of puncture.

Gel stab



Gel stab.
Surface growth

Potato.—No growth can be seen until the seventh day, when it acquires a somewhat different color from the potato, which later (sixteen days) becomes about the color of honey. Until the seventh day, only a moisture can be seen. It is a very thin layer, smooth, moist, and looks glazed.

Bouillon.—On third day a slight, diffuse cloudiness is seen, which increases somewhat, but never becomes dense. Later the growth settles to bottom, leaving liquid almost clear.

Rosolic acid.—Very slight growth and no change of color.

Litmus milk.—Color is discharged to some extent by the third day. About the tenth day a reddish tint is seen, and the casein is coagulated in flocculi. Reaction acid. There is no subsequent digestion of the casein up to five weeks.

Sugar gelatin, deep stab.—No growth seen for a week, when a single colony developed deep white and sending out fine branches.

Gelatin slant.—At first a faint whitish line, 1 mm. wide, along needle mark. Later this became an elevated white band, 2 mm. wide, with uneven surface and irregular edges. No liquefaction after three weeks.

Indol.—Negative.

Relation to temperature.—More rapid at 35° to 36° C.

Note.—In the Zeitschrift für Hygiene, Vol. VI, page 379, the Franklands first described an organism under the name bacillus *Arborescens.* The single colonies on gelatin of the bacillus here described correspond so closely to the description of the organism described by them, that I have retained the name so well applied, qualifying it by a striking distinctive characteristic—the non-liquefaction of gelatin.

Bacillus Rodonatus.

(Figs 41, 42, and 43, Pl. IV.)

Found at the depth of 1 foot in made earth, which had been paved for a number of years.

Character.—Requires oxygen for its best development, though a fair growth occurs in an atmosphere of hydrogen.

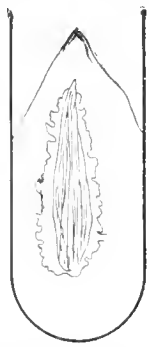
Morphology.—Short rods with rounded ends, but little longer than broad, forming ovals. Resembles the bacillus *Prodigiosus* very closely. Occurs singly and in irregular groups; no chains formed.

Spore formation not observed.

Motility.—Non-motile.

Flagella not demonstrated.

Colonies on gelatin plates.—Colonies seen in about thirty hours. The deep are punctiform and white, and under a low power (× 80) resembles masses of amorphous crystals heaped up. They are yellowish brown with very irregular edges. In the body of the colony the edges of the separate masses can be seen overlapping one another, the whole resembling a rosette. At the end of thirty-six hours the surface colonies are one-fourth of a millimeter in diameter, circular, and white. × 80. Appearance much the same as deep, the mass being more dense, and the central structure not so apparent. The center is yellowish brown and coarsely granular, while at points the outlines of the masses composing it can be seen. They became more clearly visible toward the edge, giving a petal-like arrangement. Beyond is an outer zone which is grayish and finely granular, and fine veins run through it. The colony is circular, with well-defined edges, which are notched here and there. The growth is rather slow, so that at the end of sixty hours the surface colonies are not quite 1 mm. in diameter. At end of eighty-four hours many of them are so dense that it is hard to make out any structure, but in some, by using strong light, the characteristic rosette form can be seen. The deep colonies grow slowly, the masses becoming larger and more regularly disposed, the resemblance to a rosette becoming more marked. In the surface colonies the petal-like arrangement at the edge becomes more distinct, the leaves growing longer and narrower in proportion. As the colony grows older it increases in thickness layer by layer, piling up in the center and growing thinner toward the edges, the color ranging from a dark reddish brown in the center to a pale yellowish gray at the edge. After a week the colonies acquire a fern-like border. There is no liquefaction.



Agar slant.

Agar slant.—A white translucent layer is formed which never spreads very widely. It is not much elevated and has leafy edges. After four or five days a very thin, colorless layer is seen around the edges of the first growth, which has ferny outlines.

Gelatin stab.—Same growth along line of puncture, but mainly on surface, where a thin white layer with irregular leafy edges is formed. It attains a diameter of 4 or 5 mm. No liquefaction at end of three weeks.

Gel. stab.

Gelatin slant.—Greenish-white band, 2 mm. wide, elevated, smooth and shining. The edges are irregular, and after some days become finely dentate.

Potato.—A yellowish layer, moist and shining, which finally covers most of the plug, is formed. At end of a week it becomes a dirty, brownish color, but no further change occurs.

Bouillon.—Diffuse cloudiness seen in twenty-four hours. After a few days a thin, friable pellicle forms on surface, while the growth collects at bottom in dense whitish masses.

Rosolic acid.—Loses color entirely in six or seven days.

Litmus milk.—Becomes a pure blue in three or four days. The color is then slowly discharged and is entirely lost at end of ten days. The milk becomes watery. No coagulation at any time.

Sugar gelatin, deep stab.—Growth in upper half of stab, with button on surface. No gas produced.

Indol.—Reaction negative.

Relation to temperature.—Grows more rapidly at 35° to 36° C.

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A CONTRIBUTION TO THE STUDY OF THE EFFECT OF THE VENOM OF CROTALUS ADAMANTEUS UPON THE BLOOD OF MAN AND ANIMALS.

A CONTRIBUTION TO THE STUDY OF THE EFFECT THE VENOM OF CROTALUS ADAMANTEUS UPON THE BLOOD OF MAN AND ANIMALS.

By S. Weir Mitchell, M. D., and Alonzo H. Stewart, M. D.

THE ACTION OF FRESH CROTALUS VENOM UPON HUMAN BLOOD.

These experiments were conducted with a view to determine the influence of the venom of the *Crotalus adamanteus* upon the human blood corpuscles. It was thought that with the newer methods of examining blood now in use additional knowledge of value could be obtained.

Cases of poisoning by venom are so exceedingly rare in this country at the present time that the only way to carry on this investigation was by noting the effect of the venom in various dilutions upon the blood of man and of the lower animals and also by injecting subcutaneously known quantities of venom into animals and then carefully studying their blood after it had been influenced by the venom.

In the study of the effect of the venom upon the shed blood of the animals the slides of blood were sealed with balsam to protect the blood from the drying action of the air. Some of the slides were kept at the temperature of the room; others containing the same mixture were placed at body temperature in an incubator. All slides were watched carefully, at first on a warm stage, then every few hours, to detect the changes that occurred from time to time.

First, a control slide of normal blood was made and the characteristics of the corpuscles noted. On a second slide the blood and the fresh venom were mixed in equal parts. Third, a control slide of blood and normal saline solution was prepared; then slides on which were placed blood mixed thoroughly with various strengths of venom in normal saline solution ranging from 10 to 0.01 per cent.

Average normal human blood on carefully prepared slides at 37.5° C. showed no marked changes in forty eight hours. In seventy two hours the erythrocytes were crenated and the ameboid motion of the leucocytes had entirely ceased. After one hundred and forty-four hours had elapsed all the corpuscles were broken down.

Blood and fresh venom, 20 cubic millimeters of each, were throughly mixed and preserved from the atmosphere. The erythrocytes at once became globular, 3 to 5 micro-millimeters in diameter, and more highly refractive. The color changed from a slight greenish yellow to a light chocolate tinge, and in many of the slides the corpuscles became quite adherent, sticking together in large clumps or drawn out in long stringy masses. These strings of corpuscles often show the erythrocytes drawn out to 20 micro-millimeters in length. The tendency of the corpuscles to form rouleaux seemed to have entirely disappeared. The leucocytes were reduced from 18 and 20 micro-millimeters to 10 and 12 micro-millimeters in diameter, and they became more refractive at the borders. The ameboid movement ceased at once. Examination in twenty-four hours showed the erythrocytes to be losing color, the long strings having disappeared. The aggregation in clumps was still marked, except where the layers of corpuscles were very thin. Here the formation of small oblong crystals from the blood corpuscles began to be visible. At first the corpuscle became square, and then several faint light lines parallel to each other appeared on the surface.

These lines finally marked the division into oblong crystals. The crystals after a few days became very much larger. In one hundred and forty-four hours in the majority of the slides the erythrocytes had lost nearly all their hemoglobin and were consequently quite pale. There was no sign of any general disintegration of the corpuscles.

Blood was mixed with a normal saline solution containing 10 per cent venom, equal parts. The immediate effect was a diminution in the size of the corpuscles, the erythrocytes shrinking to 5 micro millimeters in diameter, leaving only a slight biconcavity. The ameboid movement of the leucocytes was very slow. In one hundred and forty-four hours the disintegration of all corpuscles was apparent.

Equal parts of blood and a normal saline solution containing 1 per cent venom gave only a slight diminution in the size of the erythrocytes, and there was active movement in the polynuclear leucocytes. In seventy-two hours disintegration was complete.

Equal parts blood and a normal saline solution containing 0.2 to 0.01 per cent venom: The immediate effect was only a slight increase in the refraction of the corpuscles when the dilutions were below 0.05 per cent venom. When the mixture was made with dilutions above 0.05 per cent venom there was no noticeable effect upon the corpuscles. In forty-eight hours the corpuscles were nearly all destroyed.

HUMAN BLOOD.

	Immediate effect.	In 24 hours.	48 hours later.	72 hours later.	96 hours later.
Normal blood.....	Erythrocytes normal. Leucocytes normal in number and appearance.	No change.....	No change.....	Erythrocytes crenated. Leucocytes, ameboid movement stopped.	Erythrocytes same. Leucocytes same. In 144 hours all corpuscles broken down.
Blood and venom, equal parts	Erythrocytes, globular, 3 to 5 micro-millimeters in diameter, more refractive, adhering closely together quite ductile, and many had a chocolate hue. Leucocytes smaller and more refractive at the border; polynuclears showed no ameboid movement.	Erythrocytes losing color and many changed to oblong crystals. Corpuscles became square and then broke up into the oblong crystals. Where corpuscles were thick in layers they adhered in large masses.	Same	Same	Erythrocytes becoming colorless and the crystals better defined; 144 hours, many corpuscles showed no signs of breaking down.
Blood and normal saline solution, equal parts.	Erythrocytes normal. Leucocytes, ameboid movement slow.	Erythrocytes crenated. Leucocytes, ameboid movement stopped.	Erythrocytes granular, breaking down.	Homogeneous mass.	
Blood and normal salt solution containing 1 per cent venom, equal parts.	Erythrocytes globular, 5 micro millimeters in diameter, dark, no tendency to adhere. Leucocytes, active ameboid movement.	No change.....	Erythrocytes crenated. Leucocytes, movement stopped; hemoglobin dissolving out.	Homogeneous mass.	
Blood and normal salt solution containing 0.2 per cent venom equal parts.	Erythrocytes, slight diminution in size. Leucocytes, active ameboid movement.	No change	All corpuscles broken down.	.....	
Blood in normal salt solution containing 0.1 per cent venom, equal parts.	Erythrocytes, slight diminution in size. Leucocytes, active ameboid movement.	No change.....	All corpuscles broken down.	.....	
Blood and normal salt solution containing 0.05 per cent venom, equal parts.	Erythrocytes, scarcely any diminution in size. Leucocytes normal.	No change	All corpuscles broken down.	.....	
Blood and normal salt solution containing 0.04 per cent to 0.01 per cent, equal parts.	Erythrocytes, no apparent diminution in size. Leucocytes normal.	No change	All corpuscles destroyed.	.....	

THE EFFECT ON HUMAN BLOOD OF DRIED VENOM REDISSOLVED IN DISTILLED WATER.

The slides of normal blood showed but slight changes in forty-eight hours, and in one hundred and forty-four hours all the corpuscles were broken down.

Blood brought in contact with dried venom dissolved in water sufficient to make the specific gravity 1.035 showed marked changes. In a few minutes a decided effect on the venom was

noticeable. The effect produced was about the same as when the blood was mixed with fresh venom, with this exception, that the preservative action of the venom did not last so long. The dry venom which has been mixed with water is apparently slower in its action upon the corpuscles than is the pure fresh venom.

	Immediate effect.	24 hours later.	48 hours later.
Blood	Normal	Normal, slight crenation	Slight crenation 144 hours, pale, disappearing.
Blood, dry venom mixed with water, sufficient to make specific gravity 1.055, equal parts	Erythrocytes: In about three minutes the decided effect of the venom is noticeable, corpuscles become globular, more refractive, smaller. Leucocytes slightly smaller, and no ameboid movement.	Breaking down, becoming granular.	Broken down. Large numbers of oblong crystals in the field.
Blood and normal venom	Erythrocytes: Instantly the corpuscles become globular, 3 to 5 in diameter, more refractive, adhering together, quite ductile, and having a reddish hue. Leucocytes smaller and more refractive at the border. Ameboid movement stopped.	Erythrocytes, same condition but where the layers of the corpuscles are thin oblong, crystals are forming. Leucocytes same.	Same appearance. Same.

THE ACTION OF VENOM UPON THE BLOOD OF THE MONKEY.

In the normal blood the erythrocytes were 6 micromillimeters in diameter, and when the slides of blood were made in the usual way all the corpuscles were destroyed in seventy-two hours.

Blood and venom, 20 cubic micromillimeters of each, thoroughly mixed, showed the erythrocytes 3 micromillimeters in diameter, dark, globular, adhesive, and very ductile. The leucocytes were non-motile. After seven days the corpuscles were of good shape and only slightly paler

Blood and a normal saline solution mixed in equal parts gave rise to no alteration in the corpuscles immediately. In seventy-two hours the corpuscles were broken down.

Blood and a normal saline solution containing 10 per cent venom, equal parts, showed the erythrocytes 3.5 micromillimeters in diameter and globular. The leucocytes had active ameboid movement. In twenty-four hours all the corpuscles were destroyed.

Blood and a normal saline solution containing 1 per cent venom, equal parts. The erythrocytes were 5 micromillimeters in diameter and slightly biconcave. In twenty-four hours the corpuscles were all destroyed.

Blood and a normal saline solution containing 0.2 to 0.01 per cent venom, equal parts. In the dilutions below 0.05 per cent venom the corpuscles showed greater refraction with scarcely any perceptible diminution in size. Above 0.05 per cent venom the corpuscles were normal. In twenty-four hours all the corpuscles were destroyed.

Here is again illustrated how more rapidly the corpuscles are broken down when brought in contact with the weaker dilutions of venom than when a given quantity of human blood is mixed with a similar quantity of venom. There was apparently no tendency to the crystallization of the hemoglobin in the slides of blood of monkeys.

THE ACTION OF VENOM UPON THE BLOOD OF THE GUINEA PIG.

Under the same conditions as in the previous experiments slides were made of normal blood, which showed the erythrocytes to be 5 micromillimeters in diameter. The ameboid motion of the leucocytes stopped in twenty-four hours. All the corpuscles were broken down in five days.

When blood and venom were mixed, 20 cubic millimeters of each, the erythrocytes were globular, 3 micromillimeters in diameter, dark, almost chocolate colored, quite adhesive, and very ductile. There was active ameboid movement. In six days all the corpuscles were destroyed.

Blood and a normal saline solution mixed in equal quantities produced no immediate alteration in the corpuscles, but in seventy-two hours all the corpuscles were broken down.

When blood and a normal saline solution containing 10 per cent venom, equal parts, were mixed, the erythrocytes became globular, 3 micromillimeters in diameter, and very refractive. The leucocytes preserved their ameboid movement. In forty-eight hours all the corpuscles were broken down.

Blood and a normal saline solution containing from 0.2 to 0.01 per cent venom, equal parts. There was no apparent effect from these high dilutions of venom except the breaking down of the blood in forty-eight hours, which is the time needed for destruction of the human-blood corpuscles when treated in the same way.

In the immunization of the guinea pig to large doses of venom, which we attempted on many occasions by beginning with 1 per cent of the fatal dose and gradually giving larger doses, we found it almost impossible to get beyond the minimum fatal dose. The sloughing of the parts near the seat of the injections was too extreme or the animal died from the effect of the poison.

THE EFFECT OF VENOM UPON THE BLOOD OF THE DOG.

The erythrocytes in the slides of normal blood were 6 micromillimeters in diamater. The ameboid motion stopped in twenty-four hours. The corpuscles were broken down in ninety-six hours.

Blood and venom mixed, 20 centimeters of each, showed erythrocytes small, 4 micromillimeters in diameter, globular, gelatinous, and ductile. The leucocytes have active ameboid motion. In twenty-four hours the conditions were the same, and in forty-eight hours the ameboid motion had ceased. In one hundred and forty four hours all the corpuscles were broken down.

Blood and a normal saline solution mixed in equal parts showed no change in the corpuscles at first, and in forty-eight hours the corpuscles were broken down.

Blood and a normal saline solution containing 10 per cent venom, equal parts. The erythrocytes became 4 micromillimeters in diameter, dark, globular, and adhesive. The leucocytes were dark and retained active ameboid movement. In seventy-two hours all the corpuscles were broken down.

Blood and a normal saline solution containing 1 per cent venom, equal parts, showed the erythrocytes 5 micromillimeters in diameter, and otherwise the same as where the 10 per cent venom was used.

When blood was mixed with a normal saline solution containing from 0.2 to 0.01 per cent venom, equal parts, the dilutions higher than 0.05 per cent venom showed very little, if any, alteration of the corpuscles. In forty-eight hours all the corpuscles were broken down.

EFFECT OF VENOM UPON THE BLOOD OF A MOUSE.

In the normal blood the corpuscles retain their shape with slight crenation for one hundred and forty-four hours.

When blood and venom are mixed in equal parts the erythrocytes were diminished from 5 to 3 micromillimeters in diameter. They became spherical, more refractive, clumped, and showed increased ductility. The leucocytes were slightly smaller and there was no apparent movement.

Blood and a normal saline solution were mixed in equal parts. There was no immediate effect upon the corpuscles, and in seventy-two hours the corpuscles were broken down. The other dilutions of blood and venom from 10 to 0.01 per cent showed no apparent immediate effect in the dilutions above 1 per cent. In the higher dilutions the corpuscles were destroyed in forty-eight hours.

THE EFFECT OF VENOM UPON THE BLOOD OF THE PIGEON.

Normal blood: The erythrocytes of normal blood were 11 micromillimeters in diameter, oval, and nucleated. The leucocytes showed active ameboid movement. In twenty-four hours many nuclei had escaped and the ameboid motion of the leucocytes had stopped.

Blood and venom, a mixture of 20 cubic micromillimeters of each, showed the erythrocytes dark and spindle-shaped, and in many the nuclei were not distinct. Other corpuscles were circular, 7 micromillimeters in diameter, and of a light chocolate color. In twenty-four hours there were no free nuclei. The ninety-six hours there was no other change.

Blood and a normal saline solution, equal parts, showed erythrocytes swollen and circular. The nuclei were discharged very quickly, and in seventy-two hours they alone were visible.

Blood and a normal saline solution containing 10 per cent venom, equal parts: The erythrocytes became circular and the nuclei were discharged. There was only slight ameboid movement, and in forty-eight hours all the corpuscles were destroyed.

Blood and a normal saline solution containing 1 to 0.2 per cent venom, equal parts, showed the erythrocytes globular and refractive. In fifteen minutes all the nuclei were discharged. In forty-eight hours the corpuscles were destroyed.

Blood and a normal saline solution containing 0.2 to 0.01 per cent venom, equal parts, showed the corpuscles apparently normal. In twenty-four hours all the corpuscles were destroyed.

THE EFFECT OF VENOM UPON THE BLOOD OF THE CHICKEN.

Normal blood: The erythrocytes were oval and nucleated, and in ninety-six hours were completely destroyed.

Blood and venom, 20 cubic millimeters of each, mixed, showed the erythrocytes darker and the nuclei more distinct and smaller. In twenty-four hours many of the corpuscles were globular, while others were spindle shaped, only a few nuclei being discharged. In two hundred and forty-four hours there was no other change.

Blood and a normal saline solution, equal parts: There was no apparent immediate change in the corpuscles. In seventy two hours only a homogeneous mass remained.

Blood and a normal saline solution containing 10 per cent venom, equal parts: The erythrocytes were spindle shaped and more refractive and the nuclei were more distinct. In forty-eight hours the corpuscles were all destroyed.

Blood and a normal saline solution containing 1 per cent venom, equal parts, gave the same result as when the 10 per cent venom was used, except that the complete destruction of the blood occurred in thirty-six hours.

Blood and a normal saline solution containing 0.2 to 0.01 per cent venom, equal parts, showed no immediate alteration of the corpuscles. Only a few scattered nuclei remained in twenty-four hours.

THE EFFECT OF VENOM UPON FROG'S BLOOD.

Normal blood: The erythrocytes were oval, nucleated, and 18 micromillimeters in the long diameter. In forty-eight hours only a few nuclei remained.

Blood and fresh venom, 20 cubic millimeters of each: The erythrocytes showed a tendency to become spindle shaped and the nuclei to become more distinct. The leucocytes were smaller and the ameboid movement stopped. In seventy-two hours there was slight bulging on the sides of the corpuscles. The shape of the corpuscles was well preserved for two weeks.

Blood and a normal saline solution, equal parts: There was no immediate effect upon the corpuscles. In twenty-four hours the blood was completely broken down.

Blood and a normal saline solution containing 10 per cent venom, equal parts: Many erythrocytes became spindle shaped and showed alternate light and dark lines radiating from the nucleus to the periphery of the corpuscles. The leucocytes were normal. In forty-eight hours all the corpuscles were absorbed.

Blood and a normal saline solution containing 1 per cent venom, equal parts: The erythrocytes were crenated, although none were spindle shaped. The leucocytes were normal. In twenty-four hours all the corpuscles were broken down.

Blood and a normal saline solution containing 0.2 to 0.01 per cent venom, equal parts: There was no apparent immediate effect upon the corpuscles. In twenty four hours all the corpuscles were destroyed.

THE EFFECT OF THE VENOM OF CROTALUS ADAMANTEUS UPON PINE SNAKE BLOOD.

In the normal blood of the pine snake the erythrocytes are oval and 15 micromillimeters in the long diameter. The leucocytes are small, 6 micromillimeters in diameter, with the exception of a few which are about 8 to 10 micromillimeters in diameter. The larger leucocytes had marked ameboid movement. In seventy-two hours all the corpuscles were broken down.

Blood and venom, equal parts: There is no diminution in the size of the leucocytes. The only change noticed was a slight striation. There was no ameboid movement present. In twenty-four hours the corpuscles were slightly darker and there was very little diminution in size. In seventy-two hours most of the corpuscles still showed good contour.

Blood and a normal saline solution, equal parts: There was no immediate effect. In seventy-eight hours many of the corpuscles were broken down.

Blood and a normal saline solution containing 10 per cent venom, equal parts: The erythrocytes showed slight discoloration. The leucocytes retained their ameboid movement. In forty-eight hours the corpuscles were broken down.

Blood and a normal saline solution containing 2 per cent venom, equal parts: The erythrocytes were striated and the ameboid movement still continued. In twenty-four hours all corpuscles were destroyed.

Dilutions of 0.1 to 0.05 per cent venom in the same way showed the same result as when 2 per cent venom was used. When 0.05 per cent venom to 0.1 per cent was used, there was no immediate effect whatever upon the corpuscles, and the destruction of the corpuscles occurred in forty-eight hours.

PINE SNAKE BLOOD AND VENOM OF CROTALUS ADAMANTEUS.

	Immediate effect.	24 hours later.	48 hours later.	72 hours.
Blood	Erythrocytes oval, nucleated, 15 micromillimeters in diameter. Leucocytes: Small, 6 micromillimeters in diameter.	Erythrocytes. Crenation. Leucocytes: No ameboid movement.	Same	Broken down.
	In largest size, ameboid movement		Same	
Blood and venom, equal parts.	Erythrocytes No diminution in size. The only change noticed was slight striation of the corpuscles. Leucocytes No ameboid movement and only a few corpuscles noticed.	Erythrocytes slightly darker in color and very little diminution in size. Leucocytes. No change.	Same	Dark, many corpuscles of good shape.
Blood and saline solution, equal parts.	Erythrocytes normal. Leucocytes normal.	Erythrocytes normal, slight striation. Leucocytes. No ameboid movement.	Most corpuscles normal, a few circular	Broken down.
Blood and normal saline solution containing 10 per cent venom, equal parts.	Erythrocytes: Striation Leucocytes Ameboid movement.	Erythrocytes, crenated, dark, fair shape.	Broken down	
Blood and normal saline solution containing 2 per cent venom, equal parts.	Erythrocytes Striation. Leucocytes Ameboid movement.	Broken down		
Blood and normal saline solution containing 1 per cent venom, equal parts.	Erythrocytes Striation. Leucocytes normal.	Broken down		
Blood and normal saline solution containing 0.2 per cent venom, equal parts.	Erythrocytes Striation. Leucocytes normal.	Broken down		
Blood and normal saline solution containing 0.1 per cent venom, equal parts.	Erythrocytes: Striation. Leucocytes normal.	Breaking down	Broken down	
Blood and normal saline solution containing 0.05 per cent venom to 0.01 per cent venom.	Erythrocytes normal.	Pale, crenated		

THE EFFECT OF VENOM UPON THE BLOOD OF THE CROTALUS ADAMANTEUS.

The normal erythrocytes of crotalus blood were 25 micromillimeters in the long diameter, oval, and nucleated. The leucocytes were numerous, and many had marked ameboid movement. In twenty-four hours the erythrocytes showed crenation and ameboid movement of the leucocytes had stopped. In ninety-six hours all the corpuscles were broken down.

When blood and venom were mixed in equal parts the erythrocytes were normal in size but slightly paler, and the ameboid movement was present. Six days later there was no change whatever in appearance of the corpuscles.

Blood and a normal saline solution, equal parts. The saline solution produced no immediate effect. In ninety-six hours most of the corpuscles were broken down and only a few crenated ones remained.

Blood and a normal salt solution containing 10 per cent venom, equal parts. There was no immediate effect on the corpuscles. In ninety-six hours there was only a slight crenation.

Blood and a normal salt solution containing 2 per cent venom, equal parts. In this mixture the nuclei of the erythrocytes were quite distinct. In ninety-six hours the corpuscles were broken down.

In the weaker dilutions used the same effect was noted, as in the mixtures of 2 per cent venom.

Equal parts of crotalus blood and human blood brought in contact showed no other effect except crenation at the line of contact.

In these experiments with crotalus blood the most noticeable feature is the slight effect produced upon the blood of the crotalus by its own venom.

CROTALUS BLOOD.

	Immediate effect.	24 hours later.	48 hours later	72 hours later.	96 hours later.
Blood of crotalus adamanteus.	Erythrocytes 25 in long diameter, oval, and nucleated. Leucocytes numerous, marked ameboid movement.	Erythrocytes crenated. Leucocytes. No ameboid movement.	Same	Crenated and breaking down.	Broken down.
Blood and venom, equal parts.	Erythrocytes normal in size only slightly paler. Leucocytes, ameboid movement noticed.	Erythrocytes pale. Leucocytes: Ameboid movement stopped	No change.....	Same	Same, 6 days later no change.
Blood and saline solution, equal parts.	Erythrocytes normal. Leucocytes normal.	Erythrocytes slightly crenated. Leucocytes: Ameboid movement stopped	Same	Same	Most of corpuscles broken down and the rest crenated
Blood and normal saline solution containing 10 per cent venom, equal parts.	Erythrocytes normal. Leucocytes normal.	Erythrocytes Slight crenation Leucocytes normal.	Same	Same	Same.
Blood and normal salt solution containing 4 per cent venom, equal parts.	Erythrocytes: Nuclei slightly more distinct. Leucocytes normal.	Erythrocytes: crenation.	Same	Erythrocytes: same. Leucocytes pale and granular.	Breaking down.
Blood and normal saline solution containing 2 per cent venom, equal parts	Erythrocytes. Nuclei more distinct. Leucocytes normal.	Erythrocytes: crenated. Leucocytes normal.	Same	Erythrocytes: same. Leucocytes granular.	Breaking down.
Blood and normal saline solution containing 1 per cent venom, equal parts.	Erythrocytes: nuclei more distinct. Leucocytes normal.	Erythrocytes: crenation Leucocytes normal.	Same	Erythrocytes: pale, granular. Leucocytes granular.	Broken down.
Blood and normal saline solution containing 0.2 per cent venom, equal parts.	Erythrocytes: nuclei more distinct. Leucocytes normal.	Erythrocytes crenation. Leucocytes normal.	Same	All corpuscles granular.	Broken down.
Crotalus blood and human blood, equal parts.	Erythrocytes of human blood crenated at the line of contact. Leucocytes. No change.	Erythrocytes: same. Leucocytes same.	Erythrocytes: same. Leucocytes granular.	Same	Broken down.

THE EFFECT OF VENOM UPON THE RABBIT BLOOD.

The slides of normal blood showed the corpuscles granular and broken down in ninety-six hours.

When blood and venom, equal parts, were mixed the erythrocytes in a few seconds became small, dark, globular adherent in clumps and showed increased ductility. The leucocytes showed marked ameboid movement. In ninety-six hours the corpuscles began to lose their hemoglobin.

Blood and a normal saline solution, equal parts. In this mixture there was no change in the corpuscles. In seventy-two hours the corpuscles were entirely broken down.

Blood and normal saline solution containing 10 per cent venom, equal parts, showed the erythrocytes small, dark, globular and separate. Leucocytes retained a slight ameboid movement. In forty-eight hours all corpuscles were broken down. The same result was noted in dilutions as high as 0.2 per cent. In dilutions of 1 per cent to 0.01 per cent venom the corpuscles were normal, and in forty-eight hours they were completely destroyed.

RABBIT BLOOD.

	Immediate effect.	24 hours later.	48 hours.	72 hours.	96 hours.
Blood	All corpusceless in good condition.	Erythrocytes slight crenation. Leucocytes breaking down.	Same	Same	Color fading, granular.
Blood and venom, equal parts	Erythrocytes small, dark, globular, adherent in lumps, and showing ductility. In a few seconds many of the corpuscles became entirely globular and separate. Leucocytes marked ameboid movement.	Erythrocytes highly refractive, dark, and globular. Leucocytes active, ameboid movement stopped.	Erythrocytes: same. Leucocytes ameboid movement stopped.	Same	Erythrocytes losing, hemoglobin. Leucocytes granular.
Blood and normal saline solution, equal parts.	Erythrocytes normal. Leucocytes slight ameboid movement.	Erythrocytes swollen. Leucocytes swollen and granular.	Erythrocytes crenated, losing color. Leucocytes disappeared.	Homogeneous mass.	
Blood and normal salt solution, containing 10 per cent venom, equal parts.	Erythrocytes small dark globular separate. Leucocytes Slight ameboid movement.	Erythrocytes same. Leucocytes swollen and granular.	All corpuscles broken.		
Blood and normal saline solution containing 1 per cent venom, equal parts.	Erythrocytes: Slightly smaller, more refractive, biconcavity retained. Leucocytes: Ameboid movement present.	Erythrocytes same. Leucocytes swollen and granular, ameboid movement stopped.	All corpuscles broken down.		
Blood and saline solution containing 0.2 per cent venom, equal parts.	Erythrocytes: Smaller and more refractive. Leucocytes Ameboid movement present.	Erythrocytes same. Leucocytes, ameboid movement stopped.	All corpuscles broken down.		
Blood and normal saline solution containing 0.1 to 0.01 per cent venom, equal parts.	Corpuscles normal	Crenated	Broken down		

THE EFFECT OF VENOM UPON THE BLOOD CORPUSCLES OF A NORMAL RABBIT COMPARED WITH THE EFFECT UPON THE BLOOD OF A RABBIT IMMUNE TO FIFTY TIMES THE MINIMUM FATAL DOSE.

In the immunization of various animals to crotalus venom it was found that the rabbit could withstand the effect of the venom better than the other animals ordinarily used for the purpose. The immunization of the guinea pig is almost impossible. No matter how small may be the dose given at the beginning of the process, before the minimum fatal dose has been reached, there is a marked sloughing at the seat of inoculation, and the loss of tissue is so great that doses can be given only at long intervals. Whenever the minimum lethal dose has been reached the animals die. Rabbits, on the other hand, are not nearly so susceptible to the poison. Beginning with one-tenth to one one-thousandth of the minimum fatal dose and gradually increasing the dose, injecting subcutaneously every four days (the interval depending, of course, upon the health of the animal), most rabbits may be immunized to five or ten times the fatal dose with but very little difficulty. When death occurs in these immunized animals it is usually through bacterial infection, but it may be due to the direct effect of the venom itself. In the attempt to immunize rabbits to as high a degree as fifty times the minimum fatal dose much difficulty was experienced, on account of the widespread local lesions produced. We succeeded in immunizing many rabbits to twenty times the fatal dose, but with only one were we able to reach fifty times the minimum lethal dose, and the blood of these animals was used in experiments with the following result, which results we compare with those obtained in the use of normal rabbit's blood.

In the blood of a normal rabbit there are about 5,000,000 erythrocytes and about 10,000 leucocytes to the cubic millimeter. In the immunized rabbit's blood we found 4,500,000 erythrocytes and 75,000 leucocytes to the cubic millimeter. When the blood of a normal rabbit was mixed with equal parts of venom the erythrocytes became small, dark, globular, and adherent in clumps, and they showed increased ductility; in a few seconds many of the corpuscles become entirely globular and separate. When the blood of the immunized animal was mixed with equal parts of venom the erythrocytes remained normal in size and appearance (except that they present a slight reddish hue), and retain their biconcavity for about thirty minutes; they then become but slightly smaller and globular. We see here in the immunized blood that the effect of the venom is withstood for a considerable length of time, thus showing that the blood corpuscles themselves have gained a certain amount of power of resistance to the poison in this period of immunization.

[A, normal blood. B, immune blood.]

	Immediate effect.	24 hours later.	48 hours later.
Blood	(A) Normal: Erythrocytes, 5,000,000 per cubic millimeter; leucocytes 10,000 per cubic millimeter.	(A) Normal	(A) Crenation.
	(B) Erythrocytes, 4,500,000 per cubic millimeter leucocytes, 75,000 per cubic millimeter.	(B) Normal, beginning crenation.	(B) Crenation.
Blood and venom, equal parts	(A) Characteristic changes noted on table.	(A) Same	(A) Same.
	(B) Erythrocytes normal in size and appearance, except a slight reddish tinge. They retain their biconcavity for 30 minutes and then become smaller and globular.	(B) Erythrocytes smaller, darker, and the biconcavity lost. Leucocytes ameboid movement present.	(B) Same.
Blood and normal salt solution, equal parts.	(A) Normal	(A) Crenated	(A) Broken down.
	(B) Normal	(B) Crenated	(B) Broken down.
Blood and normal saline solution containing 10 per cent venom, equal parts.	(A) Erythrocytes smaller, globular, more refractive. Leucocytes. Ameboid movement present	(A) Crenated	(A) Same.
	(B) Erythrocytes full size, biconcave. Leucocytes; Ameboid movement present.	(B) Crenated	(B) Corpuscles small and crenated.
Blood and normal saline solution containing 2 per cent venom, equal parts.	(A) Erythrocytes smaller, more refractive, slight biconcavity. Leucocytes normal.	(A) Crenated	(A) Breaking down.
	(B) Erythrocytes larger than (A) and show less effect of venom. Leucocytes normal.	(B) Normal	(B) Breaking down.
Blood and normal salt solution containing 1 per cent venom, equal parts.	(A) Erythrocytes smaller and more refractive	(A) Same	(A) Broken down.
	(B) Normal	(B) Normal	(B) Broken down.
Blood and normal saline solution containing 0.1 per cent venom, equal parts.	(A) Corpuscles normal	(A) Crenated	(A) Broken down.
	(B) Normal	(B) Normal	(B) Broken down
Blood and normal saline solution containing 0.02 per cent venom, equal parts.	(A) Corpuscles normal	(A) Crenated	(A) Broken down.
	(B) Normal	(B) Crenated	(B) Broken down.

THE EFFECT OF POTASSIUM PERMANGANATE SOLUTIONS UPON VENOM AND RABBIT'S BLOOD.

A saturated solution of potassium permanganate in water brought in contact with an equal amount of rabbit blood showed the corpuscles slightly stained with permanganate without any alteration in their shape. The ameboid movement was stopped. When a 1 per cent aqueous solution was used the same effect was noted. A saturated solution of potassium permanganate was then brought in contact with blood which had been mixed with an equal quantity of venom, and it was found that the corpuscles regained their normal size and were no longer adhesive, but they were considerably stained by the solution used. When 1 per cent solution of potassium permanganate was used upon the affected blood the corpuscles regained their normal shape, but not as quickly as when the stronger solution of potassium permanganate was used. When weaker dilutions of potassium permanganate were brought in contact with blood affected by venom there was little or no effect, thus showing that the weak solution of potassium permanganate was unable to counteract the powerful effect of the venom.

THE ACTION OF VENOM UPON THE BLOOD OF A RABBIT WHICH HAD RECEIVED SUBCUTANEOUS INJECTIONS OF POTASSIUM PERMANGANATE.

Five centigrams of potassium permanganate in five cubic centimeters of distilled water were injected subcutaneously each day for one week, and the blood was then tested with the various solutions of venom. It was found that there was no apparent protective effect from the injections, and the venom acted on the blood in the usual way.

EFFECT OF POTASSIUM PERMANGANATE UPON VEMON AND BLOOD OF THE MONKEY.

The saturated aqueous solution of potassium permanganate mixed with the normal blood gives only a very slight increase in the size of the erythrocytes. If the blood and venom were mixed so as to alter the corpuscles, and then brought in contact with the potassium of permanganate solution, the erythrocytes would be seen to again assume their normal size, 6 micromillimeters in diameter. The biconcavity returned and the corpuscles were not broken down for weeks.

Blood and venom, equal parts, brought in contact with 1 per cent solution of potassium permanganate did not show the marked effect seen when the saturated solution was used.

Equal parts of blood and a normal saline solution containing 10 per cent of venom brought in contact with a 1 per cent solution of potassium permanganate. The effect of venom immediately disappeared.

THE EFFECT OF VENOM UPON RABBIT'S BLOOD DURING INTOXICATION OF THE ANIMAL WITH ALCOHOL.

The blood taken from these animals when placed upon slides showed a marked tendency of the erythrocytes to crenation. The leucocytes slightly increased in number. In forty-eight hours all of the corpuscles were broken down.

Blood and venom, equal parts: The erythrocytes showed a quick reaction to the venom in the usual way. In twenty-four hours all of the corpuscles were destroyed.

Blood and a normal saline solution, equal parts: There was no marked immediate effect. In forty-eight hours the corpuscles were all destroyed.

Blood and a normal saline solution containing 10 per cent venom, equal parts, and weaker dilutions of venom used all showed marked reaction of venom, and the corpuscles were broken down in twenty-four hours.

The evident susceptibility of the blood of animals intoxicated with alcohol is indeed curious. Why this should be we do not clearly understand, but it proves conclusively the lessened resistance of individuals under the influence of alcohol. It also bears out the teachings of those who do not believe that intoxication of patients who have been bitten by a snake exerts any beneficial effect upon the condition.

	Immediate effect.	24 hours later.	48 hours later.
Blood	Erythrocytes: Marked tendency to crenation. Leucocytes increased in number.	Corpuscles becoming granular.	Broken down.
Blood and venom, equal parts	Erythrocytes: Characteristic reaction to venom. Leucocytes: Active ameboid movement.	All corpuscles broken down.	
Blood and normal saline solution, equal parts.	Erythrocytes normal. Leucocytes, normal in appearance.	Granular	Broken down.
Blood and normal saline solution, containing 10 per cent venom, equal parts.	Erythrocytes slightly smaller and more refractive. Many are globular. Leucocytes: Ameboid movement present.	Broken down.	
Blood and normal saline solution, containing 1 per cent venom, equal parts.	Erythrocytes smaller, more refractive, slightly biconcave. Leucocytes: Amœboid movement present.	Broken down.	

EFFECT OF PERMANGANATE OF ZINC UPON VENOM AND HUMAN BLOOD.

When a saturated solution of permanganate of zinc was brought in contact with human blood the corpuscles at the point of contact became fixed and dark brown in color, but were not altered in shape. Various strengths of permanganate of zinc solutions were mixed with blood which had previously been mixed with venom; no immediate or late effect was shown other than that indicated when the permanganate of zinc in saturated solution was brought in contact with normal blood.

EFFECT OF POTASSIUM CHROMATE UPON VENOM AND HUMAN BLOOD.

When a saturated solution of potassium chromate was brought in contact with normal blood in equal parts, there was no change in the blood except a yellowish discoloration of the corpuscles and a stopping of the ameboid movement of the leucocytes. The saturated solution of potassium chromate brought in contact with blood, which had been previously effected by venom, stained the corpuscles but produced no alteration in the effected corpuscles. The same thing was shown when the blood was mixed with the solution of 10 per cent venom and 0.1 per cent venom.

EFFECT OF CHROMIC ACID UPON VENOM AND HUMAN BLOOD.

The strong solutions of chromic acid above 2 per cent immediately destroyed all corpuscles, but solutions of 1 to 0.1 per cent seemed to have no other action on either normal corpuscles, or upon those effected by venom, than simply to decolorize them.

EFFECT OF CALCIUM CHLORIDE SOLUTION UPON VENOM AND HUMAN BLOOD.

A solution of calcium chloride in water, 1 to 60, was brought in contact with normal human blood. The only noticeable effect from this mixture upon the corpuscles was slight crenation of the erythrocytes and stopping of ameboid motion. The calcium chloride solution was mixed with

blood previously effected by venom and it was found that the corpuscles retained the alteration which had been produced by the venom. The calcium chloride solution apparently had no influence whatever. Rabbits which had received the minimum fatal dose of venom were then given an injection of calcium chloride solution near to the seat of the injection of the poison with no effect.

EFFECT OF POTASSIUM PERMANGANATE UPON VENOM AND HUMAN BLOOD.

A saturated solution of potassium permanganate in water was brought in contact with human blood. The erythrocytes remained almost normal in size, their biconcavity was retained, and all the corpuscles were stained with the permanganate solution. The leucocytes were smaller, the granules stained brown, and the ameboid movement was absent. When weaker solutions of permanganate of potash were used the same effect is present only to a less degree.

When venom was brought in contact with an equal quantity of blood, and an equal quantity of the solution of potassium permanganate added to this mixture, the following changes were noted: When the blood came in contact with the venom the usual changes occurred on the addition of the potassium permanganate solution; the red corpuscles changed their globular form and again became biconcave circular disks of normal size, and did not show any longer the marked agglutination. This return of the corpuscles to almost the normal appearance will occur when the potassium permanganate solution is added forty-five minutes after the mixture of the blood and venom.

When 1 per cent solution of potassium permanganate is used instead of the saturated solution in the above experiment, the restoration of the corpuscles to the normal is not nearly so complete.

When 1 per cent solution of potassium permanganate is brought in contact with a mixture of blood and saline solution which contains 10 per cent venom, the effect of the permanganate is not sufficient to entirely counteract the influence of the venom upon the corpuscles. The rapid restoration of the affected corpuscles to the normal, or almost normal, condition by the addition of the solution of potassium permanganate is certainly a remarkble and a very interesting fact.

The rapid oxidation of the corpuscles may have some effect upon the neutralization of the venom in the corpuscles, for when peroxide of hydrogen solutions of neutral reaction were used in the place of the potassium permanganate solutions in the above experiments, almost the same results were obtained.

	Immediate effect.	24 hours later.	48 hours later.
Human blood	Normal	Crenated	Crenated.
Blood and saturated solution potassium permanganate, equal parts.	Erythrocytes slightly smaller; biconcavity retained, no rouleaux, stained a deep brown color. Leucocytes smaller, no ameboid movement; granules stained dark brown.	Erythrocytes good shape; no crenation; slightly paler, no signs of degeneration.	Same.
Blood and 1 per cent solution potassium permanganate in water, equal parts	Erythrocytes slightly smaller, many almost colorless, no crenation; biconcavity retained. Leucocytes smaller and no ameboid movement.	Homogeneous mass	
Blood and venom, equal parts.	Erythrocytes 3 to 5 in diameter; globular, more refractive, adhering together, ductile, and many have a chocolate hue. Leucocytes smaller, more refractive at the border, ameboid movement lost.	Erythrocytes losing color and beginning formation of oblong crystals, where the corpuscles are thick they still retain their adhesiveness.	Same.
Blood and venom and saturated solution potassium permanganate, equal parts.	Erythrocytes: When the blood comes in contact with venom the usual changes occur; but when the potassium permanganate solution is added the red corpuscles change their globular form and again become biconcave, circular disks of normal size and not adhesive. Leucocytes: No ameboid movement.	Same	Same.
Blood and venom and 1 per cent solution potassium permanganate, equal parts.	Erythrocytes slightly smaller, globular, separate, and not adhesive. Leucocytes, nonmotile.	Same	Same.
Blood and venom normal saline solution containing 10 per cent venom, equal parts	Erythrocytes diminutive in size, almost as great as when pure venom was used, but corpuscles still slightly biconcave. Leucocytes: Ameboid movement present	Erythrocytes same. Leucocytes Ameboid movement still continues.	Erythrocytes Crenation. Leucocytes Ameboid movement stopped.
Blood and 10 per cent venom and saturated solution potassium permanganate, equal parts.	Erythrocytes: Corpuscles normal in size; no crenation, no loss of biconcavity, not adhesive. Leucocytes: Ameboid movement stopped.	Erythrocytes same	Same.
Blood and 10 per cent venom and 1 per cent solution potassium permanganate, equal parts.	Erythrocytes slightly smaller, darker, many globular; not adhesive. Leucocytes: Ameboid movement stopped.	Broken down	

CONCLUSIONS.

(1) Blood of warm-blooded animals is unusually preserved when mixed with an equal quantity of venom, but when small quantities of venom are used the blood breaks down very rapidly.

(2) The action of the venom of the crotalus adamanteus is less apparent upon its own blood than upon the blood of other varieties of animals.

(3) In the immunization of rabbits to crotalus adamantens venom there is a marked leucocytosis produced.

(4) Blood corpuscles of rabbits, immune to fifty times the minimum fatal dose, resist the direct action of the venom, so that the changes which usually occur in the corpuscles when brought in contact with the venom do not occur for about thirty minutes.

(5) Solutions of potassium permanganate brought in contact with the blood corpuscles that have been altered by the action of crotalus venom restore the corpuscles to their normal size and shape.

(6) Solutions of hydrogen peroxide have the same effect upon blood corpuscles affected by venom as do the potassium permanganate solutions.

(7) Chromic acid solutions 0.1 to 1 per cent apparently have no other effect than to decolorize and partially destroy the blood corpuscles.

(8) Calcium chloride solutions produce no apparent change in either normal corpuscles or in those affected by venom.

(9) There is an evident increased susceptibility to venom of the blood corpuscles of rabbits when the rabbits are profoundly intoxicated with alcohol.

NORMAL HUMAN BLOOD.

EARLY EFFECT OF CROTALUS VENOM UPON HUMAN BLOOD CORPUSCLES, CAUSING THEM TO BECOME GLOBULAR AND SMALLER AND TO BE AGGLUTINATED AS SHOWN.

FINAL EFFECT OF CROTALUS VENOM UPON HUMAN BLOOD CORPUSCLES, SHOWING THE STRINGY CONDITION OF THE CORPUSCLES.

RESTORATIVE EFFECT OF PERMANGANATE OF POTASSIUM UPON HUMAN BLOOD CORPUSCLES THAT HAVE BEEN ALTERED BY THE ACTION OF CROTALUS VENOM.

LATER EFFECT OF CROTALUS VENOM UPON HUMAN BLOOD CORPUSCLES,
SHOWING BEGINNING CRYSTALLIZATION

FINAL RESULT OBTAINED BY MIXING CROTALUS VENOM AND HUMAN BLOOD, SHOWING LAST STAGE OF CRYSTALLIZATION.

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GENERAL PERTURBATIONS OF MINERVA (93), BY JUPITER, INCLUDING TERMS ONLY OF THE FIRST ORDER WITH RESPECT TO THE MASS, TOGETHER WITH A CORRECTION OF ELEMENTS.

GENERAL PERTURBATIONS OF MINERVA (93), BY JUPITER, INCLUDING TERMS ONLY OF THE FIRST ORDER WITH RESPECT TO THE MASS, TOGETHER WITH A CORRECTION OF ELEMENTS.

By W. S. Eichelberger, Ph. D.

The method used in computing the perturbations is that developed by Hansen in "*Auseinandersetzung einer zweckmässigen Methode zur Berechnung der absoluten Störungen der kleinen Planeten.*"

The elements of Jupiter were obtained from Hill's *Theory of Jupiter and Saturn*, and those of Minerva from a special discussion, by the author, of the observations from 1867 to 1879 inclusive. These elements are as follows:

Elements of Jupiter and Minerva.

Epoch, 1872, Nov. 2.0, Greenwich M. T.

(93)		24	
$g=108^\circ\ 37'\ 48''.4$		$g'=121^\circ\ 10'\ 41''.9$	
$\pi=274\ 47\ 41.4$		$\pi'=12\ 12\ 57.0$	
$\theta=5\ 5\ 25.0$	1872	$\theta'=99\ 7\ 14.2$	1872
$i=8\ 36\ 21.6$		$i'=1\ 18\ 39.1$	
$\varphi=8\ 5\ 0.5$		$\varphi'=2\ 45\ 57.2$	
$n=776''.51130$		$n'=299''.12834$	
$\mu=\frac{n'}{n}$		$1\div m'=1047.88$	

The first step in determining the perturbations was to develop the reciprocal of the distance between the two planets and, in the case of the first order perturbations, its cube, in terms of the sines and cosines of the sum of the different multiples of the eccentric anomalies of the two planets. The coefficients of the terms in these developments are functions of the following six quantities:*

$\log a=0.2763315$	$J=8^\circ\ 47'\ 42''.5$
$e=\sin\varphi=0.1406156$	$\Pi=278\ 17\ 16.4$
$e'=\sin\varphi'=0.0482551$	$\Pi'=15\ 36\ 37.8$

The square of the mutual distance $\left(\frac{\Delta}{a}\right)^2$ was thrown into the form

$$D-f\cos(\varepsilon'-F)+\tfrac{1}{2}\gamma_2\cos 2\varepsilon'$$

where ε' is the eccentric anomaly of Jupiter, $\gamma_2=a^2e'^2$, and D, F and f are functions of the elements and the eccentric anomaly ε of Minerva.

*The notation and formulas are those of Hansen in the work referred to above.

The values of the last three quantities were computed for each of sixteen values of ε as given in the following table:

ε	D	log f	F—ε
0° 0	4.293171	0.5026265	268° 56 1.05
22 30	4.381903	0.5295604	271 51 19.49
45 0	4.498856	0.5609250	272 55 55.54
67 30	4.629257	0.5906060	272 21 21.81
90 0	4.756284	0.6148842	270 31 46.15
112 30	4.861853	0.6319519	267 51 57.57
135 0	4.928436	0.6410617	264 43 31.24
157 30	4.943440	0.6419863	261 24 56.50
180 0	4.900975	0.6347467	258 13 14.09
202 30	4.806453	0.6195693	255 25 58.47
225 0	4.675518	0.5970701	253 23 10.35
247 30	4.531136	0.5687062	252 28 8.78
270 0	4.398317	0.5375153	253 5 19.31
292 30	4.298539	0.5088686	255 31 12.48
315 0	4.245736	0.4901403	259 36 25.97
337 30	4.244915	0.4877304	264 30 29.32

From these quantities were computed the values of β'^{n}_{i} defined by the equations,

$$\{D-f\cos(\varepsilon'-F)\}^{-3}=\alpha^{n}_{0}+2\alpha^{n}_{1}\cos(\varepsilon'-F)+2\alpha^{n}_{2}\cos 2(\varepsilon'-F)+\text{ etc.}$$

$$\beta^{1}_{i}=\frac{1}{8}\frac{m'}{\sin 1''}\alpha^{(1)}_{i}$$

$$\beta^{(3)}_{i}=\frac{1}{8}\frac{\alpha^{2}m'}{\sin 1''}\alpha^{(3)}_{i}$$

$$\beta'^{(5)}_{i}=\frac{3}{64}\frac{\alpha^{2}\gamma_{2}m'}{\sin 1''}\alpha^{(5)}_{i}$$

Instead of the former designation of $\varepsilon=0°$, $22°\frac{1}{2}$, etc., we use $\varepsilon=(0)$, (1), etc.

ε	log β^{1}_{0}	log β^{1}_{1}	log β^{1}_{2}	log β^{1}_{3}	log β^{1}_{4}	log β^{1}_{5}	log β^{1}_{6}	log β^{1}_{7}
(0)	1.1370406	0.494480	0.020288	9.589895	9.179893	8.781721	8.39128	8.00631
(1)	1.1409100	0.527776	0.081825	9.679372	9.297189	8.926772	8.56105	8.20677
(2)	1.1465353	0.568141	0.155946	9.786530	9.437208	9.099563	8.76956	8.44497
(3)	1.1526571	0.607972	0.227063	9.888758	9.570346	9.263509	8.96426	8.67037
(4)	1.1578512	0.639880	0.283992	9.970263	9.676241	9.393696	9.11868	8.84898
(5)	1.1609152	0.660402	0.320709	0.022819	9.744558	9.477670	9.21827	8.96416
(6)	1.1616490	0.668852	0.336323	0.045170	9.774122	9.514141	9.26162	9.01439
(7)	1.1605509	0.666823	0.333432	0.041736	9.769554	9.508715	9.25540	9.00734
(8)	1.1581440	0.656261	0.315055	0.015710	9.735947	9.467596	9.20673	8.95117
(9)	1.1556981	0.638014	0.282395	9.968928	9.675167	9.392880	9.11812	8.84868
(10)	1.1522170	0.611969	0.235203	9.900971	9.586605	9.283798	8.98857	8.69869
(11)	1.1480126	0.578657	0.174123	9.813152	9.471927	9.142356	8.82041	8.50386
(12)	1.1434177	0.541086	0.105469	9.713229	9.341208	8.980928	8.62833	8.28116
(13)	1.1392417	0.505760	0.040308	9.618566	9.217180	8.827605	8.44576	8.06936
(14)	1.1363362	0.481835	9.996126	9.554324	9.132959	8.723117	8.32168	7.92539
(15)	1.1354750	0.477403	9.988246	9.543028	9.118259	8.705351	8.30019	7.90051

ε	$\log \beta_{8}^{(1)}$	$\log \beta_{9}^{(1)}$	$\log \beta_{10}^{(1)}$	$\log \beta_{11}^{(1)}$	$\log \beta_{12}^{(1)}$	$\log \beta_{13}^{(1)}$	$\log \beta_{14}^{(1)}$	$\log \beta_{15}^{(1)}$
(0)	7.62538	7.2476	6.8723	6.4991	6.1275	5.75736	5.3884	5.0236
(1)	7.85353	7.5034	7.1558	6.8102	6.4663	6.12377	5.7825	5.4423
(2)	8.12139	7.8069	7.4919	7.1789	6.8676	6.55777	6.2491	5.9415
(3)	8.38047	8.0937	7.8093	7.5270	7.2463	6.96705	6.6890	6.4120
(4)	8.58325	8.3206	8.0604	7.8022	7.5456	7.29049	7.0366	6.7836
(5)	8.74400	8.4669	8.2222	7.9796	7.7385	7.49893	7.2605	7.0231
(6)	8.77110	8.5309	8.2930	8.0572	7.8231	7.59028	7.3587	7.1282
(7)	8.76322	8.5222	8.2835	8.0469	7.8119	7.57830	7.3459	7.1145
(8)	8.69955	8.4510	8.2049	7.9608	7.7183	7.47723	7.2374	6.9985
(9)	8.58321	8.3208	8.0609	7.8029	7.5466	7.29174	7.0384	6.7854
(10)	8.44280	8.1300	7.8497	7.5713	7.2947	7.01941	6.7451	6.4721
(11)	8.19132	7.8819	7.5749	7.2700	6.9667	6.66486	6.3642	6.0646
(12)	7.93802	7.5980	7.2605	6.9250	6.5911	6.25874	5.9276	5.5974
(13)	7.69701	7.3278	6.9611	6.5964	6.2334	5.87182	5.5115	5.1522
(14)	7.53316	7.1441	6.7575	6.3729	5.9900	5.60861	5.2284	4.8192
(15)	7.50488	7.1124	6.7224	6.3345	5.9482	5.56341	5.1798	4.7973

ε	$\log \beta_{0}^{(3)}$	$\log \beta_{1}^{(3)}$	$\log \beta_{2}^{(3)}$	$\log \beta_{3}^{(3)}$	$\log \beta_{4}^{(3)}$	$\log \beta_{5}^{(3)}$	$\log \beta_{6}^{(3)}$	$\log \beta_{7}^{(3)}$
(0)	1.3226229	1.1132809	0.8454110	0.5531487	0.2474051	9.9330855	9.612823	9.288197
(1)	1.3557926	1.1696692	0.9277062	0.6621435	0.3834433	0.0903480	9.803417	9.506190
(2)	1.4027927	1.2432650	1.0314940	0.7972120	0.5502712	0.2951892	0.034423	9.769458
(3)	1.4555562	1.3200910	1.1362230	0.9310441	0.7137138	0.1885900	0.257924	0.023173
(4)	1.5034004	1.3861666	1.2238991	1.0111088	0.8472914	0.6455891	0.438538	0.227507
(5)	1.5364016	1.4305298	1.2819644	1.1139519	0.9316705	0.7480006	0.556101	0.360300
(6)	1.5498120	1.4488473	1.3062644	1.1445968	0.9718291	0.7917660	0.606530	0.417430
(7)	1.5451323	1.4435820	1.3002829	1.1378550	0.9643061	0.7834509	0.597416	0.407512
(8)	1.5265722	1.4196521	1.2698138	1.1004533	0.9197890	0.7317170	0.538404	0.341181
(9)	1.4973136	1.3802705	1.2182313	1.0359816	0.8421106	0.6406580	0.433858	0.223080
(10)	1.4593335	1.3269407	1.1466825	0.9452851	0.7318431	0.5105897	0.283850	0.053040
(11)	1.4157066	1.2625773	1.0581661	0.8315406	0.5923880	0.3451647	0.092299	9.835263
(12)	1.3720482	1.1942518	0.9616773	0.7058210	0.4369662	0.1597897	9.876821	9.589585
(13)	1.3355199	1.1334325	0.8736169	0.5896429	0.2922887	9.9864116	9.674623	9.358490
(14)	1.3126565	1.0936651	0.8151341	0.5119170	0.1950921	9.8696250	9.538176	9.202338
(15)	1.3078152	1.0859160	0.8041835	0.4976800	0.1775323	9.8487234	9.513921	9.174723

ε	$\log \beta_{\nu}^{(3)}$	$\log \beta_{9}^{(3)}$	$\log \beta_{10}^{(3)}$	$\log \beta_{11}^{(3)}$	$\log \beta_{12}^{(3)}$	$\log \beta_{13}^{(3)}$	$\log \beta_{14}^{(3)}$	$\log \beta_{15}^{(3)}$	$\log \beta_{16}^{(3)}$
(0)	8.960228	8.62962	8.29687	7.96235	7.62634	7.28906	6.9507	6.6111	6.2712
(1)	9.205669	8.90254	8.59729	8.29030	7.98182	7.67210	7.3613	7.0495	6.7369
(2)	9.501265	9.23051	8.95768	8.68312	8.40711	8.12985	7.8515	7.5723	7.2922
(3)	9.785271	9.54486	9.30241	9.05827	8.81270	8.56591	8.3181	8.0693	7.8197
(4)	0.013398	9.79684	9.57827	9.35804	9.13611	8.913573	8.6897	8.4649	8.2393
(5)	0.161475	9.96024	9.75702	9.55217	9.34593	9.138499	8.9300	8.7207	8.5105
(6)	0.225332	0.03084	9.83439	9.63630	9.43684	9.236198	9.0345	8.8320	8.6286
(7)	0.214606	0.01930	9.82204	9.62315	9.42287	9.221411	9.0189	8.8155	8.6114
(8)	0.140929	9.93826	9.73361	9.52732	9.31965	9.110777	8.9009	8.6901	8.4785
(9)	0.009223	9.79291	9.57461	9.35463	9.13325	8.910672	8.6870	8.4625	8.2372
(10)	9.819091	9.58264	9.34416	9.10399	8.86240	8.61958	8.3757	8.1309	7.8853
(11)	9.575016	9.31222	9.04736	8.78078	8.51275	8.24348	7.9731	7.7019	7.4298
(12)	9.299073	9.00597	8.71075	8.41380	8.11537	7.81570	7.5149	7.2132	6.9107
(13)	9.039030	8.71694	8.39271	8.06672	7.73025	7.41051	7.0807	6.7499	6.4183
(14)	8.863141	8.52129	8.17729	7.83152	7.48124	7.13570	6.7861	6.4355	6.0840
(15)	8.832162	8.48694	8.13957	7.79042	7.43978	7.08786	6.7348	6.3809	6.0260

ε	$\log \beta_{0}^{(5)}$	$\log \beta_{1}^{(5)}$	$\log \beta_{2}^{(5)}$	$\log \beta_{3}^{(5)}$	$\log \beta_{4}^{(5)}$	$\log \beta_{5}^{(5)}$	$\log \beta_{6}^{(5)}$	$\log \beta_{7}^{(5)}$	$\log \beta_{\nu}^{(5)}$
(0)	8.5913	8.5059	8.343592	8.13836	7.9059	7.6546	7.38956	7.11402	6.8302
(1)	8.6697	8.5978	8.456245	8.27161	8.0671	7.8416	7.60279	7.35383	7.0968
(2)	8.7789	8.7214	8.603186	8.44857	8.2700	8.0744	7.86621	7.61833	7.4227
(3)	8.8999	8.8545	8.756837	8.62666	8.4745	8.3065	8.12671	7.93764	7.7412
(4)	9.0090	8.9720	8.889564	8.77787	8.6459	8.4993	8.34140	8.17475	8.0010
(5)	9.0846	9.0525	8.979151	8.87925	8.7600	8.6268	8.48288	8.33049	8.1713
(6)	9.1166	9.0865	9.017411	8.92216	8.8085	8.6811	8.54324	8.39710	8.2442
(7)	9.1078	9.0773	9.007729	8.91189	8.7975	8.6695	8.53088	8.38399	8.2304
(8)	9.0663	9.0337	8.959778	8.85852	8.7381	8.6036	8.45842	8.30471	8.1441
(9)	8.9992	8.9622	8.879992	8.76849	8.6368	8.4903	8.33269	8.16628	7.9928
(10)	8.9109	8.8669	8.771841	8.64178	8.4960	8.3316	8.15546	7.97013	7.7775
(11)	8.8087	8.7545	8.611795	8.49368	8.3221	8.1338	7.93312	7.72281	7.5048
(12)	8.7059	8.6387	8.504115	8.33127	8.1328	7.9166	7.68732	7.44800	7.2007
(13)	8.6196	8.5386	8.382798	8.18494	7.9602	7.7170	7.46008	7.19280	6.9173
(14)	8.5659	8.4747	8.303687	8.08866	7.8459	7.5840	7.30813	7.02169	6.7269
(15)	8.5553	8.4623	8.288655	8.07068	7.8248	7.5597	7.28061	6.99090	6.6928

ε	$\log \beta_{9}$	$\log \beta_{10}$	$\log \beta_{11}^{0}$	$\log \beta_{12}$	$\log \beta_{13}^{0}$	$\log \beta_{14}^{0}$	$\log \beta_{15}$
(0)	6.5397	6.2438	5.9432	5.639	.....	5.020	4.706
(1)	6.8332	6.5613	6.2910	6.014	5.733	5.449	5.161
(2)	7.1907	6.9536	6.71200	6.467	6.218	5.967	5.7127
(3)	7.5387	7.3311	7.11931	6.901	6.685	6.464	6.24014
(4)	7.8215	7.6370	7.448632	7.257	7.062	6.864	6.66353
(5)	8.0064	7.8369	7.663275	7.486	7.306	7.124	6.93850
(6)	8.0859	7.9227	7.755715	7.585	7.412	7.236	7.05746
(7)	8.0712	7.9073	7.739511	7.568	7.394	7.217	7.03807
(8)	7.9779	7.8070	7.632007	7.451	7.272	7.088	6.90161
(9)	7.8135	7.6294	7.441140	7.249	7.055	6.857	6.65701
(10)	7.5788	7.3751	7.16718	6.956	6.741	6.523	6.30364
(11)	7.2806	7.0513	6.81750	6.580	6.339	6.096	5.8499
(12)	6.9469	6.6879	6.4244	6.157	5.886	5.613	5.337
(13)	6.6352	6.3476	6.0554	5.759	.....	5.157	4.853
(14)	6.4254	6.1183	5.8066	5.491	....	4.850	4.525
(15)	6.3879	6.0776	5.7626	5.441	.....	4.796	4.468

Each β_{i}^{n} was multiplied by sine and cosine $i\,(\mathrm{F}-\varepsilon)$ for each of its sixteen special values, the products $\beta_{i}^{n}\sin i\,(\mathrm{F}-\varepsilon)$ and $\beta_{i}^{n}\cos i\,(\mathrm{F}-\varepsilon)$ then being developed in series proceeding according to sines and cosines of multiples of ε.

From these followed immediately $\{\mathrm{D}-f\cos(\varepsilon'-\mathrm{F})\}^{-\frac{n}{2}}$ developed in series proceeding according to sines and cosines of $i\varepsilon - i'\varepsilon'$, and by the following formulas, the desired negative odd powers of the distance between the planets.

$$\left(\frac{a}{\Delta}\right) = \frac{1}{\{\mathrm{D}-f\cos(\varepsilon'-\mathrm{F})\}^{\frac{1}{2}}} - \frac{\frac{1}{4}\gamma_2\cos 2\,\varepsilon'}{\{\mathrm{D}-f\cos(\varepsilon'-\mathrm{F})\}^{\frac{3}{2}}}$$

$$\left(\frac{a}{\Delta}\right)^3 = \frac{1}{\{\mathrm{D}-f\cos(\varepsilon'-\mathrm{F})\}^{\frac{3}{2}}} - \frac{\frac{3}{4}\gamma_2\cos 2\,\varepsilon'}{\{\mathrm{D}-f\cos(\varepsilon'-\mathrm{F})\}^{\frac{5}{2}}}$$

ε	ε	$\frac{m'}{\sin 1}\left(\frac{a}{\Delta}\right)$ cos	$\frac{m'}{\sin 1}\left(\frac{a}{\Delta}\right)$ sin	$\frac{m}{\sin 1}\alpha^2\left(\frac{a}{\Delta}\right)^3$ cos	$\frac{m}{\sin 1}\alpha^2\left(\frac{a}{\Delta}\right)^3$ sin
0	0	+112.8189		+220.1549	
1		− 2.82716	+ 1.81880	− 51.58872	+ 32.12936
2		− 0.31188	+ 1367	− 0.7361	− 3.6467
3		+ 336	− 366	+ 0.713	− 0.141
4		+ 2	+ 35	− 25	+ 0.143
5	0	− 3	+ 1	− 11	− 8
− 5	− 1	− 1	0	− 2	+ 2
− 4		0	− 4	− 16	− 16
− 3		+ 66	+ 2	+ 0.203	− 26
− 2		− 588	+ 429	− 0.419	+ 0.814
− 1		− 323	− 0.1625	− 7.152	+ 0.619
0		+ 7.5824	− 9.5098	+ 57.321	− 71.118
1		− 7.8240	+60.9888	− 39.901	+312.054
2		− 0.6029	− 1.1168	− 16.083	− 33.204
3	− 1	− 187	− 0.2397	+ 1.933	− 1.298

ε	ε	$\frac{m'}{\sin 1}\left(\frac{a}{\Delta}\right)$ cos	$\frac{m'}{\sin 1}\left(\frac{a}{\Delta}\right)$ sin	$\frac{m}{\sin 1}\alpha^2\left(\frac{a}{\Delta}\right)^3$ cos	$\frac{m}{\sin 1}\alpha^2\left(\frac{a}{\Delta}\right)^3$ sin
4	— 1	+ 201	+ 230	+ 0.338	+ 0.577
5		— 18	+ 3	— 93	— 20
6	— 1	— 1	— 2	+ 4	— 8
— 4	— 2	0	0	— 3	— 2
— 3		+ 6	— 4	+ 24	— 26
— 2		— 8	+ 113	+ 23	+ 0.256
— 1		— 326	— 604	— 0.886	— 0.044
0		— 0.1388	— 0.7751	— 1.775	— 12.999
1		+ 6.3962	+ 6.5813	+ 62.649	+ 64.867
2		— 23.6868	— 6.1698	—193.673	— 50.261
3		+ 0.4597	— 0.2238	+ 19.987	— 7.271
4		+ 0.1577	+ 31	+ 1.314	+ 1.139
5		— 147	+ 102	— 0.435	+ 0.217
6		— 3	— 9	+ 14	— 58
7	— 2	+ 1	— 1	+ 5	+ 2
— 3	— 3	+ 1	— 1	+ 1	— 5
— 2		+ 9	+ 10	+ 37	+ 35
— 1		— 138	— 30	— 0.263	+ 33
0		— 74	+ 107	— 0.795	— 1.144
1		+ 1.0201	— 912	+ 16.503	— 0.950
2		— 4.7291	+ 3.5510	— 59.289	+ 44.349
3		+ 4.0010	— 9.9734	+ 44.850	—112.263
4		+ 940	+ 0.1886	+ 3.009	+ 11.491
5		— 126	+ 963	— 0.755	+ 1.082
6		— 49	— 576	— 0.123	— 0.309
7		+ 5	— 3	+ 35	+ 9
8	— 3	+ 1	+ 1	— 1	+ 4
— 2	— 4	+ 1	+ 1	+ 8	+ 1
— 1		— 17	+ 12	— 44	+ 11
6		+ 11	— 102	— 0.100	— 0.206
1		+ 594	— 601	+ 1.592	— 1.548
2		— 279	+ 0.9524	— 0.848	+ 16.693
3		— 1.7688	— 3.1109	— 27.074	— 17.740
4		+ 4.3132	+ 2.3987	+ 62.040	+ 34.336
5		— 759	+ 161	— 6.384	+ 1.124
6		— 560	— 140	— 0.792	— 0.540
7		+ 52	— 22	+ 0.208	— 61
8		+ 2	+ 3	— 5	+ 21
9	— 4	— 1	0	— 3	0
— 1	— 5	0	+ 2	— 1	+ 11
0		— 13	— 18	— 46	— 12
1		+ 550	— 112	+ 0.1322	— 0.2202
2		— 7811	+ 7789	+ 1.8882	+ 2.0282
3		— 0.71998	— 0.11212	— 11.5604	— 2.4825
4	— 5	+ 1.9355	— 0.7959	+ 35.280	— 11.489

ε	ε	$\frac{m}{\sin 1}\left(\frac{a}{J}\right)$ cos	$\frac{m}{\sin 1}\left(\frac{a}{J}\right)$ sin	$\frac{m}{\sin 1}\alpha\left(\frac{a}{J}\right)$ cos	$\frac{m}{\sin 1}\alpha\left(\frac{a}{J}\right)$ sin
5	− 5	− 1.3752	+ 1.8753	− 24.025	+ 32.952
6		− 263	− 299	− 0.368	− 3.455
7		+ 119	− 313	+ 0.396	− 0.535
8		+ 9	+ 29	+ 26	+ 0.135
9	− 5	− 2	+ 2	− 12	− 3
0	− 6	− 4	0	− 13	− 1
1		+ 14	− 12	− 28	− 17
2		+ 95	+ 26	+ 0.348	+ 86
3		− 846	+ 713	− 2.281	+ 1.808
4		+ 0.1445	− 0.5015	+ 3.422	− 11.430
5		+ 0.2120	+ 1.1562	+ 6.606	+ 24.470
6		− 0.8096	− 0.7647	− 16.863	− 15.819
7		+ 117	− 165	+ 1.836	− 0.100
8		+ 169	+ 89	+ 0.340	+ 0.288
9		− 17	+ 4	− 84	+ 8
10	− 6	− 1	− 1	+ 1	− 7
0	− 7	0	0	− 2	+ 1
1		+ 1	− 3	0	− 13
2		+ 12	+ 5	+ 51	+ 6
3		− 20	+ 128	− 81	+ 110
4		− 536	− 797	− 1.464	− 2.292
5		+ 0.3246	+ 0.1400	+ 8.274	+ 3.644
6		− 0.6688	+ 0.0925	− 16.147	+ 2.241
7		+ 0.4155	− 0.3436	+ 9.957	− 8.303
8		+ 107	+ 48	+ 0.021	+ 0.963
9		− 61	+ 89	− 0.204	+ 0.205
10		− 1	− 9	+ 1	− 51
11	− 7	+ 1	− 1	+ 5	0
1	− 8	0	0	− 1	− 2
2		+ 31	+ 3	+ 120	− 14
3		+ 18	+ 130	+ 140	+ 580
4		− 1362	− 253	− 0.4750	− 0.1052
5		+ 678	− 349	+ 2.099	− 1.030
6		− 0.1171	+ 0.1982	− 3.355	+ 5.604
7		− 0.0043	− 0.3764	− 0.129	− 10.224
8		+ 0.1418	+ 0.2215	+ 3.913	+ 6.050
9		− 22	+ 70	− 0.503	+ 0.007
10		− 15	− 40	− 0.117	− 0.140
11	− 8	+ 5	0	+ 30	+ 3
2	− 9	− 1	0	+ 2	− 2
3		0	+ 2	+ 4	+ 10
4		− 15	+ 6	− 66	+ 28
5		+ 34	− 125	+ 0.138	− 0.456
6		+ 197	+ 534	+ 0.627	+ 1.780
7	− 9	− 0.1150	− 893	− 3.579	− 2.804

ε	ε'	$\frac{m'}{\sin 1''}\left(\frac{a}{\Delta}\right)^3$ cos	$\frac{m'}{\sin 1''}\left(\frac{a}{\Delta}\right)^3$ sin	$\frac{m'}{\sin 1''}\alpha^2\left(\frac{a}{\Delta}\right)^3$ cos	$\frac{m'}{\sin 1''}\alpha^2\left(\frac{a}{\Delta}\right)^3$ sin
8	— 9	+ 0.2067	+ 236	+ 6.247	+ 0.704
9		— 0.1162	+ 560	— 3.570	+ 1.745
10		— 45	— 12	— 8	— 0.265
11		+ 25	— 22	+ 94	— 64
12	— 9	0	+ 2	— 3	+ 17
3	—10	0	0	+ 2	+ 2
4		— 2	+ 1	— 8	+ 7
5		— 8	— 16	— 32	— 73
6		+ 101	+ 10	+ 0.398	+ 0.163
7		— 394	+ 93	— 1.418	+ 0.315
8		+ 637	— 636	+ 2.182	— 2.163
9		— 270	+ 0.1110	— 0.891	+ 3.697
10		— 206	— 601	— 0.720	— 2.051
11		+ 8	— 28	+ 0.141	— 10
12		+ 11	+ 15	+ 33	+ 61
13	—10	— 1	0	— 10	— 3
4	—11	— 3	+ 5	— 13	+ 20
5		— 16	— 15	— 95	— 71
6		+ 164	— 73	+ 748	— 302
7		— 41	+ 79	— 0.174	+ 0.321
8		— 29	— 277	— 0.103	— 1.069
9		+ 331	+ 433	+ 1.235	+ 1.606
10		— 583	— 221	— 2.124	— 0.800
11		+ 306	— 67	+ 1.157	— 0.261
12		+ 17	+ 6	+ 11	+ 77
13		— 9	+ 4	— 39	+ 16
14	—11	0	— 1	+ 2	— 5
4	—12	— 1	+ 3	+ 4	+ 19
5		— 26	— 20	— 190	— 85
6		+ 128	— 204	+ 697	— 1099
7		+ 53	+ 152	+ 230	+ 724
8		— 56	— 38	— 0.243	— 0.169
9		+ 186	+ 3	+ 0.770	+ 0.021
10		— 282	+ 166	— 1.130	+ 0.663
11		+ 158	— 299	+ 0.622	— 1.185
12		+ 16	+ 154	+ 69	+ 0.639
13		— 4	+ 10	— 43	+ 8
14		— 2	— 5	— 7	— 24
15	—12	0	0	+ 3	+ 2
4	—13	+ 8	— 6	+ 41	— 41
5		— 29	+ 14	— 164	+ 106
6		+ 78	— 371	+ 353	— 2065
7		+ 214	+ 121	+ 1113	+ 711
8		— 133	+ 33	— 658	+ 116
9	—13	+ 33	— 38	+ 0.153	— 0.172

ε	ε	$\frac{m}{\sin 1}\left(\frac{a}{\Delta}\right)^{7}$ cos	$\frac{m}{\sin 1}\left(\frac{a}{\Delta}\right)^{7}$ sin	$\frac{m}{\sin 1}\alpha\left(\frac{a}{\Delta}\right)^{7}$ cos	$\frac{m}{\sin 1}\alpha\left(\frac{a}{\Delta}\right)^{7}$ sin
10	−13	− 17	+ 120	− 0.081	+ 0.531
11		− 77	− 178	− 0.329	− 0.765
12		+ 150	+ 105	+ 0.613	+ 0.445
13		− 77	− 1	− 0.346	− 1
14		− 6	− 3	− 6	− 25
15	−13	+ 3	− 1	+ 14	− 3
6	−14	+ 2	− 3	− 13	− 13
7		+ 4	0	+ 22	+ 1
8		− 1	+ 2	− 8	+ 11
9		− 2	− 11	− 7	− 56
10		+ 24	+ 26	+ 0.115	+ 0.129
11		− 75	− 21	− 0.353	− 0.099
12		+ 109	− 32	+ 0.500	− 0.146
13		− 66	+ 74	− 0.298	+ 0.339
14		+ 5	− 38	+ 17	− 0.184
15		+ 2	− 3	+ 17	− 6
16	−14	0	+ 2	0	+ 9
8	−15	0	0	0	+ 2
9		− 2	− 1	− 9	− 7
10		+ 9	0	+ 16	− 1
11		− 20	+ 14	− 0.104	+ 72
12		+ 19	− 45	+ 0.095	− 0.226
13		+ 10	+ 65	+ 0.052	+ 0.318
14		− 35	− 40	− 0.173	− 0.193
15		+ 18	+ 4	+ 97	+ 19
16		+ 2	+ 2	+ 3	+ 10
17	−15	− 1	0	− 6	0
9	−16			− 2	0
10				+ 7	− 8
11				− 4	+ 36
12				− 42	− 80
13				+ 0.140	+ 80
14				− 0.197	+ 8
15				+ 0.121	− 85
16				− 15	+ 50
17				− 6	+ 2
18	−16			0	− 3

Before forming the derivatives of the perturbative function, ε' of the preceding series was replaced by g' by means of the Besselian transformation, and the following quantities computed:

$$\frac{1}{2}\left(\frac{r'}{a'}\right)^2-\frac{1}{2\alpha^2}\left(\frac{r}{a}\right)^2=[9.5566691]+2\,[8.294341]\cos\varepsilon-2\,[6.84032]\cos 2\,\varepsilon$$
$$-2\,[8.382387]\cos(-g')-2\,[6.46366]\cos(-2g')-2\,[4.8459]\cos(-3g')$$
$$-\frac{\sin J}{\alpha}\left(\frac{r'}{a'}\right)\sin(f'+H')=[7.19762]-2\,[8.036580]\cos(-g')-2\,[6.41880]\cos(-2g')$$
$$-2\,[4.9774]\cos(-3g')$$
$$+2\,[8.590096]\sin(-g')+2\,[6.97240]\sin(-2g')+2\,[5.5308]\sin(-3\,g')$$

where the numbers in brackets are the logarithms of the coefficients.

		(H)		(J)	
ε	g	cos	sin	sin	cos
−1	−1	+ 938	− 406		
0		+0.9631	− 7.5921	−8.108	+2.267
1	−1	−6.9429	+54.0322		
−1	−2	+ 91	− 34		
0		+ 929	− 0.7324	−0.782	+0.219
1	−2	−0.6697	+ 5.2116		
−1	−3	+ 7	− 3		
0		+ 76	− 596	− 64	+ 18
1	−3	− 545	+ 0.4211		
−1	−4	+ 1	0		
0		+ 6	− 45	− 5	+ 1
1	−4	− 42	+ 323		
0	−5	0	− 3		
1	−5	− 31	+ 238		
1	−6	0	+ 2		

The required derivatives were then formed according to the equations

$$(i)\quad a\Omega=i\left[\frac{m'}{\sin 1''}\left(\frac{a}{\Delta}\right)-(\mathrm{H})\right]$$
$$ar\left(\frac{d\Omega}{dr}\right)=\left\{\frac{m'}{\sin 1''}a^2\left(\frac{a}{\Delta}\right)^3\right\}\left\{\frac{1}{2}\left(\frac{r'}{a'}\right)^2-\frac{1}{2a^2}\left(\frac{r}{a}\right)^2\right\}-\frac{1}{2}\frac{m'}{\sin 1''}\left(\frac{a}{\Delta}\right)-(\mathrm{H})$$
$$a^2\left(\frac{d\Omega}{dz}\right)=\left\{\frac{m'}{\sin 1''}a^2\left(\frac{a}{\Delta}\right)^3\right\}\left\{-\frac{\sin J}{\alpha}\left(\frac{r'}{a'}\right)\sin(f'+H')\right\}+(\mathrm{J})$$

Before integrating, these series were transformed so that the arguments should contain but the single independent variable ε. In this form they are, the argument being $[(i-i'\mu)\varepsilon - i'(g'-\mu g)]$.

i	i'	$(c)\, a\Omega$ cos	$(c)\, a\Omega$ sin	$ar\left(\frac{d\Omega}{dr}\right)$ cos	$ar\left(\frac{d\Omega}{dr}\right)$ sin	$a^2\left(\frac{d\Omega}{dz}\right)$ cos	$a^2\left(\frac{d\Omega}{dz}\right)$ sin
0	0			+20.1296		— 3.0350	"
1		— 2.63761	+ 0.34337	— 7.02664	+ 1.31628	+12.55825	—1.99613
2		— 0.5918	+ 0.1433	— 1.0282	+ 0.2041	— 1.0857	+0.7801
3		+ 0.102	— 92	+ 0.211	— 0.179	— 62	— 38
4		— 1	+ 12	— 5	+ 25	+ 18	— 18
5	0	— 2	0	— 2	+ 1	0	+ 3
— 4	— 1	+ 1	+ 2	— 2	— 3	+ 7	0
— 3		— 23	+ 2	+ 56	— 11	— 22	+ 23
— 2		+ 0.113	— 87	— 0.275	+ 0.254	— 0.175	— 20
— 1		+ 0.125	+ 0.101	— 0.357	— 0.332	+ 1.898	—1.854
0		+ 0.036	— 0.177	+ 4.161	— 7.238	— 3.044	+9.101
1		— 1.212	+ 6.613	— 3.595	+22.113	+ 1.583	—4.877
2		+ 1.042	— 1.432	+ 0.923	— 2.552	+ 0.165	+7.860
3		— 85	— 0.756	— 0.125	— 1.124	— 0.251	—0.428
4		+ 48	+ 72	+ 85	+ 0.136	0	— 70
5		— 5	+ 2	— 9	+ 1	+ 11	+ 12
6	— 1	— 1	— 2	— 1	— 2	— 2	0
— 3	— 2	— 2	+ 2	+ 5	— 9	0	+ 10
— 2		+ 2	— 27	+ 5	+ 96	— 30	— 6
— 1		+ 52	+ 63	— 0.172	— 0.255	— 36	—0.464
0		— 0.433	— 169	— 1.391	— 1.290	+ 2.787	+2.946
1		+ 9.291	+ 3.521	+19.003	+ 8.696	—11.607	—5.707
2		—46.130	—12.762	—52.256	—14.672	+ 2.916	+1.925
3		— 2.053	+ 0.758	— 1.902	+ 0.736	— 4.537	—0.501
4		+ 0.602	+ 42	+ 0.842	+ 42	+ 90	— 70
5		— 36	+ 16	— 66	+ 30	+ 59	— 3
6		— 3	+ 21	— 4	— 4	— 7	+ 6
7	— 2	+ 1	0	+ 1	— 1	0	— 1
— 3	— 3	0	0	0	— 2	+ 2	+ 2
— 2		— 3	— 4	+ 16	+ 12	— 10	0
— 1		+ 21	+ 5	— 98	— 12	— 18	— 55
0		— 0.119	+ 35	— 0.222	— 81	+ 0.917	+ 40
1		+ 2.341	— 0.743	+ 4.726	— 1.660	— 1.134	+1.900
2		—12.513	+ 8.577	—16.377	+14.073	+ 4.737	—6.711
3		+11.582	—28.183	+12.728	—30.478	— 1.704	+1.600
4		— 0.236	— 2.546	— 0.186	— 2.635	+ 0.590	—2.173
5		— 0.119	+ 0.111	— 0.137	+ 0.524	+ 24	— 47
6		— 5	— 0.296	— 9	+ 3	— 1	+ 41
7	— 3	+ 1	— 27	+ 1	— 3	— 2	— 1
— 2	— 4	0	0	+ 4	0	— 3	+ 2
— 1		+ 4	— 2	— 19	+ 18	— 10	— 7
0		— 20	+ 21	— 20	— 11	+ 0.131	—0.110
1	— 4	+ 0.214	— 0.397	+ 0.402	— 0.728	— 0.318	+1.112

i	i'	$(i)\,a\Omega$		$ar\left(\frac{d\Omega}{dr}\right)$		$a^2\left(\frac{d\Omega}{dz}\right)$	
		cos	sin	cos	sin	cos	sin
2	− 4	− 0.″299	+ 3.558	+ 0.′279	+ 5.′732	− 1.013	−3.″611
3		− 5.916	−12.054	− 8.763	−14.624	+ 3.506	+3.477
4		+15.506	+ 8.690	+16.284	+ 9.269	− 0.775	−1.275
5		+ 2.208	+ 0.204	+ 2.316	+ 0.266	+ 1.288	+0.471
6		− 0.205	− 0.152	− 0.276	− 0.148	+ 81	+ 20
7		− 5	− 5	− 2	− 4	− 25	− 4
8	− 4	+ 3	+ 1	+ 4	0	+ 1	− 1
− 1	− 5	0	0	0	+ 6	− 3	− 1
0		0	+ 6	− 16	− 15	+ 7	− 27
1		− 243	− 715	− 18	− 0.1104	+ 0.1287	+0.2128
2		+ 0.52833	− 0.51767	+ 0.9518	+ 0.7619	− 1.0419	−0.4869
3		− 3.7868	− 0.9772	− 5.4622	− 0.7312	+ 2.7446	−0.3318
4		+ 9.636	− 3.202	+11.207	− 4.582	− 2.338	+1.662
5		− 5.743	+ 7.949	− 5.988	+ 8.161	+ 0.860	−0.320
6		− 0.412	+ 1.614	− 0.473	+ 1.689	− 0.318	+0.646
7		+ 0.106	− 80	+ 0.120	− 0.116	− 22	+ 72
8		+ 4	− 10	+ 4	− 9	+ 4	− 14
9	− 5	− 2	+ 2	− 1	+ 2	+ 1	0
0	− 6	0	+ 1	− 6	0	0	− 4
1		− 11	− 5	0	− 18	+ 46	+ 13
2		+ 0.141	− 12	+ 0.218	− 17	− 0.266	+0.112
3		− 0.775	+ 0.542	− 1.046	+ 0.932	+ 0.355	−0.830
4		+ 1.392	− 3.279	+ 1.357	− 4.141	− 0.660	+1.897
5		+ 1.338	+ 6.871	+ 1.965	+ 7.770	− 0.697	−1.472
6		− 3.852	− 3.166	− 3.877	− 3.544	+ 0.099	+0.538
7		− 1.060	− 0.444	− 1.100	− 0.491	− 0.344	−0.194
8		+ 13	+ 70	+ 30	+ 80	− 53	− 22
9		+ 9	+ 6	+ 10	+ 6	+ 6	+ 3
10	− 6	− 1	0	− 1	0	0	+ 1
0	− 7	0	0	− 1	+ 1	0	− 1
1		− 2	+ 1	− 2	− 5	+ 8	− 3
2		+ 16	− 19	+ 28	− 21	− 23	+ 59
3		− 22	+ 0.203	− 10	+ 0.301	− 71	−0.279
4		− 0.434	− 0.896	− 0.736	− 1.157	+ 0.586	+0.533
5		+ 2.480	+ 1.489	+ 3.226	+ 1.552	− 1.219	−0.226
6		− 4.518	+ 0.310	− 5.005	+ 0.580	+ 0.878	−0.237
7		+ 1.942	− 1.779	+ 1.950	− 1.758	− 0.316	+0.006
8		+ 0.382	− 0.611	+ 0.413	− 0.659	+ 0.109	−0.148
9		− 39	− 14	− 45	− 7	+ 18	− 34
10		− 5	+ 7	− 6	+ 7	− 3	+ 3
11	− 7	0	0	+ 1	− 1	− 1	0
1	− 8	0	0	− 1	− 1	+ 1	− 1
2		− 3	− 43	+ 36	− 46	+ 46	+ 119
3		+ 2670	+ 3059	+ 367	+ 138	− 628	− 314
4	− 8	− 0.2332	− 657	− 0.3359	− 587	+ 0.2564	− 275

i	i	$(i)a\Omega$ cos	$(i)a\Omega$ sin	$ar\left(\frac{d\Omega}{dr}\right)$ cos	$ar\left(\frac{d\Omega}{dr}\right)$ sin	$a^2\left(\frac{d\Omega}{dz}\right)$ cos	$a^2\left(\frac{d\Omega}{dz}\right)$ sin
5	— 8	+ 0.881	— 0.275	+ 1.104	— 0.483	— 0.454	+0.372
6		— 1.353	+ 1.694	— 1.442	+ 2.144	+ 0.255	—0.737
7		+ 0.144	— 2.787	+ 0.032	— 3.040	+ 40	+0.498
8		+ 0.791	+ 1.003	+ 0.767	+ 1.002	+ 24	—0.177
9		+ 0.363	+ 0.286	+ 0.369	+ 0.308	+ 68	+ 58
10		+ 23	— 18	+ 20	— 20	+ 20	+ 15
11	— 8	— 2	— 5	— 4	— 5	0	— 1
2	— 9	— 1	0	0	— 1	+ 2	+ 1
3		+ 8	0	+ 10	+ 3	— 15	+ 4
4		— 46	+ 28	— 61	+ 42	+ 42	— 57
5		+ 0.104	— 0.229	+ 0.106	— 0.321	— 8	+0.214
6		+ 0.126	+ 0.770	+ 0.256	+ 0.945	— 0.214	—0.356
7		— 1.063	— 1.100	— 1.323	— 1.182	+ 0.421	+0.222
8		+ 1.636	+ 0.275	+ 1.759	+ 0.230	— 0.271	— 28
9		— 0.500	+ 0.312	— 0.484	+ 0.328	+ 94	+ 28
10		— 0.200	+ 0.190	— 0.210	+ 0.194	— 29	+ 31
11		+ 6	+ 36	+ 7	+ 19	— 10	+ 11
12	— 9	+ 2	+ 3	+ 4	— 1	+ 1	— 2
3	—10	+ 10	— 12	+ 2	0	— 1	+ 3
4		— 22	+ 106	— 4	+ 14	— 3	— 17
5		— 251	— 564	— 40	— 74	+ 47	+ 46
6		+ 0.198	+ 0.128	+ 0.274	+ 0.138	— 0.164	— 30
7		— 0.615	+ 0.016	— 0.714	+ 0.092	+ 0.259	—0.108
8		+ 0.824	— 0.609	+ 0.887	— 0.761	— 0.169	+0.228
9		— 0.262	+ 0.920	— 0.243	+ 0.974	+ 42	—0.141
10		— 0.149	— 0.229	— 0.142	— 0.212	— 22	+ 48
11		— 97	— 0.128	— 96	— 0.136	— 15	— 14
12		— 14	— 3	— 15	0	— 7	— 6
13	—10	0	+ 2	+ 1	+ 2	0	0
4	—11	+ 2	+ 2	0	+ 3	— 3	— 3
5		— 13	— 6	— 18	— 6	+ 17	— 1
6		+ 61	— 16	+ 79	— 30	— 44	+ 34
7		— 0.132	+ 0.156	— 0.118	+ 0.212	+ 40	—0.117
8		+ 0.048	— 0.457	+ 0.009	— 0.546	+ 47	+0.178
9		+ 0.333	+ 0.580	+ 0.410	+ 0.621	— 0.116	—0.118
10		— 0.495	— 0.197	— 0.519	— 0.190	+ 70	+ 36
11		+ 95	— 68	+ 84	— 65	— 24	— 14
12		+ 80	— 45	+ 82	— 44	+ 6	— 7
13		+ 2	— 11	+ 1	— 10	+ 4	— 3
14	—11	— 1	— 1	— 1	+ 1	0	— 1
5	—12	— 2	+ 2	— 4	+ 2	+ 3	— 4
6		+ 8	— 14	+ 8	— 19	— 2	+ 17
7		+ 8	+ 59	+ 17	+ 75	— 22	— 39
8		— 0.110	— 0.126	— 0.151	— 0.110	+ 80	+ 40
9	—12	+ 0.321	+ 0.075	+ 0.378	+ 0.058	— 0.117	+ 13

i	i'	$(i)a\Omega$ cos	$(i)a\Omega$ sin	$ar\left(\frac{d\Omega}{dr}\right)$ cos	$ar\left(\frac{d\Omega}{dr}\right)$ sin	$a^2\left(\frac{d\Omega}{dz}\right)$ cos	$a^2\left(\frac{d\Omega}{dz}\right)$ sin
10	−12	− 0.″386	+ 0.″165	− 0.″412	+ 0.″204	+ ″ 77	− ″ 56
11		+ 0.132	− 0.256	+ 0.130	− 0.268	− 25	+ 33
12		+ 34	+ 34	+ 34	+ 28	+ 8	− 11
13		+ 20	+ 46	+ 19	+ 46	+ 3	+ 7
14		+ 6	+ 4	+ 6	+ 4	+ 1	+ 3
15	−12	− 1	− 1	+ 1	0	0	+ 1
4	−13	+ 60	− 48	+ 130	− 19	− 142	+ 147
5		− 184	+ 544	− 312	+ 625	− 28	− 1006
6		− 863	− 3329	− 1445	− 4212	+ 2886	+ 3344
7		+ 1276	+ 930	+ 1756	+ 1023	− 1414	− 331
8		− 533	− 11	− 665	+ 53	+ 325	− 128
9		+ 0.111	− 73	+ 0.122	− 99	− 35	+ 51
10		− 0.078	+ 0.213	− 0.072	+ 0.249	+ 2	− 73
11		− 0.071	− 0.215	− 0.092	− 0.260	+ 24	+ 47
12		+ 0.130	+ 83	+ 0.134	+ 80	− 14	− 16
13		− 10	+ 20	− 7	+ 20	+ 5	+ 5
14		− 28	+ 8	− 26	+ 6	− 1	+ 2
15	−13	− 4	+ 2	− 4	+ 4	− 2	0

If we designate the preceding series by

$$(i)\ a\Omega = \Sigma\Sigma\, b\,(i,i',c)\cos\left[(i-i'\mu)\,\varepsilon - i'(g'-\mu g)\right] + \Sigma\Sigma\, b\,(i,i',s)\sin\left[(i-i'\mu)\,\varepsilon - i'(g'-\mu g)\right]$$

$$ar\left(\frac{d\Omega}{dr}\right) = \Sigma\Sigma\, c\,(i,i',c)\cos\left[(i-i'\mu)\,\varepsilon - i'(g'-\mu g)\right] + \Sigma\Sigma\, c\,(i,i',s)\sin\left[(i-i'\mu)\,\varepsilon - i'(g'-\mu g)\right]$$

$$a^2\left(\frac{d\Omega}{dz}\right) = \Sigma\Sigma\, d\,(i,i',c)\cos\left[(i-i'\mu)\,\varepsilon - i'(g'-\mu g)\right] + \Sigma\Sigma\, d\,(i,i',s)\sin\left[(i-i'\mu)\,\varepsilon - i'(g'-\mu g)\right]$$

F, G, H, T, U, and V were first computed by the formulas

$$\begin{aligned}
G\,(i,i',\tfrac{c}{s}) &= A_{-1}\,b\,(i+1,i',\tfrac{c}{s}) + A_0\,b\,(i,i',\tfrac{c}{s}) + A_1\,b\,(i-1,i',\tfrac{c}{s}) + A_2\,b\,(i-2,i',\tfrac{c}{s}) \\
&\quad + C_{-1}\,e\,(i+1,i',\tfrac{c}{s}) + C_0\,e\,(i,i',\tfrac{c}{s}) + C_1\,e\,(i-1,i',\tfrac{c}{s}) + C_2\,e\,(i-2,i',\tfrac{c}{s}) \\
H\,(i,i',\tfrac{c}{s}) &= A_{-1}\,b\,(i-1,i',\tfrac{c}{s}) + A_0\,b\,(i,i',\tfrac{c}{s}) + A_1\,b\,(i+1,i',\tfrac{c}{s}) + A_2\,b\,(i+2,i',\tfrac{c}{s}) \\
&\quad - C_{-1}\,e\,(i-1,i',\tfrac{c}{s}) - C_0\,e\,(i,i',\tfrac{c}{s}) - C_1\,e\,(i+1,i',\tfrac{c}{s}) - C_2\,e\,(i+2,i',\tfrac{c}{s}) \\
F\,(i,i',\tfrac{c}{s}) &= -\tfrac{1}{2}\left[G\,(i+1,i',\tfrac{c}{s}) + H\,(i-1,i',\tfrac{c}{s})\right] - b\,(i,i',\tfrac{c}{s}) \\
U\,(i,i',\tfrac{c}{s}) &= N_{-1}\,d\,(i+1,i',\tfrac{c}{s}) + N_0\,d\,(i,i',\tfrac{c}{s}) + N_1\,d\,(i-1,i',\tfrac{c}{s}) + N_2\,d\,(i-2,i',\tfrac{c}{s}) \\
V\,(i,i',\tfrac{c}{s}) &= -N_{-1}\,d\,(i-1,i',\tfrac{c}{s}) - N_0\,d\,(i,i',\tfrac{c}{s}) - N_1\,d\,(i+1,i',\tfrac{c}{s}) - N_2\,d\,(i+2,i',\tfrac{c}{s}) \\
T\,(i,i',\tfrac{c}{s}) &= -U\,(i+1,i',\tfrac{c}{s}) - V\,(i-1,i',\tfrac{c}{s})
\end{aligned}$$

where

$$A_{-1} = \frac{e^2}{2\cos^2\varphi} = +0.010086 \qquad C_{-1} = A_{-1} = +0.010086$$

$$A_0 = -\frac{3\,e}{2\cos^2\varphi} = -0.215178 \qquad C_0 = A_2 = -0.071726$$

$$A_1 = \frac{4-e^2}{2\cos^2\varphi} = +2.030257 \qquad C_1 = \frac{-2+e^2}{2\cos^2\varphi} = -1.010086$$

$$A_2 = -\frac{e}{2\cos^2\varphi} = -0.071726 \qquad C_2 = -A_2 = +0.071726$$

$$N_{-1} = \frac{e^2}{4} = +0.004943$$

$$N_0 = -\frac{3e}{4} = -0.105462$$

$$N_1 = \frac{2+e^2}{4} = +0.504943$$

$$N_2 = -\frac{e}{4} = -0.035154$$

From these were then computed for $i' > 0$

$$P(i,i',s) = \frac{F(i,i',s)}{i-i'\mu} + \frac{G(i+1,i',s)}{i+1-i'\mu} + \frac{H(i-1,i',s)}{i-1-i'\mu}$$

$$Q(i,i',s) = \frac{G(i+1,i',s)}{i+1-i'\mu} - \frac{H(i-1,i',s)}{i-1-i'\mu}$$

$$R(i,i',s) = \frac{P(i,i',s) - \frac{e}{2}P(i+1,i',s) - \frac{e}{2}P(i-1,i',s)}{i-i'\mu}$$

$$S(i,i',s) = \frac{Q(i,i',s)}{i-i'\mu}$$

$$Y(i,i',s) = \frac{T(i,i',s)}{i-i'\mu} + \frac{U(i+1,i',s)}{i+1-i'\mu} + \frac{V(i-1,i',s)}{i-1-i'\mu}$$

$$W(i,i',s) = -\frac{U(i+1,i',s)}{i+1-i'\mu} + \frac{V(i-1,i',s)}{i-1-i'\mu}$$

and for $i' = 0$

$$P(0,0,c) = G(1,0,c)$$
$$P(1,0,s) = F(1,0,s) + \tfrac{1}{2}G(2,0,s)$$
$$P(2,0,s) = \tfrac{1}{2}F(2,0,s) + \tfrac{1}{3}G(3,0,s) + H(1,0,s)$$
$$P(3,0,s) = \tfrac{1}{3}F(3,0,s) + \tfrac{1}{4}G(4,0,s) + \tfrac{1}{2}H(2,0,s)$$

etc.

$$Q(1,0,s) = \tfrac{1}{2}G(2,0,s)$$
$$Q(2,0,s) = \tfrac{1}{3}G(3,0,s) - H(1,0,s)$$
$$Q(3,0,s) = \tfrac{1}{4}G(4,0,s) - \tfrac{1}{2}H(1,0,s)$$

etc.

$$R(0,0,c) = P(0,0,c) - \frac{e}{2}P(1,0,c)$$

$$R(1,0,c) = P(1,0,c) - \frac{e}{2}P(0,0,c) - \frac{e}{2}P(0,0,c) - \frac{e}{2}P(2,0,c)$$

$$R(1,0,s) = P(1,0,s) - \frac{e}{2}P(2,0,s)$$

$$R(2,0,s) = \tfrac{1}{2}\left[P(2,0,s) - \frac{e}{2}P(1,0,s) - \frac{e}{2}P(3,0,s)\right]$$

$$R(3,0,s) = \tfrac{1}{3}\left[P(3,0,s) - \frac{e}{2}P(2,0,s) - \frac{e}{2}P(4,0,s)\right]$$

etc.

$$Y(1,0,s) = T(1,0,s) + \tfrac{1}{2}U(2,0,s)$$
$$Y(2,0,s) = \tfrac{1}{2}T(2,0,s) + \tfrac{1}{3}U(3,0,s) + V(1,0,s)$$
$$Y(3,0,s) = \tfrac{1}{3}T(3,0,s) + \tfrac{1}{4}U(4,0,s) + \tfrac{1}{2}V(2,0,s)$$

These quantities gave immediately the final perturbations by means of the following equations:

$$nz = (g) + nt + n\delta z.$$

$$\begin{aligned}
n\delta z = &\left[R\,(0,0,c) + k - \frac{e}{2}k_1\right] nt \\
&+\left[-R\,(1,0,s) + H\,(0,0,s) - \frac{5e^2}{8}H\,(0,0,s) - k_2\right]\cos\varepsilon \\
&+\left[R\,(1,0,c) + e\,R\,(0,0,c) - H\,(0,0,c) + \frac{e^2}{8}H\,(0,0,c) + k_1 - \frac{e^2}{2}k_1\right]\sin\varepsilon \\
&+H\,(0,0,c)\,nt\cos\varepsilon \\
&+\left[H\,(0,0,s) - \frac{e^2}{2}H\,(0,0,s)\right] nt\sin\varepsilon \\
&+\left[-R\,(2,0,s) - \frac{e}{8}(5-2e^2)\,H\,(0,0,s) + \frac{e}{4}k_2\right]\cos 2\varepsilon \\
&+\left[R\,(2,0,c) + \frac{5e}{8}H\,(0,0,c) - \frac{e}{4}k_1\right]\sin 2\varepsilon \\
&-\frac{e}{4}H\,(0,0,c)\,nt\cos 2\varepsilon \\
&-\frac{e}{4}H\,(0,0,s)\,nt\sin 2\varepsilon \\
&+\left[-R\,(3,0,s) + \frac{e^2}{8}H\,(0,0,s)\right]\cos 3\varepsilon \qquad +\left[R\,(3,0,c) - \frac{e^2}{8}H\,(0,0,c)\right]\sin 3\varepsilon \\
&-R\,(4,0,s)\cos 4\varepsilon \qquad +R\,(4,0,c)\sin 4\varepsilon \\
&-\ \ldots\ldots\ldots\ldots \qquad +\ \ldots\ldots\ldots\ldots \\
&-\sum_{i'>0}\sum R\,(i,i',s)\cos\left[(i-i'\mu)\varepsilon - i'(e'-\mu c)\right] + \sum_{i'>0}\sum R\,(i,i',c)\sin\left[(i-i'\mu)\varepsilon - i'(e'-\mu c)\right]
\end{aligned}$$

$$\begin{aligned}
2\nu = &2C - e\,H\,(0,0,s)\,nt \\
&+\left[Q\,(1,0,c) + H\,(0,0,c) - k_1\right]\cos\varepsilon \qquad +\left[Q\,(1,0,s) + H\,(0,0,s) - e^2\,H\,(0,0,s) - k_2\right]\sin\varepsilon \\
&-H\,(0,0,s)\,nt\cos\varepsilon \qquad +H\,(0,0,c)\,nt\sin\varepsilon \\
&+\tfrac{1}{2}\left[Q\,(2,0,c) - e\,H\,(0,0,c)\right]\cos 2\varepsilon \qquad +\tfrac{1}{2}\left[Q\,(2,0,s) - e\,H\,(0,0,s)\right]\sin 2\varepsilon \\
&+\tfrac{1}{3}\,Q\,(3,0,c)\cos 3\varepsilon \qquad +\tfrac{1}{3}\,Q\,(3,0,s)\sin 3\varepsilon \\
&+\ \ldots\ldots\ldots\ldots\ldots \qquad +\ \ldots\ldots\ldots\ldots\ldots \\
&+\sum_{i'>0}\sum S\,(i,i',c)\cos\left[(i-i'\mu)\varepsilon - i'(e'-\mu c)\right] + \sum_{i'>0}\sum S\,(i,i',s)\sin\left[(i-i'\mu)\varepsilon - i'(e'-\mu c)\right]
\end{aligned}$$

$$\begin{aligned}
\frac{u}{\cos i} = &U\,(1,0,c) - \frac{e}{2}\,V\,(0,0,c) - cl_1 - e\,V\,(0,0,s)\,nt \\
&+\left[V\,(1,0,c) + l_1\right]\cos\varepsilon \qquad +\left[V\,(1,0,s) - e^2\,V\,(0,0,s) + l\right]\sin\varepsilon \\
&+V\,(0,0,s)\,nt\cos\varepsilon \qquad -V\,(0,0,c)\,nt\sin\varepsilon \\
&+\left[V\,(2,0,c) + \frac{e}{2}\,V\,(0,0,c)\right]\cos 2\varepsilon \qquad +\left[V\,(2,0,s) + \frac{e}{2}\,V\,(0,0,s)\right]\sin 2\varepsilon \\
&+V\,(3,0,c)\cos 3\varepsilon \qquad +V\,(3,0,s)\sin 3\varepsilon \\
&+\ \ldots\ldots\ldots\ldots \qquad +\ \ldots\ldots\ldots\ldots \\
&+\sum_{i'>0}\sum V\,(i,i',c)\cos\left[(i-i'\mu)\varepsilon - i'(e'-\mu c)\right] + \sum_{i'>0}\sum V\,(i,i',s)\sin\left[(i-i'\mu)\varepsilon - i'(e'-\mu c)\right]
\end{aligned}$$

where (g), C, k, k_1, k_2, l, and l_1 are constants of integration, connected by the relation

$$C = -\tfrac{1}{6}\left[k + ek_1\right]$$

leaving six independent constants.

Determining the constants by the condition that for $t = 0$, the date of osculation, $nz = g_0$, $\nu = 0$, $\frac{dz}{dt} = 1$, $\frac{d\nu}{d\varepsilon} = 0$, $u = 0$, and $\frac{du}{d\varepsilon} = 0$, we have as final perturbations—

Epoch=1872, Nov. 2.0, Greenwich M. T.; $nz = 108^\circ\ 30'\ 11''.4 + 775''.93288t + n\delta z$.

i	i'	$n\delta z$		ν		$\frac{u}{\cos i}$	
		cos	sin	cos	sin	cos	sin
0	0	″	″	+ 23.″79		− 9.″02	″
0				− 0.1950 T		− 0.1981 T	
1		−484.25	−110.86	+ 60.94	−242.99	+47.53	+23.73
1		− 14.8322 T	+ 2.7460 T	− 1.3867 T	− 7.4161 T	+ 1.4090 T	+ 9.2902 T
2		+ 16.74	+ 2.59	+ 0.94	− 0.19	+ 0.63	− 0.31
2		+ 0.5214 T	− 0.0976 T				
3	0	+ 5	+ 0.41	− 4	+ 4	− 2	+ 2
−2	− 1	+ 0.18	+ 9	+ 8	− 8	+ 0.11	− 8
−1		− 2.52	− 0.19	+ 0.27	+ 1.26	− 2.75	+ 3.97
0		+ 37.88	+ 26.22	+ 3.73	+ 1.07	− 4.12	+12.72
1		+211.05	+ 36.23	− 11.88	+ 71.26	+ 3.85	−12.01
2		− 2.21	+ 1.17	− 1.40	+ 2.70	+ 8	− 5.57
3		+ 0.20	− 0.16	+ 5	+ 0.30	+ 5	+ 0.30
4	− 1	− 4	+ 1	− 1	− 2	0	0
−1	− 2	− 8	− 0.38	+ 0.27	+ 0.19	+ 0.29	+ 0.49
0		+ 2.20	+ 6.45	+ 12.47	+ 2.98	+13.66	+10.71
1		+306.90	−768.37	+151.26	+ 55.12	−13.10	− 7.14
2		+119.39	−431.19	+253.56	+ 70.78	−11.06	− 6.15
3		− 5.71	+ 17.46	− 0.18	− 0.67	+ 1.30	+ 0.22
4		+ 4	+ 0.16	− 0.16	0	− 9	0
5	− 2	0	− 2	+ 1	0	0	0
−1	− 3	+ 0.13	+ 0.31	+ 6	0	+ 7	+ 1
0		− 1.52	− 2.57	− 3.16	+ 1.78	− 5.44	+ 1.19
1		− 74.89	−235.50	− 47.60	+ 25.76	− 6.91	+ 6.10
2		+301.54	+373.87	−169.98	+139.52	+20.16	−25.28
3		+ 26.69	+ 3.60	− 11.19	+ 26.03	+ 1.11	− 1.29
4		− 1.37	− 0.98	+ 0.20	+ 0.26	− 0.13	+ 0.40
5		− 0.10	0	+ 2	− 7	0	− 3
6	− 3	+ 2	0	0	0	0	0
0	− 4	− 4	− 8	− 4	+ 18	− 0.14	+ 0.25
1		− 4.15	− 0.96	− 0.36	+ 4.39	0.00	+ 3.04
2		+106.21	+ 1.58	+ 2.44	+ 34.06	− 1.11	− 4.96
3		+ 44.40	− 27.44	+ 16.22	+ 28.93	− 3.38	− 3.84
4		− 6.38	+ 8.49	− 5.90	− 3.50	+ 0.30	+ 0.39
5		+ 0.27	− 0.14	− 0.20	+ 4	− 0.13	− 6
6	− 4	+ 1	− 4	+ 3	+ 1	+ 1	0
1	− 5	− 1.53	+ 2.16	+ 2.46	+ 1.72	+ 2.74	+ 2.28
2		+320.55	−332.23	+ 29.95	+ 17.49	+ 1.24	− 1.12
3	− 5	+ 24.62	−178.85	+ 93.72	+ 14.28	−21.07	+ 2.38

i	i	$n\delta z$ cos	$n\delta z$ sin	ν cos	ν sin	$\frac{u}{\cos i}$ cos	$\frac{u}{\cos i}$ sin
4	— 5	+ 2.69	+ 15.58	— 6.46	+ 2.40	+ 0.89	— 0.54
5		— 2.06	— 1.92	+ 1.27	— 1.63	— 0.15	+ 8
6		— 3	+ 7	+ 1	— 0.12	+ 3	— 4
7	— 5	+ 2	+ 1	— 1	1	0	0
1	— 6	— 1	— 7	— 0.10	+ 4	— 0.11	+ 2
2		— 0.62	— 3.59	— 1.56	+ 0.80	— 0.52	+ 0.51
3		+ 14.85	+ 17.43	— 6.98	+ 6.61	+ 1.19	— 1.77
4		+ 7.29	+ 1.75	— 1.64	+ 4.82	+ 0.05	— 1.20
5		— 3.09	+ 0.59	— 0.46	— 2.15	+ 0.11	+ 0.30
6		+ 0.68	— 0.57	+ 0.49	+ 0.48	— 2	— 6
7		— 1	— 3	+ 6	+ 2	+ 2	+ 1
8	— 6	— 1	+ 1	0	0	0	0
2	— 7	— 0.28	— 5	— 2	+ 0.29	0	+ 0.26
3		+ 10.17	+ 0.77	+ 0.28	+ 2.58	+ 1	— 0.28
4		+ 6.70	— 4.57	+ 2.42	+ 3.94	— 1.03	— 0.88
5		— 1.14	+ 2.08	— 1.30	— 0.69	+ 0.33	+ 7
6		— 0.06	— 1.07	+ 0.81	— 0.06	— 0.11	+ 2
7		+ 0.16	+ 0.26	— 0.19	+ 0.15	+ 3	0
8	— 7	+ 2	0	— 2	+ 3	— 1	0
2	— 8	+ 8	— 8	— 0.10	— 8	— 0.11	— 0.11
3		+ 11.97	— 10.68	— 1.45	— 0.82	— 0.34	+ 0.02
4		— 1.99	+ 13.00	— 6.34	— 0.90	+ 1.87	— 0.27
5		+ 0.65	+ 0.76	— 0.80	+ 0.32	+ 0.20	— 0.17
6		— 0.65	— 0.45	+ 0.33	— 0.45	— 4	+ 0.12
7		+ 0.41	+ 3	— 2	+ 0.32	0	— 5
8		— 0.10	+ 5	— 5	— 7	0	+ 1
9	— 8	0	+ 1	— 2	— 1	0	0
3	— 9	— 4	— 0.11	— 7	+ 1	— 4	+ 3
4		+ 0.78	+ 1.12	— 0.38	+ 0.34	+ 7	— 8
5		+ 0.87	+ 0.22	— 0.18	+ 0.51	0	— 0.19
6		— 0.45	+ 0.12	— 0.06	— 0.30	+ 5	+ 8
7		+ 0.21	— 0.23	+ 0.17	+ 0.16	— 4	— 2
8	— 9	— 3	+ 0.16	— 0.13	— 2	+ 2	0
4	—10	+ 1.78	+ 0.57	0	+ 0.26	+ 2	0
5		+ 1.13	— 0.72	+ 0.36	+ 0.62	— 0.20	— 0.17
6		— 0.13	+ 0.24	— 0.11	— 8	+ 6	+ 1
7	—10	— 2	— 0.18	+ 8	— 1	— 4	+ 1
5	—11	— 0.11	+ 0.35	— 0.16	— 4	+ 4	0
5	—13	+ 11.07	+ 4.04	0	— 0.17	— 2	— 2
6	—13	— 1.08	+ 0.47	— 0.24	— 0.54	+ 0.17	+ 0.17

t = number of days after November 2.0, 1872, Greenwich mean time.
T = fraction of year counted from same date.
The argument is $[(i-i'u)\,\varepsilon - i\,(g'-ug)]$

By the aid of the preceding table, and using π, φ, i, and θ, as given on page 59, an ephemeris was computed for each opposition at which observations were made from 1867 to 1884 and compared with these observations. With the residuals thus obtained equations of condition were formed, and from their solution the following correction to the elements obtained:

$$\begin{aligned} \Delta n &= \quad\quad\quad 0.012472 \\ \Delta g &= -\ 1\ \ 35.7 \\ \Delta \pi &= +\ 1\ \ 37.8 \\ \Delta \varphi &= -\ 0\ \ \ 8.1 \\ \Delta \theta &= -\ 0\ \ \ 7.5 \\ \Delta i &= +\ 0\ \ \ 2.0 \end{aligned}$$

Applying these corrections we obtain as

Final Elements:

$$\left.\begin{aligned} g &= 108^\circ\ 28'\ 35.7 \\ \pi &= 274\ \ 49\ \ 19.2 \\ \theta &= \ \ 5\ \ \ 5\ \ 17.5 \\ i &= \ \ 8\ \ 36\ \ 23.6 \end{aligned}\right\} 1872.0$$

$$\varphi = \ \ 8\ \ \ 4\ \ 52.4$$

$$n = 775.''920408$$

Epoch: November 2.0, 1872, Greenwich mean time.

U. S. Naval Observatory.

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Volume VIII.

FOURTH MEMOIR.

OPHIURA BREVISPINA.

As my name appears upon the title-page of this memoir, it is proper for me to state that my share in the work has been that of the instructor under whose direction the work has been done. The discovery that this Ophiuran is of peculiar interest and that it is unusually favorable for the study of the problems of the morphology of Echinoderms, was made by Dr. Grave; and the results which are here detailed are his work.

W. K. Brooks.

CONTENTS.

OPHIURA BREVISPINA.

By W. K. Brooks and Caswell Grave.

INTRODUCTION.

During the summer of 1898 it was my privilege to occupy the table of the Johns Hopkins University in the United States Fish Commission laboratory at Woods Hole, and while here I rediscovered the peculiar Ophiuran larva, which was first found and figured by Krohn (7).

Finding the larvæ he described in the open sea Krohn did not know to what species they belonged; but the larvæ, the development of which is the subject of the greater part of this paper, came from eggs laid in aquaria by *Ophiura brevispina*. It is not likely that the same species of Ophiuran occurs both at Funchal, where Krohn did his work, and also at North Falmouth, where my material was obtained, but it is very probable that species belonging to the genus *Ophiura* have similar larval forms.

Among Echinoderms, where a direct development from the larva to adult occurs, that is, without the usual highly specialized intermediate pelagic larva, we usually have to do with a species which in some manner takes care of its brood; but in *O. brevispina* the larvæ are free swimming, they being provided with a well developed locomotor apparatus, yet the usual Ophiurid pluteus larva is as completely omitted as it is from the life history of the viviparous *Amphiura squamata*.

From the fact that the usual pluteus skeleton is begun in the larvæ of *O. brevispina* one is led to suspect, however, that at some period in its history the species possessed a larva more nearly like a pluteus than at the present time. On the other hand, on account of the resemblances which exist between the larvæ of *O. brevispina* and *Antedon rosacea* (treated of in another place) we may suppose a close phylogenetic relationship exists between them. If, as many zoologists believe, the crinoids have retained more nearly than any other group the characters of the primitive Echinoderm stock, then in the larva of *O. brevispina* we may have one which has retained unmodified its primitive characteristics.

In this paper, however, the facts only of development are taken up, and the question of the bearing which this larva may have on any theoretical discussion concerning the interrelationships of the Echinoderms is suggested here in order that the reader may keep the subject before him while studying the paper. The points of resemblance between the Ophiuran and Antedon larvæ are enumerated in a chapter further on.

The method used in the preparation of the material for microscopical study, and which gave good results, is as follows: The larvæ were taken up into a pipet with as little water as possible, and squirted into a small bottle containing a solution of sublimate-acetic (98 parts of a sat. sol. $HgCl_2$ being used to 2 parts of glacial acetic acid). After from two to five minutes the sublimate solution was drawn off gently, leaving the larvæ at the bottom where they had settled. Then 50 per cent alcohol was added, which in a few minutes (5) was drawn off and replaced by 70 per cent alcohol, in which a little iodine had been dissolved. In a few hours (3–12) this was changed for clear 75 per cent alcohol, in which the larvæ remained until needed for laboratory study. After staining lightly in acid carmine, so as to facilitate their orientation, the larvæ were dehydrated in the usual way and cleared in oil of cloves. From the clove oil they were oriented by a modification of the Patton method. After an impregnation with 55° paraffin, series of sections three

microns in thickness were made in three planes, transverse, longitudinal sagittal, and longitudinal horizontal. The sections were stained on the slide with KLEINENBERG'S hæmatoxylon. Other methods were tried, but none proved so satisfactory as the one just described. The shrinkage in echinoderm tissue, which usually accompanies the unmodified paraffin method, was not to be seen in the tissue of these larvæ, due, no doubt, to its unusual thickness.

It has been thought best to make the following list of terms which are used synonymously in the text of this paper in the description of the larvæ. Those in the same line can, in most cases, be interchangeably used.

Dorsal–aboral–above–over.
Ventral–oral–below–under.
Anterior–forward–before.
Posterior–backward–behind.

In the drawings of the larvæ, when the ventral side is up and the anterior end is nearest the top of the page, then the reader's left is also left in the figure.

For convenience in description, the various stages taken to illustrate the life history of the species have been designated by letters of the alphabet, this method seeming preferable to one in which age is used as a distinguishing character, since the progress of development at any age depends so intimately on the varying conditions of environment.

I take this opportunity to acknowledge my indebtedness to Dr. C. P. SIGERFOOS, at whose suggestion I began the study of Ophiuran development.

I was aided very materially while at the Fish Commission laboratory by Prof. H. C. BUMPUS, who placed at my disposal every facility for work at his command, and to him, also, I am greatly indebted for many suggestions in methods of rearing larvæ at the seashore.

To Professor BROOKS, under whose direction my work has been done, are due my warmest thanks for the interest with which he has followed me in my studies and for the many valuable suggestions he has offered from time to time during the year.

HISTORICAL SKETCH.

The species of Ophiuran, *Ophiura brevispina*, the life history of which is the subject of this dissertation, was first discovered and described by Thomas Say in 1825 (12).

Since this time the species has been rediscovered and renamed as many as three times. It is probably best known at present by one of its synonyms, *Ophiura olivacea*, which was given to it in 1865 by THEODORE LYMAN (8). In his earlier works LYMAN distinguished between *O. olivacea* and *O. brevispina*, but in his *Challenger* report on the *Ophiuridæ* and *Astrophytidæ* (9) he places the two species together as one under its earlier name, which, although less descriptive of the species than that given by Lyman, it is probably best to retain.

In 1852 AYERS described the species under the name *Ophioderma olivaceum* in Vol. IV of the Proc. Bost. Soc. Nat. Hist.

LÜTKEN also described it as *Ophioderma serpens* in 1856.

DISTRIBUTION AND HABITS.

Ophiura brevispina is a very widely distributed species, it having been reported from points along the Atlantic coast from Brazil to New England.

It has been taken from the following localities:

1. Bahia, Brazil.
2. Port Antonio, Jamaica.
3. St. Thomas, Bahamas.
4. Cape Florida, Florida.
5. Tortugas.
6. Beaufort, North Carolina.
7. Old Point Comfort, Virginia.
8. Sag Harbor, New York.
9. Dartmouth, Massachusetts.
10. New Bedford, Massachusetts.
11. North Falmouth, Massachusetts.

That part of North Falmouth Harbor which is inhabited by the species is very shallow, its depth at low tide not exceeding 1 fathom.

The bottom is covered with a mat of living and dead grasses and algæ, and in this tangle the ophiurans live, together with a great variety of crustaceans, molusks, and worms.

The usual color of the species is an olive green, with darker bands on the arms and sometimes with a clouded disk.

Through the blending of their colors with the seaweed the ophiurans are greatly protected from their enemies, and it is difficult, even when looking for them, to see them among the seaweed so long as they do not move.

It is quite common to find a small Amphipod crustacean clinging to the arms of dredged specimens, and from the structure of the crustacean it is probable that the two species live together commensally. What benefit either animal can derive from the association it is difficult to see.

One pair of the thoracic legs of the crustacean is so modified as to form a structure beautifully adapted for clinging to the round ophiuran arms. The last segment but one of each of this pair of legs is Y-shaped. At the end of one arm of the Y is attached a movable segment, the end segment of the leg, which when shut down upon the end of the other arm of the Y incloses a triangular space in which the ophiuran arm is held.

The body of the crustacean is colored and banded in such a manner as to simulate closely the color and banding of the ophiuran arms.

When placed in aquaria with their host, the crustaceans cling to the ophiuran arms until the water becomes depleted of oxygen, when they leave the arms and swim about the edge of the dish apparently much alarmed.

In examining the stomachs of the ophiurans one finds bits of other animals, such as crustacean appendages and the skeletons of young horseshoe crabs. From this it is probable that the creatures are scavengers, since an active crustacean would hardly be captured by so slow and poorly armed an animal as an ophiuran. None were ever observed to eat anything when kept in the laboratory, and it is quite out of the question to observe them in their natural habitat, since they are nocturnal animals remaining hidden during the day.

The ophiurans were first examined for sexual elements early in June, and at that time the eggs were very large but adhered closely together in the gonads. The sperm appeared to be fully formed but were nonmotile.

From this time on until the middle of August the species was regularly watched and examined, and on July 16 the first ripe eggs and sperm were obtained. A great number of specimens had that day been dredged and placed in aquaria dishes of fresh, filtered sea water. One week later a great number of adults were again brought in and placed under the same conditions as those which had spawned in the laboratory the week before, but this time very few eggs were obtained, and all subsequent attempts to get the ophiurans to spawn were unsuccessful.

From this it would seem that the breeding season is extremely short.[1]

The time of day at which spawning occurred corresponds well with the time at which I have noted it to take place in *Ophiophilus aculeata* and *Ophiocoma echinata*, that is, between 8 and 10 o'clock p. m.

PHYSIOLOGICAL NOTES.

The locomotor movements of an ophiurid, upon a casual observation, seem to consist of an uncoordinated writhing and twisting not calculated to bring the creature to food or a place of safety except by chance; but a more careful study shows them to be the result of an orderly and nicely coordinated mechanism.

The rapid strides which characterize the movements of a brittle star are in strong contrast

[1] During the summer of 1899, after this paper had gone to press, my experience with the species was very different from the above. Specimens brought into the laboratory early in June threw eggs and sperm, but the eggs, after passing through the early segmentation stages, ceased to develop. The eggs were probably immature, and were spawned only because of the bad condition of the water in the aquaria, but spawning always occurred early in the evening at the time when it would have occurred under normal conditions. Why unripe eggs should develop at all, or why eggs mature enough to begin their development should not be mature enough to complete it, is an interesting question.

This phenomenon was repeated every few days until July 26, when about one-fourth the number of eggs spawned developed into normal larvæ. This is ten days *later* than the date when eggs became mature at Woods Holl. From the fact that the water is much warmer at Beaufort than at Woods Holl one would expect to find the spawning season earlier at the latter place.

with the slow creeping movements of a starfish or sea-urchin, the difference being due to the employment of different locomotor mechanisms in the two cases; the starfish and sea-urchin depending entirely upon their tube feet and spines while in the ophiurids, the arms themselves are the efficient locomotor organs, they being used much as we use our arms in swimming.

The arm of an ophiurid consists of a large number of segments, each of which contains a central calcarious ossicle. The calcarious ossicles of adjacent segments articulate with each other like the vertebræ of the spinal column, and are joined together by two pairs of muscles in such a manner that motion is possible in all directions. This mechanism is aided in producing the locomotion of the creature not only by the arm spines, where they are present, but by the foot tentacles. These latter organs, which are the homologues of the tube feet of other echinoderms, have been previously regarded as having given up their locomotor function entirely, but I shall show further on that this is not true in the genus *Ophiura*.

The experiments I carried on last summer on the movements of ophiurans resulted in little that is new, but on account of the confirmation my notes and photographs give to PREYERS' work (11) on the same subject, it has been thought advisable to publish them.

In the usual method of progression one arm precedes, it taking no other part, apparently, than to point out the way; the two arms adjacent to and behind the anterior arm make the stroke; the remaining arms are dragged behind, acting as a rudder.

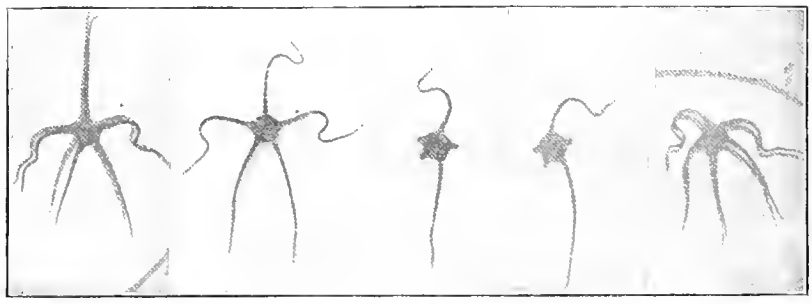

FIG. 1. FIG. 2. FIG. 3. FIG. 4. FIG. 5.

No preference as to which arm should precede could be found in an adult ophiuran, each arm being equally capable of going before, making the stroke, or following behind.

If greater speed is needed, for example, to get away from a strong stimulus, the arm which precedes may also take part in the stroke, its contractions being made simultaneously with those of the side arms. This added force, if produced repeatedly on one side, would soon change the course of progression, but this difficulty is overcome by an alternation of the stroke of the preceding arm, first on one side, then on the other (text fig. 2).

In a third method of normal locomotion the arms are arranged as is seen in text fig. 5, in which only one arm follows, acting as the rudder. This leaves two pairs of arms for the stroke, but the anterior pair is usually most vigorous in its contractions.

Since no physiological differentiation into anterior, posterior, or lateral parts is to be found in ophiurids, the creatures are under no necessity of turning the body when a change in the direction of progression is to be made. The arm which finds itself pointing in the new direction to be traveled takes the lead, although it may have been either lateral or posterior in position in the previous movements.

As has been mentioned before, the foot tentacles aid in making the strokes of the arms efficient in propelling the body. After a stroke has been made, while the arms are being drawn forward and extended for a new stroke, the tentacles can be seen moving actively about, but as the arms come to rest for the backward movement the tentacles are thrust down against the substratum and cease to move. The tentacles thus fit themselves into the inequalities of the surface and afford fixed points for the arms to pull against. The tentacles of the posterior arms act in the same way, and are efficient in preventing the force of the stroke being lost in side motion.

In ophiurans with long arm spines these latter structures may perform the function just described for the foot tentacles, but in the genus *Ophiura* the arm spines are very minute and closely applied to the sides of the arms.

It is interesting to note the wonderful coordination of locomotor movements immediately following the amputation of three of the arms. In this case if the nerve ring has been uninjured one of the remaining arms takes up the part of guiding and balancing, while the other strokes first on one side then on the other (text figs. 3 and 4).

When the central nerve ring is cut at any point the coordination in movement is impaired, and when cut in five places, between the arms, it is lost entirely.

When placed on its aboral surface an ophiuran quickly turns over. The method used is quite definite; two adjacent arms straighten out so that together they form a straight line. On these arms as an axis the body revolves, being pushed over by the three remaining arms, but mostly by the median one of the three.

EARLY STAGES.

The mature eggs are opaque and vary in color from an olive green to an orange yellow. Those of the same individual, however, are constant in their coloration. Until quite well developed the larvæ retain the color which was on the eggs at the time they were laid.

For echinoderms the eggs are very large, being 0.3 millimeter in diameter.

Soon after they are fertilized the eggs throw off two membranes, the first of which is much thicker than the second.

When first laid and during their early development the eggs float, but when their cilia are formed the larvæ are able to swim below the surface.

As I did not know that any special interest would be found in the life history of the species, I did not carefully observe the early stages while living, nor preserve material for future study, and as I have stated elsewhere, all later attempts to get other material were unsuccessful.

This makes it necessary to begin this paper with the description of a late gastrula in which the first pair of enterocœles have already begun to form as lateral pouches from the anterior free end of the archenteron (figs. 1–3).

Larvæ in this stage of development will be designated as "A."

Stage "A," 36 Hours Old.

(Figures 1, 2, and 3.)

At the age of 36 hours the larvæ swim actively, they being uniformly covered with cilia (fig. 1).

The shape of the larvæ is an oval, the length being to the shorter diameter as 2 is to 1.

The animal or anterior pole is slightly more pointed than the posterior vegetative one. The ventral surface is distinguished by the presence of the blastopore, which latter has been pushed from its posterior position to a ventral one by the rapid growth of the ectoderm of the dorsal surface of the larva.

An apical plate of taller cells is present at the anterior end, but I could not see that the cilia at this point were any longer than those which cover the other parts of the larva (fig. 3, ap).

From the blastopore, through which its cavity opens to the exterior, a large archenteron projects forward into the blastocœle.

The remainder of the blastocœle, not taken up by the archenteron or its pouches, is filled with a close network of mesenchyme cells. This mesenchyme tissue is shown in fig. 3, mes, which is a longitudinal sagittal section of "A."

From the anterior free end of the archenteron a large pouch is in process of being cut off. This pouch projects to the right and left as horn-like processes, which latter are to be considered the rudiments of the right and left anterior enterocœles (fig. 2, aer and ael).

As to the method of gastrulation I can not at present speak from observation on larvæ in which it is just taking place, but from a study of the stage now under consideration some idea can be gotten as to how it has proceeded. In figs. 1 and 3 we see a cellular plug (cp) protruding from the blastopore and also extending far into the archenteric cavity. In some cases it extends even into the enterocœle pouch. The contour of this cellular mass is ragged, which is also true of both the outer and inner surfaces of the wall of the archenteron and the inner surface of the ectoderm.

These facts seem to indicate that gastrulation does not take place by invagination, as is usual in echinoderms, but that the larva before gastrulation is a solid, planula-like affair, and later the

archenteron is formed by a splitting away of the central core. In the same way the plug of cells is probably formed by the hollowing out of the solid archenteron.

Beside their ragged outline the walls of the larva have another peculiarity in their structure, for, judging by the number and position of the nuclei, they are from two to three cells in thickness (fig. 3).

Cell walls are not distinguishable in any stage of development.

Stage "B," 42 Hours Old.

(Figures 4 and 5.)

According to Bury (2) the hydrocœle does not have the same origin in all the groups of echinoderms. He found that it originates in the crinoids, sea-urchins, and starfishes from the left *anterior* enterocœle, but in the ophiurids it grows out from the anterior end of the left *posterior* enterocœle.

This observation, which Bury records with apparent hesitation, I can completely confirm, as will be seen in the description and figures of "B."

Externally the appearance is the same as in "A," but the internal structures have undergone a great change.

The anterior pouches, the cavities of which in "A" were connected both with each other and with the cavity of the archenteron, are now separate and distinct. The connection between these structures still continues, however, in their fused walls. The left pouch is a little larger than the right and lies behind and to the left of the latter (fig. 4, acl).

Just below the anterior pouches there is to be found a third pouch, which is growing out from the left side and anterior end of the archenteron (fig. 4, hy). It protrudes anteriorly and partially covers the two anterior enterocœles. The cavity of this pouch, which is the rudiment of the hydrocœle, is in wide communication with the archenteron.

From the wall forming the convex sides of the hydrocœle there are, even at this early stage in its formation, five outgrowths which are the beginnings of the radial canals of the adult ophiuran (fig. 4. 1, 2, 3, 4, and 5).

The whole hydrocœle is curving round to the right to encircle the œsophagus, which latter is making its first appearance in this stage as a shallow but definite pit in the central part of the ventral ectodermal wall (fig. 4, oe).

To avoid confusion the hydrocœle was spoken of above as arising from the archenteron, but, as will be seen in the transverse section (fig. 5), taken in a plane posterior to the origin of the hydrocœle, a differentiation is taking place in the archenteron which enables us to distinguish in it the rudiments of two structures, the posterior enterocœles and the stomach. By a longitudinal circular furrow the archenteron is being cut horizontally into a large ventral pouch, the posterior enterocœles (pe) and a smaller dorsal one, the stomach (s). This stomach rudiment bends around the posterior end of the posterior enterocœle and opens to the exterior through the blastopore (fig. 4).

It is from the left side and anterior end of the ventral pouch that the hydrocœle grows out, hence the confirmation of Bury's statement that it arises from the left posterior enterocœle in ophiurids.

In most echinoderms the posterior enterocœles originate as paired structures, and if the statements of Bury and McBride are correct, that the left posterior enterocœle of the larva forms the hypogastric body cavity of the adult, and the right posterior enterocœle goes to form the epigastric cœlom, then, according to this, the large ventral pouch, which I regard as the fused right and left posterior enterocœles, really represents the left only, because it takes no part in the formation of the epigastric body cavity of the adult ophiurid, but, with the left, does pass directly into the hypogastric.

The origin of the epigastric enterocœle is discussed in the description of Stage "C," in which its rudiment is first found over the stomach.

My reason for regarding the ventral pouch of "B" as the fused right and left posterior enterocœles, is that at the time of its origin it is symmetrically disposed on either side of the plane of larval bilateral symmetry.

Goto (5), too, has shown that the hypogastric enterocœle in the starfishes is not formed from the left alone, but in it are to be found the left and the greater part of the right posterior enterocœles.

The cellular plug of cells, which in "A" fills the archenteric cavity, becomes divided by the furrow which separates the archenteron into enterocœle and stomach and a part of it becomes inclosed in the cavities of each of these structures (fig. 5, ep).

Stage "C," 48 Hours Old.

(Figures 6, 7, and 8.)

The external form of the larva, which in this series of embryos is six hours older than "B," has been changed by the appearance of two lateral thickenings of the ectoderm a little posterior to the median transverse plane (fig. 6).

The blastopore, which in "B" was open to the exterior, has closed, leaving no trace of its former position.

The mouth and œsophagus, which existed in "B" only as a shallow ectodermal pit, now have the form of a deep, hollow tube (figs. 6 and 7, m and oe), which projects vertically inward until it passes through the hydrocœle and beyond the posterior enterocœle, when it curves back under the latter to fuse with the anterior wall of the stomach.

The stomach and posterior enterocœle are still in open communication, as in "B," but the furrow in "C" has deepened, and the process by which the two structures are being separated is almost complete (fig. 7).

Although the walls of the œsophagus and stomach are fused, their cavities are still separate.

This condition renders it easy to see just what part is played by the ectoderm in the formation of the alimentary canal, the entire œsophageal cavity being surrounded by ectoderm.

In "B" the hydrocœle communicates with the posterior enterocœle by a wide opening, and at the same point in "C" the two structures are still in communication, but the connection has been narrowed down to a small tube (fig. 7, hc).

Beside this connection with the posterior enterocœle, a second tube has been formed, joining the left anterior enterocœle with the hydrocœle (fig. 7, st). This new tube, which is the rudiment of the stone canal, enters the hydrocœle at the same point with the tube connecting the latter with the posterior enterocœle.

The left anterior enterocœle lies to the left of the œsophagus, and dorsal to the left half of the hydrocœle (figs. 6 and 7, ael).

It is to be noted that, although we now have a larva possessing both hydrocœle and stone canal, there has been as yet no pore canal formed. This is a marked reversal in the sequence of the formation of these structures from what might be expected from the order of their appearance in other known echinoderms, the pore canal arising usually before the formation of the hydrocœle, while the stone canal appears much later than either.

Returning to the hydrocœle, we find it a horseshoe-shaped structure astride the œsophagus (figs. 6 and 7, hy). The bulging areas which are to form the radial canals of the adult are much longer and more regular in size than in "B." The radial pouch, which lies to the right of the œsophagus and at the end of the right horn of the horseshoe, will hereafter be spoken of as radial canal 1, since it arises from that part of the hydrocœle which was first to bud out from the posterior enterocœle. The other radial canals, passing to the left over the œsophagus, will be designated as 2, 3, 4, and 5. Radial canal 5 lies in this stage over the opening of the stone canal.

The rotation of the hydrocœle around the œsophagus from its original left position, which was begun in "B," has continued to such an extent in "C" that half of it lies to the right of the median sagittal plane of the larva and half to the left. Radial canal 3 lies in this plane and points directly toward the anterior end of the larva (fig. 6).

With its rotation the hydrocœle also moves bodily toward the posterior end of the larva, carrying with it the œsophagus. The œsophagus, coming in contact with the anterior wall of the united posterior enterocœles, causes the latter to be pushed in at the point of contact. As the process continues, those parts of the posterior enterocœles lying on either side of this in-pushing area are forced to flow forward around the œsophagus and under the hydrocœle; thus we have

the posterior enterocœles becoming horseshoe-shaped, the two horns of which lie under the horns of the hydrocœle (figs. 6 and 7, he and hy).

Lying dorsal to the stomach we find a small enterocœle which was not present in "B," or if present, not in this position. It is the rudiment of the body cavity, which in the adult lies aboral to the stomach and which has been recently appropriately termed the epigastric enterocœle (figs. 6 and 7, ee).

As to the origin of this structure I have no direct observations to give, but certain facts have led me to believe that it is formed from the right anterior enterocœle. These facts may be summed up as follows: In "B" no epigastric enterocœle exists, but the two anterior enterocœles (fig. 4, aer and ael) lie side by side anterior to the stomach and the posterior enterocœles. In "C" (figs. 6 and 7, ee) an epigastric pouch, equal in size to the right anterior enterocœle of "B" is to be found, but by the side of the œsophagus only the left anterior enterocœle remains (figs. 6 and 7, ael).

During the six hours which intervene between "B" and "C" it seems hardly possible that a complete formation of the epigastric enterocœle should have taken place or that there should have been time for the complete degeneration and disappearance of the right anterior pouch; sufficient time may have elapsed, however, for the migration of the right anterior enterocœle to a position behind the stomach.

Against such an interpretation as the above there is the fact that in no other case has the epigastric enterocœle been observed to take its origin from the right anterior pouch. It has been described as arising from the right *posterior* enterocœle, however, as has been referred to before, in all the groups by BURY, and his observations have been corroborated by both MCBRIDE and GOTO in the starfishes.

STAGE "D," 60 HOURS OLD.

(Figures 9-11.)

The changes which have taken place in "C" to produce "D" are very marked.

The cilia have disappeared, except in four transverse rings or bands, three of which extend entirely around the body of the larva. The third ring, counting from the anterior end, is interrupted by the aboral disk on the ventral surface.

This third ciliated ring first appears on the lateral bulges, which were described in "C," and the fourth ring appears on a second pair of lateral bulges which originate behind the first pair near the posterior end of the larva.

The shape of the larva is no longer oval, but the posterior end has widened laterally and become somewhat dorso ventrally compressed (fig. 9). The anterior end has not changed in shape and may be thought of as forming the handle of the now club-shaped larva.

The enlarged posterior end of the larva contains all its organs and is the part which will enter directly into the formation of the adult ophiurid.

From its homology with the preoral lobe and larval organ of *Asterina gibbosa* I have called the anterior end of the larva the larval organ. It disappears with the metamorphosis into the adult form.

The larval organ is also homologous with the stalk of the Antedon larva, although in the ophiurid larva it never functions as an attachment organ. When swimming, the larval organ precedes. It is filled with a network of mesenchyme cells (fig. 11, mes).

Internally the changes have been even greater than the external ones we have just considered, for it is during this period of development that the rotation and readjustment of organs takes place, which is present in all echinoderms at some stage of their development.

The hydrocœle, which has begun its rotation about the œsophagus as an axis in "C," has completed it in "D" and reached its definite position.

That part of the hydrocœle which in "C" was situated on the left of the plane dividing the larva into bilaterally symmetrical halves, now lies on the right side of the same plane and vice versa. (Compare figs. 6 and 9.)

A revolution of 180° has taken place in the hydrocœle since "C," to which if the 180° of rotation be added, which took place up to the time of "C," we have a total rotation of 360° in the

hydrocœle. Radial pouch 1, finally, after having passed around the œsophagus, comes to rest at the point where it originated. Radial pouch 5, it will be noted, is carried only half as far as radial pouch 1, or from its point of origin on the left to a point opposite on the right of the œsophagus. (Compare figs. 6 and 9, (1) and (5).)

This great amount of rotation seemed so peculiar that I hesitated for some time to believe it, and was led to suppose instead that while the hydrocœle moved to the right the other organs lying above it rotated an equal amount to the left.

The early closure of the blastopore and the central position of the mouth in the early stages make such a view as the latter seem possible, and as it may suggest itself to those who study figs. 6 and 7, I will give below the points which seem to me, directly or indirectly, to prove that the hydrocœle revolves under the enterocœles and stomach, rather than that the latter twist over the hydrocœle:

(*a*) The ectodermal bulges, nearer the posterior end in "C" (fig. 6), are the same as those nearer the posterior end of "D" (fig. 9), on which the third ciliated band is situated.

(*b*) If the latter view is the correct one then radial canal 3 points toward the same end of the larva in both "C" and "D" (figs. 6 and 9), but in "C" the end toward which it points is anteriorly directed in swimming and in "D" it points away from the end which precedes. It is hardly thinkable that in any stage in its development the anterior end of a larva should change its physiological function and become the posterior end.

(*c*) By any other view than the one I have adopted the blastopore, or the point where it existed before closing, would be anterior and the larval organ posterior in position. In all known echinoderm larvæ, however, the blastopore marks the posterior end, and in all cases where it occurs the larval organ originates from the anterior end of the larva.

(*d*) It may be recalled, also, that in the readjustment of parts which takes place during the metamorphosis of other echinoderm larvæ the rotation is almost entirely confined to the hydrocœle.

As the hydrocœle passes around the œsophagus the tube connecting it with the left horn of the hypogastric enterocœle becomes broken and the left anterior enterocœle, together with the tube connecting it with the left horn of the hydrocœle, are carried anteriorly around the œsophagus (fig. 9, ael and st). In "D," then, we find the stone canal on the right side of a line dividing the larva into symmetrical halves, instead of to the left of the same line as it is in "C." (Compare figs. 6 and 7 with 9.) The anterior enterocœle comes to rest immediately in front of the stomach and œsophagus.

From the point where the stone canal enters the anterior enterocœle the pore canal grows out, passes dorsally to the ectoderm, with which latter its walls fuse, and an opening the water pore (figs. 9 and 11, pc.) breaks through. Thus in this stage the cœlom and hydrocœle are first connected with the exterior.

In "C" the circular water-canal had not closed, but existed in the form of a horseshoe, the concave side of which opened posteriorly, but as the rotation of the hydrocœle takes place its horns grow toward each other until they meet. A fusion of their walls then takes place at the point of contact and a complete ring is thus formed. The part of the ring canal, the formation of which has just been described, lies between radial canals 1 and 5 in fig. 9. The opening of the stone canal into the water ring is situated in "C" at the base of radial canal 5, but by means of the rotation of the hydrocœle about the œsophagus, together with the growth of the ends of the horseshoe, this opening is carried away from its position at the base of radial canal 5 toward radial canal 1. It always remains, however, nearer the former than the latter; in other words, it comes to lie definitively in the *right adradius* between radial canals 5 and 1. (Compare figs. 6 and 9.)

The radial canals, which existed in "C" as simple pouches from the convex side of the hydrocœle, have in "D" each become three-lobed. Near the tip and from the sides of each canal a pair of pouches has budded out, each of which is about equal in size to the end of the canal which lies between and beyond them (fig. 9, et and tl). In these three structures we have the rudiments of the end tentacle and the first pair of foot tentacles of the ophiurid arm.

When we were last considering the hypogastric enterocœle it was in the form of a crescent, the horns of which were very short and its central part very wide. Into its concavity, which was

anteriorly directed, the œsophagus fitted. The horns of this enterocœle, beginning in "C" to grow over the hydrocœle, continue the process during the rotation of the latter, the horns of the crescent growing at the expense of the thickness of its central part, and in "D" we have this enterocœle lying directly over the hydrocœle in the form of a perfect horseshoe (fig. 9, hc).

Between the ends of the horns of the hypogastric cœlom lies the anterior enterocœle. The walls of these structures come together and fuse in such a way that they together form a hollow circular cœlom surrounding the stomach and lying over the somewhat smaller water vascular ring (fig. 9).

In the four interradii, marked by their positions between radial canals 1 and 2, 2 and 3, 3 and 4, and 4 and 5, four pouches of the hypogastric enterocœle grow downward, outside the water vascular ring, forcing themselves between the radial canals; a fifth pouch, similar to those just described, is formed from the left anterior enterocœle in the remaining interradius between radial canals 5 and 1 (figs. 9, 12, 13, and 14, hip 1–2, 2–3, 3–4, 4–5, and ipax 5–1). These five pouches are the rudiments of the *outer* perihæmal ring, which will be more fully considered in the succeeding stages.

The stomach, after being entirely cut off from the hypogastric enterocœle, was drawn forward during the rotation of the hydrocœle, and the œsophagus was carried in the opposite direction, so that in "D" the stomach lies almost directly over the œsophagus (figs. 8 and 13, oe and s). The partition, which in "C" separated the cavities of these two structures, has disappeared in "D," and the œsophageal cavity opens into that of the stomach. There is present, then, in "D" the definitive alimentary canal of the adult ophiurid.

The "cellular mass," which in "B" and "C" was being divided into two parts by the constriction separating the archenteron into enterocœle and stomach, is to be found, in sections of "D," in the cavities of both the above structures (figs. 11, 12, 13, and 14 ep).

Lying immediately above, or aboral to, the stomach is to be found the epigastric enterocœle. It has enlarged considerably during the interval between "C" and "D," but is not yet of sufficient size for its walls to touch those of the hypogastric cœlom, and hence in this stage no circular aboral mesentery is to be found.

Stage "E," 66 Hours Old.

(Figures 15–21.)

The thickening of the ventral ectoderm which was begun in "D" has continued during the six hours which intervene between "D" and "E" and has spread to the sides of the larva (figs. 15 and 19–21).

Near the edge of this thickened oral disk are to be found five groups of rounded elevations of the ectoderm (fig. 15, I, II, III, IV, and V). The three elevations, of which each group consists, form the angles of an isosceles triangle the apex of which points away from the mouth of the larva (fig. 15). These elevations or evaginated papillæ lie immediately below and inclose the tips of those branches of the radial water canals which form the rudiments of the end tentacle and first pair of foot tentacles of each arm (figs. 19 and 21). In this way each tentacle grows into its ectoderm, the latter closing around it as it pushes out.

The function of these tentacles in the adult being mainly a sensory one, it is interesting to note that they receive their ectoderm from part of the same thickened oral area which gives rise later to the adult nervous system.

The ciliated bands in "E" do not differ in appearance and position from those in "D," but since they were not figured in the earlier stage it may be well to refer to them again in connection with figs. 15 and 16, cb 1, 2, 3, and 4. The first or most anterior band surrounds the larval organ quite near its tip.

Near the first band, and parallel to it, runs the second one also around the larval organ. The third ciliated band is separated from the second by a much wider space than that which separates the first and second bands. Were it not interrupted on the oral disk the third ciliated band would lie in the line separating the bivium and trivium—that is, between arms I and II on the one side and IV and V on the other. The fourth band, passing just posterior to the group of ectodermal elevations lying under the branches of the third radial water tube, surrounds the posterior end of the larva.

In "E" the cavities of the œsophagus and stomach have become obliterated, and the two structures appear in section as one solid mass of cells (fig. 20, st and oe). No degeneration in their size, however, is to be observed, and their outer walls remain well defined, the œsophagus retaining its connection with the ectoderm. As will be seen later, their lumen reappear and they become the definitive alimentary organs of the adult ophiurid.

Returning to the consideration of the water system, we find in "E" instead of one pair of tentacles on each radial canal, as in "D," there are two pairs present (fig. 17, t1 and t2), the second pair having grown out of the radial canal between the first pair and the water ring. The second pair is much smaller than those which were first to be formed, and, contrary to what one would expect, this discrepancy in size does not disappear as time goes on. This is also true in the sea-urchins, in which the primary tube feet in the larva are enormously larger than those which are subsequently formed. The primary tube feet in this case gradually diminish in size after the adult form is reached.

As a rule, among echinoderms the tube feet or tentacles are formed *centrifugally* from the radial canals; that is, between the end tentacle and the last pair of tube feet or tentacles already formed. This process keeps the undifferentiated growing point of each arm at its tip, but in this ophiuran, and the same is true of Antedon, the formation of the tentacles *begins* in a centripetal manner; that is, the second pair of tentacles appears, not between the end tentacle and the first pair, but between the first pair and the ring canal.

This second pair of tentacles is the rudiment of the buccal tentacles, and although differing in both function and position in the adult from that of the foot tentacles, is nevertheless entirely homologous with the latter. This homology is shown by their origin and the fact that for a time after forming they are directed away from the mouth toward the end of the arm just as is the case with the foot tentacles. After a time, however, as will be seen later, they turn back and point toward the mouth, thus showing that in this second pair of outgrowths from the radial canals we have to do with the first pair of buccal tentacles of the adult. After budding, as we see, from the radial canals, they migrate to a position on the ring canal, with which we find them connected in the adult.

In "E" the buccal tentacles have no ectoderm nor rudiment of such, the ectoderm under their tips being as yet undifferentiated from the oral disk.

The hypogastric enterocœle has assumed a more pentagonal shape than in "D," it having grown out over the radial water canals (fig. 17, he). These projections of the hypogastric enterocœle will continue to grow with the growth of the arms and become the brachial extensions of the body cœlom.

The interradial pouches of the hypogastric enterocœle, which were beginning to form in "D," have pushed down further and further between the radial canals until, coming in contact with the ventral ectoderm, they bend over, inserting themselves between the ring canal and the oral disk (figs. 17–21, hip 1–2, 2–3, 3–4, and 4–5). In the same way the pouch from the anterior enterocœle in the stone canal interradius has grown under the water ring. In these five interradial enterocœlic outgrowths, as has been mentioned before, we have the rudiments of the outer perihæmal sinus of the adult. The process by which this perihæmal sinus is formed in *Ophiura brevispina* agrees in every detail with its method of origin in *Asterina gibbosa* as described by McBRIDE (10).

The epigastric enterocœle is in much the same condition as that in which we left it in "D," it being as yet too small to meet and form a mesentery with the dorsal edges of the hypogastric cœlom (fig. 19, ee).

The stone and pore canals, too, have changed very little during the interval between "D" and "E." From the ring canal at a point to the left of the origin of radial canal 1 the stone canal passes upward and opens into the right postero-dorsal part of the anterior enterocœle. The pore canal begins at the same point where the stone canal ends, the two canals thus having a common opening into the anterior enterocœle or ampullæ. The pore canal extends from the enterocœle to the dorsal surface of the larva, where it empties through the dorsal pore at a point a little to the right of the median sagittal plane. These two canals, although extending in the same direction, do not lie in the same straight line, the pore canal being set a little anterior to and to the right of the stone canal (figs. 17, 18, and 21, st and pc; also fig. 11).

STAGE "F," 5 DAYS OLD.

(Figures 22-30.)

Although "F" is separated from the stage last described by a considerable space of time, the changes in the larva which have been brought about are easy to follow.

The larva is considerably larger than in "E," and has reached its full development. From this time on the larval organ gradually degenerates and is finally completely absorbed by the developing star (Compare figs. 22 and 31 lo.)

The external form of the larva has been changed by the appearance of a number of elevations and depressions in its outer surface, the ciliated bands being elevated upon circular ridges (fig. 22, cb 1, 2, 3, and 4), while at points on the sides of the disk beyond the end tentacles projections in the ectoderm have made their appearance, these being the rudiments of the ophiuran arms (fig. 22, I, II, III, IV, and V).

The larval organ is cylindrical, but the disk has continued its dorso ventral flattening. (Compare figs. 22 and 26.)

The first and second ciliated bands are situated in the same places as in "E." The third, while retaining its old position, has grown in upon the ventral disk toward the mouth (fig. 22, cb 3). On the ventral side of the larva the fourth band has shifted from its old position behind the third radial canal to one on the interradii between arms II and III and III and IV. It has also become interrupted on the oral disk in a manner similar to the third ciliated band (fig. 22, cb 4).

The depressions before referred to are caused by the invagination of the nervous system, which structure has been forming since "D" in the thickened oral disk of ectoderm. Immediately below the water ring and radial water canals the thickening has increased more rapidly than at other points, thus producing a ring-shaped internal ridge, from which extend five radial thickened ridges. These rudiments of the nerve ring and radial nerves bulge inwardly, no evidence of their presence being apparent on the outside. When the thickening process has been completed the whole nervous system gradually sinks in, leaving a circular groove from which five radial grooves pass out. This is the stage in the formation of the nervous system which has been reached in "F" (fig. 22, eg and rg). The invagination process begins at the ends of the radial nerves, just inside of the curved tips of the end tentacles, the nerve ring being invaginated last of all. (Compare figs. 23–27.) As development goes on the edges of the grooves gradually close over the nerves, the closure taking place in the same order as the invagination proceeded—that is, first over the ends of the radial nerves, then finally, after gradually traveling up the radial nerves, closing over the nerve ring.

By the meeting and subsequent fusion of the edges of the grooves, part of their cavity becomes cut off from the exterior and is left below the nervous system as the subneural space. But this will be referred to again in an older larva, in which the process of its formation is more nearly completed, it having begun in a few only of the most advanced larvæ of Stage "F."

The nervous system shows a differentiation into two distinct layers, a fibrous one nearest the water system and a cellular layer lying below the fibers (figs. 23–29). The nuclei of the cellular layer are oval, with their long diameter perpendicular to the fibrous layer.

Above the nervous system, separating it from the water system, is to be found the outer perihæmal space (figs. 23–30, opr). Recalling the condition of the perihæmal system in Stage "E," we see that the ends of the interradial projections from the hypogastric and anterior enterocœles have grown out over the nervous system, spreading in both directions until the outgrowths of each interradial pouch meet those of its adjacent fellows in the radii over the origins of the radial nerves; here the ends of the pouches fuse, and together they grow out over the radial nerves as the radial perihæmal sinuses.

In the starfishes, where the formation of this perihæmal system has been observed, it is said that no fusion takes place between the diverticula of the interradial pouches of the hypogastric and anterior enterocœles when they meet in the radii, but that a mesentery is formed at the points where the diverticula come in contact. This mesentery is described as continuing to the end of the arms, separating the radial spaces into two parallel cavities.

Nowhere could I find such a mesentery in sections of the larvæ of *O. brevispina*, nor could I feel sure that it exists in the adult ophiuran.

McBRIDE (10) and GOTO (5) both agree that in starfishes the *inner* perihæmal ring sinus arises from the anterior enterocœle, although they differ as to the method of its formation. In none of the larvæ I have is the structure in question fully formed, but in Stage "F" a cavity is arising, as an outgrowth from the anterior enterocœle in the stone canal interradius, which I take to be the rudiment of the inner perihæmal ring space. It lies to the left of the stone canal near the median sagittal plane of the larva. From the posterior side of the ventral end of the anterior enterocœle the outgrowth takes its origin, then extending posteriorly until past the water ring it bends over and grows down until its end reaches the nerve ring at a point inside the outer perihæmal sinus. Here the end of the pouch in question begins to spread under the nerve ring in both directions, parallel to the outer perihæmal ring (figs. 24 and 26, ips). This coincides exactly with its method of origin in *Asterina gibbosa* as described by McBRIDE.

Although the outer perihæmal ring is entirely cut off from the body cavities at this stage, there still remain traces of the interradial pouches which gave rise to it (fig. 29, hip 1–2 and 4–5).

The hypogastric enterocœle itself has changed very little since Stage "E," but the epigastric has enlarged to such an extent that its edges now meet the edges of the hypogastric and a circular aboral mesentery is formed (figs. 23–29, em).

In the water system considerable growth is to be noted in the tentacles, the end and first pair of foot tentacles being capable of protrusion considerably beyond the disk. By means of these tentacles the larvæ are able to cling tenaciously to the surfaces of foreign bodies, it requiring a strong jet of water from a pipette to detach them. Special notice was taken to be sure that it was the tentacles and not the larval organ which was used as a means of attachment.

The second pair of tentacles (buccal tentacles) have acquired their ectoderm in this stage and they protrude, like the other tentacles, over the radial nerves into the radial grooves (figs. 22 and 26, t 2).

The axial sinus or ampulla is present in "F," it being that part of the anterior enterocœle which remains after the pouches have been cut off, which will form the inner perihæmal and part of the outer perihæmal systems (figs. 24, 25, and 26, ax sin).

It will be noted that beside the ampulla, which is situated anteriorly to the stone canal, there are two other cavities near the stone canal to be accounted for (fig. 26, sin a and sin b). I can not be sure of their origin, but I believe that they also come from the anterior enterocœle. I have distinguished them by the letters a and b, as they are probably the same cavities as those so lettered by McBRIDE (10) in his figures of Amphiura.

The cavity McBRIDE has lettered b′, and which he thinks represents the degenerated *right* hydrocœle, I have been unable to find in any of my sections.

The stomach and œsophagus are in a condition the same as we found them in "E;" that is, without lumen.

STAGE "G," 5½ DAYS OLD.

(Figures 31 and 32.)

Larvæ a few hours older than "F" show a decided degeneration in the larval organ (fig. 31, lo), but otherwise the external appearance of the two stages is about the same.

The grooves caused by the invagination of the nervous system have begun to disappear by the growing together of their edges, and instead of the deep furrows we find a slightly depressed line where the edges of the grooves have met (fig. 28, rg).

In the nervous system a pair of tentacle nerves has been formed from each radial nerve (fig. 31, nl). They grow out laterally from the radial nerves at points proximal to the first pair of foot tentacles, around which latter they grow and to which they belong. No nerves as yet have appeared to supply the buccal tentacles.

In "F" the buccal tentacles had only begun to curve away from the end of the arm; but in "G" this proximal bending has continued until they curve over the nerve ring and point toward the mouth.

Beside this change in the water vascular system we find in "G" the first appearance of the rudiments of the polian vesicles. They are four in number and are in the form of small interradial pouches growing distally from the convex wall of the water ring (figs. 31 and 32, pv). There is no polian vesicle present in this species in the stone canal interradius.

As no perceptible change has taken place since "F" in the organs not referred to above, the description of them given in the previous chapter will serve equally as well for "G" as for "F," and the figures of these organs in "G" may be examined in connection with their description in "F."

STAGE "H," 8 DAYS OLD.

(Figures 33 and 34.)

In the oldest larvæ I have, the metamorphosis has been almost completed. The larval organ has nearly disappeared, that part of it which yet remains being found sticking to the edge of the aboral disk of the young pentagonal star.

When living the little ophiurids clung to the bottom and sides of the aquaria dishes. Although the ciliated bands were still evident on the disk their free swimming habits had been wholly given up.

The pore canal still opens on the aboral surface, but with the growth of the latter it is traveling toward the edge of the disk, and by a continuation of this process the oral surface will ultimately be reached.

As the closure of the grooves over the nervous system took place, circular areas below the tips of the tentacles were left open, the tentacle pores, and through these the tentacles, were able to protrude and withdraw themselves.

The subneural sinuses which had begun to be formed in "F" have been completed in the eight-day larva (figs. 31 and 34 ss). In "H," then, the nervous system is cushioned below by the subneural sinus and above by the outer perihæmal ring.

The stomach, which for so long a period has been at a standstill in its development, has begun to grow, its sides pushing out between the epigastric and hypogastric body cavities. The lumen of both stomach and œsophagus have reappeared (fig. 34 s). The glandular structure which makes the walls of the stomach so complicated in the adult has not begun to form in "H," the walls being simple and one cell in thickness.

No figure of "H" as a whole object has been made for the reason that the skeletal plates should be included, and material adequate to a complete study of them is at present not in my possession.

RELATION OF LARVA TO ADULT.

The hydrocœle is the first organ to show radial symmetry in the developing larva of *Ophiura brevispina*, and from the time when this organ has completed its rotation about the œsophagus it shows a definite relation to the plane of bilateral symmetry of the larva.

The hydrocœle is not only radially symmetrical, but bilaterally symmetrical, since it is divided into symmetrical halves by the plane which passes through radial canal 3 and through the interradius of the stone canal. This plane coincides with the plane of bilateral symmetry of the larva. The other parts of the star are built about the water vascular system; hence it, as a whole, bears a similar relation to the larva as was initiated by the hydrocœle.

No secondary twisting of the various parts of the star occurs, and its relation to the larva remains constant as it began, and throughout the life history of the species the following statements hold true: Ventral and dorsal in the larva are equivalent to oral and aboral in the adult. Although no physiological differentiation exists, if we regard that part of the adult as anterior which was anteriorly directed in the free swimming larva, the trivium is anterior, the bivium is posterior.

In the foregoing I have confirmed, in an ophiurid, the conclusions drawn by GOTO from his studies on a starfish. In his work on the development of *Asterias pallida* GOTO (5) thought he was able to prove the coincidence of bilateral symmetry, which obtains in the adult starfish, with the plane of bilateral symmetry of the bipinnarian and brachiolarian larvæ.

The study of the relation of larva to adult in the starfishes is made most difficult, however, by the independent origin and subsequent twisting of the parts of the star. At the time of their origin no two parts of the star bear the same relation to the larva. The relation of each part to the larva also changes as metamorphosis proceeds.

The facts just enumerated admit of other conclusions than those deduced by GOTO, and no

two investigators have reached the same conclusion. The point of view from which the subject has been approached is not the same in all cases, but the results obtained by those who have studied the question admit of being reduced to the same basis; that is, the relation of the planes of bilateral symmetry in larva and adult.

CUÉNOT (4) in his latest work denies the existence of any known relation between them.

SEMON (13), working on a holothurian, found the two planes in question to coincide, but his conclusion is based on the supposition that the dorsal mesentery of the adult is the same as that of the auricularia larva, which supposition BURY has since shown to be incorrect.

BURY (3), after working on members of all the groups of echinoderms, concluded that the plane of bilateral symmetry of the larval form coincides not with the plane dividing the adult form into two symmetrical halves, but with the plane of radial symmetry.

MCBRIDE'S (10) observation on a starfish, *Asterina gibbosa*, led him to adopt about the same view as that of BURY. He found that the plane of radial symmetry of the star makes an angle of 70° plus with the frontal plane of the larva, but may, without error, be considered as 90°. This is equivalent to saying that the plane of radial symmetry of the star is parallel with the sagittal plane or the plane of bilateral symmetry of the larva, and is also reducible to the statement that the planes of bilateral symmetry of the larva and adult are at right angles to one another. Thus right and left in the larva become aboral and oral in the adult.

The difference in results arrived at by GOTO and MCBRIDE are due almost wholly to the stages in the metamorphosis selected in each case for the study of the question, GOTO selecting a very late stage, when the larval body had all but disappeared, while the stage chosen by MCBRIDE is an early one, in which the rudiments of the star are just appearing.

If the five groups of echinoderms have sprung from a common stem after radial symmetry had been established, then in the metamorphosis which is found in all the groups there should be discoverable a unity of relation between larva and adult. It is hard to conceive of the radial symmetry of echinoderms as having been independently acquired by each group, although it is easy to see how secondary changes may have arisen in the metamorphosis since the groups separated.

The five groups of echinoderms stand isolated from one another almost as completely as does the echinoderm phylum from the other phyla of the animal kingdom, and it is not my intention at this time to enter into a discussion of the interrelationships of echinoderms. I wish, however, to point out an interesting series of facts presented by members of the Asterid, Crinoid, and Ophiurid groups which may have a bearing upon the subject, and in the same connection I wish to call attention to how well MCBRIDE'S hypothetical ancestor of the Asterids and Crinoids (10, fig. —), when details are not too closely compared, fits into the facts of the larva of *Ophiura brevispina*.

In one of the Asterids GOTO has shown that toward the end of metamorphosis the almost complete star sits as a cap at the posterior end of the larva, with its aboral end posterior, its oral surface anterior, the bivium dorsal, and the trivium ventral.

In Antedon, like the starfish, the rotation brings the developing crinoid head to the posterior end of the larva, but differing diametrically from the starfish in that the oral instead of the aboral surface of the crinoid is posterior; but this difference does not in any way affect the homologies between the two groups as has been supposed.

In *Ophiura brevispina* the relation of larva and adult at the time of metamorphosis is approximately the same as is shown in Stage "F" (fig. 22), in which ventral in the larva is ventral (oral) in the adult.

Now, if we take an ophiuran larva at Stage "F," and imagine the disk to rotate in such a way as to bring its oral surface away from the larval organ or preoral lobe, it fairly represents that which takes place in the metamorphosis of Antedon, but if we think of it as rotating in the opposite way, bringing the aboral surface away from the preoral lobe, then it more nearly illustrates the starfish metamorphosis.

In Antedon, as metamorphosis proceeds, the stem is carried on to the aboral surface, while in the starfish the preoral lobe finally disappears on the oral surface. In *O. brevispina* the place of disappearance of the larval organ more nearly recalls the crinoid than any other echinoderm, the larval organ being found in some of my oldest specimens as a small knob near the edge of the *aboral* surface between arms I and V.

COMPARISON OF THE LARVA OF ANTEDON ROSACEA WITH THAT OF OPHIURA BREVISPINA.

While I was studying the larva of *Ophiura brevispina*, characters were constantly being found which reminded me of the larva of Antedon as described by BURY (1). Some of these points of resemblance are no doubt only superficial, but others are such as to make it worth the while to devote a short chapter to the similarities of the two larvæ.

The entire ciliation of the very young larvæ gives place in both to a series of transverse ciliated bands, five in Antedon, four in Ophiura. The band nearest the anterior end of the Antedon larva, however, is small and incomplete. Two bands only in each case surround that part of the larva from which the disk is formed.

The blastopore in both larvæ, after shifting from a posterior position to one on the ventral surface, closes and the archenteron loses its connection with the ectoderm and lies free in the body cavity.

In the seven-day embryo of Antedon and Stage "C" of Ophiura the hydrocœle is a horseshoe-shaped structure lying in the posterior ventral part of the larvæ with the open end directed anteriorly, and in each case the plane of radial symmetry of the hydrocœle is at right angles to the plane of bilateral symmetry of the larvæ.

In the formation of the paired tentacles from the radial water canals the process is *begun* centripetally in both larvæ, the second pair of tentacles appearing between the first pair and the water ring instead of between the first pair and the end tentacle, as is the case in the other groups of echinoderms.

In the five-day Antedon larva and those stages represented by "D" to "F" in Ophiura the stalk and larval organ are strikingly similar, both in shape and position, the two structures being anteriorly directed in swimming.

The stem of the Antedon larva, as a result of metamorphosis, comes to be an aboral structure, and just before the disappearance of the larval organ from the ophiuran larva it is to be found as a small knob, not in the *center* of the aboral disk, it is true, but on its edge. In the starfishes it may be recalled that the preoral lobe disappears on the *oral* surface of the metamorphosing star.

To the above larval characteristics may be added the similarity which exists in the disposition of the alimentary and cœlomic systems in the adult forms.

In both Crinoids and Ophiurans the digestive apparatus is confined to the disk.

The body cavity is continued into and to the ends of the arms. When a transverse section of a pinnule of Antedon is compared with a transverse section of an ophiurid arm, the following striking correspondence is found in the parts: Aborally, segmentally arranged calcarious ossicles and muscles are present; a continuation of the body cœlom runs between and oral to the muscles; connected with and on each side of this central brachial body cavity are two other cavities, the subtentacular canals of Antedon. These latter in the Ophiurans are connected with perihæmal space in each vertebral segment.

The radial water tube lies between the subtentacular canals, and in each segment sends out a pair of tentacles. The tentacles in both the Crinoids and Ophiurids are devoid of the terminal suckers, which are so characteristic of the other echinoderms.

Separating the radial water tube from the nerve cord is to be found the radial perihæmal sinus.

In ophiurans a subneural space is present which is not represented in the crinoid arm. This is due to the fact that in Antedon the nervous system is superficial, while in Ophiura it has been invaginated, and with its invagination a space has also been carried in below it.

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EXPLANATION OF PLATES.

The figures illustrating this paper were drawn to the same scale of magnification, 330 diameters, and were reduced one-half in reproduction.

Figs. 1, 2, 4, 6, 7, 9, 17, 31, and 32 were reconstructed from series of transverse and sagittal sections.

In all cases the part of the figure which is nearest the top of the plate is either anterior or else ventral in the larva.

ABBREVIATIONS USED.

ael	Left anterior enterocœle.
aer	Right anterior enterocœle.
ap	Apical plate.
ax sin	Axial Sinus.
b	Blastopore.
ch 1, 2, 3, and 4	Ciliated bands.
eg	Circular groove.
em	Circular mesentery.
ep	Cellular plug.
d	Dorsal pore.
ee	Epigastric enterocœle.
et	End tentacle.
hc	Canal connecting posterior enterocœle and hydrocœle.
he	Hypogastric enterocœle.
hip 1-2, 2-3, 3-4, 4-5	Interradial pouches of the hypogastric enterocœle.
hy	Hydrocœle.
ips	Inner perihæmal sinus.
ipax 5 1	Interradial pouch of axial sinus.
lo	Larval organ.
m	Mouth.
mes	Mesenchyme.
n1	First pair tentacle nerves.
nr	Nerve ring.
oe	Œsophagus.
od	Oral disk.
opr	Outer perihæmal ring.
pc	Pore canal.
pe	Posterior enterocœles.
pv	Polian vesicle.
rad n	Radial nerves.
rg	Radial grooves.
rps	Radial perihæmal space.
sin a	Sinus "a".
sin b	Sinus "b".
st	Stone canal.
ss	Subneural sinus.
s	Stomach.
t1	First pair foot tentacles.
t2	Buccal tentacles.
wvr	Water vascular ring.
I, II, III, IV, V	Arm rudiments.
1, 2, 3, 4, 5	Radial water canals.

PLATE I.

FIG. 1. Larva in Stage "A," seen from the right side, the right half of the ectoderm removed and the mesenchyme omitted.
FIG. 2. The same larva, seen from the ventral side as a transparent object.
FIG. 3. Median longitudinal section of a larva in Stage "A."
FIG. 4. A larva in Stage "B," viewed from the ventral side as a transparent object.
FIG. 5. Transverse section of a larva in Stage "B" in a plane halfway between the blastopore and the point where the hydrocele is connected with the archenteron.
FIG. 6. Larva in Stage "C," seen from the ventral side, the ventral half of the ectoderm, the mesenchyme, and part of the œsophagus removed.
FIG. 7. The left half of the same larva.
FIG. 8. Transverse section through Stage "C" in a plane indicated on fig. 6 by the letters *a–b*.
FIG. 9. The reconstructed internal anatomy of a larva in Stage "D," the ventral ectoderm removed and with it part of the œsophagus.
FIG. 10. An outline drawing of fig. 9, on which are indicated by lines the planes of the sections which follow in figures 11, 12, 13, and 14.
FIG. 11. Longitudinal section taken through a larva in Stage "D" in the plane indicated on fig. 10 by the line *m–n*.
FIGS. 12, 13, and fig. 14 of Plate II. Transverse sections taken through Stage "D" in planes indicated on fig. 10 by the lines *a–b*, *c–d*, and *e–f*.

PLATE II.

FIG. 15. Ventral view of a larva in Stage "E," to show ciliated bands and first appearance of the arm rudiments.
FIG. 16. Dorsal view of Stage "E," showing the ciliated bands.
FIG. 17. A reconstruction of the anatomy of a larva in stage "E," the ventral ectoderm removed.
FIG. 18. An outline drawing of fig. 17, on which are indicated by lines the planes of the sections shown in figs. 19, 20, and 21.
FIGS. 19, 20, and 21. Transverse sections taken through larva in Stage "E" in planes indicated on fig. 18 by the lines *r–s*, *t–u*, and *v–w*.
FIG. 31. Reconstruction of the anatomy of a larva in Stage "G." In this case as in all the other reconstructions the ventral surface is up and the ventral ectoderm removed.
FIG. 32. An outline drawing of the water vascular system of a larva in Stage "G," seen from the ventral surface.
FIG. 33. Transverse section of Stage "H," taken through the region of the stone canal.
FIG. 34. Transverse section of a larva in Stage "H," taken through the stomach.

PLATE III.

FIG. 22. Ventral view of the fully developed larva before metamorphosis has begun. Stage "F."
FIG. 23. Outline drawing of fig. 22. The lines indicate the planes of the sections, which have been drawn to show the anatomy of a larva in Stage "F."
FIGS. 24, 25, 26, and 27. Longitudinal sections of a larva in Stage "F," the planes of which are indicated on fig. 23 by the lines *a–b*, *c–d*, *m–n*, and *x–y*.
FIGS. 28, 29, and 30. Transverse sections of a larva in Stage "F," the planes of which are indicated on fig. 23 by the lines *c–o*, *d–o* and *e–o*.

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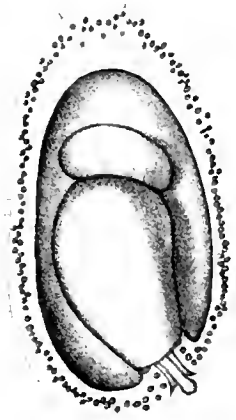


Fig. 1.

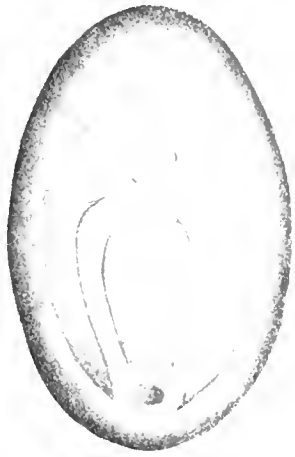
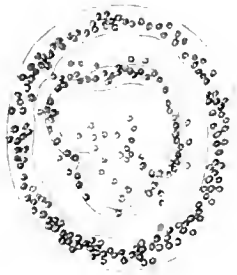


Fig. 2.

Fig. 3.

Fig. 4.



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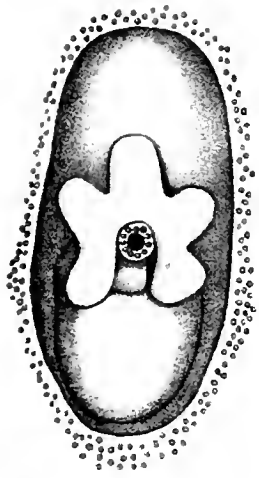


Fig. 6.

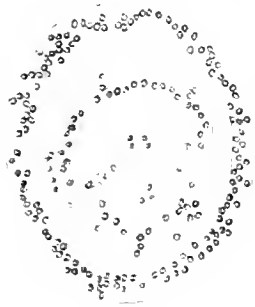


Fig. 8.

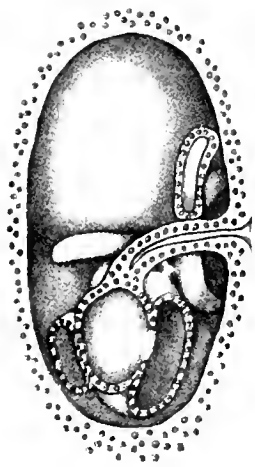
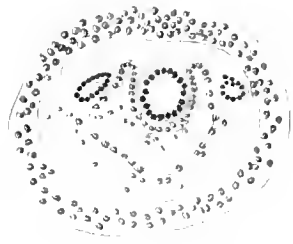


Fig. 7.

Fig. 11.



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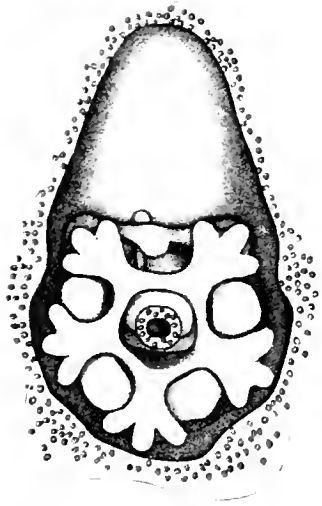


Fig. 9.

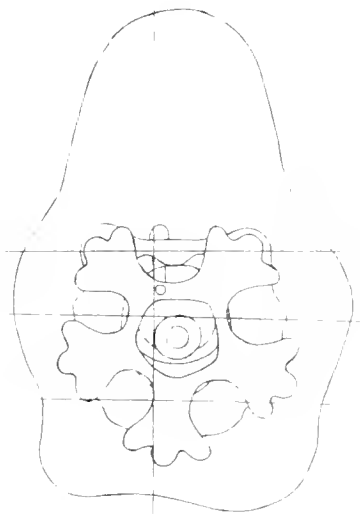


Fig. 10.

Fig. 13.

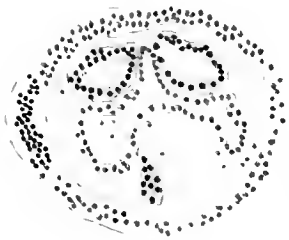


Fig. 14.

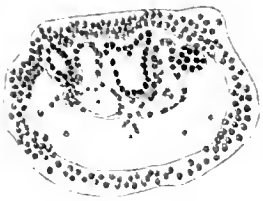


Fig. 19.

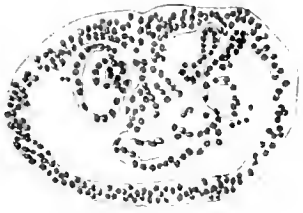


Fig. 20.

Fig. 21.

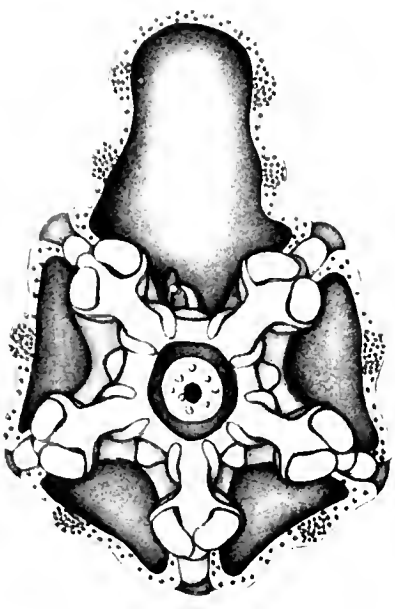
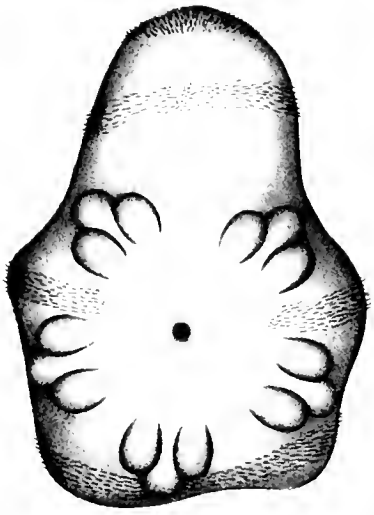


Fig. 31.



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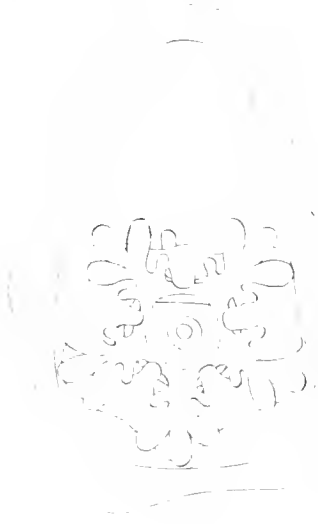

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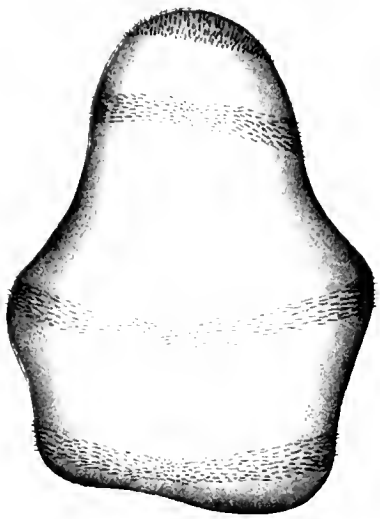
Fig. 32.



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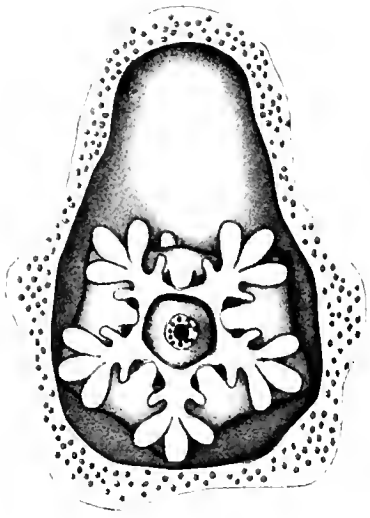

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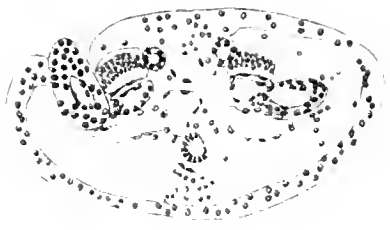

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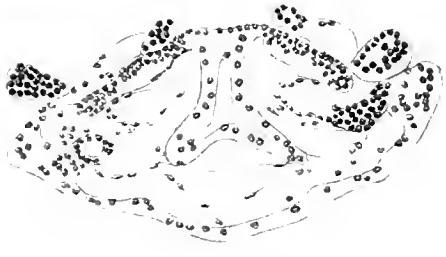

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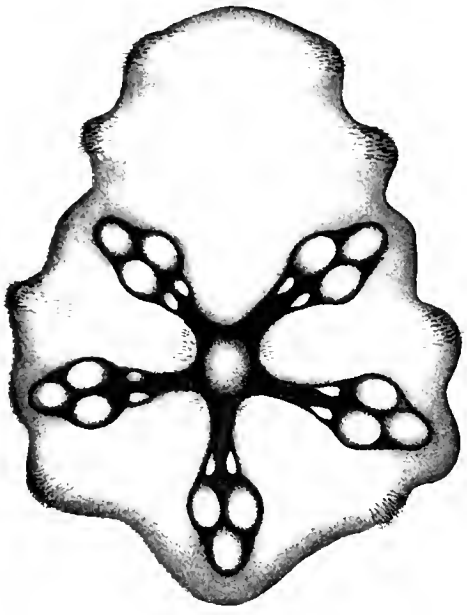
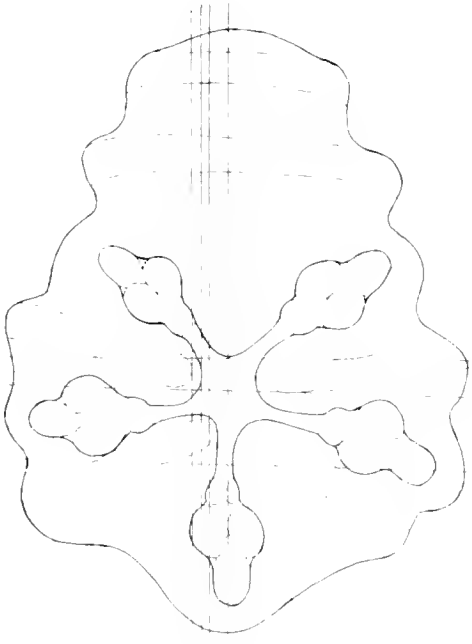


Fig. 22.

Fig. 24.

Fig. 25.



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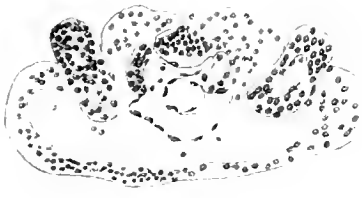

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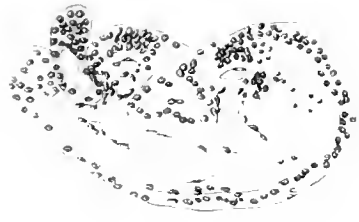

Fig. 29.

Fig. 30.

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ANATOMY OF NAUTILUS POMPILIUS.

THE ANATOMY OF NAUTILUS POMPILIUS

BY LAWRENCE EDMONDS GRIFFIN,

Bruce Fellow of Johns Hopkins University.

[Communicated by Prof. WILLIAM KEITH BROOKS.]

INTRODUCTION.

In the year 1890 Mr. LOUIS F. MENAGE, of Minneapolis, Minnesota, generously enabled the Minnesota Academy of Sciences, of the same city, to make scientific collections in the Philippine Islands. Prof. DEAN C. WORCESTER and Dr. FRANK S. BOURNES made the expedition to the islands for the Academy, gathering in the course of their three years stay a large collection of scientific material.

Certain anatomical material was comprised in the collection. This the Academy placed at the disposal of the Department of Animal Biology of the University of Minnesota.

In the collection of anatomical material were sixty-six specimens of *Nautilus pompilius*. It is these specimens which Professor NACHTRIEB allowed me the privilege of studying after I came to him as a student of zoology, and upon which the following paper is based.

While the specimens were not sufficiently well preserved to allow of histological study throughout, they were, for the most part, excellently preserved for anatomical study, Professor WORCESTER having taken care that they should not be contracted, and that they should be as well preserved as the circumstances permitted. Some of the external parts, however, were found to be in good order for the study of their microscopical anatomy, if not for cytological study.

My studies upon the Pearly Nautilus were commenced at the University of Minnesota, under the guidance of Professor NACHTRIEB. I wish to express my indebtedness to him for the rare privilege of studying this material, in which I have found great pleasure as well as profit, and to thank him for much kindness and many helps in the course of my work.

The work has been completed since I came to Johns Hopkins University, and I wish to express my gratitude to Professor BROOKS for his interest in my work and for advice and assistance which have enabled me, I hope, to correct or to avoid some of the faults to which my inexperience lays me liable.

Professor WORCESTER has also been very kind to me in furnishing me with what information he possessed in regard to the occurrence, habits, and mode of capture of the Nautilus.

The soft parts of the Nautilus remained unknown until the year 1832. It is true that long before this RUMPH had published a figure of the animal, accompanied by a description of its habits and portions of its anatomy, but the figure is not remarkable for its clearness, and the description was unintelligible until elucidated by the figures and accounts of later observers. At a later date than RUMPH, QUOY and GAIMARD published a notice regarding what they supposed to be a portion of the body of a Nautilus.

In the year mentioned OWEN published his famous Memoir on the Pearly Nautilus. This still remains the best work which we have upon the anatomy of Nautilus. When we consider

that OWEN had but a single specimen for dissection and no guides in his work, we can not but recognize the patient genius which enabled him to produce so complete, clear, accurate, and enduring a work.

The work of VALENCIENNES (1841) added to our knowledge minor facts which OWEN had not described, beside correcting OWEN in a few slight errors.

Both these anatomists had female specimens. VAN DER HOEVEN (1848, 1856) was the first to dissect and describe a male Nautilus.

Between then and now numerous papers have appeared treating of various points in the anatomy of Nautilus. But still its development is entirely unknown. Only recently WILLEY has spent a considerable time in New Guinea in the endeavor to obtain its embryology. He has published a number of interesting papers upon details of its anatomy and its habits, and has succeeded in obtaining fertilized eggs, but has so far kept silence regarding their development.

Such a paper as my own may seem superfluous to many in view of the numerous papers which have already been published upon the same subject. But I hope that it will have a useful place since I have endeavored to gather together the various disconnected accounts of Nautilus anatomy and, adding to them what new facts I have been able to discover, to publish an account of the gross anatomy of Nautilus which shall be as complete as possible. Few persons have the opportunity, and still fewer the time to examine all the various papers on this subject, so I hope that, beside adding to our knowledge of Nautilus, this paper may be found convenient by the student of comparative anatomy.

Although the shell of the animal might properly be considered in an anatomical description, in this case it is so well known that another description of it by me would serve no good purpose.

The Nautili of the Menage collection were captured in water of 1,800 feet depth off the southern coast of Negros, Philippine Islands. An extract from a letter of Professor WORCESTER to the Minnesota Academy of Natural Sciences tells of the mode of capturing the animals.

"Their (the natives') method is to lower a large bamboo basket, baited with meat, in six or eight hundred feet of water. This basket is made on the principle of the old-fashioned rat trap, allowing the animal to enter easily but preventing its escape. Every morning these traps are drawn up for inspection, and a single one sometimes contains four or five live Pearly Nautili: which are sold for food, bringing about 4 cents apiece."

This was written after a preliminary examination of the ground, but several months before the capture of the specimens which were sent to this country. The specimens taken by the expedition were caught in deeper water than that mentioned in the letter.

The natives ordinarily set their traps for a deep-sea food fish, the capture of the Nautili being in a measure accidental, at most, incidental.

Nautilus is not confined to deep water. It has generally been found there, but WILLEY has also obtained it in water only 2 or 3 fathoms in depth.

Nautilus is carnivorous, and apparently predatory, the crop and stomach of captured specimens being usually filled with fragments of crustacea, or the chicken, or fish, or whatever other meat is used for baiting the trap. The appearances indicate that it feeds mostly upon a species of decapod crustacea. These are devoured shell and all. The jaws appear strong enough to crush any moderately thick-shelled mollusk upon which the Nautilus might happen.

WILLEY (1897, 1) says: "One of the surest ways of obtaining Nautilus, and in fact, the method by which I have obtained most of my specimens at Lifu, is to bait the fish basket with the cooked and bruised exoskeleton of Palinurus, or an allied form. The strongly scented 'potage' so produced is then wrapped up in cocoanut fibre like a small parcel, and then placed in the fish trap overnight. There is therefore nothing to be seen, but on the other hand there is something to be smelt, and by this means I have obtained as many as ten Nautili at one time."

While this observation points to the probability of Nautilus being chiefly guided by its sense of smell in the capture of its prey, it is not by any means proof that the eyes are not also useful in this action. We would rather expect that smell would be the guiding sense from the fact that the Nautilus is usually found at great depths where darkness must prevail, and from the simple character of the eyes.

GENERAL SKETCH OF ANATOMY.

The Nautilus occupies a light gracefully formed shell, which is beautifully marked with alternating bands of reddish brown and white, except near the mouth, where the dark bands do not interrupt the white ground. (Fig. 11). The shell is coiled dorsally (exogastrically) so that the older parts are completely hidden by the younger. An adult shell has about two and a half whorls. As the Nautilus increases in size it grows forward in its shell, leaving an unoccupied space behind itself. At frequent intervals it forms septa which completely separate the unoccupied portion from the living chamber of the shell, except at the centers of the septa, where they inclose a tubular process of the body wall, which extends to the oldest chamber of the shell. (Fig. 1.) The unoccupied chambers of the shell are filled with a gas which resembles air in its composition, but having a slightly greater proportion of nitrogen than the latter.

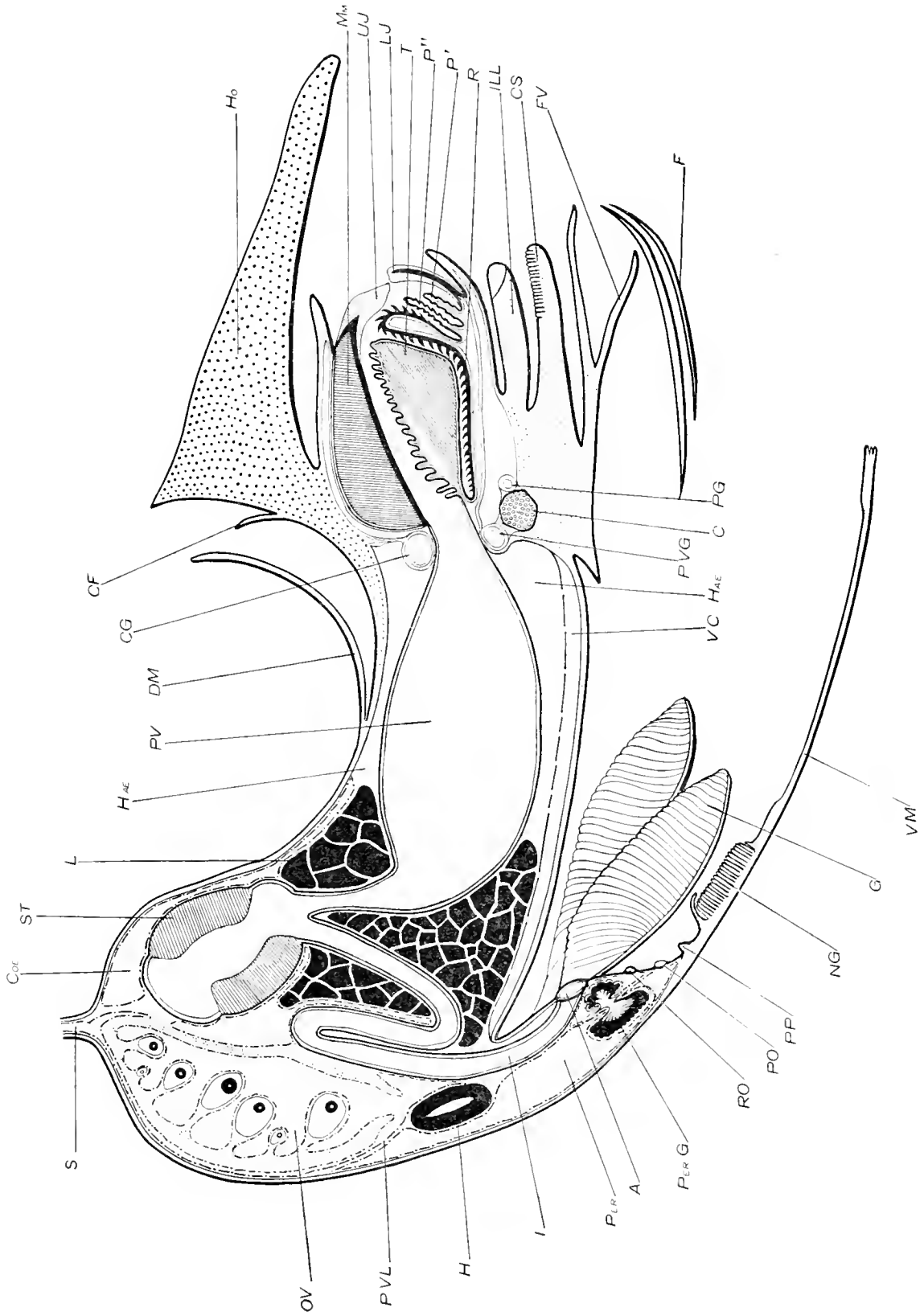
When the Nautilus is in its natural position the involution of the shell is uppermost, while the mouth of the shell is below and turned forward. (Fig. 1.) The body is now nearly horizontal; the head, surrounded by tentacles, is anterior; the siphuncle is near the posterior end of the body; the funnel is upon the ventral side, and the depression which receives the involution of the shell marks the dorsal side of the body. (Fig. 2.) The orientation of the body and the description of the anatomy are made more difficult by the upward curve of the posterior part of the body. Thus, the siphuncle springs from the dorsal surface near the posterior end, and not from the extreme posterior end of the body. (Fig. 2.)

The body of Nautilus is roughly oblong, and between 6 and 7 inches in length. The anterior portion of the animal which projects from the shell, comprising the cephalic and nuchal regions, with the jaws, organs of sense, motion, and adhesion, is tough and muscular. The posterior portion of the body is covered and protected by the shell, and consequently the body wall is here so thin that the viscera can easily be distinguished through it.

The part of the body contained within the shell conforms exactly to the latter. In the middle dorsal region the body is deeply hollowed to receive the involution of the shell. All other portions of the body within the shell are smoothly and evenly convex. The anterior part of the body is covered by the large triangular hood. At the sides and ventrally are the numerous digital tentacles, the sheaths of which, fused to each other and the hood, form a solid wall around the mouth parts, to which the name cephalic sheath has been given. Within the cephalic sheath are the projecting parrot-like mandibles, surrounded by several groups of smaller tentacles. Beneath is the large muscular funnel, the crura of which pass upward upon the sides of the body just back of the bases of the tentacles to the upper edges of the body, where they are joined by the crescentic ridge extending across the back of the hood. (Fig. 2, CR.) In the angle between the projecting posterior corners of the hood, the back of the cephalic sheath and the crura of the funnel, are the large round eyes (E). Two tentacles, the pre- and post-oculars (Fig. 1, O′, O″), spring from close to the base of each eye, while just beneath each eye is a small projecting pyramidal organ supposed to have an olfactory function.

The mantle fold projects freely entirely around the body. The edge of the mantle is attached along the edge of the shell, but from the umbilicus of the shell upward it extends as a convex fold covering the dark portion of the involution of the shell. The mantle cavity is shallow dorsally, while very deep and capacious ventrally. The organs of the pallial complex are all within the ventral portion of the mantle cavity. (Fig. 3.) The four gills, the renal, pericardial, and anal orifices, and certain papillæ sometimes spoken of as osphradia, are borne by the mantle. In adult females the inner side of the mantle also bears a large bilateral nidamental gland. (Fig. 4, N.) The reproductive orifices are situated upon the body wall near the origin of the mantle. The mantle is continuous posteriorly with the thin and transparent wall of the visceral portion of the body.

The body wall is produced from the end of the body as a slender tube, the siphuncle, which extends within the siphon of the shell to its very end. (Fig. 1, fig. 2.) At the sides and above the middle of the body are seen the crescentic areas of attachment of the strong shell muscles by which the body is held to the shell. (Fig. 1, SM.) Beside these areas of attachment, the wall of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TEXT-FIG. 1.—DIAGRAMMATIC LONGITUDINAL SECTION OF NAUTILUS.

A, anus.
C, cartilage.
CF, crescentic fold on back of head.
CG, cerebral ganglion.
Coe, genital division of coelom; the coelomic epithelium is indicated by the dotted line.
CS, ventral portion of cephalic sheath bearing the folds which receive the spermatophore.
DM, dorsal portion of mantle.
E, overlapping edges of funnel.
EV, valve of funnel.
G, gill; the bases of the gills lie in the sides of the plane of section.
H, heart.
HVC, hectocotyl.
Ho, hood.
I, intestine; brought into the plane of the diagram.
ILL, inferior labial lobe.
L, liver.
LJ, lower jaw.
MM, mandibular muscle.
NG, infundibular gland.
OV, ovary.
P, anterior pedingual process.
pp, posterior pedingual process.
Per, pericardial division of coelom.
PerGl, anterior pericardial gland; opposite is the renal appendage on the renal sac. These parts have been moved slightly medial to be in the plane of section.
Pd, pedal commissure.
Po, pericardial pore.
PP, preanal papilla.
PV, preoral velum.
PVG, pleuro-visceral ganglion.
PVL, pallio-visceral ligament.
R, radula; the radular sac extends backward under the tongue as far as the commencement of the œsophagus.
RO, renal pore.
S, siphuncle.
ST, stomach, suspended from the ovary by the gastric ligament.
T, tongue.
UJ, upper jaw.
VC, vena cava.
VM, ventral portion of mantle.

the body is attached to the shell along three aponeurotic bands, two ventral and one dorsal, which extend between the ends of the areas of attachment of the shell muscles. (Fig. 1.)

The division of the body of the Nautilus into cephalic, nuchal, and visceral regions is not as distinct as it is in many dibranchiates. At times it proves convenient to recognize such divisions, although they are entirely without morphological importance. For this reason we may consider the cephalic region to be that which bears the tentacles, buccal mass, and eyes. A section through the body just back of the eyes would also pass just back of the central nervous system. The nuchal region is that of less girth, which extends between the posterior edges of the cephalic sheath and the attachment of the mantle. Accordingly, this bears the funnel and its crura, the reproductive orifices, and the mantle. The visceral region comprises the remaining posterior portion of the body, the wall of which we have already noted as thin and semitransparent.

THE TENTACLES.

A.—Digital Tentacles.

For the purposes of description each tentacle will be considered to consist of two parts—a cirrus, which is the active part of the organ, and a sheath which forms a protection for the cirrus. The sheath of certain tentacles is lacking (or undifferentiated), the cirrus, never normally. In this application of the terms we need not take into account the probable morphological importance of the sheath.

The digital tentacles include those tentacles which form the cephalic sheath and hood. Each is composed of two parts—a retractile (or extensible) adhesive cirrus, and a tough, thick-walled, more or less rigid sheath into which the cirrus may be entirely withdrawn. (Fig. 1, C; Fig. 49; Fig. 50.) This is the essential structure of not alone the digital tentacles, but all the tentacles with which a Nautilus is so generously supplied. Whatever differences there are, they are modifications of this plan.

The digital tentacles are symmetrically arranged upon each side of the head, according to the diagram presented in text-figure 2, CS, p. 116. A careful examination of more than fifty specimens has led me to make this statement in the face of other statements denying any regularity of arrangement of these tentacles. Whether each individual tentacle, as determined by the innervation, always occupies the same identical position is more than I can assert, because of the extreme difficulty of satisfactorily following the nerve to each tentacle. However this may be, the arrangement of the tentacles follows a definite plan from which variations were found in only five specimens out of fifty-one examined at one time.* Except in one case the variation occurred upon one side only. I see no especial morphological importance to be attached to this arrangement; nevertheless, the fact is interesting and its knowledge may sometime be helpful when the development of Nautilus comes to be studied.

As has already been mentioned, the cephalic sheath is formed by the fusion of the sheaths of the individual digital tentacles. The hood, which forms the entire dorsal part of the cephalic sheath, is itself composed of the enormously developed sheaths of two tentacles. (Fig. 1, Ho; Fig. 2, Ho.A.) The hood is roughly triangular in shape. It is thickest in its middle posterior part, sloping from here to thin edges anteriorly and laterally. It presents three superficial fasciæ (Fig. 2): a dorsal about an inch in width sloping downward and forward to the anterior edge, and two lateral which slope from the middle fascia to the lateral edges. The dorsal fascia maintains an equal width throughout its length—this varying in different specimens between 18 and 25 millimeters. Accordingly the anterior edge of the hood is approximately straight and not pointed. The lateral fasciæ, however, are widest opposite the posterior end of the middle fascia, gradually narrowing to a point anteriorly, and to a blunt rounded extremity posteriorly which overlies the umbilicus of the shell. The posterior surface of the hood is pressed closely against the involution of the shell, and following its shape is deeply concave. The postero-

*The tentacles of a dozen other specimens since examined have conformed to the same plan.

lateral corners lying against the umbilici of the shell are sometimes spoken of as the auricles of the hood. (Fig. 2, Ho.A.) In most specimens a slight groove runs along the middle of the dorsal fascia of the hood, although it is frequently absent.

Scattered more or less evenly over the surface of the hood are numerous small papillæ. The possibility of these possessing a tactile function is immediately suggested, but my material shows no structure to confirm it. The papillæ are differently distributed upon different Nautili, in some being most thickly placed upon the median portion of the hood, in others upon the lateral parts. But comparing one specimen with another, the papillæ may be said to be evenly distributed over the entire surface.

In the anterior edge of the hood are two small openings leading into deep cavities, in each of which is a cirrus exactly similar to the cirri of the neighboring tentacles. (Fig. 2, Ho.C.) The presence of the cirri, the innervation and the anatomical relations of the hood, and the fact that the neighboring tentacles are sometimes closely fused with it leave no doubt that the hood is composed of two tentacles, the sheaths of which have become much enlarged and closely fused. It seems probable that the hood of the Nautilus, aside from its other uses, serves to protect the animal when withdrawn into its shell in much the same way as the operculum of a Gastropod protects its owner. It is noticeable how closely the hood of a strongly contracted Nautilus fits the opening of the shell.

A cleft of varying depth existed in the middle of the anterior edge of the hood of several specimens in line with the median groove before mentioned. This may be an indication of an originally less completely fused condition of the hood tentacles.

Below the hood are eighteen digital tentacles upon each side. Including the tentacles forming the hood there are thus nineteen upon each side, a number from which I found no variations in any of sixty-six specimens. But that variations in the number do occur is proved by the fact that Rumph and Owen each counted twenty tentacles upon a side, while Valenciennes found only eighteen upon a side in his specimen. In another specimen Owen found only seventeen tentacles upon one side, while the number was normal upon the opposite side.

The sheaths of the digital tentacles are fused to each other except for a distance of about half an inch at their tips. The exterior of the cephalic sheath is made rough by the projecting angles of the tentacle sheaths, and by this means the course of the individual sheaths can be followed to a certain degree. The internal surface, on the other hand, is perfectly smooth except at one point. The exception is possessed by the female only. Upon the outside of the cephalic sheath are seen four tentacles which are so much smaller than the others that they do not begin to reach the anterior edge of the sheath.

The tentacle next the hood on each side possesses a much larger sheath than the remaining lateral tentacles, the increase in size being especially expressed in breadth. The sheath is considerably flattened and overlaps the next lower tentacle sheath as it is itself overlapped by the edge of the hood. It is usually fused along nearly its entire length to the ventral side of the hood, leaving a crease where the edge of the hood projects. (Fig. 1; Fig. 2, DT^2.) Its outer surface bears papillæ like those upon the hood. Normally the tip of the sheath is entirely free, but occasionally its sheath and the hood are so closely fused that no line of demarcation can be observed, the tips of the sheaths being included in the fusion. Rarely other more lateral tentacles may be included in this close fusion, so that the area of the hood may be considerably increased.

The remaining tentacles present no differences beyond those of size and shape which we may expect to find. The tips of the sheaths where their shape is unaffected by fusion are roughly triangular or quadrangular. Usually one of the angles is turned outward, and this may be continued as a distinct ridge nearly or quite to the posterior edge of the cephalic sheath.

At the sides of the head the posterior part of the cephalic sheath falls away abruptly to the level of the nuchal region. (Fig. 1.) These posterior faces are quite smooth. From the hood they slope first down and back, then, from the level of the lower edge of the eye, they slope down and forward. The faces become narrower as they pass downward and gradually disappear upon

the ventral surface of the cephalic sheath. The eyes are situated partly within the angles between the auricles of the hood and the upper portions of the just described posterior faces of the cephalic sheath.

In the ventral surface of the cephalic sheath is a broad and deep channel, into which fits the dorsal part of the funnel. (Text-fig. 2; Pl. 3, Fig. 3.) The anterior edge of the sheath, in line with the channel, is deeply notched, so that ventrally the tentacles of the two sides are widely separated. (Figs. 24 and 25.) Partly surrounding and extending back from the edges of the ventral notch in the cephalic sheath of the female is the exception previously noted to the complete smoothness of the inner surface of the cephalic sheath. (Figs. 24 and 25.) We see here a large number of low, narrow, glandular lamellæ extending parallel to each other from side to side of the area. The lamellæ of the anterior half of the organ frequently radiate from centers at each side of the notch in the sheath. Consequently, while their median portions extend transversely to the axis of the body, the lateral portions turn more or less sharply forward. The posterior lamellæ do not reach the centers referred to, and so the forward bend at the sides becomes less and less pronounced as the back of the area is approached. Finally the most posterior lamellæ are almost straight.

Considerable differences exist in the shape of this area in different specimens. The one which I have described and figured in Fig. 24 seems to be quite rare, although for a considerable time I thought it to be the normal shape. Instead, the lamellæ rarely meet at such centers as I have figured. The differences in the descriptions of various authors suggest that practically the only constant feature may be the presence of numerous lamellæ, while their arrangement is capable of a high degree of variability. Frequently the area is nearly or quite separated into two portions by a median furrow. Valenciennes and Lankester refer to the organ as a paired structure. Owen describes it as consisting of "two clusters of soft conical papillæ, and on each side of these a group of laminæ disposed longitudinally".

As noted, the organ, as it may fairly be called, exists in the female only. Slight folds of the skin are often found in the same region of the male, but they are evidently adventitious, resulting from contraction, and do not in any way represent a structure similar to the one possessed by the female.

The lamellæ of the female form an organ for the retention of the spermatophore. In the case figured (Fig. 25) the spermatophore is arranged with unusual symmetry. In no other instance was it so nicely coiled as in this, though it was always spread out upon the surface of the lamellæ so that few coils overlapped. The coils of the spermatophore were in all cases so firmly glued to the lamellæ that it was impossible to remove them without breaking either lamellæ or spermatophore. Kerr mentions that in his specimen the spermatophore was partly embedded in the coagulated secretion of the lamellæ. The secretion has not been so noticeable in my own specimens, being only sufficient to hold the spermatophores, but that very tightly.

Having considered the digital tentacles as a complex, the cephalic sheath, let us now consider their individual structure. It has been noticed that each tentacle comprises two parts, namely, a slender retractile cirrus and a tough sheath within which the cirrus may be entirely withdrawn.

The completely extended cirri are often fully twice the length of the sheaths. They are supple and slender, tapering slightly to a bluntly rounded point. Average dimensions of the larger cirri would be 10 centimeters in length by 4 millimeters in diameter. Each cirrus presents throughout its length, except the basal portion, a series of narrow annular grooves and ridges. (Fig. 50.) These vary in number according to the length of the cirrus. Upon a cirrus of ordinary length there are 50 to 60 ridges. The cirri are ordinarily three sided in the portion which is commonly extended outside the sheath, the broadest and flattest side being turned inward toward the mouth. Exceptional cirri which are round are quite common, and in any case the outer angle of the cirrus is much rounded, and the portion which remains inside the sheath is always nearly round, being flattened only slightly upon the inner side. Willey states that the outer sides are deep brown in color, while the inner side is of a pale neutral tint. A

usual, but not a constant, feature is a shallow longitudinal groove occupying the middle of the inner face of the cirrus. (Fig. 49.)

The annular grooves are much deeper upon the inner side than upon the outer sides, and as a consequence the alternating ridges are also much more prominent upon the inner side. (Fig. 50.) To use a comparison, the cirri are somewhat like high piles of thin, flat disks, fastened together through their centers. This comparison, however, applies closely to the terminal third or half of the cirrus only. Upon the proximal part, which is always retained within the sheath, the annular grooves quickly disappear on the outer surfaces. The grooves persist on the inner side, gradually becoming fainter and fainter, until within a couple of centimeters of the proximal end of the cirrus. The proximal end of the cirrus is usually perfectly round and perfectly smooth; it tapers slightly to the base, which has about half the greatest diameter of the cirrus. The terminal disks are broken off with great ease; the query arises if regeneration of some sort does not take place. The inner projecting part of each disk forms an adhesive organ, the structure of which will presently be described in detail.

The tissues of the cirrus are continuous at its base with the tissues of its sheath. The sheaths of the larger tentacles have a depth of about 6 centimeters. The epithelium extends from the surface of the cirrus upon the inner surface of its sheath, and over the margin of the latter upon the surface of the body. The free portion of each sheath is usually angular and slightly tapering. At its blunt extremity is a round, oval, or slit-like opening, through which the cirrus projects. The cavity of the sheath frequently extends to near the cephalic ganglia—much farther, therefore, than there is any external indication of the individual sheath. With the exception of those two which form the hood, one sheath is very much like another. The reasons for believing the hood to be composed of the greatly enlarged and closely fused sheaths of two ordinary tentacles have already been given.

The tentacle sheaths are composed of a dense felt of large, branched elastic fibres; its interstices are occupied by white fibrous connective tissue fibres and nuclei. Small scattering bundles of longitudinal and transverse muscle fibres traverse the sheaths. In places the longitudinal muscles approach a regular arrangement. The amount of muscular tissue is, however, so small that there can be but very little movement of the individual sheaths. The external surface of the sheath is covered by a columnar epithelium, the cells of which measure 52μ by 4μ–8μ; the cells lining the cavity of the sheath are much lower, being only 24μ by 3μ–6μ in their dimensions. Both inner and outer epithelia contain very numerous glandular cells. The oval nuclei are situated in the lower half of the cells, but do not all lie in one plane. Large capillaries with endothelial walls are surprisingly numerous in the tissues of the sheath, and here, as elsewhere, the capillaries do not collapse when empty. But the vascular system is not completely closed. The tissues of the sheaths are like a fine mesh work, in the spaces of which the blood flows freely. There is no dermis.

The hood presents some modifications of this plan. The cells of the epithelium measure 36μ by 4μ–6μ. Immediately beneath the epithelium is a dermis formed by a layer of particularly closely woven elastic fibres which, on account of its density, is easily distinguished by the naked eye from the underlying tissue, although it can not be readily dissected away. The dermis is almost entirely destitute of muscular fibres and is penetrated in every direction by great numbers of vascular lacunæ. But even in the hood the dermis is not an absolutely constant character. Throughout the hood numbers of capillaries with endothelial walls can be seen. The capillaries are of large caliber and, curiously enough, remain open when empty, so that their cross sections are circular. In the posterior part of the hood many large muscles run in various directions just beneath the dermis. They form a layer which seems to have much to do with the contraction of the posterior portion of the hood. The muscles become smaller and less numerous toward the outer side and the deeper portions of the hood.

Posteriorly the hood is concave and fits snugly around the involution of the shell. The epithelial cells of this are smaller than those of the upper surface of the hood and of the remainder of the cephalic sheath, their dimensions being 28μ by 3μ–6μ. The epithelial cells of this surface as well as those of the upper surface of the hood are loaded with fine granules of a

brown pigment. In sections the pigment appears as a dark band near the outer ends of the cells, a narrow unpigmented band being outside this, while the pigment granules gradually disappear toward the bases of the cells, leaving this region also uncolored. These surfaces of the hood bear numerous small pits lined with the pigmented epithelium. Granular cells are exceedingly numerous, especially upon the concave posterior face of the hood. It seems probable that the dark brown, sometimes black, layer of organic matter found upon the involution of the shell is deposited by these cells. The thin crescentic ridge which projects from the posterior face of the hood does not possess a pigmented epithelium and may not play any prominent part in the deposition of the dark layer.

The great density of the elastic tissue makes the cephalic sheath exceedingly firm and difficult to penetrate. It must afford a very considerable protection to the Nautilus.

A cross section of a cirrus shows a highly muscular organ, usually of triangular outline in its terminal third. (Fig. 49.) Near the center is a large nerve which extends the entire length of the cirrus. (Fig. 50, N.) The nerve is situated toward the inner side of the cirrus, i. e., toward the flattened side turned toward the mouth of the animal. Close to the nerve and upon its inner side is a small strong walled artery (A), and still closer to the inner side of the cirrus is a somewhat larger vein (V). The nerve is surrounded by a sheath of connective tissue and muscle fibres (T), while outside this is a mass of longitudinal muscles forming the greater part of the cirrus (LM). The connective tissue and muscle fibres surrounding the nerve are mostly transverse to the axis of the cirrus, and they pass outward in such a way as to divide the longitudinal muscles into radiating bundles which appear in cross section like the spokes of a wheel. The radial arrangement is almost lost upon the inner side of the nerve, where the muscle bundles become small and irregularly arranged. The radial longitudinal muscles do not extend to the periphery of the cirrus. They are bounded by a narrow band of oblique muscles (Fig. 51, OM). Outside this is a layer of small bundles of longitudinal muscle fibres (LM.); while outside the latter is a thin layer of circular muscle fibres (CM). The outer muscular layers lose their identity upon the inner side of the cirrus, where transverse muscles predominate. A thin layer of connective tissue frequently separates the external circular muscles and the epithelium. The peculiar arrangement of the longitudinal muscles persists for a time after they enter the body wall at the base of the cirrus, but it is then lost as the muscles separate.

If, now, we examine the radially arranged longitudinal muscles more carefully we find that each muscle is composed of a large number of small fasciculi, held in a mesh work of connective tissue into which penetrates an occasional transverse muscle fibre. The fasciculi of the longitudinal muscles do not extend straight up and down the cirrus, but have a slightly oblique course upward and inward; i. e., as the muscles pass toward the tip of the cirrus the fasciculi pass from the outer to the inner side of the muscle. (Fig. 50, LM.) The fibres of the fasciculi, however, take a course parallel to the axis of the cirrus and are only rarely oblique to it.

The transverse muscle fibres radiate in all directions from about the nerve, passing between the longitudinal muscles and penetrating the outer circular layer. (Fig. 51.) The fibres are gathered into strands, few of which, however, radiate directly outward from the nerve, though at first sight they may seem to do so. Most pass in an hyperbolic curve from between two longitudinal muscles to between two others about 90 degrees away. Under this arrangement, when the transverse muscles contract, the outer portions of the cirrus alone are compressed and the nerve is not disturbed. After repeated examinations I am convinced that these are actually muscle fibres and not some form of connective tissue which, in the invertebrates, is often so hard to distinguish from muscle tissue. There is also considerable connective tissue in the transverse strands of the cirrus.

The fibres of the longitudinal muscles of the cirri are unstriated, smooth, slender, and exceedingly long (400 μ to 600 μ), and tapering gradually to pointed ends. An oval nucleus lies at the side of the cell near its middle. There is very little elastic connective tissue in the cirrus.

The retraction of the cirrus is accomplished by the longitudinal muscles; the elongation by

the circular, oblique, and transverse muscles. Their peculiar arrangement enables the cirrus to elongate or shorten without any undue pressure upon the central nerve. The arrangement of the cirrus muscles is very similar to that in the arms of the Octopoda and Decapoda. In these also there is a large, nearly central nerve, surrounded by a mass of connective tissue and transverse muscle fibres. Around this are the longitudinal muscles, which are also arranged radially. But instead of forming a complete circle, as in the cirri of Nautilus, the longitudinal muscles form two to four separate masses. In its essential features, however, the arrangement is remarkably similar in both the Di- and Tetra-branchiata.

It has been mentioned that between the annular grooves of the cirrus are comparatively wide projecting ridges, which show well in a longitudinal section of a cirrus. (Fig. 50.) The ridges are annular, extending completely around the cirrus. The inner portion of each annular ridge projects considerably more than the outer portions and forms an organ of adhesion. Into this projecting portion great numbers of muscle fibres extend nearly perpendicular to the inner surface. (Figs. 50 and 51.) The arrangement of the muscles in this region is very peculiar. Naturally there are almost no longitudinal fibres present. As the transverse muscles issue from between the inner longitudinal muscles they seem to branch to form an extensive brush, the outer ends of which are applied to the basement membrane. The muscle fibres are not branched, but are so attached to one another (like the straws of a broom to the handle) as to form a central strand which passes between the longitudinal muscles. (Fig. 51, RM.) This strand can be traced in an arc, as has been described for other transverse muscle fibres, across a portion of the cirrus till it passes outward between longitudinal muscles. Apparently the central strand serves as a sort of tendon to the radiating fibres of the inner portion of the annular ridge. These radiating fibres are short and thick, and quite unlike those in the other portions of the cirrus.

As each strand forming the so-called tendon runs to an opposite portion of the cirrus the contraction of all these can scarcely take place without causing some contraction of the cirrus in a transverse direction, i. e., a lengthening of the cirrus. Possibly many of the arcuate transverse fibres share in this action.

As the contraction of the radiating fibres within the inner portion of the ridge would pull the inner face of this latter inward, a sucker is thus formed. If these suckers were applied to any object the effect of the contraction of the transverse fibres in the body of the cirrus would be not to lengthen the latter, but to increase its rigidity, and thus increase the mechanical efficiency of the suckers along it. Any one such sucker would possess but little holding power, but thirty or more suckers upon each of thirty or more cirri must be able to hold very strongly.

Willey says that "most of the tentacular appendages of nautilus have essentially an adhesive function, to which is related a prehensile function. They are employed for seizing hold of food and for attachment to surfaces. Attachment is effected by the definite suctorial ridges upon their lower and inner surfaces. When attached by its tentacles, nautilus holds on with considerable tenacity, and sometimes in forcibly detaching it some of the tentacles break off and remain fixed to the surface of attachment." In Fig. 1, pl. 11, Q. J. M. S. 40, Willey represents a Nautilus holding to a glass vessel.

In considering the remarkable holding power of cephalopod suckers we must remember that attachment is effected under water, so that a perfect vacuum is possible. Another condition must affect the deep-sea forms like Nautilus much more, namely, that they are under a pressure of 20 to 80 atmospheres, where any vacuum attachment would be immensely more powerful than at the surface.

The nerve of the cirrus extends throughout its length, remaining of the same size nearly to the end. It tapers slightly here and ends abruptly immediately beneath the epithelium of the tip of the cirrus. (Fig. 50.) Ganglion cells are found at the periphery of the nerve as far as it runs in the cirrus. (Fig. 71.) But in regions corresponding to the annular ridges aggregations of ganglion cells are found which form annular enlargements or ganglia upon the nerve. There is a ganglion for each and every annulus. Numerous small nerves arise from these ganglia and pass to the external parts of the cirrus. Branches to the inner portions are especially numerous.

The nerves to the digital tentacles arise singly, as a rule, from the outer edges and lower side of the pedal ganglia. (Fig. 41, 9.) Only the nerves to a few of the more dorsal tentacles arise from a common nerve. (Fig. 41, 10.) The hood receives branches from several nerves.

A small artery with thick elastic walls is found close to the inner side of the nerve. (Fig. 51, A.). Just outside this is a much larger vein. (Fig. 51, V.) Both vessels are elliptical in cross section. This position of the artery and vein is so characteristic that even in extremely modified cirri, such as those of the spadix, the inner side of the cirrus can be determined at once in sections by the position of the vessels.

Between the epithelium of the cirrus and the circular muscle are numerous, very large, capillaries with endothelial walls. Closed capillaries are occasionally, but rarely, found in the muscular and nervous tissue. Here the circulation takes place through minute fissures in the tissues.

Immediately behind the cerebral ganglion the dorsal aorta divides into two branches—the innominate arteries, from which arise branches to the eyes, buccal mass, labial tentacles, funnel, shell muscles, and cephalic sheath (Text-fig. 10). The posterior portion of the hood is supplied by small arteries arising directly from the innominates (10). The main branches of the innominates run forward and downward upon each side, giving off branches to the individual digital tentacles (5, 4).

The veins of the cephalic sheath unite in common veins which penetrate the cartilage and enter the anterior end of the vena cava.

The epithelium of the cirri forms a feature of exceeding interest. It consists of a single layer of slender columnar cells. The epithelium upon the outer sides is of the ordinary type and contains great numbers of goblet cells. These cells are 40μ in height by 4μ in diameter. In the bottoms of the annular grooves the cells are very much shorter, often almost cubical.

But the epithelium of the inner surface of the ridges is very peculiar. A longitudinal section of a cirrus (Figs. 50 and 72) shows that the upper surface of the projecting portion of each ridge is horizontal and makes a sharp angle with the inner surface, while there is a gradual bend from the inner to the lower surface. The epithelial cells of the vertical inner surface are exceedingly slender, having a height of 108μ and a width of 2–4μ. Their width has been exaggerated in the figures of the single cells shown at the left of Fig. 72, as well as in the main portion of Fig. 72, for convenience in representation. The epithelial cells of the upper surface of the projecting portion of the ridge are only about one-eighth as high and much wider, beside being of a totally different character. The change from one kind of cells to the other takes place quite abruptly at the sharp angle of the ridge. The change in length and character of cells is much more gradual where the epithelium passes from the inner to the lower surface. The relations and characters of these cells are shown as well as my limited ability as an artist allows in Fig. 72, which was drawn from a section stained with borax carmine and Lyons blue; the colors of the stain have been copied faithfully.

The epithelium of the upper surface contains many mucous cells the secretion of which remained unstained with either stain, excepting the portion extruded from the cells and certain small granules which stained red. Mucous cells are occasionally found in the depth of the groove, but none, of this character at least, are found upon the inner surface of the ridge.

The nuclei of the slender cells upon the inner face of the ridge are situated very close to the bases of the cells. From the nucleus out almost every cell contains a large number of granules which stain a brilliant red. Sometimes the granules are arranged in a single row extending from the nucleus to the free end of the cell. Sometimes they form a dense accumulation almost filling the body of the cell. A very few scattered granules were sometimes found in the base of the cell beneath the nucleus, but never in any numbers or regularly arranged as they usually were upon the outer side of the nucleus. The granules seem to be some sort of a secretory product, but this is evidently of a different chemical nature, as well as physical, from that formed by the cells of the upper surface of the ridge or of the entire outer sides of the cirrus. Possibly its formation is connected with the function of adhesion belonging to these portions of the cirrus.

Beneath the epithelium just described is a thick basement membrane. This is exceedingly uneven, being full of small pits. The unevennesses of the basement membrane, however, are not copied by the surface of the epithelium. Over the remainder of the cirrus the basement membrane is very thin. The transition from thick to thin basement membrane is as sudden and marked as the transition from high to low epithelial cells, and occurs at the same place. (Fig. 72.)

Many of the slender cells of the inner surface of the ridge taper to a fine thread-like base, which often seems to penetrate the basement membrane and to be continued a short distance toward the center of the cirrus as a slender fibre, but it is not possible to be sure of this because of the unevennesses of the basement membrane. What appears to be a fibre penetrating the membrane may be only the slender basal portion of a cell entering one of the pits of the membrane. We can not help but suspect from their shape, position, and structure that these cells are sensory as well as secretory, but the determination of this question will require specially prepared material. Here, as in other places where the histology of Nautilus is described, descriptions of the tissues are given as they have been found under certain (rather unfavorable) conditions, and no attempt is made to insist upon any doubtful interpretations.

Variations in the shape and structure of the tentacles are quite common and take place in four directions, as far as my observation extends.

1. The free ends of the sheaths may be more or less fused; fusion may occur between any two sheaths, but is most usual among those nearest the hood.

2. The free portion of the sheath is sometimes split into two halves, leaving the cirrus projecting between them. This may be the result of injuries received by the animal early in life, but no trace of any injury is shown by any other part and the innermost digital tentacles are always the ones to be affected; from their position we should expect these tentacles to be rather less exposed to injuries than any others.

3. The opening through which the cirrus projects from the sheath may be displaced. Usually the displacement is toward the inner side and the opening is found a few millimeters below the tip of the sheath. But it may be at the very base of the sheath, which then projects in the usual manner, but with closed tip, while the greater portion of the cirrus lies outside the sheath.

Less frequently, and only among the dorsal tentacles, the openings are upon the outer side of the sheath. In one specimen one of the cirri of the hood extended from its sheath 10 millimeters back from the edge of the hood. The hood-cirrus of the other side was normal, while the cirri of the two neighboring tentacles both projected from the sides of their sheaths several millimeters back from their tips.

4. The cirrus may be entirely absent and the sheath closed. This occurred in but one specimen. Where the cirrus of the left side of the hood should have projected, only a nipple-like projection of the integument was seen. Upon slitting the hood back of this projection the cavity of the sheath was found empty, without the least trace of a cirrus, and not extending the usual distance into the hood.

The more common variations of the tentacles were those of fusion of the sheaths with one another. The general tendency, in fact, seems to be toward more complete fusion and increasing solidity of the cephalic sheath.

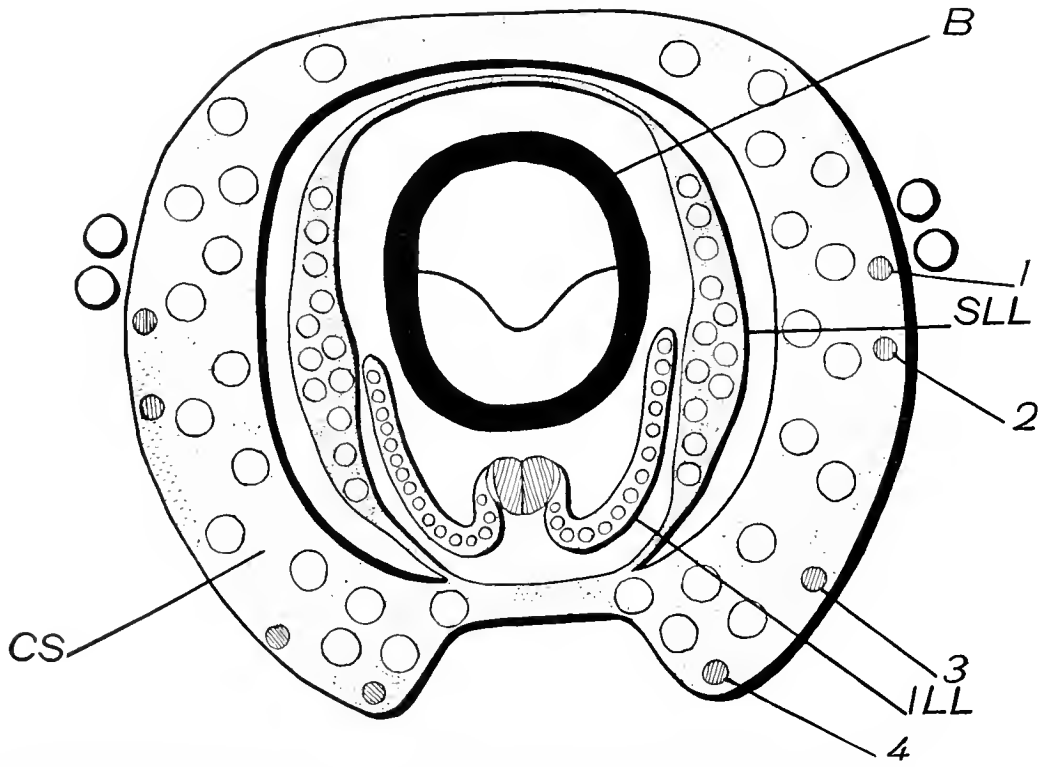
B.—Inner Tentacles of the Female.

If now we open the cephalic sheath or cut it away we see that the mouth parts of both male and female Nautili are surrounded by still other groups of tentacles. We see, further, that these groups are evidently more specialized than the digital tentacles, and that the groups are not alike in male and female, either in number, shape, or position, while their specialization is of a higher degree in the male than in the female. It is therefore impracticable to attempt a parallel description of the inner tentacles of the two sexes. The conditions are more simple in the female, so I shall attempt their description first.

The tentacles about the mouth parts are designated by the general name "labial tentacles."

Two groups situated upon either side of the buccal cone, and nearly meeting dorsally, are the superior labial tentacles. (Fig. 5, SLL; Text-fig. 2, SLL.) Two other groups, situated below the buccal cone but wrapping around it laterally, are the inferior labial tentacles. (Fig. 5, L; Text-fig. 2, ILL.)

The superior labial tentacles project from two broad, flat, thin lobes which arise from the base of the inner side of the cephalic sheath. The lobes are about 3 centimeters broad and 2 centimeters high. From the ends of the lobes low ridges are continued; dorsally to unite the two, ventrally to end above the funnel near the innermost digital tentacle of each side. (Text-fig. 2.) One might say that these two lobes are only local elevations of a single ridge which nearly surrounds the mouth parts. The upper edge of each lobe is subdivided into a number of more or less separate processes. The tip of each process is free for from 6 to 10 millimeters, while grooves upon both surfaces of the lobe indicate a division for some distance farther back. At the tip of each process is an opening leading into a cavity 1½ to 2 centimeters



TEXT-FIG. 2.—Diagram of the arrangement of the tentacles of the female nautilus, viewing them from the front.

B, buccal mass. CS, cephalic sheath, composed of the fused sheaths of the digital tentacles. ILL, inferior labial lobe. SLL, superior labial lobe. 1, 2, 3, 4, a series of four small digital tentacles upon the outer side of the cephalic sheath.

deep; each projection is the free end of the sheath of the cirrus which projects through its opening. Thus the superior labial tentacles have the same principal structures as the digital tentacles.

The number of tentacles in the superior labial group is very variable within certain limits. The most ordinary number is twelve in each group; as few as ten, or as many as fourteen are quite common. RUMPH (1805) counted sixteen in each group. The number is usually, but not necessarily, the same in both groups of one individual. I have not, however, found a difference of more than one.

The arrangement of the tentacles seems to be constant. As is shown in the diagram (Text-fig. 2) there is an inner row of nine, and, at about the middle of this, an outer row of three. The variable tentacles seem to be at the ends of the longer row, the shorter row having always been found to be normal.

The cirri of the labial tentacles are, of course, shorter and more slender, but their structure and shape are the same as of the digital tentacles.

The structure of the inferior labial lobe is more complicated. I have retained OWEN's designations of superior and inferior instead of the ones suggested by VAN DER HOEVEN, external and internal, for these lobes because the former names indicate better their actual positions. I have already spoken of two inferior groups of labial tentacles. Two groups there are, but they are borne upon a single lobe, the inferior labial lobe.

The inferior labial lobe (Fig. 5, L; fig. 26) arises immediately below the buccal cone as a process about 2½ centimeters broad and 8 millimeters thick. About 2½ centimeters from its base the process is split into two symmetrical portions. Each portion widens out like a fan and bears a single row of tentacles along its edge. (Text-fig. 2, ILL.) Each of these parts wraps itself about the buccal cone internal to the superior labial lobes. The inner surface of each is concave, the outer surface convex. Sheaths and cirri of the inferior labial groups are like those already described for the superior labial tentacles, except that the sheaths do not project freely. The middle tentacles of each inferior group are the longest; those at the outer end of the row are only slightly shorter, but the inner tentacles decrease rapidly and greatly in size. A progressive reduction in the development of the sheaths is also noticeable among the innermost tentacles. The innermost tentacle is frequently a mere papilla 2 or 3 millimeters in height.

The number of tentacles in each inferior labial group usually varies between ten and fourteen. The number upon the opposite divisions of the same lobe frequently differs by one or two. VAN DER HOEVEN reports fourteen upon the left and sixteen upon the right side.

At the junction of the outer portions of the lobe, upon its inner side, is an oval or polygonal organ composed of sixteen to twenty closely folded thin triangular lamellæ, the widest portion or base of the organ being directed posteriorly. (Fig. 5, L; Fig. 20; Text-fig. 2, ILL.) Usually sixteen lamellæ compose the organ, which OWEN supposed to be the olfactory organ of Nautilus.

The lamellæ are symmetrically disposed with respect to the median line of the body. Occasionally there is a difference of one in the number of lamellæ of the two halves of the organ. The organ represented in Fig. 20 was more expanded than most, so shows the relative arrangement and form of the lamellæ better than is usually the case. This organ measured 12 millimeters in breadth and 9 in length. The triangular lamellæ are attached to the labial lobe by one edge, the point opposite then projecting upward and inward. The line of attachment of each of the median lamellæ is parallel to the axis of the body, while the outer lamellæ are attached at acute angles to the axis. The outer lamella of each side usually lies somewhat above the others, overlapping them and lying in the continuation of the rows of tentacles upon the outer parts of the labial lobe. A ridge across the open back of the organ connects the two outer lamellæ.

Each lamella is distinctly and closely grooved upon its outer side, the grooves reminding one of those upon the cirri. Less numerous, distinct, and regular grooves are seen upon the inner sides of the lamellæ. A large nerve runs through the center of each lamella to its tip. The nerve possesses an outer layer of ganglion cells which are evenly distributed upon its surface and not grouped in ganglionic masses as they are upon the nerve of a cirrus.

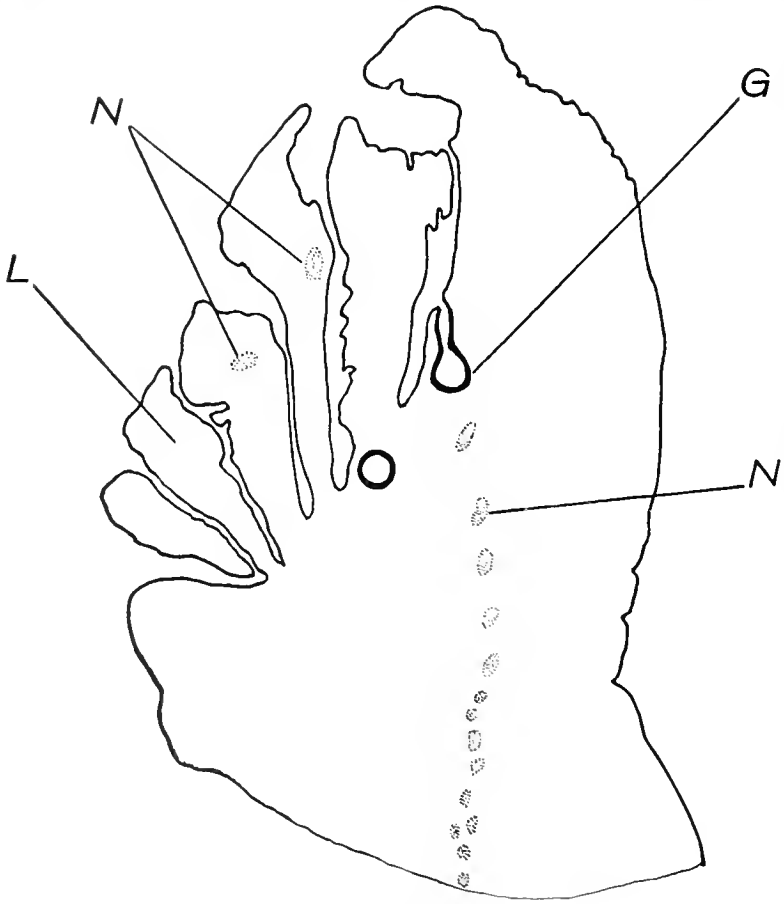
Both surfaces of the lamellæ are deeply pitted, and all portions are covered with a highly glandular epithelium.

The musculature of a lamella has essentially the same arrangement as that of a cirrus. In consequence of the flattened form of the lamellæ their longitudinal muscles extend outward to the edges upon either side of the nerve. The transverse fibers, which are radially arranged about the nerve in the cirri, here, therefore, pass directly across the thin lamellæ between the bundles of longitudinal fibres. External to the latter are circular muscle fibres.

In the farthest depths of the fissure between each two lamellæ is a small opening leading into a sunken organ which I do not hesitate to call sensory. These organs ordinarily consist of two parts: 1, a tubular neck opening outwardly as has just been mentioned, and opening inwardly into 2, a (comparatively) large cavity which extends in the solid tissue of the labial lobe at right angles to the surfaces of the lamellæ. (Text-fig. 3, G.)

The whole structure reminds one strongly of a diminutive tunnel driven in both directions

from its shaft. The tunnel is round in cross section, and as a rule the shaft is near its center. A section of the organ through the middle of its shaft therefore is flask-shaped, the neck (shaft) being slightly bulged at its center. The shaft may, however, be at one end of the tunnel. Shaft and tunnel are lined throughout with a peculiar epithelium. The cells are extraordinarily slender, almost like threads in their proportions, and the free end of each is prolonged into a sensory spike, the multitude of which causes the surface of the tunnel and shaft to appear ciliated. A very slender nucleus is situated in the basal third of each cell. None of the cells lining the cavity are glandular. The length of the cells varies greatly in different cavities, as well as in different regions of the same cavity. This peculiar epithelium may extend outward from the mouth of the shaft for a little distance into the fissure between the lamellæ. I have not observed any special nerves going to these organs, but as they lie close to the large nerves of the lamellæ better material may reveal the innervation.



TEXT-FIG. 3.—Camera lucida outline of a section of the lamellated organ of the inferior labial lobe of the female; × 13.
G, sensory pit. L, lamella; N, N, nerves of lamellæ.

There seems to me to be but little doubt that these cavities are sensory organs of a simple type, and but little more doubt that their function is olfactory as was assumed by OWEN and others for for the group of lamellæ as a whole. I find, however, no sensory structures upon the lamellæ, nor any indication of these latter possessing any special sensory function.

The sensory organs situated between the outer three or four lamellæ may be less developed than those between the inner lamellæ. The shaft may be shorter; the tunnel short, or little more than a spherical pocket. In two cases the only indications of the sense organs were small hemispherical projections between the bases of the lamellæ covered by the sensory epithelium. These were the two outer organs of one side. But there was no gradual transition from this to the more complicated and apparently more typical form of organ.

The muscles of the tentacles pass into the labial lobe as in other cases already described, interlacing here with the numerous intrinsic muscles. The inferior labial lobe is a strongly muscular and evidently contractile organ in both its divided and undivided portions. A rather complicated system of muscles extends from its base to the surrounding regions of the cephalic sheath, providing for the motion of the lobe in all directions.

The inner side of the cephalic sheath and all the organs within it, labial lobes and buccal cone, are covered with what may fairly be called a skin. This may easily be removed from their surfaces, leaving the muscular bases of the organs bare. It consists of a single layer of columnar epithelial cells similar to those upon the outer surface of the cephalic sheath, resting upon a thick connective tissue dermis. The dermis tissue is somewhat fibrous, but reminds one strongly of

embryonic gelatinous tissue. Probably better preserved material would show more structure than I have been able to discover. When the skin has been removed from the labial lobes their muscles come into view.

The muscle fibres of the superior labial lobes pass into the tissues of the cephalic sheath without forming any distinct muscles. But in regard to the inferior labial lobe the case is very different.

A longitudinal median muscle, the dorsal median retractor (Fig. 26, 5), extends over the dorsal face of the lobe from just back of the lamellated organ to the base of the lobe, where it enters the ventral portion of the cephalic sheath immedately above the funnel. A similar, but much smaller, longitudinal muscle follows a similar median course upon the ventral face of the lobe.

There remain three pairs of muscles arranged symmetrically at the sides of the lobe. 1 and 1′ (Fig. 26) extend out and back from the sides of the lobe to insertions in the lateral regions of the cephalic sheath immediately below the bases of the superior labial lobes. These appear to be the muscles used in raising the lobe and its tentacles.

2 and 2′ (Fig. 26) originate near the base of the lobe and pass outward from the median line over the base. The outer ends of these muscles are expanded and flattened, and are inserted over the inner faces of the superior labial lobes. This arrangement evidently serves for the approximation of the superior and inferior lobes and their tentacles. The posterior portions of the inner ends of 2 and 2′ separate from the remainder of the muscles and unite with each other above the median muscle 5.

The muscles 3, 4, and 3′, 4′, (Fig. 26), the lateral retractor muscles, have their origins in the posterior region of the lobe beneath the inner parts of the muscles 2 and 2′. They pass beneath these latter backward and slightly toward the median line. Arising as single muscles, they separate into two distinct portions. The smaller outer portions pass into the base of the buccal mass behind the inferior buccal retractors, as is shown for similar muscles in the figure of Van der Hoeven's organ. (Fig. 29.) The larger inner portions pass back to insertions upon the median processes of the cartilage.

The base of the lobe is thick and muscular and its tissues extend directly into the ventral portion of the cephalic sheath.

The inferior labial lobes are supplied with blood by a branch from each tentacular artery. (Text-fig. 10, pp. 182, 3.)

A large nerve leaves each pedal ganglion near the infundibular nerve (Fig. 41, 7), which runs forward and enters the side of the inferior labial lobe. Within the lobe it enlarges into a ganglion, from which the separate nerves of the tentacles and the lamellæ arise. (Fig. 41, 35.)

It must be noted that while the inferior labial lobe is bilaterally symmetrical it is not paired as are the superior labial lobes. Young specimens seem to indicate that it is unpaired in its origin.

We have still to consider what the relation is between the lamellæ upon the median part of the lobe and the tentacles upon either side of the lamellæ. Can the two sorts of structures be homologous, or must they be considered as developed separately—one for adhesion and the other for smelling, tasting, or some other function?

It has already been noted that as we approach the lamellæ the inner cirri of each side, i. e., those nearest the lamellæ, rapidly decrease in length. Hand in hand with the decrease in length of the cirri goes a decrease in the depth of their sheaths. Moreover, we often find that the tentacle next to the lamellæ is a small, scarcely noticeable papilla. In some cases such a papilla is partly or wholly surrounded by a shallow groove. Further development of papilla and groove would lead to the formation of a cirrus and a sheath, and tentacles sometimes actually illustrate steps in this process. The minute papillæ, annularly grooved, are supplied with a nerve similar in all respects but length to the nerve of fully developed cirri.

On the other hand, the outer lamellæ are sometimes small and not much different from the rudimentary tentacles just described. So, if we consider shape alone, it is not at all difficult to imagine that lamellæ and tentacles are but differently developed individuals of a single series.

There are, however, other facts which favor this view. The transverse furrows upon the outer sides of the lamellæ are obviously comparable with the grooves upon the cirri. We also note that each lamella possesses a nerve extending throughout its length which has essentially the same structure as the nerve of a cirrus; it has a like complete investment of ganglion cells, although these are not collected into ganglia; beside this, the nerves of the lamellæ arise from the same ganglion as the nerves of the cirri, and it is impossible to distinguish the nerves of cirri and lamellæ before they arrive at their respective terminations. The nerves of the lamellæ are simply the innermost of the series arising from the ganglia.

The arrangement of the muscles of the lamellæ is according to the same plan as is that of the cirri. We have also noted that the sensory organs at the bases of the outer lamellæ have a tendency to be simpler or less developed than those between the inner lamellæ.

The number of both lamellæ and cirri is quite variable, but the number of lamellæ does not seem to bear any constant relation to that of the cirri. The entire number of lamellæ and cirri borne by the inferior labial lobe is about forty.

The facts stated seem to indicate that the lamellated organ is composed of a number of slightly modified labial tentacles, and is not a structure developed upon the labial lobe separately from the tentacles. Furthermore, there are indications that the outer members of the series of lamellæ and the inner members of the series of tentacles graduate into each other, possibly being developed in one direction in some individuals and in the opposite direction in other individuals.

The inferior labial lobe of a half-grown female showed an interesting condition in the development of the lobe. The superior labial lobes were as well developed, proportionally, as in a mature specimen. The inferior labial lobe, on the contrary, was in a rudimentary condition. It reached only about to the middle of the buccal mass. Each side of the anterior edge of the lobe was produced in a curve; in the center were a number of fine lamellæ. The tentacles at the edges of the lobe were very rudimentary, in many cases apparently not yet being differentiated into cirrus and sheath.

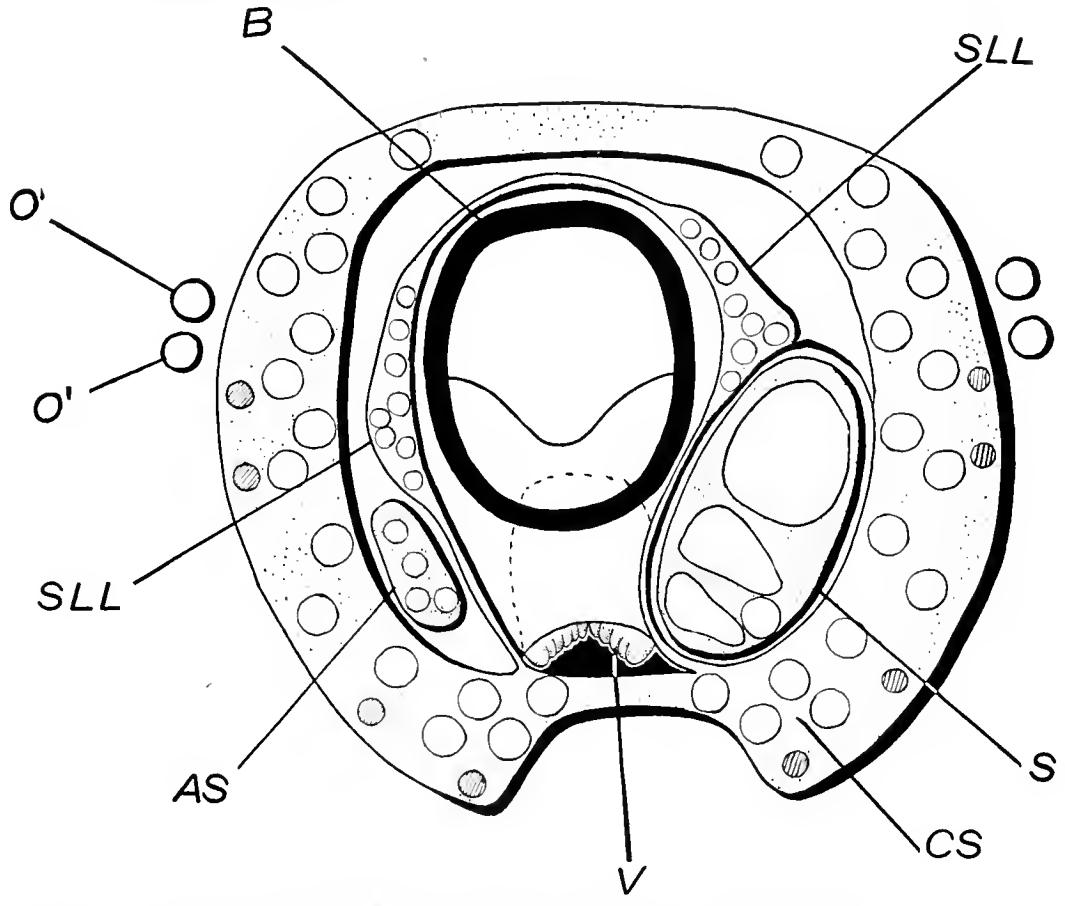
Haswell makes the following statement: "One of the six or eight female specimens examined by me presents a condition of the median minor tentaculiferous lobe which may, perhaps, have a bearing on the functions of the part. In this specimen, which was a good-sized one and fully developed in other respects, the lobe in question (the group of lamellæ) was represented by a rudiment, in which, however, all the parts of the perfected structure were distinctly and symmetrically represented."

C.—Inner Tentacles of the Male.

The arrangement which we see when we open the cephalic sheath of the male is quite different from that which we have observed in the female. The buccal cone occupies the same relative position in both sexes. At each side of and dorsal to the buccal cone of the male is a group of tentacles closely resembling the superior labial tentacles of the female. (Fig. 7; Text-fig. 4.) They are borne upon two lobes which are elevations of a ridge of the base of the cephalic sheath nearly encircling the buccal cone. The ridge is very low dorsally and ventrally to the tentacle lobes, which latter rise to a height of from 1½ to 3 centimeters. Ventrally the ends of the ridge approach each other like the tips of a horseshoe and end upon the cephalic sheath near the innermost digital tentacle. This ridge obviously corresponds to the similar ridge of the female which bears the superior labial lobes, and we shall also term these tentacle-bearing lobes of the male superior labial lobes.

Outside the ventral ends of the ridge bearing the superior labial lobes are two groups of tentacles, one at each side of the head, which do not appear in the female. There are four tentacles in each group. (Fig. 7, Sp, ASp; Text-fig. 4, S, AS.) The tentacles of the right-hand group do not differ markedly from the tentacles of the superior labial group. The tentacles of the left-hand group, however, are enormously developed and form a conspicuous organ known as the spadix. The smaller corresponding group of the right side is called the antispadix.

Immediately beneath the buccal cone is still another organ which is peculiar to the male. It was discovered by VAN DER HOEVEN, and has since been known as VAN DER HOEVEN'S organ. It lies in a pocket formed by the ventral portion of the cephalic sheath ventrally, and dorsally by a fold connecting the ends of the horseshoe-shaped ridge which bears the superior labial lobes. (Text-fig. 4, V.) The organ can not be seen until the cephalic sheath has been opened, so closely does it lie under the buccal mass. Even then the observer can only notice that its anterior end appears to be formed of small lobes and is bilaterally symmetrical. In the diagram (Text-fig. 4, V) it is represented, for the sake of convenience in drawing merely, as projecting at some dis-



TEXT-FIG. 4.—Diagram of the arrangement of the tentacles of the male nautilus, viewing them from in front.

AS, antispadix; B, buccal mass; CS, cephalic sheath, composed of the fused sheaths of the digital tentacles; O', preocular tentacle; O'', postocular tentacle; S, spadix; SLL, superior labial lobe; V, Van der Hoeven's organ.

tance from the buccal mass, which it does not actually do. Its shape is roughly outlined by the dotted line. I hope to present sufficient evidence to be convincing that VAN DER HOEVEN'S organ is the homologue of the inferior labial lobes of the female.

SUPERIOR LABIAL LOBES.

The only considerable difference between the superior labial tentacles of the male and those of the female is in their number. Eight tentacles are usually borne upon each superior labial lobe of the male, while twelve is the usual number upon each of these lobes of the female. Less than eight tentacles may occur upon each lobe of the male, although I have never found more than this number. Two of my specimens presented only six tentacles upon each lobe; one specimen had six upon one lobe and seven upon the other.

The superior labial tentacles of the male are slightly more robust than those of the female; their sheaths are more completely separated in the male than in the female. Two of the tenta-

cles are more or less crowded to the outside of the row formed by the other six, as is shown in Text-fig. 4, and in Fig. 7, SLL. Aside from these there are no differences between the superior labial lobes and tentacles of the two sexes.

Each cirrus possesses a nerve, which springs directly from the pedal ganglion. These nerves leave the edge of the ganglion just dorsally to the nerves of the digital tentacles; being of only about half the size of the latter they are easily distinguished from them, although not so readily traced to their respective cirri.

SPADIX AND ANTISPADIX.

The spadix and the antispadix are morphologically equivalent organs, although the antispadix is simple in all its parts, while the parts of the spadix are highly developed and modified, and several structures are there developed which are not represented in the antispadix. A previous study of the antispadix will probably aid in the understanding of the spadix.

Before proceeding, we must notice the position of the two organs. The spadix is usually upon the left side of the head and the antispadix upon the right side, but this arrangement may be reversed. Out of forty-seven male Nautili, nine, or 19 per cent, had the spadix upon the right and the antispadix upon the left side. Willey found an even greater proportion of reversals. "Out of thirty-seven males which were examined ad hoc, twenty-three had the spadix upon the left side and fourteen had it upon the right side" (1896, 1)). This is 37 per cent of the total.

One of my specimens possessed a well-developed spadix upon one side and an abnormally developed spadix upon the opposite side.

The antispadix is composed of four tentacles similar to those of the superior labial groups, except as they are somewhat larger and longer than the latter. (Fig. 7, A. Sp; Fig. 12.) The tentacles are arranged in a row, which in the natural position of the animal is dorso-ventral. To distinguish the tentacles I shall number them 1, 2, 3, 4, from above downward, and shall speak of them as the first, second, third, or fourth tentacles. The sheaths of the first, second, and third tentacles are fused as far as their tips, thus forming a narrow, flattened process. It is convenient to speak of the fused sheaths as the sheath of the antispadix. The fourth tentacle is united to the process at the base only. (Fig. 12.) It is situated a little externally to the other tentacles, extending past the third, so that its dorsal edge comes to lie in a groove formed by a projection of the sheath of the antispadix.

At the bases of the cirri the muscular tissues of the cirri and their sheaths unite to form a strong, flat sheet of muscle, which lies against the inner side of the cephalic sheath, but entirely separate from it until near the cartilage. Here it unites with the tissues of the cephalic sheath. The muscular base of the antispadix is entirely separate from the muscular base of the superior labial lobe, although close to it. It is easily seen when the skin between the antispadix and the buccal mass has been cut.

Upon the outer surface of the sheath of the antispadix, near its tip and between the first and second cirri, is a small glandular area. (Fig. 12, G.) Its structure will be described with that of a similar area upon the sheath of the spadix.

The antispadix projects from a pocket between the cephalic sheath and the ridge of the labial lobe and at the ventral end of the lobe. (Fig. 7; Text-fig. 4.) The lobe of the antispadix is about two centimeters in length from the base of the pocket to the tip of the sheath. As a consequence of the shortening of the rows, the superior labial tentacles are further removed from the ventral side of the cephalic sheath in the male than in the female. (Text-figs. 2 and 4.) The low ventral portions of the labial ridge are therefore considerably increased in length in the male. As the spadix increases in size it crowds the superior labial tentacles of this side still farther toward the dorsal side of the head and stretches the ventral portion of the labial ridge.

The spadix presents a very different appearance from the antispadix upon the opposite side of the head. (Fig. 7, Sp.; Figs. 13 and 14; Text-fig. 4, S.) It forms a large, very solid organ, five to seven centimeters in length, two to three centimeters in dorsi-ventral measurement, and one

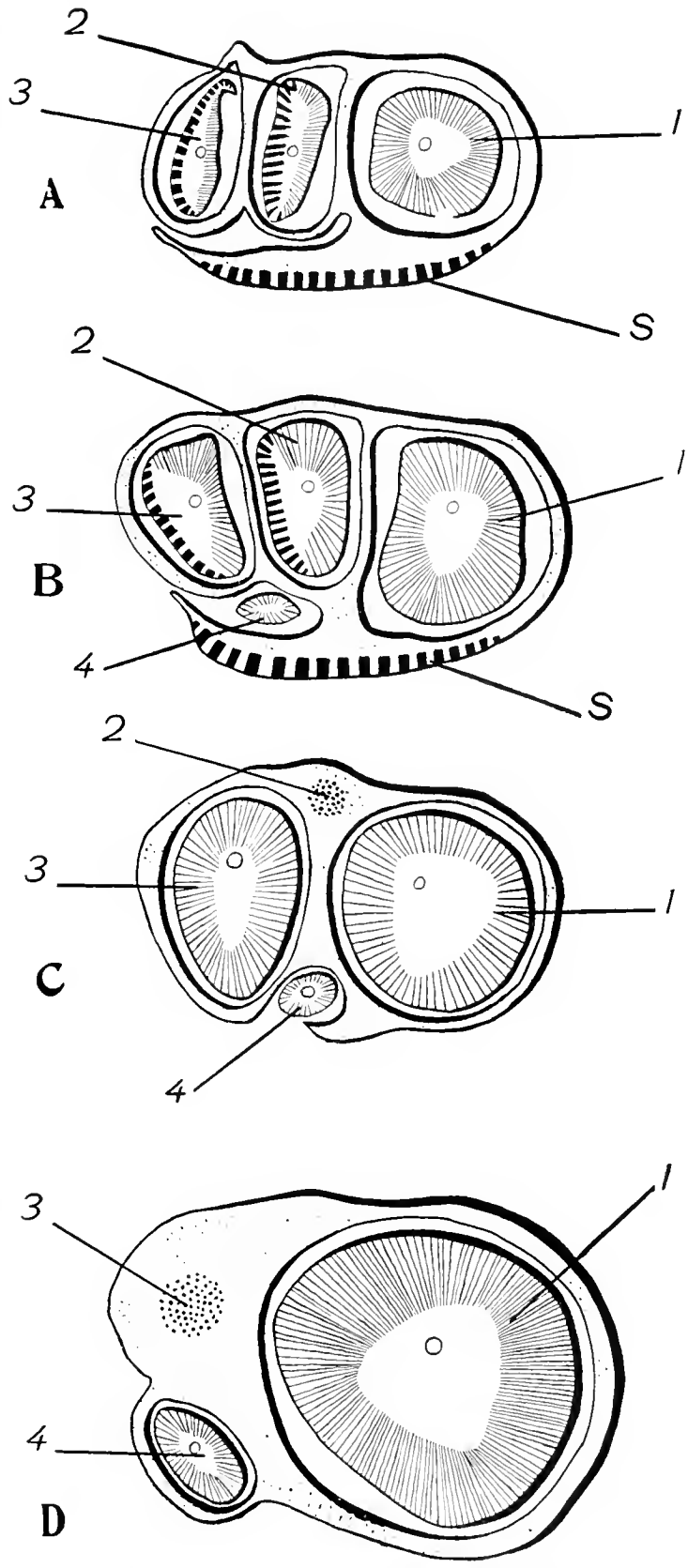
and a half centimeters in thickness. It remains of about the same width and thickness nearly to the irregularly conical end. The tentacles of the spadix have the same relative arrangement as those of the antispadix. Each is greatly increased in size, with the exception of the fourth tentacle, which is but little larger than its representative in the antispadix.

The cirrus of the first tentacle has become an enormous conical, fleshy organ. (Fig. 15.) The cirrus of the second has become flattened as well as enlarged, and bears numerous rows of small glands upon one surface. (Fig. 16.) The cirrus of the third is also flattened at its tip, and shows upon its ventral side many rows of fine pores. (Figs. 17 and 18.)

The sheaths of the first, second, and third tentacles are completely fused and have developed in accordance with the cirri, and now form a structure which Vayssiere has proposed to call the sheath of the spadix. (Figs. 13 and 14.)

There is a groove in the outer side of the sheath of the spadix, between the second and third cirri, into which the tip of the fourth cirrus is pressed. (Fig. 14.) The tip of this cirrus is overlapped by a broad flap, which corresponds to the smaller flap noticed upon the outer side of the antispadix. The base of the fourth tentacle lies within a notch in the sheath of the spadix and is not covered. Its own sheath is short and is free from the sheath of the spadix for a short distance only. In this respect the fourth tentacle of the spadix differs quite noticeably from the corresponding tentacle of the antispadix.

Upon the outer side of the sheath of the spadix, and near its tip, is a large circular glandular area, slightly raised above the general surface. (Fig. 14, G.) The glandular area extends out



TEXT-FIG 5.—Transverse sections of the spadix at successive levels.

A, nearest the tip; D, nearest the base of the organ; 1, first cirrus; 2, second cirrus; 3, third cirrus; 4, fourth cirrus; S, slime gland of spadix sheath.

upon the flap covering the tip of the fourth tentacle. Upon its surface numerous pores, the openings of tubular glands, are easily seen.

The bulk of the spadix is composed of the cirri of the first, second, and third tentacles. The fourth tentacle may almost be said not to enter into the formation of the spadix, so small is it compared with the mass formed by the other tentacles. (Fig. 19.)

The cirri of the spadix are not of equal length, like those of the antispadix. Neither their bases nor their tips are at the same level. Text-figure 5 is intended to show the relative length and position of the cirri of the spadix by means of diagrammatic sections of four regions of the organ. In A, a section through the tip of the spadix, the fourth cirrus does not appear. In section B, taken a quarter of its length from the tip of the spadix, the tip of the fourth cirrus is cut through. In section C, taken just below the middle of the spadix, the second cirrus has ended, and in the position it occupied we see only bundles of muscle fibres passing from its base in the sheath of the spadix. The fourth cirrus is no longer completely shut in by the flap of the spadix sheath. In section D, taken through the base of the spadix, the third cirrus has disappeared in like manner as the second. In spite of the disappearance of two cirri the spadix has increased in size continually as we have approached its base. This is accounted for almost entirely by the great increase in the size of the first cirrus alone. But the fourth cirrus has also increased in size and is, at the base, included within the sheath of the spadix. Strands of muscle from the bases of the second and third cirri also form a portion of the organ. The fourth cirrus is still free from the sheath of the spadix back of where the tissues of the first cirrus and the sheath unite. Finally, the tissues of all the tentacles are united to form a solid base for the spadix, which is firmly attached to the posterior region of the cephalic sheath and the cartilage.

Let us now turn to more detailed descriptions of the separate portions of the spadix.

THE SHEATH OF THE SPADIX.

This somewhat indefinite name is nevertheless convenient, and for this reason it seems appropriate and worth retaining. From the previous description and diagrams it will be noticed that in the anterior region of the sheath it is composed of the sheaths of the tentacles alone, but in its posterior or basal part it includes the muscle tissue extending from the bases of the second and third tentacles.

Sometimes slight longitudinal grooves upon the outside of the sheath indicate the position and boundaries of the cirri within. (Fig. 13.) Upon the outer side of the spadix, i. e., the side turned away from the mouth, is a deeper groove which receives the fourth cirrus. The anterior end of this groove is hidden by the large flap developed on this side from the sheath of the spadix. This flap, extending along the entire length of the spadix, is widest near the tip of the organ, while it becomes a mere ridge near the base. The free edge of the flap is thin and evenly curved. It is about twelve millimetres in width at its broadest part.

Examination of the sheath with a lens reveals minute pits upon the surfaces near its tip, numerous upon the outer surface and less so upon the inner surface. Except for these and the glandular area upon the outer side the sheath is quite smooth.

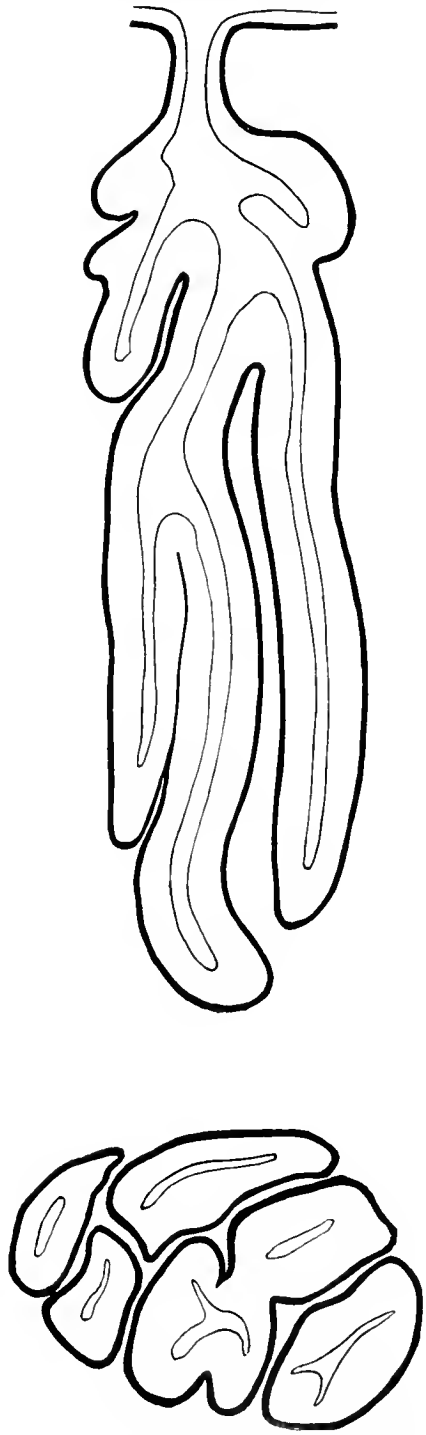
The sheath is composed of an external layer of longitudinal muscle fibres, and of inner circular fibres ringing each cirrus cavity. It is covered by a single-layered epithelium, composed of slender columnar cells, the basal halves of which are occupied by elongate, oval nuclei. Goblet cells, filled with granular secretion, are found in exceedingly great numbers in the epithelium of the external surface of the anterior portion of the sheath, but in small numbers upon the basal portion. The pits and short grooves upon the anterior portion of the sheath, noticed under the lens, are lined mostly by mucus-secreting cells and serve the purpose of increasing the secretory surface. The epithelium upon the inner surface of the sheath is very similar to that upon the outer surface, except that the cells are shorter, the nuclei nearly round, and the goblet cells very rare. Indeed, the latter are only present near the edges of the cavities occupied by the cirri.

Immediately under the epithelium is a dermis of felted fibrous and elastic connective tissue. In the thinnest portions this, containing a few muscle fibres, forms the entire substance of the

sheath. In the thicker portions the amount of muscle tissue within the dermis is very considerable, and is roughly arranged in the longitudinal and circular layers already mentioned. It must not be forgotten that a quite considerable portion of the sheath is derived from the tissues of the second and third tentacles after these have become continuous with the tissues of the former. The spaces between the muscles are occupied by fibrous and elastic connective tissue. The sheath is penetrated by a perfect network of vascular lacunæ.

Until we have some idea of the function of the glandular area upon the outer side of the spadix sheath the term "slime gland" will do very well to designate it. It is surprising that this structure should not have been mentioned by VAYSSIERE in his excellent paper upon Nautilus. The slime gland forms a nearly circular area upon the outer side of the spadix sheath, from 25 to 30 millimeters in diameter, and is considerably raised above the surrounding surface, besides being of a much darker color, all in all being a quite conspicuous organ. (Fig. 14.) Numerous pores, the openings of the glands within, open upon its surface. The glands are formed of long, branching tubes, which are packed closely together, and occupy three-quarters of the thickness of the sheath at this point. (Fig. 57.) The sheath contains but little muscle tissue in this region, being composed almost entirely of fibrous connective tissue which, below the slime gland, is reduced to a network inclosing great numbers of vascular lacunæ of all sizes. The larger spaces have endothelial walls. The lacunæ are much more numerous than they are represented in Fig. 57, by far the greater number being too small to be shown in such a figure.

The structure of the glands is quite simple. From a short, narrow neck arise several tubular outgrowths. (Fig. 57; Text-fig. 6, A.) Most of these are long and slender and extend into the sheath nearly at right angles to its surface. Around the outer part of the neck are often grouped short tubules or mere outpocketings of the wall. The main tubules may themselves be branched. The tubules of each gland lie parallel and close to each other, separated by only a small amount of submucous tissue. (Text-fig. 6, A and B.) The tubules are packed together so that they form a package of almost equal transverse diameters from end to end.



TEXT-FIG. 6.—Slightly diagrammatic sections of a single gland of the slime gland of the spadix sheath. A, longitudinal section; B, transverse section.

The tubules are lined by a single layer of tall, columnar secretory cells. The lumens of the tubules are extremely narrow, being rarely of greater width than half the height of the cells lining them. (Fig. 57.) The epithelial cells are extremely slender, averaging about 100μ in length and 4μ to 8μ in their transverse diameters. (Fig. 57, A.) The epithelium rests upon a thin basement membrane. At the very base of each cell is a small oval nucleus, 3μ by 8μ in its dimensions. From just above the nucleus to its free end each cell is packed with deeply staining granules of

secretion. The region of the cell immediately about the nucleus is entirely free from any secretion, so that the outer edge of the tubule shows a clear border in sections. Figure 57 A shows a single cell of the secretory epithelium drawn with the aid of a camera lucida. It was taken from a place where the epithelium was lower than ordinary, but otherwise is characteristic. The single row of deeply staining granules almost completely fills the body of the cell. The bent base of the cell is a very characteristic feature, although not found universally. The short basal portion of the cell is directed upward and inward, and the longer outer portion of the cell is perpendicular to the axis of the tubule. As the neck of the gland is approached a change takes place in the character of the epithelial cells. The epithelium becomes lower and the cells contain fewer and smaller granules. Finally the epithelium is only of about half the height of that in the tubules; the granule secreting cells disappear, and ordinary goblet mucous cells are found scattered in the epithelium, which is of the same character as that clothing the surface of the slime gland between the pores of the glands.

At the edge of the slime gland are all stages between fully developed tubular glands and the merest invaginations of the surface epithelium. One might almost say that there is here an ontogenetic series in the development of the glands. The smallest invaginations are lined with epithelium entirely similar to that upon the surface of the slime gland. Farther from the edge the invaginations become deeper, and from the inner parts outgrowths occur which become the glandular tubules of fully developed glands. The young tubules possess an epithelium like that of the adult in its essential characters, but at first only a few cells appear to be glandular. These are typical goblet cells filled with finely granular secretion. In more developed glands the secreting cells become more numerous, the granules of secretion are larger, and finally all the cells below the neck of the gland are filled with coarse granules.

The description of the glands upon the outer side of the antispadix was referred to this place. They are of the same character as those of the slime gland of the spadix, but are less developed. The glandular epithelium and the secretion are apparently alike in both organs. The glands upon the sheath of the antispadix are proportionately shallower and are less branched than those of the spadix, but otherwise the structure seems to be the same.

FIRST CIRRUS OF THE SPADIX. (FIG. 15.)

The first cirrus is much the largest of the four forming the spadix. It is nearly circular in section, gradually diminishing in size from the base to near the tip. The latter diminishes in size very rapidly, causing the cirrus to end in a point like the tip of a low cone. The tip is frequently excentric and is sometimes produced like a nipple. The surface of the cirrus is smooth except near the tip, where very faint annular grooves may be noticed. The base of the cirrus, its largest part, measures 32 millimeters dorso-ventrally and 17 millimeters from side to side. It is 6 centimeters in length.

From the ventral side of the base a strong muscle passes ventrally and across the body, to become lost in the tissues of the opposite side of the cephalic sheath. The main mass of the tissue of the cirrus passes immediately into the tissues of the posterior portion of the cephalic sheath on its own side. The development of a special muscle for this cirrus, as well as the remarkable muscular development of the cirrus itself, indicates that the cirrus is very actively employed at some time or other in the animal's existence, and it may also indicate that the cirrus is extended or retracted as a whole from its base and is not extensile in the same manner as the cirri of other tentacles; but all statements of how this and the other cirri of the spadix are used are as yet guesses, pure and simple.

Transverse and longitudinal sections explain the rest of the structure of this cirrus. (Figs. 52 and 53.) Near the center of the cirrus, but still to the inner side of it (i. e., the side nearest the buccal mass), is the large nerve N. This is surrounded by the transverse musculature of the cirrus. Around the core of transverse muscles is a thick ring of longitudinal muscles, which are divided by radial septa of transverse muscles. Outside this follow three thin layers of muscle—a circular, an outer longitudinal, and an outer circular layer. The essential features of the arrangement of the musculature are therefore the same as those of the digital or labial cirri.

A longitudinal section of the cirrus shows that the central transverse musculature consists of alternating layers of crossing fibres. (Fig. 52.) The section figured in Fig. 53 has been cut a trifle obliquely so that it passes through several of these alternating layers. The layers of muscles are arranged like the crossing boards of a double floor.

The surface of the cirrus is covered by a fine columnar epithelium in which are scattered great numbers of goblet cells. The epithelial surface is increased by numerous pits the lining epithelium of which is especially supplied with secreting cells.

The nerve of the cirrus is enlarged at regular and frequent intervals, like the nerves of the digital cirri. Each enlargement corresponds in position to a pair of the alternating layers of the transverse musculature. In a young Nautilus the first cirrus of the as-yet-undeveloped spadix is like one of the labial cirri, slender and marked with annular grooves. The corresponding segmentation of the cirrus and its nerve in the digital and labial tentacles has already been noticed. Probably there is a similar correspondence here, while the transverse musculature is also segmentally arranged. As the cirrus under discussion increases in size the external segmentation becomes obliterated. The branches of the nerve pass outward in the layers of the transverse muscle. The nerve ends abruptly near the tip of the cirrus. An artery runs along the inner side of the nerve A. The vein divides and its branches come to lie at a considerable distance from the nerve, V, V′, Fig. 53.

Between the outer layer of muscles and the epithelium is a layer of connective tissue which is curiously developed in one region. (Fig. 52.) Over most of the cirrus the layer is thin and the tissue firm and close, containing a few muscle fibres; but just below the tip it is much thickened and great numbers of vascular lacunæ, large and small, make their appearance in it. The larger lacunæ have endothelial walls. Fig. 52 only represents the larger lacunæ, and not the far greater number of small ones. It may be possible that this forms a kind of erectile tissue.

SECOND CIRRUS OF SPADIX. (FIG. 16.)

The second cirrus of the spadix is much more modified than the first, for that is modified in shape and size mainly, while this has undergone modification of structure also. It is slender, and instead of becoming larger at its base it narrows. Its muscles are continued into the sheath of the spadix between the first and the third cirri. (Text-fig. 5, C. 2.) Its length is about 4 centimeters. Its basal portion, to within about 15 millimeters of the tip, is round and smooth. Exceedingly indistinct annular grooves can sometimes be seen in this portion of the cirrus. At the point referred to the cirrus begins to be flattened upon both dorsal and ventral surfaces. It ends in a flat, thin-edged, lancet-like tip. A little distance from the tip one edge remains thick while the other is thin, giving the cirrus a triangular shape. Concurrently with the flattening the cirrus becomes more and more distinctly annulated, the grooves appearing a little more strongly marked upon the ventral than upon the dorsal surface.

In general this cirrus adheres to the plan of structure already described for other cirri. The nerve, extending through the cirrus near its center, does not possess any unusual characters. It is of good size, showing ganglionic enlargements at regular intervals which correspond with the annulations upon the surface of the cirrus, and extends to the very tip of the cirrus. (Fig. 61, N.) Upon the inner side of the nerve is an artery, and still farther toward the inner edge of the cirrus a large vein. (Fig. 56, A and V.) The nerve and the artery are surrounded by transverse muscle fibres, but the radial arrangement of the musculature has been lost to a large extent and is replaced by an arrangement of the longitudinal muscles in lines extending across the cirrus in the direction of the shorter transverse axis, the dorso-ventral axis. In the round basal portion of the cirrus the arrangement of the muscles is similar to that in the digital cirri.

The dorsal side of the cirrus, amounting to from one-half to one-third of its entire thickness, from the point where the annulations first show plainly, is occupied by glands and not by muscles. (Figs. 56 and 61, G.) The glands open by very minute pores in the annular grooves, a single row of closely placed pores occupying each groove. The pores of the glands are upon the slopes of the grooves and not in the bottoms. They are so small that they are only to be seen in sections.

The circular and outer longitudinal rings of muscles have been greatly reduced in this cirrus, the longitudinal having almost completely disappeared. Immediately underneath the glands is a thin layer of the circular muscles. With the development of the glands the dermis tissue has become greatly increased, so that now the glands are surrounded by fibrous tissue, traversed here and there by muscle fibres. Each gland has a thin tunic of muscle fibres. A few vascular lacunæ are found in the dermis.

The glands have the shape of thick, round-bodied flasks with very short and narrow necks. (Fig. 55.) Owing to their mutual pressure the glands are usually polygonal. They are 0.8 to 1 millimeter in length and 0.4 to 0.6 millimeter in diameter. The exterior of the cirrus is covered by an epithelium of very slender columnar cells, none of which are secretory. At the mouths of the glands a transition occurs to shorter or even cubical cells which line the duct and upper part of the body of the gland. The sides and the base of the gland are lined with exceedingly long, slender, secretory cells, whose oval nuclei lie in the very bases of the cells. There is considerable variation in the length of the cells of the upper side of the gland. Sometimes they are scarcely longer than those of the duct; sometimes, again, as long as any in the gland. Mucous cells are sometimes scattered among the cells of the upper sides and the duct of the gland, the other cells of these regions not appearing to be secretory; again, all are secretory. The portion of the secretory cell above the nucleus is closely packed with fine granules. The large lumens of the glands were in most cases filled with a finely granular secretion. Glands near the tip of the cirrus may be more or less distinctly divided into two portions, which are partially separated by a constriction—a basal thick-walled secretory portion and an outer thin-walled portion, which may be a collecting or storing chamber, from which the duct leads to the exterior.

The ridges upon the surface of the cirrus are almost entirely occupied by large vascular lacunæ. A network of connective tissue extends between the lacunæ of the ventral ridges, but there is almost no connective tissue in the ridges of the dorsal side.

THIRD CIRRUS OF SPADIX. (FIGS. 17 AND 18.)

The third cirrus is the most highly modified and remarkable of the group. It is longer and larger than the second, being intermediate in size between this and the first. As has already been noted, its base lies posterior to that of the second. It is oval in cross section at the base instead of round, as is the case with all the other cirri of the spadix. It is narrowed at the base, however, like the second cirrus. For about half its length it is oval and perfectly smooth. At its middle it begins to be still more flattened dorso-ventrally, until near its tip it is almost perfectly flat upon both sides. The dorsal side is apt to be somewhat concave and the ventral side convex. A longitudinal ridge may be present along the median line of the dorsal side near the tip, caused by the tissues passing over the nerve lying directly underneath.

At the same time that the cirrus becomes flattened it loses its smooth surface. The dorsal surface becomes marked by transverse ridges, which are at first very faint, but become distinct as the tip of the cirrus is approached. At the very tip, however, the ridges become crowded and less distinct. They also disappear at the edges of the cirrus, leaving a smooth, unmarked margin. Close examination with the naked eye discovers many smaller ridges extending longitudinally between the transverse.

It is upon the opposite (the ventral) side of the cirrus that we find a most peculiar structure. (Fig. 18.) Arranged across the cirrus in rows which seem to correspond closely to the ridges of the opposite side are great numbers of fine pits extending into the tissue of the cirrus. The largest of these may be a little more than a half a millimeter in diameter. Examination with a hand lens shows the openings to be nearly square, the sides being parallel to the main axis of the cirrus, and to be set as closely to each other in both directions as is possible. The openings are often so regularly spaced that they form longitudinal as well as transverse rows. Only a thin wall remains between the pits. At the posterior end of the pitted surface the pits become small, imperfectly formed, and finally disappear. Similarly the pits are not well developed at the tip of the cirrus. When the fingers are passed over the pitted surface it feels like shagreen, and

suggests that it is covered by a rough cuticle. This, however, is not the case, as we shall presently see.

The middle part of the cirrus, where the transition from the oval to the flattened shape takes place, is triangular in section for a distance. (Fig. 59.) The inner side of the cirrus forms the short side of the triangle. The dorsal and ventral surfaces of this region bear their characteristic structures. The inner surface is smooth and muscular.

In general the structure of this cirrus is so like that of the second that no detailed description is necessary of any part except the pits. In Fig. 59 we have a transverse, slightly oblique section of the third cirrus, and in Fig. 60 a longitudinal section of the same cirrus, both drawn with the aid of the camera lucida. Fig. 62 shows a longitudinal section through the center of a pit magnified to 34 diameters. The pits are simple cavities 1 millimeter in depth, into which a fleshy tongue projects from the posterior side as the animal is in its swimming position. Supposing the cirrus to be placed tip upward, the tongue projects from the floor of the cavity. The cavity of the crypt forms only a narrow fissure about three sides and the edges of the fourth side of the tongue. This is thus attached to the wall of the crypt along a narrow median region. (Figs. 59 and 60.) The tongue is strongly muscular, the muscle fibres mostly extending from the base toward the tip. The tissue between the crypts is largely muscular; all the muscle fibres, both of the tongues and of the intermediate tissues, are much finer than those making up the body of the cirrus. Many connective tissue nuclei are scattered among the muscle fibres.

Beneath the epithelium of the sides of the crypts and their tongues is a clear layer of a peculiar structure. (Fig. 62.) This layer does not extend quite to the bottoms of the crypts, but commencing near here, becomes gradually thicker and thicker as the openings of the crypts are approached. The clear layer is especially thick upon the anterior edge of the crypt, i. e., upon the edge toward the tip of the cirrus. Under low powers the layer appears homogeneous and structureless, but high powers of the microscope reveal numerous and exceedingly fine fibres in it. No nuclei whatever are found in the layer. At the extreme outer edge of the layer, immediately under the epithelium, no fibres at all, nor any other structural element can be distinguished. Passing inward, the fibres are progressively more and more distinct. Along the inner edge of the layer, next to the muscle, is a distinct layer of small nuclei which appear like connective tissue nuclei. It is this clear layer which gives the surface of this portion of the cirrus its hard character. It seems to form a supporting tissue or sort of exoskeleton for the other tissues of the crypts, or perhaps for the cirrus as a whole.

The surface of the cirrus is covered with a single layered epithelium. Those portions of the cirrus not occupied by crypts are covered by an epithelium similar to that of the second cirrus. In the region of the crypts it is considerably modified. In the deepest parts of the crypts the cells are of about the same proportions as those upon the dorsal side of the cirrus—slender columnar cells, among which are numerous goblet cells. The number of secretory cells in these regions is not at all remarkable.

As the cells extend outward upon the sides of the crypts and their tongues, they gradually decrease in length and increase in breadth, until a veritable pavement epithelium is formed. The outer portions of the sides of the crypts and all the area between their openings is covered by an epithelium of this character.

The function of the crypts is entirely unknown, and I do not see that we have facts of any kind upon which to base even guesses as to the nature of their uses in the economy of Nautilus. The number of glandular cells in the crypts is so small that, as VAYSSIERE says, the latter can scarcely have been developed for the purpose of increasing glandular area. The development of muscle tissue about the crypts, and especially in their tongues, together with the development of a firm, hard layer upon their surfaces, indicates a considerable and important activity for these structures and for the cirrus as a whole as well.

FOURTH CIRRUS OF SPADIX. (FIG. 19.)

As has been said, this cirrus is almost unmodified. It is the smallest of the group and is nearly hidden by the flap upon the outer side of the spadix. It is scarcely longer than the

corresponding cirrus of the antispadix, but is of considerably greater diameter. The tip is flattened. Elsewhere the cirrus is nearly round. Its lower portion is smooth, while the distal half is more or less distinctly grooved. This cirrus has its origin at the very base of the spadix, and is free for almost its entire length from the main portion of this organ. It possesses a very short separate sheath which is not nearly as long as the sheath of the corresponding cirrus of the antispadix. (Figs. 12 and 14.) This sheath is united to the base of the spadix sheath. The base of the fourth cirrus passes under the base of the first cirrus to its outer side. Aside from the reduction of the annular ridges, the appearance of this cirrus is not markedly different from that of the digital cirri.

The essential features in the structure of this cirrus are also almost the same as those described for the digital cirri. (Figs. 54 and 58.) The arrangement of the muscles is somewhat modified by the great development of the transverse musculature, the strands of which are sometimes as large as those of the longitudinal muscles. The regular radial arrangement of the latter is largely lost. The epithelium of the annular ridges is not especially developed at any point, although distinctly higher upon the ridges than between them. Large blood spaces run within the ridges upon the inner side of the cirrus. They extend only a portion, one-half or less, of the distance across the inner face of the cirrus. These spaces are lined with flat endothelial cells, and communicate with veins lying deeper in the cirrus. They lie almost directly beneath the epithelium. They are not present in the small ridges near the tip of the cirrus, appearing in the tenth to the fifteenth from the tip, and increasing in size as the ridges increase in breadth and height.

The nerves of the spadix come off from the left pedal ganglion; those of the antispadix from the right pedal ganglion. It is very difficult to trace the nerves into the individual tentacles, although I have succeeded in doing this in a few instances. The four nerves to the cirri of the spadix or the antispadix spring from the edge of the ganglion. They appear to belong to the superior labial series, but being a little larger. A few special nerves pass from the ganglion into the base of the spadix. One of these (Figs. 41, 30) forms an enlargement in the base of the spadix, from which several small nerves pass into the surrounding tissues.

In a less than half-grown male the spadix formed a very small, flat organ, resembling the antispadix, which scarcely reached as far as the tips of the jaws. Vayssiere has already shown that the cirri of the spadix are at first like those of the antispadix, and that they undergo modification quite late in the life of the Nautilus.

VAN DER HOEVEN'S ORGAN.

Directly beneath the buccal mass of the male Nautilus is a peculiar organ discovered by Van der Hoeven and since known by the name used at the beginning of this paragraph. (Figs. 8, 9, 10, 66, 67, 68, and 73.) To this organ an olfactory function has been ascribed, without any evidence, to be sure, but apparently in accordance with a common custom of describing any organ of Nautilus, the function of which is unknown, as an olfactory organ. The organ opens into a pocket formed laterally by the labial ridges, ventrally by the cephalic sheath, and dorsally by a ridge connecting the labial ridges. Into this pocket the anterior end of the organ projects freely. (Fig. 8.) The walls of the pocket soon attach themselves to the organ and, being continued upon its surface, form a tunic. This attachment takes place near the anterior end of the organ dorsally, but near the middle ventrally. (Fig. 9.) The organ is oval, the long axis lying parallel to the long axis of the body, and is flattened dorso-ventrally. It is 25 millimeters in length, 15 millimeters in width, and 10 millimeters in thickness.

If the pocket, or atrium, into which the organ projects be opened as far back as the attachment of its walls to the organ, we see that the anterior part of the latter is divided by a median longitudinal fissure which extends from the ventral side nearly through to the dorsal side of the organ. (Fig. 8, VF; Fig. 10.) The fissure does not extend on the surface quite as far back as the attachment of the integument to the organ. Transverse and longitudinal sections reveal the fact that the fissure just mentioned does, however, extend within the organ for some distance

into its posterior half, and that it communicates dorsally with a broad transverse fissure near the dorsal side of the organ. (Figs. 9 and 10, H.) The transverse horizontal fissure extends almost to the posterior end of the organ.

The anterior free portion of the organ is firm in texture and is seen to be partly divided into lobes by fissures extending from the edges of the vertical fissure. In longitudinal and cross sections of the organ the deeper parts of the longitudinal fissure are seen to be bordered by thin, shelf-like laminæ, which extend about halfway to the lateral edges of the organ. (Figs. 10 and 66.) The laminæ do not reach the posterior part of the organ, extending only as far as the posterior end of the vertical fissure, which ends in a line directed upward and backward.

The regions posterior to the laminæ and dorsal and lateral to the horizontal fissure are glandular. The openings of the glands can be seen with the naked eye or a hand lens upon the walls of the horizontal fissure. The glandular part of the organ is quite distinctly different from the remainder in appearance and texture, but still is firm and hard.

Both the lobules of the anterior region and the horizontal laminæ radiate from a small region of firmer tissue near the anterior end and on each side of the vertical fissure. (Fig. 9.) The lobules noticed at the sides of the anterior portion of the vertical fissure are thick and fleshy and often have their edges rounded. Posteriorly they are seen to graduate into the horizontal laminæ; as a matter of fact, lobules and laminæ are differently developed members of a single series. Counting all as laminæ, there are from 20 to 24 laminæ upon each side of the vertical fissure.

Several muscles are attached along the lateral edges of the anterior part of the organ. At their attachment they usually form a distinct muscular ridge from which two principal muscles separate themselves on each side. One pair of muscles extends backward along the sides of the organ to penetrate the muscular base of the buccal mass above and outside the ventral buccal retractors. (Fig. 8.) The other pair of muscles extends outward and each soon divides into two branches. The anterior branches are spread out upon the bases of the superior labial lobes. The posterior branches go to the sides of the cephalic sheath below the anterior. This arrangement of the muscles shows distinct resemblances to that of the muscles of the inferior labial lobe of the female. (Fig. 26.)

A large nerve arises from the pedal ganglion just outside the infundibular nerve. (Fig. 41, 7 and 35.) The two nerves pass along the sides of the organ of Van der Hoeven, entering it a little anterior to its middle.

A branch from the tentacular artery of each side supplies Van der Hoeven's organ with blood. These are the same branches which, in the female, supply the inferior labial lobe. (Text-fig. 10, p. 182, 1 and 3.)

The firm tissue forming so large a proportion of the anterior part of the organ is composed of a thick-meshed reticulum of elastic tissue fibres, in the interspaces of which run bundles of muscle fibres. The tunic is composed of a layer of muscle very distinct from the underlying tissues. The bodies of the lobules and the laminæ are almost entirely composed of elastic tissue. The bodies of the thin horizontal laminæ which lie hidden within the organ are not thicker, and frequently not as thick as the epithelium of either surface.

The epithelium of the lobules and the laminæ is of exactly the same character. It averages 80μ in height, and is composed of a single cell layer comprising two entirely different sorts of cells. The more evident, and at first sight the only sort, are slender columnar cells from 5μ to 8μ in transverse diameter. Oval nuclei situated in the very bases of the cells make a distinct row along the laminæ. All these cells appear to be able to form a secretion, which is contained in the cells in the shape of granules, which stain with remarkable intensity. But while all the cells appear to possess the power of secretion, not all in my preparations were exercising it. Next to areas in which all the cells were choked with secretion are areas the cells of which contained no secretion whatever. And as a rule, there is no gradual transition from one area to the other. The boundaries of the areas are distinct; upon one side all the cells are crowded with secretion, upon the other side not a single cell contains any secretion. In only a few places are secreting cells mixed with others not secreting along the edges of the areas. As a rule, the areas free from secretion are near the edges of the laminæ turned toward the fissure (the

inner), while the outer parts of the laminæ are covered by cells full of secretion. Occasionally, however, non-secreting areas may be found near the outer attached edges of the laminæ as well. No secretion has been found in the cavity of the organ. The sum and substance of these facts probably amounts to this, that the secretory function of the epithelium of the laminæ is exercised periodically only, and that my material was collected during the period of preparation, but before the entire secretory area had assumed its function.

The epithelium of the laminæ appears to be ciliated, and this appearance is connected with the presence of a second sort of cells in the epithelium. I have stained a number of preparations with borax carmine, and then with Lyons blue. Such preparations show a second line of nuclei at the level of the middle of the epithelium of the laminæ. These nuclei are exceedingly slender, being 6μ to 8μ in length by 1μ to 1½μ in width. They belong to and are situated near the center of long thread-like sensory cells, which stand thickly around the secretory cells. (Fig. 73.) The ends of the former project beyond the latter, forming sensory spikes, which are so numerous that they give the appearance of a thick coating of strong cilia belonging to the secretory cells. The cell bodies of the sensory cells are so slender and absolutely thread-like that they are not clearly visible without special stains, and then only in places where the other epithelial cells have been accidentally separated. Fig. 73 is an accurate drawing of such a place under a magnification of nearly 500 diameters, but taken from the glandular portion of the organ and not from the laminæ. The sensory cells, however, are alike in both regions. Favorable cross sections of the epithelia show the nuclei of the sensory cells thickly clustered around and between the secretory cells. The bases of the sensory cells pass into the subepithelial tissue as fine fibres, and are there lost; but it seems only reasonable to suppose that they are directly continuous with nerves, and that the cells are true sensory elements. We have now a better ground than before for supposing this organ to have a sensory function, which may very possibly be olfactory.

The epithelium of the surface of the anterior parts of the organ and of the skin forming the walls of the atrium is of the same form as that of the laminæ, though apparently not at all glandular.

The glandular portion of the organ is composed almost entirely of long branched glandular tubules with narrow lumens. (Figs. 66, 67, and 68.) The tubules are parallel to each other, while the submucous tissue separating them is so slight in amount as to form little more than a separating lamella. (Fig. 68.) The tubules are lined by a single-layered epithelium, composed, like that of the laminæ, of secretory and sensory cells.

The secretory cells are of a very different character from those of the laminæ and probably produce a different secretion. The regular arrangement of their brilliantly staining nuclei in the bases of the cells causes stained sections to appear almost diagrammatic. I do not think that the histological condition of my material is good enough to warrant my making a detailed comparison between these cells and the secretory cells of the laminæ. The regular arrangement of the tubules make the glandular region a striking feature of sections. The clearness of its secreting cells compared with those of the laminæ, their slightly greater width, and the larger intensely staining nuclei are features which quite clearly distinguish the secreting cells of the glands from those of the laminæ.

The gland cells average 90μ in length and are from 7μ to 10μ in width. The secretion collects in the shape of numerous droplets or granules in the portion of the cell above the nucleus. No secretion was found in the lumens of the glands.

Around and between the secretory cells are sensory cells exactly similar to those described in the epithelium of the laminæ (Fig. 73). The slender nuclei of the sensory cells form a quite distinct row at the middle of the epithelium. The sensory cells are not so numerous in the glands as upon the laminæ, but still their number is surprising. Fig. 73 is drawn from a section in which the secretory cells had separated from the submucosa and each other, leaving the sensory cells revealed. The section was cut somewhat obliquely, and so does not show the free ends of the cells. The sensory cells are perhaps a little more numerous here than in most portions of

the glands, although the portion to be drawn was chosen at random. In a few places in my sections of the glandular portion of the organ I have seen the ends of the sensory cells projecting beyond the surface of the epithelium as sensory spikes, but in most places the projecting parts were not present. Whether this is the normal condition or is due to poor preservation of the material I can not say.

The nerves (Fig. 8, N) which enter each side of VAN DER HOEVEN'S organ end in ganglia at the sides and near the posterior ends of the laminæ (Fig. 41, 35; Fig. 66, Gn). From the ganglia a small nerve extends into each lamina (Fig. 66, N), and two or three nerves on each side pass into the posterior glandular region. Each nerve to the laminæ is accompanied by a small artery. The laminar nerves possess an outer layer of ganglion cells as well as ganglion cells scattered throughout them. Each of the small lobular divisions of the anterior part of the organ receives a single nerve as well as the thin laminæ.

The facts described seem to me to constitute good and sufficient evidence for considering the inferior labial lobe of the female and VAN DER HOEVEN'S organ to be homologous. The position in the body is the same; the principal muscles are very nearly alike; the innervation is the same; the course of their blood vessels is the same.

It also seems probable that each lamina corresponds to one of the cirri or lamellæ borne upon the inferior labial lobe of the female. The main evidence for this rests upon the innervation of the laminæ, which is exactly similar to that of the cirri and lamellæ of the inferior labial lobe. The structure of the nerves themselves is also the same in the two organs. The presence of a small blood vessel running close to each laminar nerve also constitutes a bit of evidence in favor of this view. The number of laminæ in VAN DER HOEVEN'S organ is the same as the number of cirri and lamellæ combined of the inferior labial lobe, and the reasons for considering the cirri and lamellæ of the latter to be homologous have already been brought forward.

Finally the sensory cells add support to the view. It will be remembered that between the lamellæ of the inferior labial lobe are pits lined by a peculiar epithelium. The cells of this epithelium appear to be exactly similar to the sensory cells scattered over the surfaces of VAN DER HOEVEN'S organ, and I think it not improbable, taking into consideration the other evidence for the homology of these organs, that during the course of the metamorphosis of the inferior labial lobe of the male, the sensory cells, which in the female are confined to limited areas occupied by them alone, have become distributed over the entire surface of the organ.

The glandular part of VAN DER HOEVEN'S organ, which forms so large a proportion of the whole, does not seem to correspond to any portion of the inferior labial lobe of the female. The gland is probably a new formation developed in accordance with the changed and special functions of the lobe.

The inferior labial lobe of the female is evidently in much more nearly the primitive condition, its parts being but little modified from the type of structure of the many simple tentacles around it.

Here, too, the question constantly arises, What are the functions of this organ?

When any organ differs so much in the two sexes it seems only reasonable to consider that it is a sexual organ of some sort. We have, then, at least reasonable grounds for saying that VAN DER HOEVEN'S organ, and possibly the inferior labial lobe, is an accessory sexual organ; but we know nothing whatever of its chief functions. Apparently its secretory functions are only periodically and not constantly active. To what use the secretion is put is impossible to guess, even if guesses happened to be desirable. The organ may be a sensory organ all the time and a secretory organ only part of the time, or both functions may be active only periodically. In the latter case, again, the sensory function may be active only when the organ is not secreting, or this may be the time when the sensory function is most active, or the only time when it is active. It seems probable that the sensory function is either that of tasting or smelling. Possibly the activity of the secretory cells, or at least the flow of secretion, depends upon the perception of certain substances in the water by the sensory cells, or the sensory function may have a much closer relation to the everyday life of the animal.

OCULAR TENTACLES.

There are four of these tentacles, two springing from near the base of the stalk of each eye. The eyes, it will be remembered, are attached to the sides of the head in the angle formed by the posterior edge of the lateral portion of the cephalic sheath and the projecting auricles of the hood. The ocular tentacles arise above the level of attachment of the eyes, one in front of, and the other behind, each eye (Fig. 1, O′ and O″; Fig. 2, O′; Fig. 3, O″). Accordingly, they are distinguished as the preocular and the postocular tentacles.

The preocular is situated upon the base of the cephalic sheath, immediately back of the posterior corner of the sheath of the second digital tentacle, and in the angle formed by the projecting sides of the hood and the lateral walls of the head. Its sheath forms a portion of the posterior part of the cephalic sheath, only a few millimeters of its tip being free.

The postocular arises above the posterior edge of the eye in the angle made by the hood and the sides of the head. It stands straight out from the sides of the head, having a free sheath 6 to 10 millimeters long. The preocular is directed outward and forward, the postocular outward and slightly backward. Both tentacles are well protected by the projecting sides of the hood.

The cirri of the ocular tentacles are in their general features like those of the digital tentacles, but under the general similarity are most important differences of structure as well as of function. They are oval, lacking the angles of the digitals (Fig. 65). The annular grooves are very deep upon the anterior sides, and this is especially noticeable near the tips of the cirri (Figs. 64 and 63). Owen (1832, p. 14) well describes these cirri as "in reality composed of a number of flattened circular disks appended to a lateral stem." The closely pressed ridges project from the base to the tip of the cirrus like the lateral plates of a cephalopod gill.

Observations made by Willey and published in the fortieth volume of the Quarterly Journal of Microscopical Science are well worth quoting in this connection:

"The occurrence of a special tentacle in front of the eye and another behind the eye in Nautilus is well known. These tentacles resemble the large number of remaining tentacular appendages in being ringed and also in being retractile within sheaths, but differ from them in almost every other respect. In the first place, most of the tentacular appendages of Nautilus have essentially an adhesive function, to which is related a prehensile function. They are employed for seizing hold of food and for attachment to surfaces. . . . .

"It will not be surprising to learn that the adhesive tentacles are not ciliated; but it is necessary to mention this negative fact, because the preocular and postocular tentacles are ciliated. On the side corresponding to the suctorial ridges of the adhesive tentacles the annulations of the preocular and postocular tentacles form deep grooves, between which the ridges project as prominent lamellæ. The upper and lower surfaces of the lamellæ and the bases of the grooves are covered with vibratile cilia. There can be but little doubt that the preocular and postocular tentacles of Nautilus represent tentacular processes, homologous with the adhesive tentacles, which have been modified to serve an accessory olfactory function. We will therefore speak of them as the olfactory tentacles, in contrast to the adhesive tentacles. . . . .

"The olfactory tentacles . . . . when extended stand out from the body nearly at a right angle, the preocular tentacle being directed slightly forward and the postocular tentacle usually tending backward. The ciliated olfactory lamellæ are directed strictly forward.

"In the living Nautilus the olfactory tentacles otherwise offer a strong contrast to the adhesive tentacles by their almost uniform white color. When examined under the microscope there is found to be a little brown pigment in the annulations and at the edges of the lamellæ, but when viewed in toto under water the general color effect is white.

"Moreover, the adhesive tentacles can be touched without necessarily being retracted, but at the slightest contact with a foreign body the olfactory tentacles are instantly retracted within their sheaths. The presence of accessory olfactory tentacles in Nautilus can, I think, be related to an essential bionomical difference between the existing Tetrabranchiata and the Dibranchiata.

"Nautilus finds its food chiefly by the sense of smell, while it is a matter of more or less

common observation that the Dibranchiata, with their remarkably perfect eyes, pursue their quarry by the sense of sight."

The structure of the preocular and postocular cirri seems to be the same in all respects. The annular grooves, which are so deep upon the anterior side, are frequently no more than grooves in the epithelium upon the opposite side; i. e., the groove is formed by certain of the epithelial cells being shorter than those of the remaining surface of the cirrus, the bases of all being at the same level. In other portions of the cirri the grooves affect the subepithelial tissues of the posterior side as well. The ridges upon the anterior face of the lower part of the cirrus are very thin and flat, are closely pressed together, and lie in a plane perpendicular to the axis of the cirrus. The ridges of the tip of the cirrus are not flat, nor of even thickness, are more separated from each other, and turn upward around the cirrus like portions of the rim of a saucer. They form little cups, open toward the tip of the cirrus.

The epithelial cells of the cirri are all slender columnar cells. The cells of the bottoms of the grooves are taller than those upon the outer portions of the ridges. The former are about 60μ in height and 4μ in width. They are ciliated, the fine cilia being about 14μ in length. The latter cells are only 44μ in height. All possess oval nuclei irregularly located in the basal halves of the cells. Occasionally a goblet mucus cell is found among the ciliated cells. Goblet cells are frequent upon the posterior surfaces of the cirri and upon the unciliated portions of the ridges. The basement membrane upon which the epithelium rests is remarkable for its sharp outline and irregular surface. One can scarcely imagine a surface more wrinkled and pitted in a minute way. The outer surface of the epithelium, however, does not repeat this irregularity.

The subepithelial tissue of the ridges is very scant, what little there is consisting of fibrous and elastic connective tissues, and containing few muscle fibres.

From the structure of the cirrus, the side bearing the high ridges evidently corresponds to the inner side of the cirri of the other groups, although it is turned forward. As a matter of fact, if the ocular cirri were pulled forward until they were parallel to the digital cirri, the now anterior sides would then be inner. For the sake of convenience in description and the comparison thus introduced, I shall speak of the anatomically anterior side, when needful, as the inner side.

The arrangement of musculature is practically that which has been described as typical of the digital tentacles, except that it is even more regular in the ocular tentacles. As portions of the ridges are not constructed for adhesion there is no interruption of the arrangement of the muscles upon the inner side of the cirrus. Radially arranged longitudinal muscles surround the nerve, although this is, as in the former case, nearer the inner side of the cirrus than the outer. The two layers of circular muscle fibres and the outer longitudinal muscles pass uninterruptedly around the cirrus.

The ocular cirri are especially well supplied with rather large blood vessels. It would be interesting to know if the arteries described by Willey as going to the eye do not also give off branches to the ocular tentacles, or if the latter are supplied from the tentacular artery. Upon the inner side of the nerve is an artery which corresponds in position to the artery of a digital cirrus. Several other arteries, perhaps branches of this, lie near the nerve. A large vein lies between the artery and the inner side of the cirrus.

The structure of the nerves of the ocular tentacles is notable. (Fig. 64 and 65, N.) The nerves of the preocular and postocular tentacles arise as branches of a nerve which springs from the side of the pedal ganglion, the remainder of it being distributed to several of the digital tentacles. (Fig. 41, 11.) A cross section of the ocular tentacles shows that their nerves are of unusual size. Near the tip of the cirrus the nerve has the same character as the nerves of the cirri already described. It has an outer layer of ganglion cells, thickened in each segment into ganglia. Shortly, farther from the tip of the cirrus, numerous bundles of nerve fibres join themselves to the inner side of the nerve trunk. As these pass toward the base of the tentacle they seem to gradually enter the nerve trunk, their places being taken by other nerve bundles from the outer parts of the cirrus. Thus a kind of accessory nerve is formed which extends from near the tip of the cirrus to its base along the inner side of the primary nerve trunk. (Fig. 65, N'.) These

nerve bundles are not surrounded by ganglion cells like the nerve trunk, so it is easy to distinguish the boundaries of the latter in both longitudinal and cross sections. Nevertheless, they contain numerous nerve cells lying singly or in groups, some of the groups forming what one might call strands of nerve cells, parallel to the nerve bundles. At the base of the cirrus all the lateral bundles have entered the nerve trunk, which is here of the ordinary size. The nerve, as a whole, is enlarged in each segment of the cirrus by aggregations of nerve cells, the primary nerve trunk being the part most affected. From each ganglion twelve to sixteen nerves pass radially to different parts of the segment, especially to the lamella-like ridge of the inner side. These nerves are very large and distinct. The nerves passing to the ridges can be traced to directly beneath the basement membrane of the epithelium. I could not determine any direct connection of the nerves with cells of the epithelium, although, in view of the peculiar character of the tentacles and the epithelium of the grooves, and the very liberal and conspicuous innervation of these regions, it seems probable that future research will reveal special nervous elements in the epithelium.

The most curious feature of the ocular tentacles is yet to be described. The tips of the cirri, consisting of several segments, or of a single terminal segment, break very readily. The ease with which the segments break off is explained by the presence in the cirrus of breaking planes, as I have called them. In longitudinal sections lines are seen stretching across the cirrus from groove to groove, along which the connective tissues are weak or discontinuous. (Fig. 64, X.) The planes correspond to the grooves between each two segments. The longitudinal muscles and the nerve cord are not broken, but the muscles at least break very easily along the planes. Occasionally connective tissue nuclei are gathered along the breaking planes, though this may be a coincidence rather than a structural character.

At all events, there seems to be here a provision for the amputation of segments of the preocular and postocular cirri with considerable ease. It would seem as if the retraction of the cirri within their sheaths at the slightest touch, as already quoted from Willey's published observations, would protect them from injury. And especially so, as they are situated in a nook under the auricle of the hood, back of the cephalic sheath, and above the eye, so that it seems as if they need be only partly retracted within their sheaths to be completely sheltered. I feel quite sure, from the constancy of these structures between all the segments of my sections, that they are not artifacts, although I do not by any means deny such a possibility. If they are natural structures they appear to be a mechanism providing for the common and easy loss of (but not self-amputation, necessarily) terminal segments of the ocular tentacles, and they also point to the possibility of rapid regeneration of the lost portion, as is the case in other animals in which provision is made for the easy loss of certain parts of their bodies. But it is also very strange that Nautilus should possess such a mechanism in the ocular tentacles when it also has the ability to retract them quickly upon a slight stimulus.

The innervation of the ocular tentacles, as well as their position and structure, leaves no doubt but that they are members of the digital series which have become modified for sensory functions.

To summarize:

The *digital tentacles* of both sexes are exactly alike in number, distribution, and structure. Their fused sheaths form the cephalic sheath, a fleshy wall surrounding the anterior portion of the head. Upon the inner side of the cephalic sheath of the female, above the funnel, is a lamellated region for receiving the spermatophore.

The *superior labial tentacles* are alike in position and structure in both sexes, but are less in number in the male than in the female.

The *inferior labial lobes* and tentacles are present in both sexes, but are quite different in each. In the female the lobe is large and muscular. Upon its anterior edge are numerous tentacles, some of which develop cirri, while others form lamellæ, at the bases of which are certain sensory pits. In the male the lobe and its tentacles are represented by Van der Hoeven's organ. The laminæ of this correspond to the cirri plus the lamellæ of the inferior labial lobe of the female, while the gland is not represented in the latter organ.

The *spadix* and *antispadix* do not correspond to any group of tentacles in the female, as far as our present knowledge goes. It has been suggested that they have been formed by the separation of the four ventral tentacles of the superior labial group. It is true that the number of tentacles comprised by the spadix or the antispadix added to that of the superior labial group equals the number of tentacles in a superior labial group of the female, and that in young animals they are like these in size and structure. The innervation of the spadix and antispadix also seems to be like that of the superior labial tentacles. Yet the two organs are so completely separated from the labial tentacles, even standing entirely outside the labial ridge, that we must consider it still an open question if they are represented in the female until embryological evidence can be obtained.

The *ocular tentacles* are members of the digital series which have become modified for sensory functions.

This seems the best place to consider another secondary sexual character, which after all is closely connected with the tentacles. Both Vayssiere and Willey point out that a difference exists in the shape of the opening of the male and female shells. In general the shell of the male is larger than that of the female, and the breadth of the opening of the shell is greater in proportion to its height in the male than in the female shell. But these characters are so variable that in examining a large number of empty shells I was unable to determine which had belonged to males and which to females. Willey himself emphasizes the variability of this character. The hood of the male exceeds that of the female in size in the same manner as has just been mentioned for the opening of the shell.

The generally larger hood and shell opening of the male seems to be largely the result of the growth of the spadix.

PALLIAL COMPLEX.

MANTLE.

The mantle cavity of Nautilus extends completely around the body; it is shallow dorsally, but ventrally a deep, capacious cavity, which contains the various organs spoken of as the pallial complex.

The mantle itself is a thin and only slightly muscular fold, which fits closely against the walls of the inhabited chamber of the shell. I wish to make a sharp distinction between the mantle and the body wall, especially between it and the thin, membranous portion of the body wall covering the visceral hump and so frequently spoken of as the mantle. I shall limit the term "mantle" in this description to the projecting fold around the middle of the body, extending forward from its junction with the body wall and elsewhere free from the body, surrounding it like a cape. The name can not properly be applied to any other portion of the body wall.

The ventral and lateral edges of the mantle follow the edge of the shell and are attached to it it (Fig. 1, V M). From umbilicus to umbilicus, dorsally, the mantle forms a free fold, which lies against the involution of the shell (Figs. 1, 2, and 5, D M). The most shallow parts of the mantle cavity are just beneath the umbilici of the shell, dorsal to each shell muscle. The edge of the mantle following the edge of the shell slopes rapidly upward and backward to the umbilici. The posterior limit of the mantle cavity also slopes upward and somewhat forward to the same point. Thus the depth of the mantle cavity or the width of the mantle, 10 centimeters in the mid-ventral line, is reduced to 1 centimeter over the shell muscles. The dorsal portion of the mantle is produced upward and forward and is closely pressed against the lower portion of the involution of the shell. In the mid-dorsal line, therefore, the mantle has a width, or the mantle cavity a depth, of about 4 centimeters. The dorsal part of the mantle cavity contains no organs, and is nearly closed off from the ventral part by the narrowness of the lateral portions, which are still more nearly closed by the upper ends of the crura of the funnel. The dorsal part of the mantle cavity must be nearly minimal in volume, since the hood and body wall forming its floor fit closely around the involution of the shell. The dorsal portion of the mantle is probably strongly contracted in alcoholic specimens, since it does not extend nearly as high up on the

involutions of the shell as the posterior face of the hood. It has been suggested that the black layer seen upon the lower portion of the involution of the shell is deposited by the dorsal portion of the mantle. The epithelium of the posterior surface of the hood is pigmented and glandular, and probably plays the principal part in the deposition of the black material.

The mantle is for the most part a very thin, almost membranous, fold and is only slightly muscular. The contrast between it and the mantle of most of the Dibranchiata is very striking in this respect. The anterior border of the part of the mantle which is attached to the edge of the shell is slightly thickened and is comparatively quite muscular, forming a band along the edge of the mantle 1 centimeter to 1.5 centimeters in breadth. The median ventral portion of the mantle is also frequently especially muscular, and forms a strip which joins the muscular border like the stem of a T. The edge of the mantle is marked by two parallel grooves separated by a sharp ridge. The mantle seems to be attached to the edge of the shell, not only by its own edge, but also along a narrow band extending back from the edge on the outer side, along which the epithelium is peculiarly modified. Probably this attachment is not very strong.

The dorsal portion of the mantle is of uniform thickness, and, while very thin, is still much more muscular than the ventral portion.

The ventral portion of the mantle frequently presents a peculiar appearance. The tissues on either side of the middle line seem to have become chitinized; the mantle in these spots appears thin, transparent, and structureless, and has the appearance of a thin sheet of chitin. Sometimes the chitinized areas (if we may so call them) are small, like oval windows set in the sides of the mantle; sometimes they extend over the greater part of the ventral portion of the mantle, and sometimes even across the mid-ventral line. In any case the thickened border of the mantle is not affected. This change in the tissues of the mantle appears to begin on each side of the middle line ventrally and then to spread in all directions from the two starting points until nearly the whole of the ventral part of the mantle is affected. The question, Is this an accompaniment of senility? can not help but be suggested.

Speaking more exactly, the preceding description applies to the greater part of the ventral portion of the mantle, but not to all of it. There is a narrow posterior region which is thickened and which has hitherto been described as being part of the body wall. I wish to call especial attention to the fact that the posterior portion of the mantle of Nautilus is a true outfolding of the body wall, and that the renal sacs and the rectum are situated within this portion of the mantle and not inside the general body, as in the Dibranchiata. The pallial complex of Nautilus is entirely different from that of the Dibranchiata, not alone in its parts, but also in the relation of these parts to the body and to each other. This will be brought out as we proceed with the description of the separate parts of the complex.

As the renal sacs lie in the posterior part of the mantle, this is consequently thickened and entirely different in its appearance from the anterior part. The renal sacs occupy only the central or most ventral region of the posterior portion of the mantle. They lie entirely between the posterior pair of gills. When the mantle is turned back and the animal turned ventral side up, as is usually done in examining these parts (Figs. 3 and 4), the renal organs sink more or less into the body, and the inner side of the mantle above them sinks down until flush with the surface of the body, so that the real relation of the parts is obscured. I presume that it is owing to this fact that the true position of the renal organs has been overlooked for so long by most observers. I can not understand from his words whether Willey (1895) recognizes the same relations between the parts of the pallial complex as I do or not. However, if one cuts the mantle of a well-preserved specimen in the mid-ventral line while the animal is held in its natural position, there is no doubt whatever about the extent of the mantle nor of the positions of the renal sacs, rectum, anus, and gills, as well. The inner and outer walls of the posterior portion of the mantle fold are very thin and soft. Keferstein described the thickened portion of the mantle as a projecting part of the body wall forming a posterior wall to the mantle cavity, upon which were located the anus, gills, and nephridial and pericardial pores. Owen describes the gills as situated upon the mantle. Joubin, however, certainly recognizes the real extent of the mantle and the position of the various parts of the pallial complex.

The discovery of the pallial arterial system is due to WILLEY, who by means of injections was enabled to describe this peculiar system. The lesser aorta divides into two branches almost immediately after leaving the heart. One branch, the septal, goes backward and supplies blood to the siphuncle and the septal region of the body wall. The other branch, the pallial artery, bends downward to the middle line of the body wall and then runs straight forward below the skin on the surface of the renal sacs, and then in the median line of the ventral portion of the mantle nearly to its anterior edge. From its posterior part the pallial artery gives off branches to the intestine and the rectum. In front of the anus, at the posterior limit of the thin portion of the mantle, it gives off a large branch upon each side, the branchio-osphradial arteries. These supply the posterior portion of the mantle and "send up branches to the tips of the branchiæ, supplying the integument of the latter, and also a small branch into each of the osphradia. . . . In the female they also supply the nidamental gland." As the pallial artery passes forward it gives off several small branches to the lateral portions of the mantle. Arriving near the edge of the mantle it divides into two branches, which turn to either side and follow the posterior edge of the muscular margin of the mantle, the marginal pallial arteries. Very numerous and regularly arranged short branches, the radial pallial arteries, spring from the anterior side of the marginal pallial arteries, while longer and more irregular branches pass from the marginal pallial arteries backward into the middle parts of the mantle.

The marginal pallial arteries do not finally end in capillaries or blood sinuses, but unite with the pallio-nuchal branches of the dorsal aorta, thus forming a complete arterial circle, discovered by WILLEY, which he has named the circulus pallialis. The union takes place at the dorsal sides of the shell muscles.

In addition to forming a union with the marginal pallial arteries, the pallio-nuchal arteries give off branches to the dorsal portion of the mantle, and to the dorsal nuchal region of the body wall (the region which is hollowed out to receive the involution of the shell), and to the crura of the funnel.

In regard to the pallial veins WILLEY says the following:

"When a Nautilus becomes moribund it usually rises to the surface, owing to an abundant production of gas in the interior of the body. If it is allowed to die and is then removed from the shell the veins are found to be injected with gas of some sort, and the finest ramifications of the veins, in the mantle at least, are displayed with a clearness which could hardly be attained by artificial injection.

"The mantle is simply riddled by these veins in a manner which defies one's powers of draftmanship. The veins are collected into two main trunks, which lie on either side of the anterior pallial artery, and proceed backward to open into the afferent branchial vessels. At the sides of the mantle there are also a number of lateral pallial veins, which open into a large sinus situated over the shell muscles."

The mantle of the specimen OWEN described possessed a peculiar abnormality. Its opposite sides had grown together above the funnel so that OWEN describes and figures it as "perforated by a large aperture through which the funnel passes."

BODY WALL.

The inner side of the mantle cavity is formed by the body wall, to which I wish to devote a few words so as to lay a foundation for a point to be brought forward later.

Laterally—i. e., at the sides of the body—the inner wall of the mantle cavity is formed by the sides of the great shell muscles alone (Figs. 3 and 4). These muscles pass from the cephalic cartilage outward and backward, forming the sides and part of the floor of the middle region of the body wall, to be attached one to each side of the shell just anterior to the edge of the last septum. Perhaps we might say that they end immediately back of the lateral portions of the mantle cavity, for these parts of the mantle cavity are limited posteriorly by the outer ends of the shell muscles. The muscles are only about 5 centimeters in length, but 2.5 centimeters in breadth by 1.75 centimeters in thickness. These dimensions convey an idea of what the power

of these muscles must be. The outer sides of the muscles are convex, the inner sides concave. The shape of the muscles in cross section is about the same as the shape of the area of attachment of the muscles to the shell.

The muscles meet anteriorly, but as they pass outward and backward a considerable triangular space is left between their ventral edges. This portion of the body wall is composed of quite a strong layer of transverse muscle fibres, which are continued, in part at least, outward over the shell muscles. The actual thickness of this region of the body wall is very little, but it is considerable when compared with that of the body wall covering the visceral region. The vena cava lies in the middle of the triangular space between the shell muscles.

Between the dorsal edges of the shell muscles is another thin portion of the body wall, which forms the floor of the dorsal portion of the mantle cavity. This is also supplied with a quite strong musculature. This dorsal region of the body wall is concave, like a mold of the involution of the shell. It passes into the hood anteriorly and laterally, becoming gradually thicker and firmer.

The shell muscles have a very copious supply of blood received through a number of arteries.

The posterior columellar arteries are the largest and most important of those supplying the muscles. The left posterior columellar artery arises with the hepatic artery from a short common branch of the dorsal aorta—the hepatico-columellar artery. (Text-fig. 10, p. 182.) The columellar artery takes a diagonal course upward, outward, and forward to the upper edge of the left shell muscle, immediately anterior to its attachment to the shell. Then, bending downward and backward upon the inner surface of the muscle, it gives off numerous branches which penetrate the muscle. The right posterior columellar muscle arises from the right side of the dorsal aorta about 7 millimeters anterior to the origin of the hepatico-columellar muscle. As the posterior portion of the dorsal aorta lies upon the left side of the body, the right posterior columellar artery has a longer course to run to reach the right shell muscle than the left posterior columellar artery has to reach the left shell muscle. Otherwise the course of the two arteries is the same upon their respective sides.

From the point where each posterior columellar artery bends downward a branch is given off to the region of the mantle in front of the shell muscles and to the portion of the body wall dorsal to it.

The anterior portions of the shell muscles are supplied with blood by a branch of each innominate artery. These (the anterior columellar arteries) pass backward, downward, and outward to the muscles. (Text-fig. 10, p. 182.)

In addition to these special arteries to the shell muscles, the nuchal arteries, or their branches pass along the inner dorsal edges of the muscles and appear to send small branches into them.

The shell muscles are innervated from the visceral ganglia. Exceedingly numerous flattened band-like nerves pass from the posterior side of each ganglion into the muscles. (Figs. 41, 14.)

GILLS.

The two pairs of gills are situated upon the mantle at the sides of the ventral mantle chamber. (Figs. 3 and 4). They are arranged as an anterior and a posterior pair, one gill of each pair lying upon each side of the mantle, close to each other. The gills of Nautilus differ from those of the Dibranchiata, not only in number, but also in that they are situated upon the mantle instead of upon the body wall, and in that they are attached by their bases only, otherwise lying freely in the mantle chamber. They have much the same shape and structure as the gills of the Dibranchiata. The gills are situated upon the thin and muscular part of the mantle just below the convex anterior angle of the outer end of the shell muscle, the base of the anterior gill lying about 8 millimeters in front of the base of the posterior gill. The bases of the gills are sometimes placed so closely to each other that they seem, as OWEN said, "each pair arising by a common pedunele from the inner surface of the mantle," though I have never found this to be literally true. Examination always has shown that the bases of the gills were separate from each other.

Though there is rarely any considerable difference in the size of the gills, it will usually be found that the gills of the anterior pair are thicker than those of the posterior pair, while the latter may be a trifle the longest. Average measurements for the anterior gills are 18 millimeters in width and 11 millimeters in thickness. The posterior gills are 15 millimeters in width and 9 millimeters in thickness. Both pairs of gills are about 5 centimeters in length. Each gill is composed of two rows of flat, crescentic leaflets attached alternately to the sides of an oval stem. Although the posterior gills possess somewhat the smallest bulks, they bear more leaflets than the anterior gills, having about sixty-five pairs, while the latter have only about fifty-five. Owing to the arrangement and shape of the leaflets the gills are flattened dorso-ventrally. The number of leaflets varies considerably in different specimens, being as low as thirty in some. The leaflets are attached upon the stem obliquely to the base of the gill. The leaflets of the tip of the gill are rudimentary; they become more complex toward the base of the gill, being completely formed at about the tenth from the tip.

It will be noticed that in this description I have apparently reversed the position of the gills as given by previous observers. This is explained by the fact that others have described the gills in the position they occupy after the mantle has been reverted, and as though they were attached to the body wall. Owen recognized the pallial position of the gills, but later observers, with the exception of Joubin, seem to have assumed that the gills are upon the body wall, and this makes the posterior and anterior gills of their descriptions correspond to the anterior and posterior gills of my description.

The stems of the gills are flattened at their bases in the plane of the greatest width of the gills to form thin plates. (Fig. 4, at the end of the index line B V.) The lines of attachment of the stems of the gills to the inner side of the mantle are directed upward, forward, and slightly outward. The anterior gills lie a little to the outside of the posterior gills. The branchial vein runs along the ventral side of each gill as a projecting ridge. The branchial veins of the anterior gills run inward from the bases of the gills toward the median line, suspended by a thin ligamentous band, which may be considered as an inward extension of the base of the stem of the gills. (Fig. 4, B V.) At the outer borders of the inner renal sacs the veins pass inward through the mantle toward the heart. The lower leaflets of the anterior gills extend inward for some distance upon the ligamentous support of the branchial veins.

Each leaflet is composed of two parts, a central or basal supporting portion of the same tissues as the stem of the gill and an outer folded respiratory portion. (Fig. 23.) A branch of the branchial vein passes along the outer edge of each leaflet. Between the smooth basal part of the leaflet and the collecting vein the leaflet appears to be ridged. In reality it is not ridged, but folded or tucked, and the folds of the tucks alternating upon one side with those of the other side form the apparent ridges. The sides of the folds, however, have fine folds nearly at right angles to the edges of the primary folds. Along both edges of the folds are small blood vessels running at right angles to the marginal vessels of the leaflet.

The branchial vein lies upon the surface of the gill, forming a projecting ridge. Above the branchial vein the leaflets of the opposite sides of the gill are united to each other in such a way as to form a longitudinal septum extending between the vein and the stem of the gill. There is no branchial canal in the gill of Nautilus. Upon the dorsal side the leaflets project considerably beyond the stem of the gill, which is thus hidden in a groove between them. The stem is considerably wider upon its dorsal than upon its ventral edge, and thus the leaflets come to be quite widely separated dorsally. As the tip of the gill is approached the stem narrows. Toward the base of the gill the dorsal side of the stem is produced into a sharp ridge. From the distal end of the ridge to the tip of the gill the stem is marked by transverse grooves, extending from side to side between successive pairs of leaflets.

The branchial arteries pass outward from the vena cava through the posterior walls of the nephridial chambers. Here they form outpocketings into the glandular appendages upon both sides of the walls. From here the arteries pass into the mantle and run in it along the bases of the gills until they reach the middle of the attachment of the gills to the body. At this point they turn and run along the ventral side of the stem of the gill to its tip. I have never been

able to find the valves mentioned by OWEN as existing in the branchial arteries at the bases of the gills. The minute structure of the gills of *Nautilus pompilius* and *macromphalus* has been studied by JOUBIN. He considers that the thickened stem of the gill of Nautilus forms a structure which is comparable with the glands he has described in the gills of other Cephalopods, which are organs in which the blood corpuscles are formed.

The stem is covered externally by a layer of muscle fibres which also pass outward along the concave edge of each leaflet. The stem is composed almost entirely of connective tissue, in which the glandular elements are disposed at several points.

Near the outer surface of the stem is a layer of quite large vascular lacunæ, incompletely lined with flattened endothelial cells. The lacunæ are separated only by thin lamellæ of connective tissue. The lacunæ also extend outward into the supporting portion of each leaflet. Only very small lacunæ are found in the center of the stem. In the middle of the outer side of the stem a large vein is constantly present, extending from the tip of the stem to near its base, where it opens into the branchial artery.

In the central portion of the stem, but still near the median vein, are a number of lacunæ which, instead of being empty, like those at the surface of the stem, are filled with large granular cells, each possessing a large nucleus. These may be found throughout the remainder of the gland (or stem), scattered here and there in the connective tissue. JOUBIN considers that the central region is the only portion presenting an aspect comparable to that observed throughout the whole of the glands of other Cephalopods.

The remainder of the stem (gland, JOUBIN terms it) is formed of connective tissue, in which large numbers of muscle fibres are scattered.

The concave border of each leaflet is thickened, the thickening being due to a lateral extension of the tissues of the stem of the gill into each leaflet. (Fig. 23.) It forms the supporting part of the leaflet, as well as containing portions of the branchial gland. It contains very numerous vascular lacunæ, which differ in their arrangement from those of the stem in that the larger lacunæ are in the central portion, while the smaller lacunæ are external. The lacunæ receive blood from the afferent vessel of the leaflet. Here and there are free cells in the lacunæ similar to those observed in the principal part of the gland. All this region of the leaflet is covered with tall, columnar, epithelial cells. The outer ends of the cells bear a distinct border.

The thin respiratory membrane is covered with large, flattened, epithelial cells. A great number of lacunæ penetrate the inner part of the membrane, scarcely separated by a network of connective tissue cells.

A band of muscle continued from the surface of the stem passes outward along the side of the afferent vessel turned toward the respiratory membrane. In places the muscle projects into the afferent vessel and is bathed by the blood flowing in it.

The blood reaches the gill through the branchial artery which runs along the inner side of the stem from the base to the tip of the gill. (Fig. 23, 2.) Two sets of vessels are given off from the branchial artery. Upon opening the artery two rows of large alternating openings are seen in the wall turned toward the leaflets. These lead into the afferent vessels of the leaflets, which run along the concave side of each, close to the edge of the respiratory membrane. Two other rows of alternating openings, smaller than and median to the first, lead into vessels which pass into the stem of the gill.

From the afferent vessels of the leaflets smaller vessels arise which pass at right angles to the first along the entire length of the upper edges of the primary folds of the respiratory membrane. Opposite each secondary fold is an opening in the wall of the vessel of the primary fold through which the venous blood passes into the lacunæ of the secondary fold, where the interchange of gases between the blood and the water takes place.

In a similar but inverse manner the arterial blood is collected from the secondary folds into efferent vessels lying along the lower edge of each primary fold. These unite in a vein following the outer or convex border of each leaflet, which vessels themselves unite with the branchial vein.

From the afferent vessels of each leaflet the blood escapes through several openings into the

lacunæ of the supporting portion of the leaflet. These are in communication with the lacunæ of the stem of the gill, and so the blood passes from the leaflets into the stem. From the lacunæ of the stem it is gathered into the median longitudinal vessel lying near the surface of the stem. During its passage through the stem and its lateral extensions the blood has caught up many of the free cells of the branchial glands, which now form new blood corpuscles. They are carried by the longitudinal vessel into the branchial artery at the base of the gill, and thus into the circulation. It will be noticed that all the blood passing through the stem of the gill is venous, and that, having made this short circuit, it passes again into the branchial vein, the greater part then passing through the branchial leaflets into the systemic circulation.

An observation made by WILLEY on a young Nautilus is significant. Describing it, WILLEY says:

"The youngest individual I have as yet obtained was a male with the following dimensions:

	Millimeters.
Length from root of siphuncle to mid-anterior point of hood (measured along the dorsum)	25
Length of hood in middle line	10.5
Breadth of body across middle of eyes	15

"The surface of the hood was perfectly white and unpigmented. The branchiæ of opposite sides were in close apposition in the median line, and, curiously enough, the larger posterior pair extended forward far into the interior of the funnel.

"The shell was perforated at the umbilicus, as it is throughout life in *N. umbilicatus*."

If this specimen was a typical one of the young Nautilus it is evident that the gills are moved outward toward the sides of the body as the animal approaches maturity, a fact which possesses still more interest when we remember that the rudiments of the gills of the Dibranchiata arise close to the median line of the body, on either side of the anus, and that they move to the sides of the body late in development only.

The branchial nerves are two large, flattened, band-like nerves, one of which arises from the posterior side and near the inner end of each visceral ganglion. (Fig. 41, 22.) They run directly backward, along the ventral body wall, to the posterior limit of the mantle cavity. Here they turn outward and forward in the inner wall of the mantle fold. After giving off a couple of small branches which apparently supply the walls of the renal sacs, the nerves fork near the bases of the gills, and a branch passes into each gill. (Fig. 41, 19 and 20.)

The later shifting of the gills to the sides of the body may account for the peculiarly exposed course of the branchial veins of the anterior gills. (Fig. 4, BV.)

INTERBRANCHIAL AND PREANAL PAPILLÆ.

Just in front of the base of each posterior gill is a small papilla upon the inner surface of the mantle. (Fig. 3, IP.) The papillæ are about 2 millimeters in height and width. It is to these papillæ, situated between the bases of the anterior and posterior gills, that I apply the name interbranchial papillæ.

In the median line of the ventral part, just in front of the line limiting the thin portion of the mantle, two papillæ project from the inner surface of the mantle. (Figs. 3 and 4, PA.) Each papilla has the shape of a bilobed transverse ridge, and usually the two are fused, forming a distinct ridge across the median line of the mantle. It is only rarely that the papillæ are separate, and even then the separation is so slight as to be scarcely noticeable. WILLEY describes a case in which the interval between the papillæ was 2.5 millimeters. The sometimes total separation and nearly constant partial separation of the two parts of the ridge leads me to describe it as two papillæ fused rather than as a single papilla.

The united papillæ have usually passed, heretofore, by the name of postanal or supra-anal papillæ. As it is readily demonstrated that they are situated upon the inner surface of the mantle and not upon the body wall, they can not be postanal except when the mantle is turned back and the natural position of the parts of the pallial complex is reversed. To avoid this difficulty I suggest that they be called the preanal papillæ.

In 1883 LANKESTER and BOURNE first called particular attention to the interbranchial

papillæ, calling them osphradia, and suggesting that they correspond to the osphradia found so widely distributed among the Mollusca. Their specimens were not sufficiently well preserved to allow an histological examination of the papillæ, so the hypothesis depended entirely upon the evidence of their innervation. LANKESTER and BOURNE describe a small nerve as arising from the nerve to the anterior gill near the fork of the branchial nerve and running into the papilla. This innervation corresponds to the innervation of the osphradia of other Mollusca.

WILLEY (1895) describes a small nerve proceeding to the osphradium of LANKESTER and BOURNE from the point of bifurcation of the branchial nerve. He also suggests that the preanal papillæ represent a pair of osphradia, "corresponding metamerically with the pair described by LANKESTER and BOURNE between the bases of the gill plumes." This suggestion is based upon the form, and variations in form, and upon the innervation of the papillæ. It has already been stated that the halves of the preanal ridge may be entirely separated, and that they are always distinctly marked.

WILLEY finds that a small nerve arises beside (inside of) each visceral nerve and runs backward close to it. Arriving at the point at which the visceral nerves bend outward, the inner nerves continue near the median line, passing into the mantle; they were traced through the nidamental gland of the female. In regard to the relation of this nerve to the preanal papilla WILLEY says: "The inner and smaller visceral nerve passes over the region of the renal sacs on each side to the base of what I may call the posterior osphradia, to which it undoubtedly sends nerve fibres, although I can not say positively that I have definitely traced these."

In another place in the same article he says: "As to the innervation, I will say at once that it is very difficult to see the actual nerves or nerve fibres (because the nerves are often not compact trunks, but broken up into loose strands) which pass into the osphradia; but the anatomical relations of the visceral nerves to the osphradia, which, I think, have never been fully described, are such as to leave no doubt as to the source from which the osphradia derive their innervation."

WILLEY called attention to the fact that these two papillæ have essentially the same topographical relations to the anterior gills which the osphradia of LANKESTER and BOURNE have to the posterior gills. "Their greater proximity to the middle line is shared in common with the posterior (anterior) renal sacs and apertures and even the posterior (anterior) branchial veins, as compared with the corresponding anterior (posterior) structures. That they are bifid, and therefore more highly developed than the anterior (posterior) osphradia, is in keeping with their position in the living Nautilus in the anterior region of the mantle cavity, and also with the fact that the posterior (anterior) branchiæ, with which they would be associated in the metameric system, are considerably larger than the anterior (posterior) branchiæ." The words in parentheses indicate the relative natural position of the organs, WILLEY having described them as they appear after the mantle has been turned back.

WILLEY's argument for the metameric relation of the anterior gills and the preanal papillæ appears to be strengthened by the fact that in the young specimen already mentioned he found the gills closely approximated in the middle line, and in that case the preanal papillæ could not have been far from the bases of the anterior gills.

In a later article WILLEY gives more interesting facts in regard to the structure of the osphradia. "By means of macroscopic sections of fresh material the presence of vibratile cilia on the sensory epithelium of both the inner and outer osphradia can be demonstrated, and this I regard as the final proof of the osphradial character of the so-called postanal papillæ. The sensory epithelium of both osphradia is distinguished from the surrounding ectoderm both by the presence of the cilia and by the general absence of goblet cells.

"The olfactory lamellæ of the accessory olfactory tentacles (the pre- and post oculars) and the sensory epithelium of the osphradia are the only places where I have observed vibrating cilia in Nautilus hitherto."

A set of serial sections of the preanal papillæ of a male brought to light an interesting structure in this. In the base of each papilla is a gland composed of a number of irregular branching tubules. (Fig. 69, G.) Each opens separately to the exterior through a very minute pore. The

Each renal or pericardial pore is surrounded by a lip, a raised thickened portion of the mantle. The pericardial pores are the largest of the six, being 3 millimeters in length. The renal pores are each 2 millimeters in length. The lips of the latter are divided into inner and outer parts, forming tight valves. The main axes of the pores are all directed obliquely backward and outward.

ANUS.

In the median line of the mantle, just posterior to and above the anterior renal sacs, is the anus (Fig. 3, A). Its edges are plaited and project slightly from the surface of the mantle. The anus is situated upon the thickened posterior portion of the mantle, about 8 millimeters from the line along which the mantle joins the body wall. The anus of VALENCIENNES's specimen was situated upon the body wall between and at the middle of the shell muscles. VALENCIENNES has shown himself too good an observer for us to consider that he made a mistake in this description and figure. It was simply a very peculiar and rare abnormality.

REPRODUCTIVE APERTURES.

The reproductive apertures of both male and female Nautili are paired. The two differ from each other in the same sex, and the right apertures are differently formed in the two sexes. The apertures of the female present the simplest conditions. The aperture of the functional oviduct is upon the right side of the body, at the tip of a projection from the body wall (Fig. 4, O V), immediately anterior to the crease formed by the junction of the mantle with the body wall and about halfway between the right shell muscle and the median line of the body. The transverse slit-like aperture is borne upon a dorso-ventrally flattened plaited projection of the body wall. This projection, which forms the tip of the oviduct, is, in preserved specimens, of a dark-brown color. The color is the same as that of the nidamental gland, which WILLEY tells us is a bright yellow in the fresh condition; so the tip of the oviduct may also be of a very different color in the living than in the preserved specimens. It forms a projection 12 millimeters in width, 5 millimeters in thickness (dorso-ventral measurement), and 10 millimeters in length. The length of the dorsal side is not quite so great as that of the ventral side. The walls are thick and transversely folded, and are evidently glandular. In spite of its comparatively large size the tip of the oviduct is not a conspicuous part of the pallial complex, being situated so low in the crease formed by the mantle and the ventral body wall.

The aperture of the left reproductive duct is an exceedingly minute pore on the left side of the body, in the crease formed by the union of mantle and body wall, and located immediately posterior to or above the base of the posterior (the smaller) gill. The position and form of this aperture are the same in both male and female Nautili. The aperture leads into the organ commonly called the pyriform sac, which there seems to be good reason to consider as the vestige of the left reproductive duct of Nautilus. It has the same structure in both sexes.

The functional male efferent duct opens at the tip of the penis, a tubular organ lying in the median line of the ventral body wall. (Fig. 3, P.) The tip of the penis only is free from the body wall. The cavity of the penis is divided a little back of the tip of the organ by a longitudinal partition into two portions, which are parallel for a certain distance. They then fork, the left branch turning outward and backward toward the minute left reproductive aperture, and soon ending blindly. The right branch continues to the right to that region of the crease between the mantle and the body wall where the tip of the oviduct is located in the female. It here penetrates the body wall and becomes continuous with the vas deferens. Just back of the penis, which term refers to that median structure within which the efferent ducts are parallel to each other and finally unite, and are contained within a common wall, the right duct is swollen to form a considerable sac, the spermatophore sac. This forms a protrusion of the body wall which is quite noticeable. The structure of these parts will be described in more detail in the section treating of the reproductive organs.

tubules increase in size toward the ultimate branches. They are lined by a single layer of not very tall columnar cells, the nuclei of which stained deeply while the body of the cells remained unstained and clear. That the cells are secretory is proved by the fact that the cavities of the glands were filled by a secretion, the granules of which were so fine that it appeared homogeneous under ordinary high powers.

These glands may be the homologues of the glands Kerr described as being scattered over the area between the preanal papillæ and the nidamental gland in the female. I find the same area continuously glandular and much thickened. (See p. 147.)

The epithelium had been entirely rubbed off from the surface of the interbranchial papillæ and the preanal papillæ, of which I made series of sections. Therefore, I have no personal knowledge of its character. As regards the innervation of the papillæ, serial sections do not reveal any such abundance of nerves as we should expect, were they sensory organs of importance. The edge of the ventral part of the mantle possesses a remarkable number of nerves, many of considerable size. This being the fact, we have a right to expect that the innervation of sense organs of the importance of osphradia will have an at least equally plentiful supply of nerves. Instead of this being the case, serial sections do not show any nerves whatever passing into the interbranchial or preanal papillæ. The large nerve of the posterior gill is seen running by the base of the interbranchial papilla, but neither in dissections nor in serial sections have I seen any nerve pass from this into the papilla.

I do not wish to be understood to deny that the interbranchial and preanal papillæ are osphradia, but I do wish to call attention to the fact that they are not yet proven to be osphradia. WILLEY admits, and calls attention to the fact, that he has not been able to absolutely trace any nerves into these papillæ. He goes very much farther than the known facts warrant when he regards the presence of vibratile cilia "as the final proof of the osphradial character of the postanal papillæ." While it is true that sensory organs are frequently covered by a ciliated epithelium, among the cells of which the special sensory elements are nestled, the fact that certain portions of the body of an animal are ciliated does not in and of itself constitute proof that these portions of the body are sensory organs. The final proof as to whether or not these papillæ of Nautilus are osphradia must be, besides the presence of special sensory cells, their innervation; and at present both these points are very much in doubt. The nature of the nerves of Nautilus, to which WILLEY has called attention, and the position of these papillæ with respect to the course of the nerves, render an investigation of their innervation quite difficult.

The morphological importance of osphradia is too great to permit of any assumption of their presence in Nautilus without complete proof. It is because I do not consider that the osphradial nature of the papillæ under discussion has been proved beyond any doubt that I have used the name "interbranchial papillæ" for the papillæ which have been called the osphradia of Nautilus ever since the publication of the paper by LANKESTER and BOURNE. This is suggested as a provisional name until such time as the true nature of these papillæ shall have been proven.

RENAL AND PERICARDIAL PORES.

The renal organs are situated in the posterior portion of the mantle fold, their presence causing the considerable thickness of this portion of the mantle. The glands situated upon the anterior branchial arteries are shoved together in the median line below or anterior to the rectum. The glands situated upon the posterior branchial arteries are just outside and behind those already mentioned. So that we can with justice speak of anterior and posterior renal organs (Fig. 36). The anterior renal sacs lie beside each other on either side of the middle line; the posterior renal sacs are separated by the two anterior renal sacs. Each renal sac communicates with the exterior by a slit-like opening situated upon the inner side of the mantle. The openings of the posterior renal sacs are at the inner ends of the bases of the posterior gills (Fig. 3, R P). The openings of the anterior renal sacs are located at the inner ends of the bases of the anterior gills, or near where the anterior branchial veins pass through the mantle into the body (Fig. 3, R A). Upon the inner side of each anterior renal pore is another opening, the pericardial pore (Fig. 3, P P).

NIDAMENTAL GLAND.

Immediately in front of the preanal papillæ of the female a large pleated gland is situated upon the inner side of the mantle. (Fig. 4, N.) This has been called the nidamental gland. In the fresh condition it is of a light yellow color, but when preserved its color is a dark brown.

The nidamental gland extends across the mantle nearly the entire distance between the bases of the anterior gills. It has been called kidney-shaped. It is shaped as a number of thin, closely pressed, parallel folds would be if their ends were bent around close to their middle portions until the opposite ends nearly meet each other. Most of the folds of the gland are thus continuous around the curved ends of the organ. The infolding has taken place toward the anterior side of the main portion of the gland. The gland is about 60 millimeters in width, and 25 millimeters to 32 millimeters in length. At its edges the mantle is raised, forming a border entirely around the gland. On the posterior side and between the anterior and posterior portions of the gland the border thus formed is only a low ridge. Upon the ends and the anterior side of the gland the raised mantle forms a fold which overlaps more than half of the inturned portions of the gland. The outer surface of the ridge of the mantle is smooth, and the inner surface as well of the overlapping anterior parts. The inner surface of the other parts of the border is ridged perpendicularly and is apparently covered by an extension of the glandular tissue of the gland.

By means of the raised border of the gland a canal is formed which enters the anterior side of the gland and branching, extends to each side between the anterior and posterior portions of the gland. OWEN suggests that the divisions of the nidamental gland serve "both to conduct the secretion nearer the orifice of the oviduct, and also to prevent its being drawn within the respiratory currents of water, and so washed away as soon as formed." If the channel between the different portions of the gland serves to conduct the secretions of the gland, it is difficult to see how it conducts them near the orifice of the oviduct with its open end directed away from the oviduct and its lateral branches ending under the overlapping border of the gland.

The parallel glandular folds of which the organ is composed are quite separate in the anterior portions, but are grown together closely in the posterior portion.

Medianly, between the ends of the anterior portions of the gland, is a thickened, apparently glandular, projecting portion of the mantle. In the center of this is a low, longitudinal ridge. (Fig. 4, Y.)

The gland is supplied with blood through branches of the branchial arteries. A large blood lacuna lies in the median line in the mantle below the nidamental gland. This breaks up into numerous smaller lacunæ in the thickened portion of the mantle between the ends of the gland.

In a half-grown female the nidamental gland was just forming. The mantle was scarcely thickened, but the outlines of the different portions of the gland were already marked out by the border formed by the raised fold of the mantle. The glandular area was covered by very fine parallel ridges, scarcely visible to the naked eye. The gland was of the same color as the surrounding portions of the mantle.

KERR has described a series of glands between the preanal papillæ and the posterior side of the nidamental gland. The apertures, "to the number of about 150, form a band about 0.5 millimeter in width, curving gently forward on either side of the postanal papilla, tapering off and terminating close to the advehent vessel of the posterior gill. In section these openings are seen to be the apertures of tubular ducts which pass inwards perpendicular to the surface for some little distance and then break up into several blindly ending branches. These are lined by involution of the surface epithelium, which, in the neighborhood of each aperture, increases to about twice its thickness elsewhere, its cilia at the same time becoming long and powerful (0.03 millimeter in length). Once within the narrow aperture the lumen of the tube expands to about 0.05 millimeter in diameter, and the lining epithelium becomes shorter, the remainder of the lumen being lined by comparatively short columnar cells, each with a round ellipsoidal nucleus." In some females this area is greatly swollen, forming a single elongate gland. It is not possible, then, to distinguish the separate apertures of the glands upon the surface. I have not yet been able to determine if the glands in the bases of the preanal papillæ of the male are homologous

with the just mentioned glands upon the mantle of the female. Their structure is certainly very much like that of the glands described by KERR. As the epithelium of the inner surface of the mantle had been rubbed off in my specimens, I can not say anything about its structure. It is strange that WILLEY should have overlooked the ciliated surfaces described by KERR. KERR's observation certainly weakens WILLEY's "final proof" regarding the osphradial nature of certain papillæ, for this is proof that other regions of the body, aside from the surfaces of the grooves of the ocular tentacles and the interbranchial papillæ and the preanal papillæ, are ciliated. The glandular area is differently developed in different females of various ages, and this I take to be an indication that it forms an accessory part of the female reproductive apparatus.

Let us now sum up the observations on the pallial complex. The mantle is continuous around the body, forming a broad ventral fold fastened along its edge to the edge of the shell, and a small free dorsal fold, connected by very narrow lateral portions. In conformity with this structure there is a capacious ventral mantle cavity containing all the organs collectively forming the pallial complex, and a small dorsal mantle cavity; the two are connected by shallow lateral cavities.

The pallial complex consists of the following parts: The anus; two pairs of gills; two pairs of nephridial pores; one pair of pericardial pores; two interbranchial and two preanal papillæ, which may be osphradia, corresponding metamerically to the gills; one pair of reproductive apertures; in the female, the nidamental gland.

All these parts of the pallial complex, except the reproductive apertures, are situated upon the inner side of the mantle. The latter are situated upon the body wall. The renal sacs also might be considered as forming parts of the pallial complex, for they are situated *within* the base of the mantle.

This arrangement of the parts of the pallial complex of Nautilus is very interesting when compared with the Dibranchiata, in which all the organs mentioned are located upon the body wall. The arrangement of the organs of the pallial complex of Nautilus is the same as in many Gastropoda.

FUNNEL.

The funnel is an organ of great size, not to be overlooked in the most casual glance at the animal. While showing a general similarity to the funnel of the Dibranchiata, it also presents differences of the utmost interest to the student of comparative anatomy. Lying closely pressed against the ventral side of the head and nuchal regions, it has a length of about 8 centimeters and a breadth of 4 centimeters. (Figs. 3, 4, and 6.) The width of the funnel varies greatly in preserved specimens, depending largely upon the state of contraction of the organ. It forms an extremely solid mass of tissue. Its posterior end extends well into the mantle cavity. The anterior end lies partly in the ventral groove of the cephalic sheath, and its tip extends a very little beyond the posterior border of the ventral notch of the cephalic sheath. (Figs. 7, 24, and 25.) The funnel forms a long cylinder, but instead of being closed, like the funnel of the Dibranchiata, it is open upon the ventral side, where its edges merely overlap each other. It is as if the edges of a flat, oblong piece of tissue had been inrolled about the longitudinal axis until their edges slightly overlapped. A better illustration, and one which expresses the commonly accepted morphological idea, is to suppose the edges of the foot of a gastropod to be inrolled toward the ventral side, and about the longitudinal axis.

The partly closed funnel of Nautilus presents, therefore, in the adult condition a form which is found in the embryonic stages only of the Dibranchiata.

At the posterior end of the funnel the sides separate and pass upward over the sides of the nuchal region of the body, just behind the auricles of the hood, forming the crura of the funnel, to the dorsal edges of the shell muscles. (Fig. 6, CR.) The dorsal ends of the crura are united by a thin crescentic ridge running around the posterior excavated side of the hood. (Figs. 5 and 7, CR.)

Only the posterior portion of the funnel is attached to the body. The anterior five-eighths projects completely free from the body, able to move in any direction. If we examine the inside of the funnel, we shall get a logical means of separating the anterior and posterior portions of

the funnel, which are really fundamentally different parts of the organ. In the first place, we notice the valve of the funnel projecting from the dorsal wall near the tip. (Fig. 6, V.) This is a thin, tough, tongue-shaped structure precisely like the valve of the funnel of Loligo. The line of attachment of the valve is exactly transverse to the axis of the funnel and is about 3 centimeters from the tip of the funnel. The valve itself is 2.25 centimeters in length by 1.5 centimeters in breadth at the base. In preserved specimens the valve is directed forward and lies closely pressed against the roof of the funnel. Halfway between the base of the valve and the posterior end of the funnel are two white lines in the roof of the funnel which approach each other like the sides of a V. (Fig. 6, C.) The point of the V (which is directed backward) is not complete, as the posterior and inner ends of the lines remain separated by a distance of about 5 millimeters. The lines are 3 millimeters in width and 2 centimeters in length. They are caused by the superficial position of the ventral limbs of the cartilage, which here lie almost immediately beneath the epithelium of the funnel, allowing the white cartilage to show plainly through the thin overlying tissues. There is a marked difference in the appearance and structure of the funnel anterior to these lines and posterior to them. The anterior portion is smooth, and light in color. It is composed mostly of elastic tissues; small bundles of muscles form a quite definite layer upon the outer side just under the epithelium, while there are only scattered muscles upon the inner side of this portion. The part of the funnel in front of the arms of the cartilage is that which has already been referred to as free from the body. It is freely movable, but evidently only slightly contractile. The attachment of the funnel to the body begins anteriorly on a line passing through the middle of the white lines on the internal surface of the funnel.

The part of the funnel back of the processes of the cartilage is composed entirely of muscle, and is often in a state of extreme contraction in preserved specimens. The darker color of this part readily distinguishes it from the anterior part. The roof of the posterior part of the funnel is attached to the body along a median strip 7 millimeters in width and extending to the back edge of the roof of the funnel. The crurae, being attached to the nuchal surface by their anterior and inner edges, meet the anterior end of the attachment of the funnel and form the outer sides of two deep pockets lying between them and the roof of the funnel and the median attachment of the latter to the body. These lateral pockets are very similar to the pockets, or valves, beside the funnel of Loligo. The attachment of the roof of the funnel to the body forks posteriorly, often leaving quite a pocket above the median portion of the roof of the funnel. From the ends of the fork two ribbons of skin, each attached by one edge, run back along the ventral surfaces of the shell muscles for a distance of 30 to 35 millimeters. They may be 2 or 3 millimeters in height at their anterior ends, but gradually diminish in height until they disappear.

The posterior portion of the funnel possesses an internal layer of longitudinal muscles extending from the posterior sides of the limbs of the cartilage to the posterior edge of the funnel. The external layer of oblique and transverse muscles is continuous with the muscles of the crura, which seem to branch on the sides of the funnel, part of their muscles passing on to the sides and ventral part of the funnel and part passing into the roof of the funnel. The roof of the funnel might almost be described as a shelf extending between the crura. If the funnel is formed in the same way in Nautilus as in the Dibranchiata whose development has been observed, the roof of the funnel really consists, in large part, of a portion of the ventral surface of the body folded in between lateral ridges.

The crura are composed of the same dark muscle as the posterior part of the funnel. They form strong muscular bands, which, attached to the sides of the nuchal region by their anterior and inner edges, extend upward and backward close to the stalks of the eyes and immediately back of and under the auricles of the hood. (Fig. 1, CR.) Their upper ends are attached along the dorsal edges of the shell muscles and extend back to the posterior limit of the mantle cavity at these points. It will be remembered that the mantle cavity is most shallow above the shell muscles, being scarcely more than 10 millimeters in depth. The sides of the crura turn outward and backward. They thin out gradually from the attached borders to the free edges, so that the latter are thin, sharp, and pliable. Similarly, the overlapping edges of the funnel, with which the free edges of the crura are continuous, are thin and fit so closely against one another that

the funnel is, to all intents and purposes, a tightly closed tube. Apparently it makes no difference which edge is outermost, though in most cases the right side of the funnel overlaps the left. There is no structural difference between the two sides.

The crescentic ridge running in an almost horizontal line around the concave posterior side of the hood is so closely related anatomically to the crura as to almost seem to be a continuation of them. Its similar shape and relation to the surface of the body point to a similarity of function, at the least. The ends of the crescentic ridge arise upon the dorsal or inner sides of the ends of the crura (Figs. 5 and 7); these surfaces correspond to the anterior surfaces of the lower parts of the crura. In this way the crescentic ridge unites the upper ends of the crura.

Aside from the great mass of muscle forming the posterior portion of the funnel and its crura, which can not be separated into separate muscles, the funnel possesses two distinct and independent muscles. These (the *Levatores infundibuli* Owen) pass from the central part of the cephalic cartilage outward and forward in the lateral parts of the roof of the funnel to near its tip. They are slender round muscles, 2 millimeters in diameter and 35 millimeters in length. They lie in smooth-walled cavities or tunnels in the tissue of the funnel, so that they are attached only at the two ends. The anterior ends spread out in the tissues of the roof of the funnel a few millimeters in front of the base of its valve. They seem to have no connection with the valve. On account of their being attached at the ends only, the contraction of these muscles probably affects only the tip of the funnel, pulling or bending it upward. The tip would be straightened or bent downward by the intrinsic muscles of this part of the funnel. The length of the levatores must allow a considerable contraction, and consequently they are able to cause a considerable motion of the tip of the funnel. Their position and course is indicated externally by slight ridges upon the surface of the funnel where it touches the edges of the ventral groove of the cephalic sheath. Blood lacunæ open into the sheaths of the levatores.

The funnel receives its blood through two arteries which spring from the tentacular arteries near their origins, and which, according to Willey (1896, p. 178), "pass through the cartilage into the funnel." (Text-fig. 10, p. 182.)

The infundibular nerves are two in number, each of considerable size. They are the innermost nerves springing from each pedal ganglion. (Fig. 41, 8.)

VISCERAL BODY WALL.

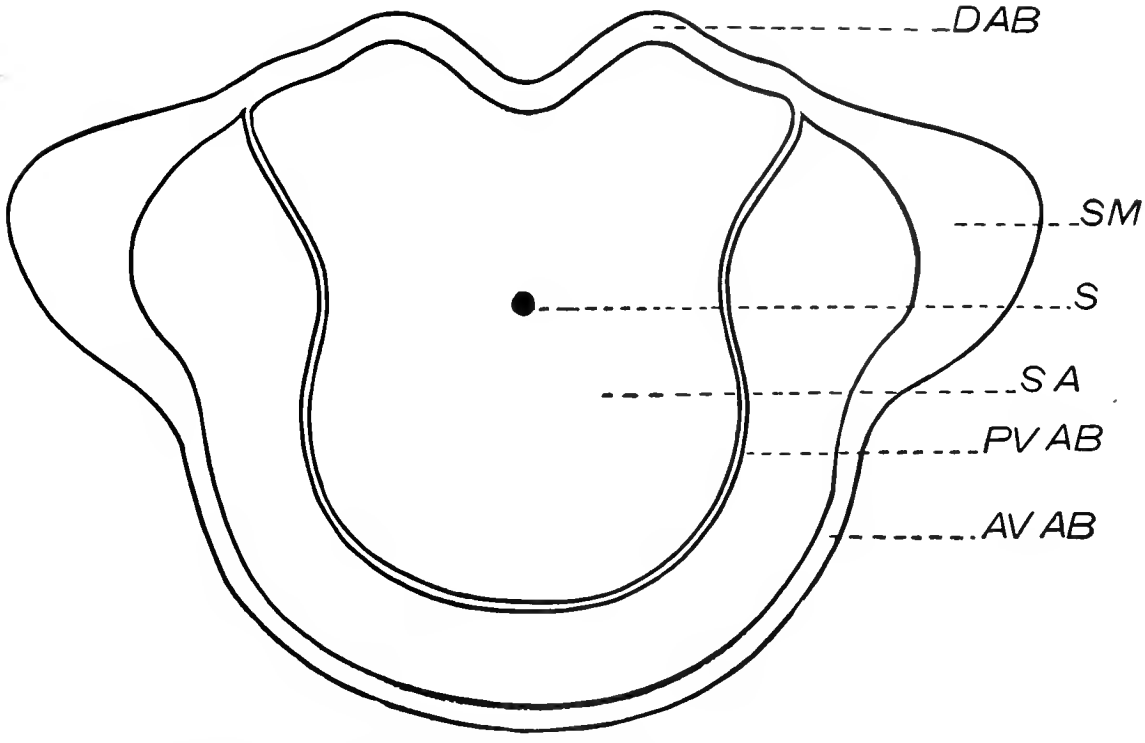
The body wall of the posterior end of the body of Nautilus is very thin, soft, and delicate. In some cases semitransparent, the outlines of several of the viscera can be distinguished through it. The greater part of this portion of the body wall is applied to the last septum of the shell, and the septa are formed by its epithelium. The thin body wall extends out upon the outer side of the mantle fold, so that there is no external sign of the posterior limit of the mantle fold. The thin body wall of the visceral region is composed of fibrous tissue in which are numerous fine branching blood vessels and a very noticeable nervous plexus. Externally it is covered by a layer of short columnar epithelial cells. Internally—that is, upon the cœlomic side—it is covered by comparatively large flat polygonal pavement cells. At the posterior end of the body (dorsally as the animal is curved) the body wall is produced into a long slender tube, the siphuncle, which passes through the siphon to the last chamber of the shell, where it probably ends blindly, like the siphon. The body wall is firmly attached to the shell over the end of each shell muscle and along three aponeurotic bands extending between the ends of the attachments of the shell muscles. (Text-fig. 7.) Everywhere over these aponeurotic areas, a thin plate or ribbon of chitinous material is found between the body wall and the shell. This is secreted by the epithelial cells of the aponeurotic areas and seems to form a kind of cementing substance by means of which the body wall is firmly attached to the smooth surface of the shell.

The attachments of the body wall to the shell over the ends of the shell muscles form areas of the same shape as the ends of the muscles. (Fig. 1, S M.) They are roughly crescentic, or perhaps better, approach in shape spherical right-angled triangles, the right angles being directed forward and downward.

The dorsal aponeurotic band (Figs. 1 and 2, DA) extends between the dorsal ends of these areas over the dorsal side of the animal. Passing over the excavated dorsal region of the body it bends quite sharply backward as the middle line is approached. At the middle line there is a pointed backward projection of the aponeurotic band. The band is about 3 millimeters in width.

Some of the older septa show a minute cup-like backward projection at the middle of their inner edge. (Fig. 1.) These depressions in the faces of the septa can be traced, constantly less developed, to the newest septum. In this it is only a notch in the extreme edge of the septum, into which the projection of the dorsal aponeurotic band just mentioned fits. From this it would seem that in young specimens there is a projection of the mantle corresponding to the depression in the septum, which has been gradually reduced until in the adult it remains only as a point at the middle of the dorsal aponeurotic band.

The ventral ends of the columellar aponeurotic areas are connected by the anterior ventral aponeurotic band, which extends over the ventral surface of the body. (Fig. 1, AV.) This is also



TEXT-FIG. 7.—Outlines of the areas of attachment of the shell muscles and aponeurotic bands to the shell spread out flat. The outline of the septal area has been drawn from a wax model.

AVAB, anterior ventral aponeurotic band. PVAB, posterior ventral aponeurotic band. DAB, dorsal aponeurotic band. SA, septal area. S, siphon. SM, shell muscle.

about 3 millimeters in width. A third aponeurotic band, the posterior ventral aponeurotic band, connects the dorsal ends of the columellar aponeurotic areas, extending also around the ventral surface of the body. (Fig. 1, PV.) As the body is curved the actual position of the ventral surface is posterior. The last band is only one-third as wide as the others. It is drawn somewhat too wide in Fig. 1.

The posterior ventral aponeurotic band first passes directly backward from the end of the columellar aponeurotic area parallel to the dorsal edges of the body. It then makes a smooth curve downward and somewhat forward over the sides of the body; its median ventral portion is parallel to the anterior ventral aponeurotic band.

The posterior ventral aponeurotic band and the dorsal aponeurotic band have a peculiar relation to the septal region of the body wall, since this is bounded by these two bands. In most shells the aponeurotic bands and areas leave slight scars upon the inside of the shell, and

by these one can observe that the two bands just mentioned always lie exactly at the edge of the septum.[1]

This portion of the body wall is marked off from the rest by its arterial vessels also. (Text-fig. 11, p. 186.) The septal artery runs backward from the heart, and entering the body wall below and a little to the left of the base of the siphuncle divides into two branches which are distributed exclusively to the septal region of the body wall and to the siphuncle. The siphuncular artery is a branch of sometimes the left, sometimes the right, septal artery. A variable number of smaller branches of the septal arteries may also pass into the walls of the siphuncle. The branches of the posterior columellar arteries to the dorsal body wall seem also to enter the septal area, but I can not be sure of their distribution without injected specimens. WILLEY states that "the septum-producing area of the mantle" is distinguished in fresh specimens "from the surrounding portions of the mantle by its greater thickness and opacity." Such a distinction can not be observed in alcoholic specimens.

MOVEMENTS OF SWIMMING AND RESPIRATION.

Nautilus swims in a manner very much like that of the Dibranchiata, backward (or with the posterior end of the body pointed in the direction of motion), propelling itself by means of jets of water squirted through the funnel. On account of the presence and the position of the air chambers of the shell the involution of the latter is always dorsal. WILLEY has already clearly stated that on this account it would be impossible for the animal to turn over in the water.

In the figure (a photograph) which WILLEY gives of a living Nautilus in the swimming position the anterior end of the body is raised so that the eyes are above the edges of the shell, and the back of the hood nearly covers the dark portion of the involution of the shell, apparently projecting higher upon this than the dorsal portion of the mantle.

When we are told that the manner of progression of Nautilus is like that of the Dibranchiata we involuntarily imagine that the water is expelled from the mantle cavity by the contraction of the mantle.

Possibly this is the case, but the scantiness of the musculature of the mantle seems to afford good ground for doubt. It has been pointed out in some cases that a chitinization of portions of the mantle takes place, which would surely interfere with its contraction.

Apparently also the mantle is attached to the edge of the shell. If this is true it is impossible that the mantle by its contraction should drive the water from the mantle cavity.

How, then, can the expulsion of water take place? There are two conceivable ways, one of which has been observed.

We have noticed that the crura of the funnel extend upward along the sides of the body from the posterior end of the funnel. They are attached to the body by one edge; in expanded specimens the crura are seen to gradually thin out from the attached edge to a very thin, pliable free edge.

If the crura should be set so that their surfaces form a large angle with the body, the outer free edges would be in contact with the inner surface of the mantle, and thus the mantle cavity would be completely closed except for the passage through the funnel. The dorsal ends of the crura turn along the upper sides of the shell muscles toward the posterior limit of the, here very narrow, mantle cavity. These ends would serve to close the communication between the dorsal and ventral portions of the mantle cavity.

[1] In Part VIII, Vol. IX, of the Proceedings of the Cambridge Philosophical Society, p. 398, Willey claims that a previous account of these aponeurotic bands published by me does not give him proper credit for the description of the "septal contour." I read Willey's previous paper carefully before writing my first description, and have read it several times since. He does not in any way describe the manner of limitation of the septal area. It seems, therefore, that my description completes his without in any way intrenching upon his priority, a thing I have not the least desire to do. It may be well to state that in gathering the accounts of many authors into one and incorporating them with my own work to form as complete an account of the anatomy of nautilus as possible, I have purposely refrained in most cases from referring in the text to the original descriptions of the various parts. Those who are familiar with Cephalopod literature will give credit where credit is due. References in the text are, for the purposes of this work, needless.

If the crura should now be swept inward like fans, touching the inner surface of the mantle as long as is possible, the volume of the mantle cavity would be slightly reduced and some of its contained water would be expelled. If this fan-like motion were repeated continuously, a current of water sufficient for the purposes of respiration would be kept flowing into and out of the mantle cavity.

That such a motion of the crura does actually take place is proven by a passage which I shall quote from WILLEY.

"There is a slight error in MOSELEY's account of the movements of the Nautilus, which may as well be corrected. He says, 'On either side of the base of the membranous operculum-like headfold . . . . . the fold of the mantle closing the gill cavity was to be seen rising and falling, with a regular pulsating motion, as the animal in breathing took in the water, to be expelled by the siphon.' It is not a fold of the mantle which is thus seen to pulsate, but the posterior free membrane-like expansion of the funnel on either side."

The current of water caused by the movement of the crura scarcely seems capable of propelling the Nautilus during vigorous swimming. In view of the fact that WILLEY and MOSELY, who have seen the living Nautilus swim, say nothing of the manner in which this movement is effected, it would be presumptuous for one like myself, who has only seen the preserved animals in a laboratory far distant from their native haunts, to form theories as to the swimming movements. I should like to point out, however, that the water in the mantle cavity could be forced out by the withdrawal of the head end of the animal into its shell, caused by the contraction of the shell muscles.

If at the same time the crura of the funnel be set so as to close the lateral portions of the mantle cavity, the expelled water must pass through the funnel and might propel the animal. The thinness of the mantle and its relation to the shell suggests, at least, that its contraction is not a factor in the propulsion of the animal.

MOSELEY says that in swimming the various sets of tentacles are extended radially from the head. WILLEY corroborates this account.

In regard to the Nautilus's power of moving up or down in the water, WILLEY says: "I have never found any necessity for framing an elaborate theory as to the rising and sinking of the shell. A remarkably small weight is sufficient to sink such an empty shell, and when the living animal retracts itself and ceases all muscular action, thereby converting itself, as it were, into a dead weight, it is heavy enough to sink several shells in addition to its own."

The air chambers of the shell seem to support the shell itself, relieving the animal of the hindrance which the weight of the shell would otherwise be. That the living Nautilus would float or sink according as it moved or remained quiet was suggested as the result of careful computations by MEIGEN thirty years ago.

ALIMENTARY SYSTEM.

It may be well to give a short general description of the alimentary system before passing to a detailed description of its various parts.

The buccal mass forms a large, bluntly conical mass, situated within the various groups of tentacles. (Fig. 7, B.) It is armed with an enormous pair of jaws, which are looked upon still more respectfully when one dissects their strong musculature. The upper jaw fits snugly within the projecting lower jaw, while the tips of both jaws are beaked and are reinforced by a considerable deposition of extremely hard calcareous material. Upon the floor of the buccal cavity is the large tongue, bearing a long-toothed radula. (Fig. 32, Tn.) Two fleshy folds arise from the floor of the buccal cavity in front of the tongue. (Fig. 32, AP, PP.) The salivary glands are contained in two larger folds which are situated upon either side of the tongue. (Fig. 32, SP, SO.) The œsophageal opening is immediately behind the tongue. The œsophagus is long and extremely distensible; when full it forms a large pear-shaped crop, with thin, smooth walls; empty and contracted it is a narrow, folded tube. (Figs. 7 and 27, Oe.) The œsophagus passes straight back through the body, finally entering a small chamber which acts as a common vestibule to the stomach and the intestine. (Fig. 32, V.) The muscular stomach (Fig. 27, St) lies

posterior to the vestibule, while the intestine passes from its right side. (Fig. 27, I^1, I^2, I^3.) Communicating with the intestine near its beginning is the cæcum (Fig. 27, Coe), into which the duct of the liver opens. The large lobes of the liver lie under and partially surround the alimentary canal. (Fig. 27, L, L^1.) The intestine passes around the posterior and right sides of the cæcum, then turns downward and backward beneath the cæcum and the stomach. It turns forward again and passes above the heart to the anus. The branches of this loop run parallely, close beside each other, and are connected by a mesentery. The terminal portion of the gut is slightly constricted and is more muscular than the preceding parts, and has been termed the rectum.

Since the jaws serve as points of attachment for the fleshy portions of the buccal mass, it is necessary to describe their form before describing the soft parts.

The jaws of Nautilus are like those of other Cephalopoda, in being large and hooked (much like the beak of a parrot), in the upper fitting inside the lower jaw, in being formed for the most part of chitin, and in each jaw dividing into two flanges a little distance back of the cutting edge. (Figs. 30 and 31.) Unlike other cephalopod jaws, those of the Nautilus are coated with a hard calcareous deposit for some distance back from the biting edges. Nor are they so sharply pointed as the jaws of other cephalopods. The calcareous deposit thickens toward the edge of the jaw, so that this, instead of being sharp, is broad and flat except for a few irregularities of the surface. The heaviest deposit is usually upon the upper jaw, the entire point of which is calcareous. Aside from this deposit the jaws are of hard, black chitin, extremely strong and light. In Figs. 30 and 31 the two jaws are shown; the lower jaw has been split through the middle to show its inner flange.

The lower jaw is 30 millimeters in length by 28 millimeters in width; the upper jaw is 32 millimeters in length by 17 millimeters in width. The flanges of both jaws are unequal in size, the inner flange of the lower and the outer flange of the upper jaw being much smaller than the other flange of each jaw. It is as though the edge of the lower jaw had been turned inward while the edge of the upper jaw had been turned outward upon itself. The larger flanges of each jaw extend nearly to the back of the buccal mass, that of the lower jaw upon the outside, while that of the upper jaw is deeply buried under muscles and forms the roof and sides of the mouth. The smaller flanges of the jaws are broadest anteriorly, gradually narrowing as they pass to the sides.

The chitinous portion of the lower jaw is pointed in front, the contour of the jaw being unchanged after the calcareous matter has been removed. The chitinous part of the upper jaw, on the other hand, is blunt or even notched anteriorly, the sharp point of the jaw being entirely formed by the calcareous deposit.

The buccal mass projects from the body in the midst of the tentacles. The enormous jaws with their muscles form the bulk of the organ; within is a comparatively small cavity well filled by the tongue and several projecting fleshy folds. Back of the cutting edges each jaw divides into two thin flanges, an inner and an outer, to which the jaw muscles are attached. The external flanges lie upon the surface of the buccal mass and may be seen by merely turning back the buccal membrane. The internal flanges lie deep and are not seen until the buccal mass is nearly dissected.

The skin of the head is carried forward upon the buccal mass, forming a mantle or collar around the jaws, the buccal membrane. (Fig. 28, BM.) Upon and just within the edge of the buccal membrane are a large number of more or less slender papillæ. Those upon the edge are frequently quite like small tentacles. The buccal membrane is attached to the buccal mass along the posterior edges of the external flanges of the upper and lower jaws. It is readily seen, therefore, that the anterior portion of the membrane is in reality a double fold. Except near the edge of the fold the outer and inner portions are actually separated by a space which is part of the hæmocœl. Near the edge the two parts are tightly bound together by muscle fibres and connective tissue. The inner part of the fold—i. e., that part which is attached to the jaws and immediately surrounds them—is extremely thin and delicate except along the anterior edge. Between the jaws and the buccal membrane is a space which, at the sides, where the external

flanges of the lower jaws extend far back, forms two deep pockets. The buccal membrane fits closely around the jaws and reduces the space between itself and them to a minimum.

The inner fold of the buccal membrane is somewhat thickened dorsally, and here it bears, a few millimeters back of the papillæ, two parallel transverse folds extending across the middle line. The folds are very thin, about 18 millimeters in length by 2 millimeters to 3 millimeters in height, and are close together.

When we slit open the cephalic sheath and buccal membrane dorsally we expose the base of the buccal mass, the œsophagus, and cephalic commissure crossing the œsophagus. (Figs. 7 and 28.) The hæmocœlic space existing between the buccal membrane and the base of the buccal mass has been mentioned. This is in communication with a labyrinth of similar spaces extending between the muscles and membranes of the buccal mass and cephalic sheath. These are further in communication with the main part of the hæmocœl which surrounds the œsophagus and liver. Many of the membranes and small muscles found around the base of the buccal mass are very inconstant in their occurrence and extent.

Strong muscles attach the buccal mass to the cephalic cartilage and body wall and govern its motions as a whole. Six muscles, arranged in pairs, seem to be retractors of the buccal mass. Four of these are dorsal and two are ventral. It seems convenient to distinguish the two pairs of dorsal muscles as the dorsal retractors and the dorso-lateral retractors. The dorsal retractors arise near the center of the cartilage and run inward and forward upon the buccal mass to their insertions dorsally between the flanges of the upper jaw. (Fig. 28, DR.) The dorso-lateral retractors have their origins immediately beneath those of the dorsal retractors (in contact with them, in fact). They run under the dorsal retractors to the buccal mass, where they spread out fanwise over the sides of the buccal mass and are inserted at the edge of the external flange of the lower jaw. (Fig. 28, DLR.) The development of the dorso-lateral retractors seems to be more or less variable; when best developed they are fully as distinct and as strong muscles as the dorsal retractors. The cerebral ganglia lie just back of the buccal mass and directly under these muscles (Fig. 28, CG); from them a number of fine nerves pass upward between the retractors to the dorsal parts of the buccal mass and the edge of the buccal membrane. (Fig. 28, N.)

The ventral buccal retractors have their origins upon the body of the cartilage and run forward and outward upon the under surface of the buccal mass to be inserted along the lower edge of the external flange of the lower jaw. These muscles are sometimes divided into more or less distinct parts. The retractors of Van der Hoeven's organ, which are partly attached to the base of the buccal mass, may pass above the ventral retractors or between the muscle bundles in case the muscles divide. (Fig. 29.)

A narrow band of muscle fibres extends along the median line of the inner surface of the outer fold of the buccal membrane into the body wall, the median muscle of the buccal membrane. From either side of the median muscle a broad bandlike muscle passes outward and downward to the ventral side of the buccal mass, where its fibres mingle with those of the ventral retractors and are attached to the edge of the lower jaw. (Figs. 28 and 33, LM.) These muscles are evidently levators of the buccal mass, as they hold it suspended in a sort of sling. It will be noticed that the six retractors and the two levators spread out considerably over the surface of the buccal mass and that their fibres commingle to a certain extent. The muscles are connected by a muscular membrane and thus, by the union of the distal portions of the muscles and this membrane, a complete covering is formed to the posterior part of the buccal mass, extending from the edges of the jaws to the circum-œsophageal nerve ring and firmly united to the tough covering of the nerve ring. (Figs. 28, 33, and 34, MM.) A second, more ventral membrane is stretched between the ventral retractors near their origins, thus forming an apparently closed chamber. (Fig. 33, OM.) Another membrane may extend between the levator muscles and the outer fold of the buccal membrane. Ventrally this membrane may be continued by the edges of Van der Hoeven's organ, as in Fig. 29, though it is rarely anything like as complete as it was in this specimen.

Upon laying open the muscular membrane, which has been described as covering the buccal mass back of the jaws, a very intricate system of intrinsic buccal muscles is exposed. Observing

the dorsal aspect of the buccal mass (Fig. 34) we see posteriorly a dark semicircle, the posterior edge of the inner flange of the upper jaw covered by only a thin membrane. From the entire outer surface of the inner flange of the upper jaw muscle bundles extend to the inner surface of the outer flange and out between the flanges of the lower jaw, the mandibular muscle. This powerful muscle, which occupies the entire space between these flanges of the two jaws, forms the closing muscle of the jaws. When we see this we are no longer surprised at the Nautilus's ability to nip off the leg of a chicken as if with a pair of shears. A groove along the mid-dorsal line indicates the line of nearly complete separation of the muscle bundles of the right and left sides. The separation is not complete, for many bundles cross from each side to the other. An artery runs immediately above this groove, but outside the muscular membrane, the branches of which are distributed to the mandibular muscles.

Upon the ventral side of the buccal mass a much more complicated arrangement holds. (Fig. 33.) Centrally the radular sac may be seen extending more than half the length of the buccal mass. At the sides are muscles which control some of the mouth parts, and portions of the buccal nervous system. I find, by comparing my notes and figures, that these muscles are slightly variable, therefore I shall describe only such as seem to be fairly constant.

By reference to Fig. 33 it will be seen that several muscles on each side have their origins in the muscular membrane already described as covering the posterior part of the buccal mass. Two pairs of these muscles (1 and 2) pass into the cavity of the anterior of the two folds in front of the tongue (the anterior prelingual process) and are attached to its walls, evidently being retractors of the organ. The median pair (2) unite as they enter the fold, but after their union give off several small branches.

A third pair of muscles (4) arise near the side of the buccal mass and run upward and inward to within the fold immediately in front of the tongue (the posterior prelingual process), but mostly to the fold which bears the anterior free part of the radula. A peculiar muscle (figured in Fig. 33, 3) arises with a double head from the muscular membrane closing the front of the space between the ventral buccal retractors and runs forward, at first above and then beneath the radular sac, to be attached to the fold in front of the tongue. Two pairs of slender muscles (5 and 6) arise from the posterior part of the muscular membrane. The longer pair (5) extend forward under the muscles already described to the surface of the tongue bearing the free part of the radula. The shorter pair of muscles extend only to the membrane covering the slight downward projection of the upper jaw.

With muscles 1 and 2 arises a third quite strong muscle (7), which passes upward and directly inward to be attached to the dorsal surface of the radular sac. From its position I should think that this muscle may function either as protractor or retractor of the radular sac, always tending to pull it back to its resting position.

From each ventral posterior corner of the inner flange of the upper jaw a strong muscle (8) runs forward and outward to be attached to the ventral edge of the outer flange of the lower jaw. The contraction of these muscles probably acts to open the jaws. The central part of the buccal nervous system lies beneath these muscles; the pharyngeal commissure, however, runs above them, between them and the lateral parts of the mandibular muscles.

Immediately above the posterior portion of the radular sac is a muscular membrane, containing both transverse and longitudinal fibres, which forms the ventral wall of the space containing the lingual and radular muscles. Quite a number of small muscles extend between this membrane and the dorsal wall of the radular sac, while the membrane itself is attached anteriorly to the radular sac. From the dorsal side of the membrane and the posterior side of the anterior upwardly directed portion of the radular sac a median septum extends to the dorsal integument of the tongue. (Fig. 35, S.) This septum, thin ventrally, becomes thicker and muscular dorsally, and is split into two parts, which are attached to the bottoms of the V-shaped folds extending back from the opening of the radula. (Fig. 35, X.)

Upon each side of the septum are three muscles which form the mass of the tongue, and are chief in controlling the movements of the tongue and radula. Next to the septum is a broad, flat muscle (the internal lingual, IL), which runs parallel to the septum, to be inserted

into the base of the depression running back from the radular opening. Outside of this is another flat muscle, the radular (R), having its origin just in front of the internal lingual. It runs forward and inward, and, uniting with its fellow on the opposite side, is attached to the anterior side of the ascending portion of the radular sac. Above the two muscles just described is a very much larger muscle which forms the bulk of the tongue. To this I have given the name external lingual (EL). Its origin lies above the origins of the other two muscles. From this it runs forward and upward and inward, partly to join its fellow of the opposite side in forming a sling which covers the whole of the ascending portion of the radular sac anteriorly, and partly to be inserted dorsally along the ridge of the tongue. The sling formed by the external linguals in front of the radular sac is not attached to the latter in any way. These three muscles do not have their origins upon any hard part, such as the jaws, but in a sort of tendinous mass (T), which is firmly attached to the floor of the mouth and the muscular membrane described a short time ago. From this tendon a short, strong muscle, the lingual protractor (LP), runs forward and outward under the edge of the opening muscle of the jaws (Fig. 33, 8) to the projecting point of the inner flange of the upper jaw. It would seem as if the only effect of the contraction of this muscle must be to pull the origin of the lingual muscles forward, possibly permitting a greater extension of the tongue; the combined effect of the contraction of the internal and external lingual and the radular muscles would be to pull the tongue and the radula up and back; a simultaneous contraction of the lingual protractor would possibly keep the radula tightly pressed against the object it was rasping. The sling formed by the external lingual is not attached to the radular sac in any place. The integument which supports the free portion of the radula is strongly supplied with muscle fibres running outward and downward to the sides of the jaw; the distinct muscles going to these parts have been mentioned. While these muscles are comparatively weak, they probably are protractors of the tongue. For the structure of the radula indicates that its rasping or pulling effect is produced only when the tongue is thrust upward and backward, and only in this motion would great resistance be encountered. Consequently the muscles which pull the tongue back are large and strong. As no great resistance would be encountered in pulling the tongue forward, the small muscles attached to the integument seem to be sufficient. The integument of the tongue is supplied with a weak longitudinal musculature.

Small muscles extend into the salivary lobes from near the origins of the lingual muscles.

The walls of the mouth cavity are formed by the inner flange of the upper jaw, except ventrally. From the floor of the mouth the tongue, bearing the radula, and four fleshy processes, project into the cavity. In front of the tongue are two processes (Fig. 32, PP and AP), one behind the other, which are really upfoldings of the floor of the mouth. The anterior process is 8 millimeters in height and 12 millimeters in width, covered with papillæ upon both sides, the papillæ upon the anterior side being much smaller than those upon the posterior side. The posterior of the two processes is slightly higher and considerably wider than the anterior. Its base is carried up a short distance on each side of the tongue. This process bears papillæ only upon the edge and the posterior side; the anterior surface is covered with fine transverse ridges.

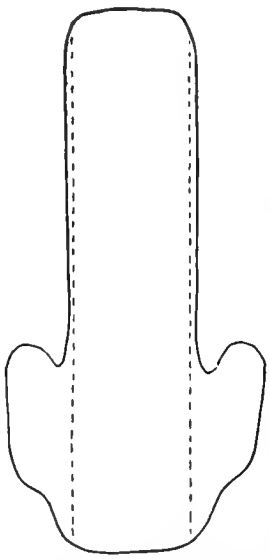
The tongue is a large organ which occupies most of the space within the mouth. (Fig. 32, Tn.) It is about 22 millimeters in length, 10 millimeters in width, and 15 millimeters in height. Anteriorly the tongue rises abruptly and with somewhat of an overhang to its full height. For nearly half its length it maintains this height, then slopes gradually to the floor of the mouth, immediately in front of the œsophageal opening. The shape of the tongue may vary, e. g., it may slope downward and forward to the opening of radular sac, and then sloping down and back. The sides of the tongue are nearly vertical and are entirely free from papillæ. The dorsal surface of the tongue, on the other hand, is thickly covered with large papillæ. Just in front of the œsophageal opening are a number of peculiarly long and slender papillæ.

The anterior surface of the tongue is covered by the radula. (Fig. 32, R.) The radula passes up over the tip of the tongue and then almost immediately bends downward again and is lost to view in the radular sac. The radular sac passes downward and a little backward under the integument of the point of the tongue till it reaches the under side of the tongue, where it abruptly

bends backwardand so passes beneath the tongue to near the œsophagus. (Fig. 33, RS). Grooves run inward from each side of the tongue to the opening of the radular sac, giving it a V shape.

The radular sac (Fig. 33) is about 25 millimeters in length and has an average width of 8 millimeters. Its ventral and lateral walls are thin and transparent and allow the brown color of the radula to show through. The extreme posterior portion of the sac, however, is colorless, since the teeth are formed here and have not yet taken on their color. This part of the sac also is somewhat wider than the rest, for the radula, at first spread out flat, becomes more and more inrolled at the edges as it grows forward. From each posterior corner of the radular sac a ligament of elastic fibres runs back to the muscular membrane near the œsophagus, evidently tending to hold the radular sac in place (RL). The dorsal wall of the radular sac is quite thick, and fits closely upon the teeth. In the anterior portion, where the radula is inrolled, the dorsal wall of the sac projects to occupy the groove. As the radula passes out of its sac a plain chitinous border, 3 to 4 millimeters wide, is added upon each side. (Text fig. 8.) This border appears to be formed at the bottoms of the grooves running back from the opening of the radular sac.

Let us now examine the separate teeth of the radula. The teeth are arranged in rows running across the chitinous, ribbon-like base of the radula; there are in all about fifty of these rows. In each row are thirteen teeth symmetrically arranged with regard to the central tooth. Each of the six lateral teeth is exactly like the corresponding tooth of the opposite side in shape and position. It scarcely seems necessary to give a detailed description of each tooth after the careful descriptions and figures of Vayssiere and with the figures accompanying this paper. I should not have drawn new figures of the teeth if Vayssiere had not used the shape of the lingual teeth as a character to distinguish between the two species of NAUTILUS, *N. pompilius* and *N. macromphalus*. But when I found as great differences in shape between his figures of the teeth of *N. pompilius* and my specimens of the teeth of the same species as he shows between the teeth of the two species it seemed to me to be wise to make new figures for the sake of comparison. All the teeth are very firmly attached to the chitinous ribbon by large bases. The bases of the central seven teeth are approximately square, while the bases of the other teeth are much longer than wide. The projecting tip of the central tooth is directed straight backward; the other teeth while projecting backward are also directed more or less inward toward the central tooth. Let us number the teeth from the central tooth outward, distinguishing them as first lateral, second lateral, and so on.



TEXT-FIG. 8.—Outline of the radular ribbon. The dotted lines indicate the position of the outer rows of teeth.

Immediately outside the central tooth (Fig. 42) is a tooth very much like the central one but smaller and having a shorter and a much less slender point. (Fig. 43.) The second lateral tooth has a broader base and a much shorter, blunter point, which is directed toward the central tooth. (Fig. 44.) The third lateral tooth (Fig. 45) is long and slender and curved. Attached by a base which makes an obtuse angle with the body of the tooth, it projects backward and inward so as to cover the first and second lateral teeth of more posterior rows. The outer (anterior) face of the tooth is gouged so as to form a sharp edge running nearly parallel to the inner outline of the tooth. The fourth lateral tooth (Fig. 46) is rod-like and attached to the ribbon along its entire length. Its dorsal surface is sharply ridged for nearly the length of the tooth; for part of its length the ridge is produced into a thin, sharp, transparent blade of chitin which also projects backward. The fifth lateral tooth (Fig. 47) is very much like the third, but longer, more slender, slightly less curved, and often more sharply pointed. It is similarly gouged out upon the outer surface, but the sharp edge is not so close to the inner edge of the tooth as on the third lateral tooth. This tooth overlaps the fourth lateral tooth and the base of the third lateral tooth in more posterior rows. The outermost tooth of all is also rod-like, attached to the ribbon along its entire length, and bears a slight

backwardly pointing projection upon its inner end. (Fig. 48.) The bases of the teeth form various angles with the axis of the radula. The outer tooth makes an angle of about 45 degrees with this axis, while the bases of the third and fifth lateral teeth make angles of 30 degrees with it. The bases of the other teeth are transverse to the axis of the radula.

The formation of the radula takes place in the extreme posterior part of the radula sac. The first 8 or 10 rows of teeth are colorless and soft; from here on the teeth gradually turn to dark brown, become hard, and assume their full size.

From the floor of the mouth a broad, flat process, 12 millimeters in length and 10 millimeters in height, arises at each side of the posterior part of the tongue. The inner sides of these processes bear papillæ to a varying extent in different individuals. They may be entirely covered except for a small space in the center, or only the upper half may be covered. A small, slightly elevated area in the center of the inner side of the process is always free from papillæ, and here is a minute pore, the opening of the salivary gland. The salivary glands are ovoid bodies, indistinctly divided into lobules, 5 millimeters by 4 millimeters by 2½ millimeters, situated within these processes, with their longest axes directed downward and backward. The duct is near the anterior end of the gland; the duct, however, is so short that it scarcely deserves the name, for the glands lie close against the integument of the processes. (Fig. 70.)

The jaws of the Nautilus are admirably adapted for crushing and biting hard objects. The calcareous layer which covers the inner and outer surfaces of the chitinous parts of both jaws forms a thick, square edge which is practicably unbreakable; slight projecting roughnesses of the edges prevent their slipping upon large and smooth objects. After the jaws have become thoroughly dry the calcareous substance is very brittle and readily peels off the chitinous base, so that in a few days, even without handling, the calcareous matter may have fallen away completely. But while the calcareous matter of the jaws contains any moisture it is extremely tough and hard to remove. This it must always be when the Nautilus is under natural conditions, so there is no doubt but that the calcareous material of the jaws means added strength in no small degree.

Without the addition of the calcareous matter the chitinous parts of the jaws would be unable to handle the food they do now. In other words, the addition of calcareous material to the jaws is a modification of the type of structure observable in the jaws of other cephalopoda which enables the Nautilus to subsist upon animals possessing shells heavy enough to protect them from most other predatory animals.

The upper jaw fits snugly inside the lower, so that its outer edge just passes the inner edge of the lower jaw in closing. Consequently when the animal is biting any substance the action of the jaws is not that of a pair of nippers, in which the two jaws meet each other, pinching the substance in two between them, but instead like that of a steel shear, where two heavy blades having broad flat faces and sharp square corners move past each other. By this construction and motion the maximum cutting power is attained with the least exertion and the least risk of breaking the edges of the jaws.

The traps in which the Nautili were caught were baited with chicken, so I often have found the crop filled with large pieces of chicken flesh. Feathers and flesh and bones, even the leg bones, are cut as cleanly as with a pair of shears; everything attests the power of the jaws and their muscles. Apparently also the Nautilus does not pluck its chickens. The remains of some crustacean found in the stomach and intestine are evidence of the ability of the Nautilus to handle any food of this nature. It also seems scarcely doubtful that the Nautilus could eat many of the thinner shelled mollusca, although there is no evidence of such a diet.

For an animal provided with such powerful jaws a radula seems much like a superfluity. Certainly it can not, as in many of the gastropoda, be the chief organ for seizing and tearing food. The slender and almost delicate form of many of the radular teeth precludes the idea that the radula may be used to rasp away objects which are too hard to be broken by the jaws. It seems possible that the radula may be used to scrape the flesh out of shells, crustacean or molluscan, which have been broken by the jaws. But the contents of the digestive tract

indicate that the Nautilus does not trouble itself in this way, but swallows shells and all, leaving the separation of food from refuse to the operations of digestion. Nevertheless, if the radula is excluded from any part in gathering food, it may be of extreme importance in the swallowing of the food. The sides and roof of the mouth are formed by the inner flange of the upper jaw, and consequently the activity of the organs of the floor of the mouth alone must carry the food to the opening of the œsophagus. The radula may seize fleshy food and hold it while it is being bitten; it would also prevent partly bitten food from escaping while the jaws take a new hold. After the food had been bitten off the radula would certainly pull it back upon the surface of the tongue, which, with possibly some aid from the salivary processes, would press the food back into the opening of the œsophagus.

It is probable that when the radula is in use and consequently under tension the long, lateral teeth are erected so that they no longer cover more central teeth, and are in better position for holding any substance firmly.

The function of the processes in front of and at the sides of the tongue is also problematical, if we do not use a still stronger term. It is reasonable to suppose that at least one of their functions is to aid in the swallowing of the food. While we do not suppose that the processes at the sides of the tongue have been developed for the sake of bearing the salivary glands, these glands are now much more advantageously situated on account of the high tongue, to aid in the deglutition of food than they would be were they in the floor of the mouth.

Steinmann's paper on the formation of calcareous matter by the mollusca suggests another possible function of the processes in front of the tongue (especially the anterior one) and the buccal membrane. The decaying secretions of these parts combining with calcium salts of the sea water may form the calcareous matter which covers the tips of both jaws. This is the only explanation I have found which seems to be at all adequate to account for the formation of so much calcareous matter at this point. For there is here no closely applied epidermis, as at the edge of the shell, which could be supposed to take an active part in the formation of this material.

The œsophagus leaves the buccal mass at its posterior end and so low down as to be almost ventral. It immediately passes through the nerve ring as a small, round tube 5 millimeters in diameter. The lengthy œsophagus runs straight back through the hæmocœl to the stomach. (Fig. 27.) The portion of the œsophagus between the nerve ring and the stomach is extremely distensible and forms a crop in which a large amount of food can be stored and gradually passed to the stomach to undergo trituration. When completely filled the crop forms a large pear-shaped sac with smooth, thin walls. But when it is only partly filled or is empty the crop shrinks in size and the walls thicken, becoming folded internally with close, longitudinal folds. In the specimen figured (Fig. 32) the posterior part of the crop contained a little food while the remaining portion was empty, so both conditions of the wall have been shown. The folds of the anterior portion of the œsophagus are more permanent, probably disappearing more or less only when large pieces of food are being swallowed. The opening in the nerve ring through which the œsophagus passes is so small that it is difficult to imagine how some of the large pieces of food found in the crop could have passed through without exerting a considerable pressure upon the ganglia. At the posterior end of the crop are several longitudinal folds which end abruptly within the opening into the vestibule of the stomach and seem to be more permanent than the other folds mentioned above. (Fig. 32, X.)

The stomach, into which the œsophagus opens, is an oval, laterally flattened organ 27 millimeters by 27 millimeters by 15 millimeters in dimensions. At first sight it appears to lie in the genital portion of the cœlom, but in reality it lies in the hæmocœl, closely covered by a backwardly projecting pocket of the membrane which separates cœlom from hæmocœl. The posterior end of the stomach is supported by a thin ligament extending between it and the gonad. (Fig. 27, GL.) The stomach lies in front of, below, and to the left of the gonad. At the center of each flattened side is an irregularly oval, white, tendinous area about 8 millimeters long, from which the muscles radiate which surround the stomach by a thick wall except at the anterior and posterior ends. At the former, where the œsophagus enters and the intestine leaves, a thin-walled chamber is formed, elsewhere spoken of as the vestibule. The muscles pass from one tendon to

the other, forming a very thick wall upon the dorsal and ventral sides of the stomach. The posterior wall of the stomach is thin, like the anterior. Within the muscular layer is a white layer of what seems to be elastic tissue, at least as thick everywhere as the muscle layer. Under the thickest part of the muscular layer, i. e., between the tendons of the stomach dorsally and ventrally, the elastic tissue layer is so thickened as to form thick pads which project into the cavity of the stomach. (Fig. 32.) Except upon the anterior and posterior walls, the inner surface of the stomach is thrown into fine, parallel, longitudinal ridges. Inside the walls of the stomach, covering only the ridged portions, is a thick, chitinous lining, which in life must lie closely upon the epithelium of the stomach and be formed by it, since it copies accurately all the ridges and folds of the walls of the stomach. In my preserved specimens the lining has always been entirely free from the walls, probably as the result of shrinkage. Compared with external chitinous parts this lining is quite soft, but nevertheless it must be a great protection to the fleshy walls of the stomach while the food, often mixed with hard, sharp pieces of shell, is being triturated.

From the anterior edge of the rigid pad of the ventral side of the stomach springs a row of small, slender tentacles. (Fig. 32, T.) I have found fine processes upon the corresponding part of the chitinous lining, which may possibly lie upon and protect the tentacles. What the function of these tentacles can be is hard to imagine. Perhaps they are sensory and have something to do with the passage of the food into or out of the stomach. In view of the character of the débris found in the intestine it does not seem probable that they are used to sift out the finely divided particles of food. Besides extremely small particles of food one finds in the intestine large pieces of crustacean shells and even entire pleopods. *A priori*, any sifting apparatus would therefore seem superfluous. It is unfortunate that the condition of my material prevents any histological examination of these organs.

The position of these tentacles clearly marks a line of separation between the anterior portion of the stomach into which the œsophagus and intestine open and the posterior portion where the food is ground, and makes the term *vestibule* seem reasonable in speaking of this portion. (Fig. 32, V.)

The opening into the intestine is upon the right side of the vestibule. I have been unable to find the valve guarding the entrance to the intestine mentioned by Owen. From the vestibule the intestine passes to the right around the back of the cœcum and then forward upon the right side of the latter organ. (Fig. 27, I^1.) Then, bending downward and backward around the part of the liver connecting the right and left lobes, the intestine forms a backwardly directed loop. (Fig. 27, I^2 and I^3.) The two legs of the loop lie parallel and close to one another, connected by a delicate mesentery in which runs an artery giving off branches to each part of the intestine. (Fig. 27, IA.) The second loop of the intestine is directed upward as well as backward, so that its end lies beneath the siphuncle. A ligament from the right anterior face of the gonad extends to the left leg of the loop and slings the loop of the intestine in position. (Fig. 27, IL; Fig. 38, l. l.) The left and larger leg of the loop runs straight forward under the stomach, crop, and liver in the mesentery above the heart and between the anterior renal sacs to the plicated anus upon the inner side of the mantle. The last part of the intestine is thickened and folded longitudinally and is called the rectum.

The cœcum is a blind sac opening into the intestine 10 to 12 millimeters from its origin and lying within the first loop of the intestine. (Fig. 27, Coe.) In and about the cœcum is the most complicated part of the entire digestive tract. The cœcum itself is a thin walled, oval, laterally flattened organ, 18 millimeters in length and 11 millimeters in width. The duct of the liver enters the cœcum opposite the intestinal opening; usually the minor ducts of the separate lobes of the liver unite into a common duct before entering the cœcum, but they may open separately. (Fig. 32, HD.) The intestinal and hepatic openings are both near the lower side of the cœcum. From the dorsal and posterior walls transverse, shelf-like lamellæ extend into the cavity of the cœcum, leaving its lower portion only unobstructed. The surfaces of the lamellæ are folded and pitted, so that their appearance lends support to the a priori judgment from their position that the lamellæ must be glandular, adding their secretion

to that of the liver as this flows through the cœcum. The lamellæ are about thirteen in number. The cœcum opens into the intestine, not directly, but through a short neck of about the same diameter as the intestine. The mouth of the cœcum is surrounded by a muscular thickening of the walls which is evidently a sphincter; ventrally the thickening extends from the opposite sides toward the intestine as a V-shaped ridge. From the opening of the neck of the cœcum into the intestine a thin, wide, projecting fold extends about 30 millimeters along the intestine toward the anus. (Fig. 32, 1.) The fold is widest at the beginning, where it evidently forms a valve guarding the cœcum against the entrance of food from the intestine. As it passes along the intestine the fold crosses over the ventral to the posterior side, at the same time becoming lower and lower until it can scarcely be seen. The middle part of the fold is of considerable thickness and is evidently glandular. From the point of the V formed by the sphincter of the cœcum a low ridge extends into the center of the pocket-like valve guarding the intestinal opening. From the point of the V also a second fold (Fig. 32, 2) extends along the right side of the intestine nearly parallel to the first fold. It is, however, not so prominent as the other. It gradually becomes lower until it disappears. A number of oblique, apparently glandular, foldings of the ventral side of the intestine connect the two folds.

In some specimens, perhaps usually, a low, longitudinal ridge occupies the base of the channel formed by the parallel folds. To this the oblique folds run and meet like the sides of a V, the apex being directed toward the rectum.

The first or posterior fold does not entirely disappear like the second, but is continued as a low, scarcely perceptible ridge to the rectum. Close beside this, anteriorly we may term it, another ridge runs exactly parallel for its entire length. (Fig. 32, 3, 3.) This third fold commences near the end of the anterior fold of the first part of the intestine, but seems to have no connection whatever with it. The two parallel folds commence upon the posterior side of the intestine; as they run back along the second loop of the intestine they pass to the opposite side, upon which they continue until the rectum is reached, when they become ventral and are lost among the longitudinal foldings of this part of the intestine. As they make the sharp turn at the back of the second loop the folds become much thickened; another thickening of the folds is observable at the beginning of the second loop. Upon the posterior side of the turn of the second loop is a thick, foliaceous ridge 20 millimeters in length. (Fig. 32, 4.) This is connected with the posterior of the two parallel ridges by a number of fine, transverse folds running across the ventral side of the intestine.

The intestine is extremely thin walled and plentifully supplied with blood vessels. In a number of instances the diagonal ridges of the intestines were immediately above small arteries; whether there is an intimate connection between ridges and blood vessels in all cases can be determined only after an histological examination which my material did not permit.

The structure of the cœcum seems to indicate that it may serve as a collecting place for the secretions of the liver with which its own secretions are mixed. When the proper time arrives the sphincter relaxes and the accumulated secretions are guided along the channel between the parallel ridges of the intestine. As has already been described, the posterior and larger of the two ridges of this part of the intestine serves as a valve to prevent food entering the cœcum; the disposition of the folds also renders it probable that the mixing of the food with the secretions of the liver and cœcum does not take place until some distance beyond the point where the latter enter the intestine. There is no use in making any further conjectures as to the functions of these ridges which, endostyle-like, extend along the intestine, until we know their histological structure.

The liver is a large, dark-brown, lobed mass which lies underneath the posterior part of the crop and the stomach and cœcum, and surrounds parts of the intestine. (Fig. 27, L, L; L^1, L^1.) It is generally divided into five parts, two right and two left lobes, and a median portion which may or may not assume the form of a lobe. The left lobes are very considerably larger than the right. The main ducts of the right and left lobes unite in pairs, the ducts thus formed uniting to make a common duct a short distance from the cœcum. The large ducts are covered by small lobules, which empty their secretion directly into the ducts. The hepatic artery and its

branches run along the dorsal sides of the hepatic ducts giving off a branch to each lobule. The duct of the right lobes of the liver passes under the first loop of the intestine as this runs forward around the cæcum. The intestine passes backward under the median part of the liver, nearly enclosing it in a loop.

VALENCIENNES has figured an exceedingly interesting abnormality in his specimen. The anus is shown situated upon the body wall between the shell muscles. This is the only record of any such misplacement of the anus. VALENCIENNES's specimen seems to be perfectly normal in every other particular.

We have no knowledge regarding the innervation of the portions of the alimentary system back of the buccal mass. It has so far been impossible to trace any nerves to these organs.

RENAL ORGANS.

It has already been mentioned several times that the renal organs of Nautilus are situated in the posterior region of the ventral portion of the mantle. Like the gills, they are four in number, the renal glands being situated upon the branchial arteries.

From the posterior side of each branchial artery, at about one-third the distance from its origin to the base of the gill, hangs a large bunch of finger-like follicles. (Fig. 36, a. p. g. and p. p. g.) These hang into the pericardial cavity. On account of their resemblance in many ways to the pericardial glands of the Dibranchiata the four follicular appendages from the posterior sides of the branchial arteries are also generally called pericardial glands.

From the anterior side of each branchial artery, immediately opposite the follicular appendage, hang two appendages subdivided by narrow fissures into small, polygonal lobes, pressed closely together so that they appear to form a single hemispherical mass of about the same size as the follicular appendage on the posterior side of the artery. (Fig. 37.) These have been called the renal appendages. Each pair of renal appendages hangs into a chamber, the renal sac, which is completely closed off from the cœlom, and has but a single opening to the exterior, situated upon the inner surface of the mantle. (Fig. 36, r. s; Fig. 3, RA, RP.)

The renal sacs are arranged in pairs; an inner (anterior) pair which lie side by side medianly, possessing a common dividing wall, and an outer (posterior) pair, which lie at either side of and slightly posterior to the inner pair, nowhere touching each other.

The dorsal or outer walls of the anterior sacs are formed by the integument of the mantle. The ventral or inner wall is formed by the viscero-pericardial ligament (Fig. 36, p. v. l.), which is continued forward to unite with the integument of the mantle. A common, thin, vertical partition separates the two sacs medianly.

The posterior walls are formed by a narrow septum, extending between the viscero-pericardial ligament and the inner wall of the mantle. A section of either sac parallel to the longitudinal axis of the body is triangular—the base of the triangle being posterior and formed by the last-mentioned wall of the sac, while the apex is directed anteriorly and is formed by the union of the edge of the viscero-pericardial ligament to the inner wall of the mantle fold.

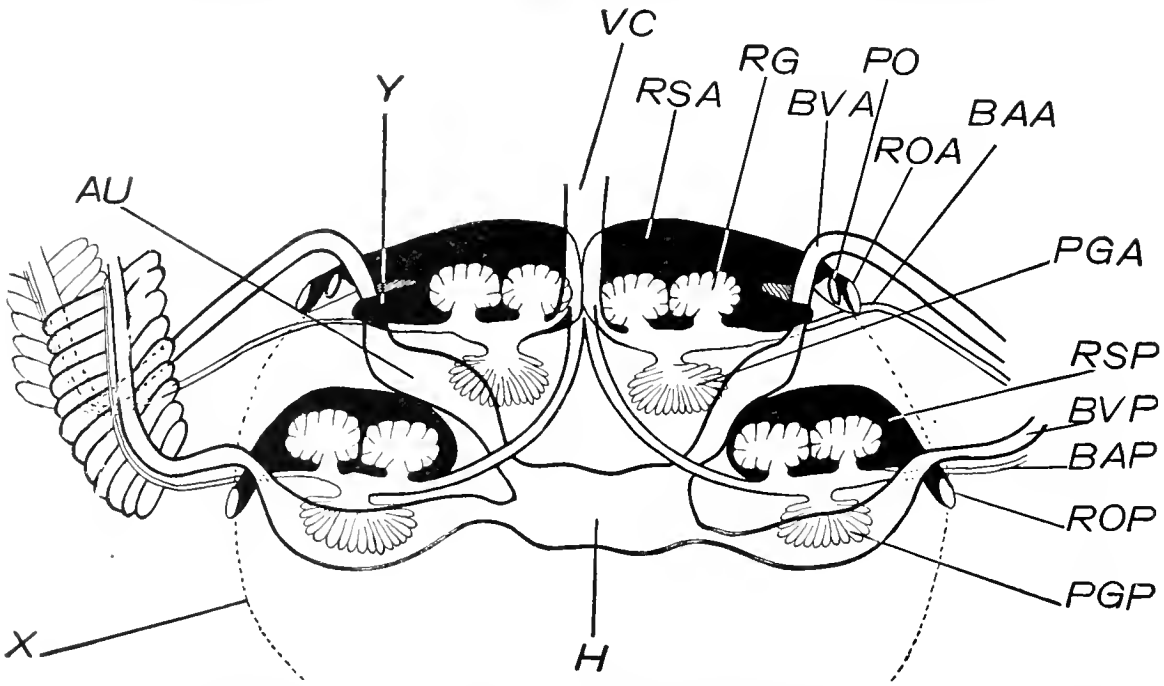
The longest diameter of the chambers is transverse to the long axis of the body. Passing toward the sides the chambers gradually decrease in size; finally, near the outer ends, forming a canal only, which leads to the external opening.

To the outer sides of the lobular appendages the branchial vein, passing through the mantle to the heart, pushes the walls of the sac inward from the posterior edge. (Text-fig. 9, BVA, Y.) A short, blind pocket is formed upon the posterior side of the branchial vein. The narrow portion of the renal sac anterior to the vein forms the canal leading to the exterior. This passes the anterior side of the vein, then turns backward below the vein and opens outward just posterior to it, through the outer of the two pores lying side by side upon the inner surface of the mantle. (Fig. 3, RA.)

The anterior branchial arteries pass outwardly from the vena cava in the posterior walls of the anterior renal sacs. Each passes below the canal of the sac leading to the exterior, and on in the mantle to the gill along the ligament-like base of the anterior gills. It thus lies immediately below the branchial vein.

The other two renal sacs, the posterior sacs, lie at the sides of the body, widely separated from each other. A little posterior to the inner sacs, they are considerably outside them, to close the ventral sides of the shell muscles.

The dorsal wall of each sac is formed by the inner wall of the mantle fold, and is that portion of the inner wall of the mantle fold lying between the anterior renal pores and the base of the posterior gill. The posterior and anterior walls of the sac are formed by septa extending backward and downward from the inner wall of the mantle. They unite around the lobular appendages to form a closed sac, from the posterior edge of which a thin ligament extends backward and somewhat inward, attached along one edge to the visceral body wall. (Fig. 36, L.) The outer end of the sac is narrowed to form a canal which, running in the substance of the mantle



TEXT-FIG. 9.—DIAGRAM OF THE RENAL SACS AND NEIGHBORING ORGANS OF NAUTILUS, AS VIEWED FROM THE DORSAL SIDE.

AU, auricular expansion of left anterior branchial vein.
BAA, anterior branchial artery.
BAP, posterior branchial artery.
BVA, anterior branchial vein.
BVP, posterior branchial vein.
H, heart.
PGA, anterior pericardial appendage.
PGP, posterior pericardial appendage.
PO, pericardial pore.
RG, anterior renal appendage.
ROA, anterior renal pore.
ROP, posterior renal pore.
RSA, anterior renal sac.
RSP, posterior renal sac.
VC, vena cava.
X, outline of pericardial division of coelom.
Y, cul de sac of anterior renal sac.

close to the ventral surface of the shell muscle outside and ventral to the branchial artery, opens to the exterior through one of the posterior renal pores. (Fig. 3, RP.) The posterior branchial arteries run through the posterior walls of the outer renal sacs. (Text-fig. 9, BAP.)

Between the inner and outer renal sacs is left a narrow offset of the pericardial cavity extending into the mantle fold. The auricular enlargements of the anterior branchial veins lie in this space. From the outer end of the enlarged auricular portion of the vein where it turns upward to pass through the inner wall of the mantle fold, a triangular septum stretched between the outer and inner walls of the mantle fold extends outward to the lateral edge of the pericardial space. By this means a narrow passage is formed between the anterior side of the outer renal sac and the septum. This passage, passing along the outer side of the anterior branchial vein, opens to the exterior through the pericardial pore. (Fig. 3, PP.)

Within the lips of each of the pericardial and renal apertures are folds from each side; they are especially well developed upon the lips of the renal apertures, and lapping past each other form valves which are difficult to push aside with a probe, and which must be effectual in preventing ingress or egress of any substance except under the control of the animal.

The histology of the pericardial glands and the renal appendages has been investigated to a limited extent by VIGELIUS, but our knowledge of the microscopic structure of these organs is still most elementary.

The branchial arteries run outward from the vena cava through the posterior walls of the renal sacs. At about the middle of these the arteries form sinus-like enlargements, in the walls of which are usually three openings—one on the posterior wall leading into the central blood space of the pericardial gland, and two in the anterior wall leading into the central cavities of the lobular renal appendages.

The pericardial glands are made up of a large number of finger-like follicles radiating from the central cavity, which is in communication with the branchial artery. The glands are not stalked, but are attached to a quite considerable area of the wall of each renal sac around the fissure leading into the central cavity of the gland. The follicles of the glands are sometimes slightly constricted at their bases or may be enlarged a little distally. Blood spaces extending outward in the follicles from the central cavity form a closed finely branching system. The external or pericardial surface of each follicle is covered by minute pores, leading into tubules which everywhere penetrate between and separate the branching blood vessels. The blood vessels possess a very thin endothelial wall, which lies close to the inner side of the columnar epithelium of the tubules. The structure of the pericardial glands is very similar to that of the venous appendages of the Dibranchiata.

GROBBEN[1] remarks upon the resemblance in essential structure of the pericardial glands of Nautilus to those of *Eledone moschata*. The glands are much further subdivided in Nautilus than in Eledone.

The renal appendages have much the same structure as the pericardial glands. They hang in pairs from the anterior sides of the branchial arteries, pressed closely against each other so as at first sight to appear like a single structure, but in reality connected only by the wall of the branchial artery.

The renal appendages are divided by narrow, not very deep, fissures into large, flattened, polygonal lobes, and so present an appearance quite different from that of the pericardial glands. Like the pericardial glands, the renal appendages are sessile upon the branchial arteries.

The openings in the anterior walls of the arteries lead into a sinus-like central blood space in each renal appendage. From the central blood space the branches to the lobes pass outward, breaking up into numerous closed vessels. These are separated by invaginations of the columnar surface epithelium, which comes into close contact with the thin endothelial walls of the blood vessels. The outer ends of the tubules pushed inward from the surfaces of the lobes are radial; the inner ends run irregularly.

The renal sacs are often completely filled with a gritty substance, like fine sand. Sometimes it is white, sometimes a faint rose-pink in color. This constitutes the excretory product of the renal appendages. It is composed of rounded grains, formed by numerous concentric layers, reminding one strongly of starch grains by their appearance. The grains are single or compound, often being joined so as to form short varicose rods. Rarely irregular masses are formed. When the deposit in the renal sacs is of a pink color most of the granules have a slight pink tinge. Some are deep red, while others contain a deep red center and a light peripheral portion. The granules are frequently found in the tubules of the appendages.

According to KEFERSTEIN, the excreted substance found in the renal sacs contains a slight amount of fat. The greater proportion is, however, made up of inorganic substances. The principal of these is calcium phosphate. Lesser amounts are found of calcium sulphate, calcium

[1] Morphologische Studien über den Harn- und Geschlechtsapparat sowie die Leibeshöhle des Cephalopoden. Arb. a. d. Zool. Inst. d. Univ. Wien. T. V., 1884.

carbonate, ferric phosphate, and magnesium ammonium phosphate. The excretion contains no uric acid.

The amount of the excreted products in the renal sac may be quite considerable. In one case the deposit obtained from the four sacs amounted to 3.28 grams.

The secretion of the pericardial glands is often quite large in amount, being sufficient to glue the viscera together and cause considerable trouble to the dissector. Of course there is a probability that the glands have been stimulated to abnormal activity by the handling of the animal. The coagulated secretion appears much like mucus. KEFERSTEIN found no traces of uric acid in either the pericardial glands or their secretion.

BODY CAVITY.

The body cavity of Nautilus is very extensive, and consists of two distinctly separated portions—an anterior hæmocœl and a posterior and ventral cœlom. The principal portion of the hæmocœl forms a space around the œsophagus with its crop-like distensible portion, and the liver, occupying the entire space between these organs and the body wall. (Fig. 7.) The hæmocœl is continued anteriorly in the form of many splits and spaces between the muscles and membranes around the buccal mass. These cavities and others which communicate with the main portion of the hæmocœl are in free communication with blood sinuses in the various organs.

The hæmocœl is traversed by many fine shreds of connective tissue, which pass from one to another portion of the body wall or from the walls of the body to the viscera lying within the cavity. All these connections are exceedingly delicate, and are so easily ruptured or dissected that for all purposes of dissection the organs in the hæmocœl lie freely in the cavity. The vena cava lies along the ventral wall of the body and through its dorsal wall are numerous openings, from twenty to seventy-five, allowing free passage to the blood from the hæmocœl into the vena cava. At least, as the blood in the vena cava moves toward the gills and through them to the heart, it is more justifiable to presume that the blood which enters the hæmocœl through numerous sinuses is drawn into the vena cava than that the flow occurs in the opposite direction. Some of the openings in the walls of the vena cava are large enough to admit the end of a probe 1 millimeter or more in diameter; others are so small as to be scarcely visible.

The cœlom is situated posteriorly to the hæmocœl, and is completely separated from it by a thin membranous wall. (Fig. 7.) This wall, which I have called the hæmocœlic membrane, is attached to the body wall dorsally along the line of the dorsal aponeurotic band. (Fig. 7, X.) At the sides of the body its edges are fastened to the inner surfaces of the shell muscles, passing downward and slightly backward. The ventral edge is attached to the ventral body wall along the line of junction of the body wall and the inner wall of the mantle fold.

The anterior face of the hæmocœlic membrane is rough, and is attached to the organs within the hæmocœl by a few strands of connective tissue. The posterior, cœlomic face of the membrane is smooth and covered by the cœlomic epithelium.

The attachments of the hæmocœlic membrane to the body walls are considerably in front of the posterior ends of the organs contained within the hæmocœl. Consequently it is pushed backward by the lobes of the liver, forming sack-like coverings for these. (Fig. 7, L, L.) It covers other organs in a manner to be described presently.

There is a considerable mechanical advantage in the dorsal attachment of the membrane, on account of the membrane forming sac-like coverings for the backwardly projecting viscera; it also serves to support these viscera. The support is rendered much more effectual by the attachment of the membrane to the body wall along the dorsal aponeurotic band, where the latter is itself attached to and supported by the shell, than it could be if the membrane were attached to the loose wall of the body back of the aponeurotic band.

The cœlom also is a cavity of very considerable extent. It occupies the entire posterior portion of the body, extending forward dorsally above the lobes of the liver and ventrally into the mantle fold. (Figs. 7 and 36.)

The cœlom is divided by an almost complete membranous partition into two chambers, the ventral of which contains the heart and its auricles and the pericardial glands, and is therefore called the pericardial chamber (Fig. 36), while the much larger dorsal and posterior chamber contains the gonad and stomach and second loop of the intestine, and is called the genital chamber. (Fig. 7.)

The membrane separating the two divisions of the cœlom was named by HUXLEY the pallio-visceral ligament. (Fig. 36, p. v. l.) It is attached posteriorly to the ventral body wall between the anterior and posterior ventral aponeurotic bands. It extends forward from here in a nearly horizontal plane, attached by its edges to the lateral walls of the body, and finally is attached anteriorly to the inner wall of the mantle fold, the anterior portion of the ligament forming the ventral or posterior walls of the anterior renal sacs.

When the pericardial chamber is opened the ventral body wall and the posterior portion of the pallio-visceral ligament will be found to be very closely applied to each other.

As a matter of fact the heart is within the pallio-visceral ligament, and not far from its center. The heart projects from the under side of the ligament, while the branchial veins, expanding near the heart to form the auricles, extend freely through the pericardial chamber to the points where they enter the wall of the mantle. Necessarily the branchial veins are also surrounded by extensions of the pallio-visceral ligament and covered by the cœlomic epithelium.

It has already been intimated that the pallio-visceral ligament is not quite complete. There are, in fact, three openings in it by which the pericardial and genital divisions of the cœlom are put into communication with each other. The smallest of these, and for a long time considered to be the only one, lies just back of the left side of the heart. (Fig. 36, p. v–p. ap.) It is an oval opening, the longer axis of which is directed posteriorly, and when undisturbed the edges of the opening lie against each other. The common septal artery passes through this opening into the genital division of the cœlom.

The other two openings through the pallio-visceral ligament lie at either side of and mostly anterior to the heart (Figs. 36, 38, and 39). These were first described by HUXLEY. They generally extend nearly to the middle line in front of the heart, leaving the heart suspended by a narrow ligament anteriorly. But their size and position is subject to considerable variation. In the specimen from which Fig. 36 was drawn the openings were widely separated anterior to the heart, and the left opening was at least twice as large as the right. In Figs. 38 and 39 the openings are seen to be much closer to each other in front of the heart, those shown in Fig. 39 being even less separated than those in Fig. 38. In Fig. 39, too, the left opening is very much larger than the right, while in Fig. 38 the left opening is only slightly larger than the right. The edges of both openings are attached to the dorsal and anterior side of the heart.

The dorsal aorta passes through the left opening, and following the posterior side of the hæmocœlic membrane for a short distance, penetrates this and runs forward in the hæmocœl above the œsophagus. (Fig. 7, Ao.)

From the posterior wall of each renal sac glandular appendages hang into the pericardial cavity. The secretory epithelium of these appendages is a portion of the cœlomic epithelium.

The genital division of the cœlom is much more extensive than the pericardial division. It is traversed by several ligaments which support and inclose viscera.

Principal of these is the genital ligament, within which the gonad is inclosed. This extends from the posterior wall of the cœlom, just above the origin of the siphuncle, to the pallio-visceral ligament just back of the heart. (Figs. 7, 38, and 39.) At its upper end this ligament forms a band a couple of centimeters in breadth, attached to the body wall obliquely, in a line directed downward from the right to the left side.

The gonad, being contained within this ligament, causes a great enlargement of its lower portion, and finally projects into the pallio-visceral ligament, causing the latter to appear to be attached to the ventral surface of the gonad. The posterior opening through the pallio-visceral ligament is just to the left of this attachment, the ligament being continued on the right side of the opening up over the surface of the gonad. In this way the common septal artery comes

to pass through the opening directly upon the surface of the gonad without at any point passing freely across the cœlom. The area of attachment of the gonad to the pallio-visceral ligament is quite wide.

At the aperture of the gonad the cœlomic epithelium is continued inside the cavity of the gonad. Thus the cavity of the ovary or of the testis is a nearly inclosed portion of the cœlom. The ova and follicle cells are developed from the cœlomic epithelium.

The genital ligament is raised from the upper or anterior surface of the gonad along two lines. (Figs. 38 and 39.) The right elevation forms a fold which incloses and suspends the second loop of the intestine. As the sides of the fold come together between the two parts of the loop a mesentery is formed binding these together. The anteriorly directed portion of the loop lies next the gonad. As this passes beyond the gonad anteriorly into the rectum it remains inclosed by the fold, which is here produced directly from the portion of the pallio-visceral ligament between the two anterior viscero-pericardial openings.

The second elevation of the genital ligament runs to the left side of the gonad and is produced from here to the posterior portion of the stomach as a distinct ligament.

The upper end of the genital ligament is sometimes found to be thickened and shrunken, appearing as if it contained muscular tissue and had contracted strongly.

Although the second loop of the intestine and the stomach appear to lie in the cœlom, they are in reality outside of it. They lie in pockets of the hæmocœlic membrane, which is only more closely applied to these organs than to the lobes of the liver. In the case of the stomach this is quite evident. With the intestine it is less so, but examination shows that the ligament surrounding the second loop of the intestine is continuous with the hæmocœlic membrane around and between the two branches of the loop.

In fact, these ligaments are composed of double lamellæ containing the viscera inside them, and covered outside by the cœlomic epithelium. They have something the same relation to the cœlom as the mesenteries of a vertebrate. The blood sinuses contained by them may be considered as portions of the hæmocœl. The ligament of the stomach is sometimes plainly hollow, and filled with coagulated blood.

The right, functional genital duct, and the left, non-functional genital duct, are both contained in the pallio-visceral ligament, their inner borders following closely the right and left anterior viscero-pericardial openings, respectively.

The pallio-visceral and genital ligaments are, like the intestinal and gastric ligaments, composed of double lamellæ, containing the organs within them. The ova and their follicle cells and the pericardial glands are the only organs literally lying in the cœlom.

The cœlom is lined with an epithelium composed of flattened polygonal cells. Upon the anterior wall of the cœlom some of the cells, according to HALLER, can be distinguished by their taking a more intense stain from the ordinary cœlomic epithelial cells.

The renal sacs should also be considered as portions of the cœlom, or secondary body cavity. Their complete separation from the main portion of the cœlom is explained by some as a result of the displacement of the reno-pericardial openings from the inside of the anterior renal sacs to the surface of the body at one side of the external openings of the renal sacs. According to this view, Nautilus originally possessed but one pair of renal sacs—the anterior, beside the apertures of which the pericardial pores are found—while the posterior sacs have been derived by a division of the anterior sacs, and a separation of the two pairs of sacs thus formed. In somewhat the same manner and at the same time the anterior gills and their vessels have divided to form the posterior gills and their vessels.

The explanation is certainly far-fetched, and can not be received with too much caution. Other explanations are possible, and it is quite probable that some other will be found in future years which will show that this one is entirely erroneous in its conceptions.

It is at least as easy to suppose that the posterior gills and renal sacs have been developed independently of the corresponding anterior organs and that similarity of function has brought about similarity of structure, just as it has in several instances in adult and embryonic organs of widely separated groups.

We have still a portion of the cœlom to consider—that portion which stretches out in the siphuncle. Upon the right side of the attachment of the genital ligament to the body wall is an opening which leads into a cavity continued to the end of the siphuncle. The structure of the siphuncle has been described in some detail by HALLER, and its consideration seems to occur most logically at this point.

The genital ligament lies directly over the opening from the cœlom into the siphuncle, and makes the opening quite difficult to find sometimes. However, it is always single and upon the right side of the ligament. The cavity of the siphuncle is divided into three tubular portions, one of which is dorsal and two ventral. The cavities are lined by a continuation of the cœlomic epithelium, which is here composed of low cubical cells. The siphuncle is narrowed where it passes through each septum. At these points the siphuncular cavities also are narrowed, but not occluded.

The common septal artery passes along the genital ligament to the posterior portion of the body wall near the base of the siphuncle. It here divides into a right and a left branch, from one of which, sometimes the right and sometimes the left, the siphuncular artery is given off. (Text-fig. 11, p. 186.) This extends through the entire length of the siphuncle, finally ending openly.

The spaces intervening between the cavities of the siphuncle and the siphuncular artery are filled by a loose reticular connective tissue, the spaces of which contain venous blood, and are in communication through the walls of the body and the various ligaments crossing the cœlom with the cavity of the hæmocœl.

HALLER describes a very curious structure of the epithelium covering the siphuncle externally. According to his description, the basement membrane is thrown into fine longitudinal folds. The epithelium does not cover the edges of the folds, these being in direct contact with the inner wall of the siphon. The epithelium covering the grooves between the edges of the folds forms a continuous protoplasmic layer, in which cell boundaries are not distinguishable. This layer shows striations perpendicular to its surface. It stains intensely with hæmatoxylin. The widely separated nuclei are disk-shaped and lie in the upper or outer portion of the layer.

The tissues of the base of the siphon seem always to be continued into the genital ligament, forming a small rounded nodular eminence close to its attachment. In one case, shown in Fig. 38, a cord of tissue extends from this eminence along the ligament of the stomach. What this is I have not yet been able to determine.

There have been several theories advanced as to the function of the siphuncle. Most consider that it is in some way connected with hydrostatic properties of the shell and attempt to explain the rising and sinking of the animal as in some way dependent upon the action of the siphuncle. Reeve's theory of its action is very interesting, and a paragraph from him is worth quoting.

"The following appears to us to be the manner in which the Nautilus constructs its shell. The animal in its embryo formation deposits a simple hollow shell, out of which it necessarily advances as it increases in bulk; and in order to assist its specific gravity at the bottom of the ocean the vacated portion of the shell is chambered in by the secretion of transverse septa, the animal having first taken the precaution to secure a strong tubiform membrane to the inner wall in order to adjust its position (a consideration of the habits of this pelagic mollusk will show the necessity for this membrane). As the soft parts increase in bulk, the muscular girdle which binds them to the shell would naturally be forced from any adhesion, but from its being furnished with a certain degree of elasticity it advances by a series of periodical slips, the suddenness of which is undoubtedly counteracted by the attachment of the central membrane. The growth of the shell then proceeds in a circular direction, and serves to buoy up its inhabitant in the water by having the vacated portion chambered in to meet its specific gravity. The geometrical increase of it arises simply thus: The natural position of the Nautilus, like other cephalopods, is with its head downward, the shell being consequently above; and the periodical slip of the belt of adhesion most probably takes place when the animal is in this supine position. It lets itself down, and round and round, as it were, upon its axis by the limited extension of

this membranous pulley: the operation ceases when it arrives at maturity, and the membrane, being no longer wanted, probably decays. Such is the manner in which our observations lead us to suppose the Nautilus grows; the chambers have certainly no communication with the surrounding fluid. The camerated portion of the shell of Nautilus is evidently a simple, mechanical construction (though planned by the wisest intelligence) to assist the specific gravity of its inhabitant whilst under the different mutations of pressure that it is liable to at different periods of growth in its passage through the element; and it is, moreover, a contrivance that could only be effected by the aid of this adjusting membrane upon the simple geometry of motion above described."

The siphuncle is, therefore, according to this theory, a mechanical contrivance regulating the form of the shell and partially supporting the body during the formation of new septa.

These theories as to the function of the siphuncle have been gradually discarded as study revealed more of the structure of fossil cephalopod shells and as our morphological conceptions matured. Our present knowledge indicates that the siphuncle is a vestigial structure, having no immediate connection with the ability of the Nautilus to rise or sink. This has been proven by Willey in a series of direct experiments.

In a communication from New Guinea, in September, 1895, Willey (1896, 1) gives an account of his experiments, as follows:

"Being desirous of obtaining, if possible, experimental evidence as to the physiological significance of the siphuncle in the Pearly Nautilus, I have made several successful attempts to cut the siphuncle without otherwise injuring the animal. The evidence supplied by the experiment can not be regarded as conclusive, on account of the altered conditions of depth and temperature to which the Nautilus is exposed by being brought up to the surface, but it may be well to consider what the results indicate.

"At first I sawed through the shell into one of the chambers, and then cut the siphuncle. This method has the disadvantages of injuriously affecting the efficiency of the chambers and of causing a more or less considerable loss of blood to the animal. The latter will, however, live in confinement about as long as untouched individuals.

"A young Nautilus operated upon in this way on June 26 was placed in the sea in shallow water for its movements to be watched. It sank slowly to the bottom, and then for a long time made active revolving motions about the vertical axis, but scarcely made any progressive movements.

"On another occasion (July 10), after several trials, I found that the best way of performing the operation is to saw through the shell in the neighborhood of the posterior portion of the body of the animal, over the cardiac region, and not to tamper with the chambers. If the shell be held mouth downward this point lies approximately in the same vertical and transverse plane with the points where the free margin of the mouth of the shell merges into the umbilicus. When a large enough hole has been made in the shell to admit the scissors, the shell being still held upside down, the ventral visceral portion of the body usually detaches itself from the shell, or can be readily caused to do so, and, sinking inward, exposes the root of the siphuncle, which can then be severed. On returning the shell to its normal position the body immediately resumes its normal intimate contact with the wall of the cavity in which it lives, and the pressure so exerted prevents any extensive loss of blood. Under these conditions the operation does not, as a rule, appear to affect the vitality of the animal in any degree.

"A Nautilus[1] which was treated in this way on July 10, on being placed in the sea, swam about very vigorously for some time in the middle stratum of water, but most of the time at a little distance from the bottom. On September 13 I operated on four more individuals taken in Talli Bay, on the north coast of the Gazelle peninsula. One of them showed a tendency to sink to the bottom, which it always performed very gradually. In this one I had accidentally punctured the mantle over the heart. The others remained floating and swimming about on the

[1] It should perhaps be mentioned that in this particular individual I accidentally cut into the last chamber and plugged the opening with wax.

surface during the whole time of observation. They did not go far in one steady direction, but tended to go in circles, as in fact did another one whose siphuncle was uncut. If one of the individuals floating at the surface was forced down to the bottom with a hand net, it would slowly rise to the surface again. This also often happens with a Nautilus that has not been operated on.

"The results indicated by the above experiments, which, it may be added, are worth repeating, may be summarized as follows:

"The cutting of the siphuncle (α) does not temporarily affect the vitality of the animal; (β) does not prevent it from making movements of translation;[1] (γ) does not prevent it from floating at the surface; (δ) does not prevent it from sinking to the bottom.

"It still remains to be ascertained whether a Nautilus whose siphuncle has been cut, having sunk to the bottom of the sea in shallow water, will undertake a journey to the surface. My experiment of July 10 would seem to indicate that this might be expected to occur.

"The above experiments do not appear to oppose the view which I expressed in a former communication—that the siphuncle of *Nautilus pompilius* is, in some measure, of the nature of a vestigial structure.

"It might, indeed, be legitimate to suppose, on the principle of the correlation of organs, that in the Nautiloidea the course of evolution has led to a reduction of the siphuncle pari passu with an increase in the efficiency of the chambers as hydrostatic organs."

REPRODUCTIVE SYSTEM.

The first specimens of Nautilus to be obtained were females. After Van der Hoeven had received a male specimen for many years again only females were obtained by naturalists, until the opinion came to be held that the females of Nautilus must greatly exceed the males in number. In recent years, however, especially in the collections made by Willey and in the Menage collection, the ratio has been inverted, the males being about three times as numerous as the females.

Willey states, in Natural Science for June, 1895, that out of sixty-seven individuals, fifty-one were male and sixteen female. In the Menage collection out of sixty-six specimens fifty were males and sixteen females. These numbers do not justify us in yet stating that there is a difference in the numbers of the sexes. The males may be much the more active in their habits at all times; the females may also retire into hiding during oviposition, and may possibly remain watching over their eggs until the young hatch, so that during a large portion of the year they are less liable to capture than are the males.

REPRODUCTIVE ORGANS OF THE MALE. (Fig. 38.)

The testis is a large oval organ situated in the extreme posterior and upper part of the cœlom, directly beneath the origin of the siphuncle (Figs. 7 and 38). Its posterior face is smoothly convex, fitting the concavity of the septum. The anterior surface, however, is flattened and shows irregular facets caused by pressure against other viscera, the stomach and liver upon the left, the intestine and the accessory reproductive gland upon the right.

The testis is covered by an extremely thin, delicate tunic, through which may be seen the indistinctly demarcated lobes of the organ. Over the posterior surface the tunic is closely attached to the tissues within, connective tissue strands extending from the tunic between the lobes. Anteriorly the tunic is entirely free from the mass of inclosed tissue, forming a sac which opens through a slit at the end of a short funnel-shaped production of the tunic (Fig. 38, T. ap.).

The testis does not lie free within the cœlom, but is attached to its walls by several ligaments. The case is summed up shortly by saying that the testis is contained within a ligament which has been invaginated into itself at one point to form the cavity of the testis. The point of invagination corresponds to the opening of the testis. This genital ligament (Fig. 38, g. l.), as

[1] In speaking above of progressive movements I mean, of course, in the usual backward direction.

we may term it, extends from the anterior portion of the pallio-visceral ligament upward and backward to the body wall just above the origin of the siphon. Thus the testis, a specialized portion of the wall of the genital ligament, comes to be slung by its upper and lower ends.

The upper attachment of the testis is effected by a membranous ligament about 2 centimeters broad extending from the anterior face of the testis, 1 centimeter below the upper end of the organ, to the body wall just above the origin of the siphuncle. The attachment of the ligament to the body wall is diagonal, passing across the body from right to left, and also somewhat downward. In this way the opening of the siphuncle into the cœlom comes to lie upon the right side of the genital ligament. Tissues of the base of the siphuncle seem to extend into the genital ligament, so that there is always a bulge in the ligament at this point.

Being continued on the testis the ligament separates into two portions which run downward over the anterior surface of the organ. These are merely elevations of the tunic of the testis. One passes over the surface of the testis to the left, leaving it at its edge and forming the suspensory ligament of the stomach (gas. l.). The other passes downward, first to the right, then slightly to the left until it reaches the anterior edge of the testis, where it is continued as a dorsal fold of the pallio-visceral ligament over the heart. This forms the suspensory ligament of the intestine and rectum (I. l.). It is attached first to the portion of the intestine leading forward to the rectum: enveloping this it forms the mesentery between the branches of the intestine, and then envelops the backwardly directed branch of the intestine. It must be remembered that all these ligaments are double folds, in some of which the walls covered externally by the cœlomic epithelium are closely pressed together, while in others organs or portions of organs, such as the intestine, stomach, etc., are pushed between the walls.

The posterior side of the anterior end of the testis is broadly attached to the pallio-visceral ligament. This attachment is immediately posterior to the heart. As the heart is surrounded and slung by the same ligament, the ventral surface of the testis and the dorsal surface of the heart come into very close contact.

The funnel-shaped tube through which the cavity of the testis is placed in communication with the vas deferens is formed by a thickened portion of its tunic about 4 millimeters in length and 3 millimeters in breadth at the tip. The tip is sometimes slightly expanded. The opening in it is slit-like.

The surface of the testis inside the tunic appears somewhat granular. Kerr, describing the structure of the testis of an immature individual, says that "the aperture of the organ is seen to lead into a vestibule, into which open several ducts. Each of these, traced inward, divides up into numerous tubules which end blindly and are aggregated into distinct lobes and lobules. Vestibule and tubes are lined by epithelium continuous with that of the general cœlom."

The measurements of the testis of one specimen were: Length, 41 millimeters; breadth, 36 millimeters; thickness, 24 millimeters. At the right of the testis, and extending anterior to it, is a large accessory gland, which is formed around the convoluted vas deferens (ac. gl.). The accessory gland lies within the pallio-visceral ligament upon the right of the right anterior viscero-pericardial aperture. Posteriorly it projects freely, carrying the dorsal wall of the ligament over its surface. Lying in the pallio-visceral ligament in this way, the accessory gland is very closely attached by the ligament to the anterior portion of the testis. On account of the elevation of the posterior portion of the accessory gland above the pallio-visceral ligament, the portion of the ligament uniting this portion of the gland and the testis appears at first sight like a separate ligament, but is in reality only a fold of the pallio-visceral ligament (y).

The accessory gland projects entirely dorsally from the pallio-visceral ligament. It forms an oval organ, smaller anteriorly than posteriorly, the measurements of which are: Length, 27 millimeters; breadth, 20 millimeters; thickness, 15 millimeters. Its tissues are much firmer than those of the testis.

When in its natural position the accessory gland lies against the right anterior face of the testis, the loop of the intestine being held between the upper portion of the gland and the testis. In Fig. 38 the gland is turned outward so as to show the face which is ordinarily pressed against

the testis. Near the lower edge of this face is a funicular depression leading into the vas deferens (v. d.). The funnel of the testis fits snugly within this opening, so that, as KERR remarks, "though the cavities of the testis and of the vas deferens open quite independently into the celom, they are at least during sexual maturity functionally continuous with one another."

The vas deferens winds about through the accessory gland, finally passing into a tough-walled sac which occupies most of the anterior end of the gland. The accessory gland "is composed of numerous cæcal tubular outgrowths from the duct itself" (KERR). The proximal end of the vas deferens is exceedingly thin walled and small, being on this account very difficult to trace (v. d^1.). It is rather less than a millimeter in diameter in this portion, but from the point v. d^2. its walls are very thick, the whole tube being about three times its former thickness, while the lumen remains about the same size as before. The thickened portion of the vas deferens opens into the right side of the tough-walled sac (S. V.), 12 millimeters long, occupying the anterior portion of the gland, which we may call the seminal vesicle. The seminal vesicle is easily distinguished without dissection of the gland.

The opening of the seminal vesicle is just in front of the junction of the mantle with the body wall. The remaining parts of the genital duct can be traced from the mantle cavity. They cause projections of the body wall so that their shape and course can be followed without dissection, but they are easily dissected by removing the integument.

The seminal vesicle opens by a very small orifice into a thick-walled tube which turns obliquely to the left, toward the center of the body. It quickly enlarges into a good-sized sac, 11 millimeters long, the spermatophore sac (Sp. s.). This is incompletely divided into two parts by a longitudinal septum extending into it from the posterior wall, upon the left side of the opening into the sac, nearly to the anterior end (Sep.). Coiled spermatophores are frequently found in the sac, bent around the anterior edge of the septum into a U-shaped mass. The anterior edge of the septum is frequently arcuate, so that the opening from one side to the other of the spermatophore sac is 3 or 4 millimeters in diameter and nearly round.

From the spermatophore sac a short thick-walled tube leads forward to the penis.

The penis is a tubular organ 4 to 5 millimeters in diameter, lying in the middle of the ventral surface of the body, its axis corresponding with the longitudinal axis of the body (Fig. 3, P.).

The walls of the penis are thick and muscular. Its tip usually projects freely from the body wall, and bears a small aperture (P. ap.). This leads into a cavity which divides almost immediately into a right and left portion. The right portion connects with the cavity of the spermatophore sac (P. r.). The wall of the cavity is thrown into longitudinal folds, which, however, are only found in the contracted condition of the organ. When a spermatophore is in the tube the walls are smooth.

A fleshy tube is prolonged posteriorly from the left side of the penis obliquely outward and backward for 8 to 15 millimeters (P. l.). This ends blindly with a slight enlargement. The left-hand cavity of the penis is continued into this tube. Its walls are folded like those of the right cavity of the penis, but not so strongly. In the enlarged portion the cavity also is larger. Near the end of the tube I have found a very minute, yet distinct opening upon the right side, leading into a short narrow sac parallel to the posterior portion of the larger tube. This sac evidently corresponds to the spermatophore sac of the opposite side. In one of the specimens examined the left portion of the penis was entirely lacking. There seems to be considerable variability in the extent of its development.

It is in the vas deferens that the spermatophores are formed. Each spermatophore consists of a thick-walled tube of chitin, one millimeter in diameter and five to ten centimeters in length. The lumen of the tube is very small and is filled with spermatozoa. I have several times found a spermatophore irregularly coiled in the seminal vesicle, or rather one end of it was coiled up here. The other end extended back in the vas deferens as far as the end or a trifle beyond the end of the thick-walled portion. The wall of the spermatophore seemed to be fully formed until near the posterior end. For the last centimeter the wall became gradually thinner and paler, finally disappearing.

In a less than half-grown male, the testis formed an elongate organ situated in the genital ligament immediately back of the heart. It measured 13 millimeters in length by 3 millimeters in breadth.

In this specimen the two halves of the penis were exactly alike: the right half could not be traced into any communication with the vas deferens. It seemed to end blindly in the body wall. I was not able to find any external opening of the vas deferens. The spermatophore sac existed as a small tubular diverticulum of the right half of the penis, just as I have found it in the left half of the penis of the adult.

Upon the left side of the lower end of the testis, within the pallio-visceral ligament, is a curious sac-like organ (pyr. s.). The blind enlarged end of the sac is close to the left side of the heart. Its position varies somewhat in different individuals, being in some close—even dorsal—to the heart, in others quite to the left of the heart, depending upon the shape and extent of the left anterior viscero-pericardial aperture. The neck of the sac is elongated, forming a narrow tube which opens into the mantle cavity through the pore already noticed upon the left side of the body at the line of junction of the mantle fold with the body wall (pyr. ap.). The sac is much flattened, causing a scarcely noticeable thickening of the pallio-visceral ligament. Its walls are thin and soft and are folded upon the inner side.

REPRODUCTIVE ORGANS OF THE FEMALE. (FIG. 39.)

The ovary (Ov.) occupies the same position as the testis, but is somewhat smaller than the fully developed testis and more rounded, forming a body 35 millimeters in length and 25 millimeters in breadth. It is suspended by ligaments in the same manner as the testis, the course of the ligament of the stomach, however, being slightly different. The fold of which the gastric ligament is a continuation extends from the upper end to the left side of the testis; it extends to the lower end of the ovary and the gastric ligament arises from its middle (gas. l.).

The aperture of the ovary is upon a small protuberance of the wall upon the right side of the lower end of the ovary (Ov. ap.). Anatomically the ovary opens into the cœlom; actually the aperture of the ovary is closely applied to the inner opening of the genital duct, so that the duct is functionally continuous from the ovary.

The posterior portion of the inside of the ovary is entirely covered by egg-follicles in various stages of development. The mature follicles are about 15 millimeters in length by 10 to 12 millimeters in diameter, each containing a single yolk-laden ovum. The older follicles are suspended from the wall of the ovary by slender, membranous stalks, which are usually simple, but, according to KERR, occasionally branch. The epithelium of the inner surface of the follicle, which is applied to the ovum, is continuous over the outside of the follicle with the cœlomic epithelium lining the ovary. The older follicles at least possess a three-lipped aperture at the end opposite the stalk, through which the ovum escapes. Follicles from which the ova have been shed are ruptured half way to their bases. KERR finds that between the bases of the follicles the lining epithelium of the ovary "thickens up into syncytial masses of protoplasm containing large round nuclei, each with a large deeply staining nucleolus, around which the protoplasm tends to segregate off more or less distinctly. The primitive ovum develops within such a heap, the nucleus increasing in size and assuming more and more the character of a 'germinal vesicle,' and the protoplasm first becoming more distinctly aggregated round the nucleus and marked off from the surrounding protoplasm and then increasing rapidly in size. As the ovum increases in size, the substance of the ovarian wall grows up round it to form the follicle, while the syncytium accompanying the ovum apparently gives rise to the lining cells of the follicle." In the young follicle the surface next the ovum is smooth, but as the ovum and follicle increase in size the inner surface of the latter becomes raised into anastomosing ridges, which penetrate deeply into the ovum. WILLEY found that the meshes formed by the ridges are much wider in submature than in the less mature ova, and would presumably be found to flatten out in completely ripe ova.

At the end of the ovum next the opening of the follicle is an area of protoplasm free from

yolk, in which the large nucleus is located. Over this region of the ovum the ridges are absent, while those which lie at the margin of the area form incomplete meshes open on the side toward the egg nucleus.

The clear polar area of the ovum is approximately triangular, "and from each of the corners of the triangle what may be called a line of weakness occurs in the follicular wall, bound on either side by incomplete meshes." (WILLEY.)

"The yolk is viscous and glutinous, and posseses a translucent brownish tinge. The nearly ripe ova rupture with the utmost facility." (WILLEY.)

"In the female the ramifications of the genital artery pass up on to the surface of the individual ova, and form a kind of capillary system, the finer branches following, but not always confined to, the reticular markings formed by the ridges of the follicular membrane which project into the yolk. The arteries which traverse the surface of the ova give off minute branches which pass inward, as it were, into the depths of the follicular ridges; and these deep-lying vessels anastomose with one another, while the superficial branches appear, as a rule, not to form anastomoses. It may be added that the impression of anastomoses is much more readily conveyed by examination with a hand-lens than it is by the use of the compound microscope." (WILLEY.)

The epithelium about the mouth of the ovary is composed of columnar cells bearing long cilia; farther within the ovary the epithelium gradually passes from columnar to cubical cells.

KEFERSTEIN[1] and LANKESTER and BOURNE have figured a large albumen gland attached to the ovary near its mouth. This has the shape of a large sac, of about the same volume as the ovary, lying upon the right side of the latter. BOURNE's diagram may be simply a copy of KEFERSTEIN's figure; nothing in the text gives any information as to whether the authors had seen the albuminous gland in their own dissections or not.

No other authors describe such a structure. I have myself been unable to find any traces of it in several female Nautili I have dissected. In several cases I have found the ovary filled with a hard, solid, brown coagulum, probably secreted by the walls of the ovary. As in one of the specimens dissected all the large ova had just been shed, this specimen was certainly sexually mature. If the gland is only formed periodically, we should certainly expect to find it in such a specimen. It is probable that the ovary of KEFERSTEIN's specimen was abnormal and possessed a hernia-like protrusion.

HALLER has previously noted the absence of such a structure as KEFERSTEIN figures and has come to the conclusion that the ovary of KEFERSTEIN's specimen was in a pathological condition. Some of HALLER's specimens also had the ovary filled with the secretion already mentioned, of which he speaks as follows: "It has the same appearance as the egg-yolk, staining similarly with certain stains (carmine) or remaining unstained with others (hæmatoxylin). This yolk is the same as that in the eggs, from which I distinguish it by the name of the free yolk, and is used by being taken into the eggs. At first I thought that it might possibly be composed of an accumulation of yolk cells, but nuclei could not be discovered in it by means of the various nuclear stains used, it being a homogeneous mass—a secretion from cells. I then sought for a glandular differentiation, which, as processes of the ovarial wall, might project inward and function in the secretion of the free yolk. However, there was no such structure present, and nothing remains but to hold the portions of the wall of the ovary which are free from eggs responsible for the production of this yolk. It is probably the right lateral side of the ovary, upon which I have never found eggs, which performs this secretion.

"The cells of this portion of the ovarial wall would not, then, function as germinal epithelium, but would furnish a sort of nutrient material, not by giving off cells, but instead, pure yolk-stuff. The histological structure of that portion of the ovarial wall seems to me to indicate this. I found there a layer of cells, the elements of which were in all things very much like the follicle cells; it is composed of high cylindrical elements, which are completely filled with yolk granules. In places, where the cells had been separated from each other by shrinkage caused by alcohol, one could observe numerous protoplasmic connections between them. The cell nuclei are, like

[1] BRONN's Classen und Ordnungen.

those of the follicle cells, very irregular, and indistinctly bounded. It is characteristic that the chromatin is gathered in a coil in the center of the nucleus."

The mouth of the ovary is usually pressed closely against the inner opening of the oviduct, so that the two are functionally continuous. The oviduct lies between the walls of the pallio-visceral ligament and is thus closely attached to the ovary.

HALLER mentions that in several cases the mouth of the ovary was not in contact with the inner opening of the oviduct, and so opened into the cœlom.

The posterior half of the oviduct is thin-walled and broad, much like a flattened sac. Its walls seem to be glandular, and are quite smooth. The internal opening of the oviduct is often much larger than I have shown it in figure 39, which, however, is an accurate representation of the condition of the specimen from which it was drawn.

The oviduct leads forward and to the right side of the body. About 20 millimeters from its beginning it becomes much narrower, and its walls become thick and raised internally into annular ridges. The width of the posterior portion of the oviduct is 17 millimeters, while that of the anterior portion is 12 millimeters. Shortly anterior to the commencement of the thickening the oviduct reaches the surface of the body at the line of junction of the mantle and body wall, from which it projects as a large rounded eminence from 7 to 12 millimeters. The projecting portion of the oviduct is ridged externally and presents an appearance which suggests that a portion of the oviduct has been evaginated. The external aperture of the oviduct forms a transverse slit at the end of the projecting portion. The distal portion of the oviduct is evidently glandular and suggests strongly the glandular distal portion of the oviduct of several Dibranchiata.

Upon the left side of the heart, in the female as well as in the male Nautilus, is a pyriform sac lying within the pallio-visceral ligament, and in all respects like the pyriform sac of the male. The position of its aperture, upon the left side of the body, corresponds to that of the functional oviduct upon the right side.

The nidamental gland has been described in the section devoted to the pallial complex. We have as yet no proof of the function of this gland. Analogy, however, guides us in giving it this designation.

The ovary of a half-grown female was a small elongated body, 18 millimeters in length by 6 millimeters in width. It was situated within the genital ligament close to the heart, extending along about one-third of the genital ligament. The intestine and stomach were attached directly to the genital ligament above the ovary. The ovary evidently grows backward and upward in the ligament so that when it is mature the ligaments of the intestine and stomach are attached to its surface.

The ovary opened into the cœlom just back of the heart, and so at a considerable distance from the inner opening of the oviduct. The functional oviduct was scarcely different from the pyriform sac at this time. The walls of the portion near the external aperture, which later became rugose and greatly thickened, were in this case only slightly ridged and scarcely thickened at all. The oviduct papilla projected very little into the mantle cavity, and was not at all pleated.

The genital arteries were discovered by means of injections by WILLEY; since then I have been able to trace the arteries in uninjected specimens. They are three in number and arise directly from the heart. They arise close together in a row from the posterior portion of the dorsal surface of the heart. (Text-fig. 10, p. 182.)

The genital artery is the middle one of the three, and its main trunk passes over the dorsal surface of the gonad.

The right-hand artery forms the gonaducal artery and goes to the functional genital duct. The left-hand artery is that of pyriform sac, being distributed mainly to this. Upon morphological grounds it should be considered to be the left gonaducal artery.

Both the gonaducal artery and the artery of the pyriform sac "give off a branch which passes into the perigonadial membrane." (WILLEY.)

The further ramifications of the genital artery of the female have already been mentioned.

The pyriform sac was first described by OWEN in a female specimen, and given this name by him. OWEN did not discover the opening of the sac to the exterior, and was led by its position

to believe that the pyriform sac was a vestige of an organ which, at some former period in the history of the species, had formed a communication between the venous sinus and systemic ventricle, independent of the branchial circulation.

KEFERSTEIN discovered the opening of the sac to the exterior.

Many years after LANKESTER and BOURNE first discovered the presence of the organ in the male Nautilus, and showed that it has the same structure and position in both sexes. These authors called attention to the exactly similar position of the genital duct upon the right side of the body and the pyriform sac and its duct upon the left side, and suggested that the latter is the left genital duct in a vestigial condition. The similarity of the functional and non-functional genital ducts is evident in the female, in which the aperture of the oviduct occupies a position upon the right side of the body corresponding closely to the position of the aperture of the pyriform sac upon the left side.

Later observers have added still further evidence in favor of the homology of the pyriform sac with the functional genital duct. KERR finds that in a very young female the inner part of the genital duct has exactly the appearance of the pyriform sac in the adult, the rudiment of the gonad being quite distinct and apparently median and unpaired.

The first part of the statement adds great strength to the view which considers the pyriform sac to be a left genital duct. The latter part of the statement answers the question left open by LANKESTER and BOURNE—whether the pyriform sac represented only the left genital duct, or the genital duct and the gonad of the same side.

KERR also remarks that "in the young animal, the NEEDHAM's sac (spermatophore sac) being not yet expanded, the form and size of the right portion of the apparatus (penis) are in almost exactly the same condition as is the left in the adult."

The discovery by WILLEY of the symmetrical arrangement of the arteries of the gonad and genital duct and the pyriform sac entirely justifies the conclusion that the latter two are homologues. The fact that from both the gonaducal artery and the artery of the pyriform sac a branch is sent to the ovarial membrane forms a strong piece of evidence that these are equivalent arteries, and also indicates that the pyriform sac corresponds to the genital duct alone, and not to an entire left reproductive apparatus.

It is then about as well established as anatomical evidence alone can establish such facts, that Nautilus possesses a single unpaired, median gonad, and a pair of gonaducts; one of these, the right, is functional and highly developed; the other, the left, exists in the condition of a sac opening to the exterior, and no longer functions as a gonaduct.

The spermatophore is formed in the vas deferens. Apparently the formation takes place in the thickened portion of the vas deferens, as in the specimens I have dissected the spermatophore ended at about the commencement of this portion of the tube—either a little distal or proximal to this point. As the spermatophore is formed it is moved forward and finally it debouches in the seminal vesicle, where it is irregularly and loosely coiled. From here it passes into the spermatophore sac where I have always found the coil occupying the two sacs, bent around the longitudinal septum in the form of a U. I have next found the spermatophore occupying the tip of the penis, causing a great distention of this organ. The spermatophore is now tightly coiled into an ovoid mass, about 8 millimeters in length by 5 millimeters in diameter.

From the penis the spermataphore is in some way passed to the superior labial tentacles. I have several times found a single spermatophore tightly held by the upper tentacles of either the right or left superior labial group. But when among the labial tentacles the spermatophore is always surrounded by a closed, tough sac of a chitinous material. The sac with the spermatophore inside it forms a roughly spherical mass, averaging 13 millimeters in diameter. The spermatophore is loosely coiled and lies free inside the sac.

We find here two questions to be answered. The first is, How and where is the sac formed around spermatophore? One would naturally expect such a structure to be formed either in the spermatophore sac or the penis. But I have never found a sac around a spermatophore contained in the spermatophore sac or in the penis—only around those held among the labial tentacles; but around each of these. Possibly the secretion of VAN DER HOEVEN's organ forms the sac

The second question is, How are the spermatophores conveyed from the penis to the labial tentacles? The latter are widely removed from the penis, beside being inside the cephalic sheath. One course has suggested itself as possible. The spermatophore being discharged from the penis may be carried through the funnel to its tip. It will be remembered that the tip of the funnel lies in a groove on the ventral side of the cephalic sheath, and that the cephalic sheath is deeply notched just above the tip of the funnel, so that the latter projects slightly beyond the posterior edge of the notch. It may be that when the spermatophore reaches the tip of the funnel it is grasped by some of the tentacles, either digital or labial, and conveyed by them to its final position among the dorsal tentacles of the superior labial group. VAN DER HOEVEN'S organ lies just back of the ventral notch, and if it plays any part in the formation of the sac of the spermatophore, the spermatophore may remain for a time in the depression into which the organ opens. Possibly the tip of the funnel may be turned upward and the spermatophore forced inside the cephalic sheath by a jet of water. I do not wish this suggestion to be interpreted as my theory of how the spermatophore travels to the labial tentacles from the penis. It is only a suggestion, which may be far from the truth, but which, arising from the anatomical relations of the various parts concerned, I think it can do no harm to publish. Such a transfer would, however, involve an active coordination of different parts which is quite unique among Mollusca in processes accessory to fertilization.

It is noticeable that the spermatophores are not found in any connection with the spadix, which has been frequently considered analogous to the hectocotylized arm of the Dibranchiata. What the rôle of this organ is, is as much a mystery as ever. Its large size and complicated structure indicate that its function is important, and that there may be several minor processes which cooperate to perform the function for which the structure has been developed.

It has been suggested that the spadix is thrust into the mantle cavity of the female during copulation. Evidently this is the idea of VAYSSIERE, who suggests that the function of the large, firm, and pointed first cirrus of the spadix is to facilitate the introduction of the spadix into the mantle chamber of the female. The fourth cirrus on account of its small size and position may have little share in the functions of the spadix. VAYSSIERE considers that the active parts in transferring the spermatophore to the female are the second and third cirri. The latter is especially fitted for this, and he suggests that the spermatozoa are carried in the crypts after the destruction of their protective envelopes, and being ejected from these by a momentary turgescence of the tongues are deposited at the orifice of the oviduct.

The second and third cirri of the spadix are evidently capable of considerable extension, and are probably very active portions of the organ in doing whatever work for which it is designed, but there is scarcely any reason to suppose that the spadix, and especially the third cirrus thereof, act as VAYSSIERE has suggested. For we have already noticed that the female frequently carries a spermatophore coiled upon the surface of the lamellated region inside the edges of the ventral notch of the cephalic sheath. It seems probable that the spermatophore is transferred from the male direct to this place. It is quite remarkable that the sac which surrounds the spermatophore when among the tentacles of the male has already been lost, the spermatophore lying naked, coiled upon the surface of the receiving apparatus of the female.

As the spermatophore is still intact, the third cirrus of the spadix certainly has no such use as VAYSSIERE suggests. Indeed, it seems strange that so complicated an organ as the spadix should have been required for so simple an operation as placing the spermatophore inside the cephalic sheath of the female. The female Loligo carries spermatophores upon the buccal membrane, but in the case of *Loligo pealii* there is not the slightest trace of a hectocotylized arm or other specialized apparatus for depositing the spermatophores upon the buccal membrane of the female. It seems quite possible that the spadix of Nautilus may not function at all in the transfer, it being entirely accomplished by the superior labial tentacles. Or possibly the spadix serves to push aside the tentacles of the female and allow of the deposition of the spermatophore within them.

The development of the spadix in the adult male alone indicates that it is an accessory reproductive organ, but of its function we are absolutely ignorant.

How is the protective envelope of the spermatophore destroyed? There is no evidence as yet to indicate whether this is done by the male, or if the envelope is intact when the female receives the spermatophore. In the latter case the envelope may be destroyed by the action of the secretion of the receiving lamellae, or more actively, by the tentacles after being received, or by the handling it may undergo during the transfer from the male to the female.

I do not know of anyone who has ever found spermatophores upon any other region of the body of the female Nautilus than the one described.

Another question arises. How long is the spermatophore retained among the tentacles of the male or upon the receiving apparatus of the female? I am inclined to think that the spermatophore may be retained for a variable but not usually long time among the tentacles of the male. I have several times found a spermatophore in the process of formation within the vas deferens, and another coiled up in the spermatophore sac. In another case the spermatophore sac contained one spermatophore while another occupied the tip of the penis. The comparatively immense size of the fully developed testis indicates that it can produce an enormous number of spermatozoa in a very short time. The accessory gland, too, is of a size which shows that it can very quickly produce the secretion required for the tubular walls of a spermatophore. Spermatophore after spermatophore is probably produced in rapid succession throughout the breeding season; or if this is continuous, the year round, as WILLEY suggests, throughout the period of sexual activity. It seems probable that the males carry a spermatophore among the tentacles only till it can be transferred to a female. Then another spermatophore takes the place of the first, and so on. The female may carry the spermatophore for a longer time. Apparently a single one is carried at any time.

THE CIRCULATION.

ARTERIAL CIRCULATION.

The figures of the arterial circulation have been made partly from my own dissections and partly from the published figures and descriptions of WILLEY. In some instances I had obtained the same results as WILLEY before he published his figures, in others I have merely verified his work, and in places I rely entirely upon his figures and descriptions in order that my own descriptions may be as complete as possible. Some facts are, I think, published for the first time.

In the case of the branches of the lesser aorta and the arteries of the reproductive apparatus the completeness of the account is entirely due to the researches of WILLEY.

In both figures of the arterial system the arteries are viewed from the dorsal side. As the vessels represented in text-fig. 11 lie almost entirely ventral to those of text-fig. 10, I believe that they are shown with less danger of confusion in separate figures.

The heart is situated immediately back of the mantle fold in the portion of the cœlom known as the pericardium. It is an oblong muscular organ of quite considerable size, being 2 centimeters in width, 1 centimeter in length (antero-posterior measurement), and 6 to 8 millimeters in thickness. The long axis of the heart is exactly transverse to the long axis of the body. The right side of the heart is slightly longer than the left side, so the symmetry of the heart is not quite perfect.

A branchial vein enters each corner of the heart. The portion of each branchial vein near the heart is capable of considerable distension, and these portions have been called the auricles of the heart. But very frequently one or all these vessels show no increase in diameter near the heart. This fact indicates that the so-called auricles of Nautilus, while physiologically similar, have not the same morphological importance and should not be considered as organs of the same nature as the auricles of the heart of the Gastropoda and the Lamellibranchiata. In these classes the auricle forms a distinct chamber, which even in its development is distinct from both the ventricle and the branchial veins, which the auricles of Nautilus are not. The term is a convenient one anatomically, indicating the portion of the branchial vein inside the pericardium

which is evidently pulsatile, but it should not be used in the same morphological sense as in other groups.

Five vessels arise from the dorsal side of the heart, the courses of which will be described presently.

The heart has thick muscular walls, and in the contracted state consequent upon death a very small fissure-like cavity. The inner surface of the heart is pitted, and by its appearance reminds one strongly of the inner surface of a mammalian heart, though by no means distinctly trabeculated. I have not been able to find any valves at the openings of the vessels leading into or from the heart, except possibly the dorsal aorta. The openings are, however, tightly closed, and it is possible that at the commencement of systole the walls of the heart contract first around the openings of the branchial veins, and thus the regurgitation of blood is prevented.

Until otherwise indicated all references will be to text-fig. 10.

The largest vessel proceeding from the heart is the dorsal aorta. This arises from the dorsal surface of the heart, on the left side and near the posterior edge. The base of the aorta is conical and possesses thick muscular walls, and could probably be properly spoken of as a conus arteriosus. At the end of the muscular portion of the base of the aorta is an elevation of the inner wall, which may be a valve. In some specimens this is quite distinct and much like a semilunar valve; in others it is barely noticeable. Possibly the conical base of the aorta should be considered morphologically as a portion of the heart itself.

Along the median part of the posterior edge of the heart, dorsally also, arise three small arteries. They lie in the portion of the pallio-visceral ligament attached to the posterior side of the heart. The artery at the left is the artery of the pyriform sac; the middle one is the genital artery, while the one on the right is the gonaducal artery.

Also from the dorsal side of the heart, but near the anterior edge, arises the fifth artery, the lesser aorta.

Let us now follow the course of the dorsal aorta and its branches. From its origin on the dorsal side of the heart the aorta extends upward and backward and to the left along the posterior side of the hæmocœlic membrane. Turning forward it penetrates the membrane and enters the hæmocœl, in which it lies free, running forward over the liver and the œsophagus. In the posterior portion of the hæmocœl the aorta lies well to the left of the cavity, but as it extends forward it approaches the median line until, near the œsophageal nerve ring, it lies in the median line. Immediately back of the nerve ring the aorta divides into a left and a right branch, the innominate arteries, from which lesser branches are given off to the cephalic region and the funnel.

Commencing from the posterior end of the aorta, the first branch leaves it just after the aorta enters the hæmocœl. Coming off from the right side of the aorta, it runs directly toward the right side of the body, giving off first a branch anteriorly which passes to the posterior portion of the proventriculus, the posterior proventricular artery; next, a branch posteriorly which immediately bends forward and passes around the anterior side of the stomach to the cæcum, the cæcal artery; finally, the end of the artery passes to the stomach, forming the gastric artery, which breaks up into numerous fine vessels in the walls of the stomach.

Five or 6 millimeters anterior to the origin of this artery a much larger artery leaves the left side of the aorta. After a course of about 5 millimeters this artery divides into two branches, the anterior of which goes to the left shell muscle (the left posterior columellar artery), while the posterior branch proceeds to the liver (hepatic artery). I have called the branch of the aorta from which both these arteries arise the hepatico-columellar artery.

The hepatic artery goes to the junction of the two left lobes of the liver. It divides here into three branches. The left and middles branches enter the left lobes of the liver in which they break up into the fine lobular branches. The right-hand branch of the hepatic artery follows the median connecting portion of the liver to the junction of the two right lobes of the liver. Here it divides into a branch for each lobe. In its course it gives off a considerable branch to the median portion of the liver.

The left posterior columellar artery runs forward and upward to the dorsal edge of the left shell muscle near its attachment. After giving off a branch to the dorsal portion of the body wall it bends downward along the inner surface of the shell muscle, giving off numerous branches which enter the muscle.

The right posterior columellar artery arises from the right side of the aorta about 5 millimeters anterior to the origin of the hepatico-columellar artery. Since the posterior portion of the aorta is upon the left side of the body cavity, the right posterior columellar artery is considerably longer than the corresponding left artery. The course of the right posterior columellar artery is the same, only inverted, as that of the left.

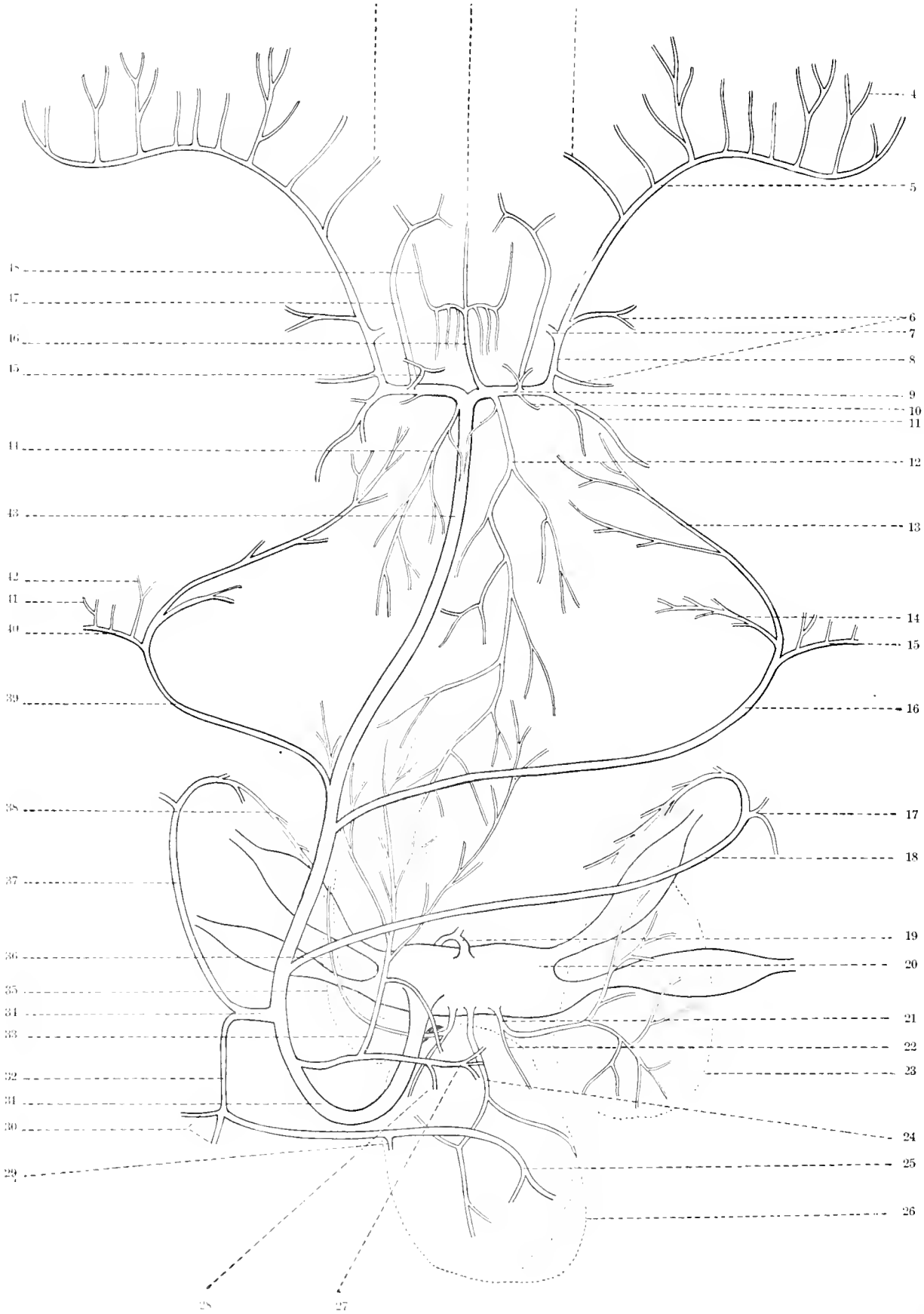
About 20 millimeters anterior to the origin of the last artery the right pallio-nuchal artery arises as a branch of the aorta. The left pallio-nuchal artery arises from the aorta 4 or 5 millimeters anterior to the right pallio-nuchal. These arteries pass upward and outward to the dorsal side of the body, entering the body wall at the base of the mantle fold where the latter crosses the dorsal edges of the shell muscles. Several branches leave the pallio-nuchal arteries at this point. Some of these pass into the dorsal portion of the mantle lying against the involution of the shell. The main portion of each artery is continued in the thin wall of the dorsal nuchal region, supplying especially the crescentic fold upon the posterior face of the hood. As it passes along the edge of the shell muscle it appears to send some small branches into the tissues of the muscle. A considerable branch extends into the crus of the funnel. From the outer side of the pallio-nuchal artery a branch enters the mantle, which becomes continuous with the marginal pallial branch of the anterior pallial artery.

Usually no other vessels arise from the aorta until it divides into the innominate arteries.

The anterior proventricular arteries, supplying blood to rather more than the anterior half of the proventriculus, frequently arise from the junction of the aorta with the innominate arteries. These arteries are, however, extremely variable in their position, a fact to which Willey has called attention. One or both may arise from the innominates, or one may be entirely absent. In Willey's Fig. 23 (1896, 1), the left anterior proventricular artery arises from the aorta a considerable distance below its division into the innominate arteries. Two small arterioles going from the anterior proventricular arteries to the walls of the aorta show also considerable variation in their points of origin. Ordinarily one arises from the base of each proventricular artery. In the case figured by Willey both arterioles arise from the right anterior proventricular artery, the left proventricular artery being absent in this case.

The buccal artery usually springs from the right innominate close to its separation from the left. It passes forward upon the dorsal side of the buccal mass, presently dividing into three branches. The median branch, the superior mandibular artery, runs straight forward in the median line of the buccal mass, giving off branches to the superior mandibular muscles. The lateral branches first pass outward to the sides of the buccal mass, giving off on the way several small branches posteriorly to the mandibular muscles, then turn forward and pass into the buccal membrane and its papillæ. Of the origin of the buccal artery Willey says: "It is a singular fact that the great median buccal artery always springs from the right innominate artery. The constancy of this origin would seem to indicate that it is potentially a paired structure." I have dissected specimens in which the buccal artery sprung from the junction of the innominate arteries; in other words, was median. Either position, lateral or median, may be secondary, resulting from a displacement of the base of the artery during growth, and it is difficult to decide which is primitive without the evidence of embryology.

Five or six millimeters from their junction a branch arises from the anterior side of each innominate (the inferior mandibular artery), which runs forward on the under side of the buccal mass to the muscles and organs of the floor of the pharynx. These arteries are closely bound to the buccal nervous system, careful dissection being required to separate the nervous from the arterial elements. The inferior mandibular arteries supply not only the lower parts of the mandibular muscles but also the tongue and the radular sac, the processes anterior to the tongue, and the salivary processes.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TEXT-FIG. 10.—THE DORSAL AORTA, THE GENITAL AND GONADUCAL ARTERIES, AND THE ARTERY OF THE PYRIFORM SAC VIEWED FROM THE DORSAL SIDE.

This figure and the one following are combinations of the results of my own dissections, and the figures of various parts of the vascular system published by WILLEY.

1, left artery of VAN DER HOEVEN's organ in the male; of inferior labial lobe in the female.
2, superior mandibular artery.
3, right artery of VAN DER HOEVE.'s organ in the male; of inferior labial lobe in the female.
4, arteries to individual digital tentacles.
5, right tentacular artery.
6, arteries of eye.
7, infundibular artery.
8, pedal artery.
9, innominate artery.
10, artery entering posterior part of hood.
11, right anterior columellar artery.
12, right anterior proventricular artery.
13, nuchal artery.
14, crural artery.
15, marginal pallial artery.
16, right pallio-nuchal artery.
17, branch to dorsal body-wall.
18, right posterior columellar artery.
19, lesser aorta.
20, heart.
21, gonaducal artery.
22, branch to wall of gonad.
23, outline of genital duct.
24, genital artery.
25, artery of right lobes of liver.
26, outline of gonad.
27, gastric artery.
28, cecal artery.
29, artery to middle portion of liver.
30, arteries to left lobes of liver.
31, dorsal aorta.
32, hepatic artery.
33, posterior proventricular artery.
34, hepatico-columellar artery.
35, outline of pyriform sac.
36, artery of pyriform sac.
37, left posterior columellar artery.
38, descending portion of columellar artery giving off branches to muscle.
39, left pallio-nuchal artery.
40, marginal pallial artery.
41, radial pallial artery.
42, artery to dorsal portion of mantle.
43, dorsal aorta.
44, left anterior proventricular artery.
45, cerebral artery.
46, buccal artery.
47, inferior mandibular artery.
48, labial artery.

From the dorsal side of the innominates, near the origins of the inferior mandibular arteries, arise arterioles which pass into the cerebral ganglia. From the posterior side of the innominates other small vessels pass into the posterior portion of the hood.

Finally, each innominate divides, one branch passing backward into the shell muscles and forming the anterior columellar artery, the other branch passing forward and downward along the bases of the tentacles, forming the pedal artery. Near the base of the pedal artery two arterioles pass outward to the eye. Between these a large branch arises from the pedal artery which passes to the funnel, the infundibular artery. The remainder of the pedal artery, which gives off branches to the individual tentacles, WILLEY has very conveniently named the tentacular artery. The first of the branches of the tentacular artery passes into the inferior labial lobe in the female, and into VAN DER HOEVEN'S organ in the male.

The origin of the genital and gonaducal arteries and the artery of the pyriform sac has already been mentioned.

The genital artery passes from the heart directly back upon the gonad, in which it breaks up into capillary branches.

The gonaducal artery passes to the right from the heart and is distributed to the walls of the functional genital duct.

The artery of the pyriform sac, or the non-functional genital duct, passes to the left from the heart and extends along this organ.

WILLEY shows that both the gonaducal artery and the artery of the pyriform sac give off a branch which passes into the perigonadial membrane, and he says: "This apparently trifling fact, combined with the subsymmetrical relations of the gonaduct and the pear-shaped gland, may indicate that the latter is the metamorphosed genital duct of the left side, and not, as I believe has been suggested, the morphological equivalent of an entire left genital apparatus."

Almost immediately after its origin from the anterior side of the heart, the lesser aorta divides into two branches.[1] One, the pallial artery, runs straight forward in the median line of the mantle and is distributed to the intestine, rectum, and mantle. The other, the common septal artery, runs almost straight backward and is distributed entirely to the septal portion of the body wall and the siphuncle.

The pallial artery is inclosed by the pallio-visceral ligament. A few millimeters anterior to the heart it gives off a slender branch (the intestinal artery), which runs back in the membrane uniting the two portions of the second loop of the intestine. Small arterioles pass from either side into the intestinal tissues.

In front of the intestinal artery several small rectal arteries arise directly from the pallial artery and pass to the walls of the rectum.

At the point where the two walls of the mantle fold unite and the mantle becomes thin, a pair of vessels arise from the pallial artery and pass outward to the right and the left in the substance of the mantle. These arteries, discovered by WILLEY, were called by him the branchio-osphradial arteries, "since among their minor ramifications they send up branches to the tips of the branchiæ, supplying the integument of the latter, and also a small branch into each of the osphradia." In the female the nidamental glands are supplied by branches of the branchio-osphradial arteries. I retain the name "branchio-osphradial" for these arteries because, although the osphradial character of the papillæ referred to is not yet well proven, there is still a considerable probability of it, and it does not seem worth while to burden the literature of the subject with a new name which might in time prove more correct, but for the present would be no more intelligible or convenient.

The pallial artery now passes forward nearly to the mantle edge. It here divides into a right and a left branch (the marginal pallial arteries), which run parallel to the edge of the mantle till they unite dorsally with the pallio-nuchal branches of the dorsal aorta. In this way a remarkable arterial circuit is formed, to which WILLEY has given the name "circulus pallialis."

[1] The arteries described after this are represented in text-fig. 11

From the anterior side of the marginal pallial artery a regular series of small arteries pass into the portion of the mantle in front of the marginal artery, which we have noticed to be especially muscular and slightly thicker than the middle portions of the mantle.

From the posterior side of the marginal artery and from the anterior portion of the pallial artery numerous vessels pass into the middle portions of the mantle.

The common septal artery bends around the anterior side of the heart immediately after its origin and then passes backward along the ventral surface of the heart. It is here covered by the portion of the pallio-visceral ligament which incloses the heart and hangs suspended in a mesentery-like fold of the ligament. Running backward under the left side of the heart, the artery arrives at the posterior viscero-pericardial opening, through which it passes by following the right edge. This edge being attached to the gonad, the artery passes directly upon the surface of the ovary or testis, as the case may be. Passing over the lower edge onto the anterior face of the gonad, the artery reaches the gastric ligament, along the edge of which it passes to the posterior wall of the body near the base of the siphuncle. The common septal artery does not appear to give off any branches to the gonad.

Arrived at the posterior wall of the body, the artery divides into a right and a left septal artery. These ramify over the portion of the body wall which faces the septum. It will be remembered that this portion of the body wall is bounded by the dorsal and the posterior ventral aponeurotic bands. The branches of the septal arteries are rigidly confined to the septal area of the body wall (Willey).

The siphuncular artery arises as a branch of one of the septal arteries, sometimes of one, sometimes of the other. Entering the base of the siphuncle, the artery extends through it to the end. Other smaller branches of the septal arteries may also enter the base of the siphuncle.

VENOUS CIRCULATION.

Only a portion of the venous system appears to be closed. The blood passes from the arterial capillaries into sinuses, which in one way or another are placed in communication with the vena cava. In the mantle there seems to be a quite extensive closed circulation.

The vena cava lies in the ventral wall of the body, extending from the cephalic cartilage to the posterior limit of the mantle cavity. It possesses thin muscular walls of its own, which appear to be innervated by two nerves springing from the pleuro-visceral ganglia. In its anterior portion the vena cava is bounded laterally by the inner faces of the shell muscles, which, touching each other ventrally, are separated dorsally. A triangular space is thus formed, which is occupied by the vena cava.

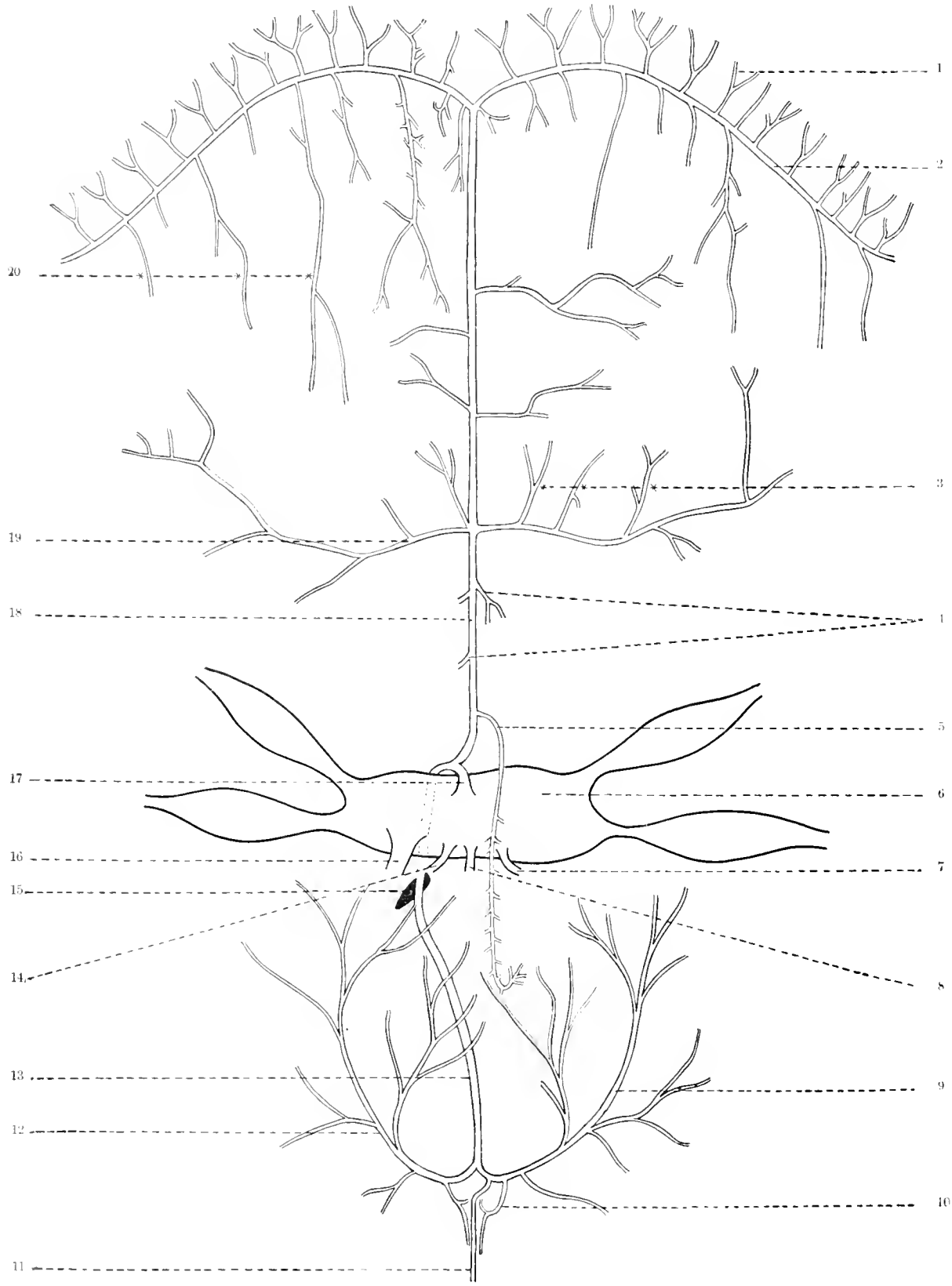
The dorsal wall of the vena cava, which is flush with the inner surface of the body wall, is perforated by numerous holes of varying size.

The vena cava is in communication anteriorly with numerous extensive blood spaces in the tissues surrounding the buccal mass and at the bases of the tentacles. Some of these spaces appear much like definite branches of the vena cava. The vena cava also receives several large veins from the shell muscles and the body wall, but these vessels are not constant in either number or position. Two veins on each side of the cephalic region pass through the body of the cartilage into the anterior end of the vena cava.

Through the openings in its dorsal wall by which the vena cava is in communication with the haemocœl blood enters the vena cava through the latter cavity from the sinuses of the body wall, and probably from the viscera contained in the haemocœl and its extensions.

At the posterior limit of the mantle cavity the vena cava divides into a right and a left branch, which branches almost immediately subdivide into two branches passing to the anterior and posterior gills of either side, the branchial arteries. Each of the branchial arteries, on its way to the gill, passes through the posterior wall of a renal sac, where it sends branches into the renal and pericardial appendages. (Text-fig. 9, p. 164.)

Willey says that the veins of the mantle "are collected into two main trunks, which lie on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TEXT-FIG. 11.—THE LESSER AORTA AND ITS BRANCHES, VIEWED FROM THE DORSAL SIDE.

1, radial pallial artery.
2, marginal pallial artery.
3, arteries of nidamental gland.
4, rectal arteries.
5, intestinal artery.
6, heart.
7, gonadical artery.
8, genital artery.
9, right septal artery.
10, accessory siphuncular artery.
11, siphuncular artery.
12, left septal artery.
13, common septal artery.
14, artery of pyriform sac.
15, posterior viscero-pericardial aperture.
16, dorsal aorta.
17, lesser aorta.
18, pallial artery.
19, branchio-osphradial artery.
20, median pallial arteries.

either side of the anterior pallial artery, and proceed backward to open into the different branchial vessels. At the sides of the mantle there are also a number of lateral pallial veins, which open into a large sinus situated over the shell muscle."

The peculiar perforated structure of the vena cava, together with the large size of the hæmocœl, may have an important bearing upon the ability of the Nautilus to endure being suddenly hauled to the surface without suffering apparent ill results. The specimens which I have had the privilege of studying were captured at a depth of from twelve hundred to eighteen hundred feet. At the latter depth they would be under a pressure of eighty atmospheres. Professor WORCESTER has told me that while the Nautili came to the surface uninjured, other animals brought up with them, as fish and crustacea, were always dead upon reaching the surface.

It is evident that something in its structure must account for the ability of the Nautilus to withstand such sudden and tremendous changes of pressure, though this function may be, and probably is, only a concomitant of the structure and not its principal function.

In order that a change of pressure should not prove injurious to an animal it is only necessary that the internal pressure of the tissues should remain equal to the external pressure. It seems to me that this result would be easily accomplished in Nautilus in the following manner. The pressure of the surrounding water upon the body would be transferred immediately to the blood contained in the hæmocœl. The cavity of the hæmocœl is in direct communication with that of the vena cava, and consequently with all the vascular spaces of the body, through the holes in the dorsal wall of the vena cava. By this means the pressure of the blood in the hæmocœl is directly transmitted to the blood of the entire body, and thus the pressure within and without the body is equalized. No change in the volume of the body would occur because the volume of the hæmocœl and cœlom is minimal, and because of the incompressibility of the fluid.

The hæmocœl is completely closed from the exterior, so no water enters it, or anywhere comes in direct communication with the blood. It seems entirely improbable that water ever enters the cœlom through the pericardial pores, as has been suggested.

NERVOUS SYSTEM. (FIG. 41.)

The central nervous system of Nautilus consists of three ganglionic bands which unite so as to form a ring around the œsophagus, two passing ventrally to the œsophagus and one dorsally.

The dorsal band represents the cerebral ganglia plus their commissure (12). The ends of the band are sometimes slightly larger than the central portion, but there is never any such separation of the parts as to allow us to say, these are the cerebral ganglia, or this is the cerebral commissure.

The posterior of the ventral bands represents the pleuro-visceral ganglia (13); this also is not separated into a pair of ganglia and a commissure, although the ends of the band are sometimes larger than the central portion. The anterior ventral band is composed of two distinct ganglia united by a slender commissure, the pedal ganglia (28) and the pedal commissure (29). The pedal ganglia are flat and crescentic in outline.

The cerebral, pedal, and pleuro-visceral ganglia form a junction at the sides of the œsophagus. The pleuro-visceral ganglia seem almost to join the pedal ganglia rather than the cerebral, but closer examination proves that they unite with the cerebral ganglia to as great an extent at least as with the pedal ganglia.

I shall speak of the cerebral and pleuro-visceral ganglia as if each band were in reality a single ganglion.

From each outer side of the cerebral ganglion an enormous optic nerve passes outward into the stalk of the eye (24 and 25). The base of the optic nerve is swollen and may form an optic ganglion, a point which the study of sections alone will settle. The optic nerve is almost immediately divided into numerous parallel small nerves which in passing outward twist slightly about the axis of the nerve. They are much more closely pressed in the stalk of the eye than nearer the cerebral ganglion. At the back of the retina the nerves separate and form a mesh about this bowl-shaped organ.

Near each end two nerves pass from the anterior side of the cerebral ganglion forward to

the ventral side of the buccal mass, where they enter the buccal nervous system (5 and 6). These are the outer and inner cerebro-buccal connectives of each side. The buccal connectives are of considerable length. In preserved and contracted specimens they are found to make numerous loops, which provide the extra length required when the buccal mass is thrust forward.

The buccal nervous system consists of two pairs of ganglia united by connectives and two commissures passing anterior to the œsophagus. The cerebro-buccal connectives pass through the muscular membrane which covers the ventral surface of the buccal mass and unite with the pharyngeal ganglia—slender ganglia lying at the sides of the ventral surface of the buccal mass, immediately upon the lower edge of the mandibular muscles (4). The pharyngeal ganglia are united by the long pharyngeal commissure passing anteriorly along the edge of the lower jaw (2). From the posterior ends of the pharyngeal ganglia strong connectives extend backward and inward to the buccal ganglia at the sides of the œsophagus as it issues from the buccal mass (32). The buccal ganglia are quite small. They are connected by a commissure passing around the anterior side of the œsophagus (33).

Numerous nerves are given off by the pharyngeal ganglia to the mandibular muscles. A nerve arising on the posterior side of the buccal ganglion bends over the dorsal side of the latter and passes to the salivary gland (34). A small nerve passes from the buccal ganglion to the œsophagus (31). Other nerves seem to pass into the tongue, but could not be accurately traced.

A number of small nerves (more than a dozen) leave the anterior side of the cerebral ganglion between the bases of the inner cerebro-buccal connectives and pass forward upon the dorsal surface of the buccal mass (27). Some of these nerves or their branches enter the mandibular muscles. The majority of them pass into the space between the folds of the buccal membrane and are distributed to the papillæ along the edge of the membrane.

A few small nerves (23) leave the posterior sides of the outer ends of the cerebral ganglion and pass to the posterior portion of the dorsal buccal retractors close to their attachment to the cartilage. These seem to be the same nerves which VALENCIENNES describes as proceeding to the cavity of the cartilage which he mistook for the otocyst.

In one specimen I have been able to trace the otocystic nerves. They are small, of about the same size as the nerve figured as going to the post-ocular tentacle. Each arises from the dorsal surface of the cerebral ganglion, just above the base of the optic nerve. As the otocyst is pressed between the posterior surface of the pedal ganglion and the cartilage, the otocystic nerve passes into the angle between the cerebral and pedal ganglia and then runs along the posterior surface of the pedal ganglion. The tunic of the nerve is so closely attached to that of the pedal ganglion that the nerve seems at first sight to spring from this ganglion. The nerve spreads out fan-wise upon the surface of the otocyst.

The nerve of the rhinophore seems to leave the cerebral ganglion close to the base of the optic nerve, but I am not entirely sure of its course.

No nerves are given off from the inner edges of the pedal ganglia, but from the outer edges arise exceedingly numerous closely set nerves. These nerves are distributed entirely to the funnel, the labial tentacles, and the digital tentacles and the cephalic sheath. In other words, they pass only to those parts which some consider to be homologous with the foot of other mollusca.

The infundibular nerves are a pair of large nerves leaving the inner end of each ganglion, passing forward and downward into the tissues of the funnel (8). They are situated at either end of the pedal commissure, from which no nerves arise. For the first part of their course the infundibular nerves lie in a cavity slightly larger than themselves, probably a blood space.

Just outside the infundibular nerves two conspicuous but smaller nerves (7) pass forward from the pedal ganglia to the inferior labial lobes in the female or to their homologue in the male, VAN DER HOEVEN'S organ. The nerves enter the base of the inferior labial lobe; they enter VAN DER HOEVEN'S organ at about the middle of each side. In each case after the nerves have entered they expand into small ganglia (35), from which nerves are given off to the separate tentacles of the organs. Fig. 41 is drawn from a male specimen in which the nerves pass inward from the ganglion instead of forward as in the female.

The outer edge of each pedal ganglion is fringed with numerous fine nerves. These nerves may be separated into two groups. The first of these are small, very slender nerves, which spring from the anterior or upper side of the edge of the ganglion. These nerves go to the tentacles of the superior labial groups; in the male, the nerves of the spadix and antispadix also are included in this series. The nerves of the tentacles of the spadix are, however, much larger than the nerves of the superior labial tentacles, or of the tentacles of the antispadix. In one dissection I found a quite peculiar nerve (30); it passes from the left pedal ganglion into the base of the first cirrus of the spadix, where it ends in an enlargement from which a number of small branches proceed into the surrounding tissues.

The apparently similar innervation of the superior labial tentacles and the tentacles of the spadix and the antispadix points to the latter being separated portions of the superior labial groups. But it is not safe to rely overmuch upon the, at present very slight, evidence of the innervation. The nerves arising from the pedal ganglia are too little separated for us to distinguish accurately between one group and another.

The second series of nerves are much larger than the first and arise from the lower or posterior portion of the edge of the ganglion, or even from the side pressed against the cartilage. They proceed to the individual digital tentacles (9).

Several large nerves leave the upper (or outer) ends of the pedal ganglia, near the junction with the cerebral and pleuro-visceral ganglia. From these nerves (10) branches proceed to some of the digital tentacles and to the hood.

Finally, a large nerve leaves the pedal ganglion very close to its junction with the other ganglia. The two main branches into which this divides become the nerves of the preocular and postocular tentacles. Finer branches proceed to the posterior portion of the hood, and sometimes to cirri of digital tentacles.

Numerous nerves, large and small, arise from the posterior edge of the pleuro-visceral ganglion. The nerves of the two sides are separated by a narrow median interval free from nerves. On either side of the interval a large visceral nerve (22) leaves the ganglion and runs straight backward, lying upon the inner surface of the body wall at the side of and parallel to the vena cava. At the posterior limit of the mantle cavity the visceral nerve turns outward and forward in the mantle, finally dividing into two branches which extend into the gills (19 and 20).

Before the visceral nerve divides to form the branchial nerves I have found it to give off two branches, which seemed to pass into the posterior walls of the renal sacs (17 and 18).

Just before the visceral nerve bends into the mantle it gives off small nerves to the spermatophore sac and genital duct (16).

Frequently connected with the visceral nerves are a pair of slender nerves which pass to the dorsal wall of the vena cava (15 and 21). These are, however, very variable in their origin. Always present, they sometimes both arise from the visceral nerves at about the middle of their course in the body. Sometimes both arise directly from the pleuro-visceral ganglion just inside the origins of the visceral nerves, as is figured by Willey; or one may arise from the pleuro-visceral ganglion, while the other springs from some portion of the visceral nerve, as is shown in Fig. 41.

Willey is quite sure that these nerves innervate the preanal papillæ, and partly for this reason considers the papillæ as the anterior pair of osphradia. I have not been able to trace the nerves anywhere but to the walls of the vena cava; although this does not constitute proof that they end there.

Lankaster and Bourne state absolutely, Willey with confidence, that they have traced a small nerve from the bifurcation of the branchial nerves into the interbranchial papillæ. This branch also I have been unable to find, either in several dissections or in a series of sections of the papilla.

Outside the visceral nerves a number of nerves of various sizes leave the pleuro-visceral ganglion and extend into the shell muscles and the body wall (14). The number of these is much larger than is represented in Fig. 41, only the larger ones being drawn.

From the extreme ends of the pleuro-visceral ganglion a few very small nerves extend into

the posterior portion of the hood. From its innervation, which is derived from the cerebral, pedal, and pleuro-visceral ganglia, the posterior portion of the hood seems to be fairly comparable with the dorsal portion of the nuchal region of the Gastropoda.

EYE.

The eye of the Nautilus is bowl-shaped, to use a rough comparison, the top of the bowl being closed by a thin membrane which is perforated centrally by a small round hole, while the base of the bowl projects as a short stalk which is attached to the side of the head (Fig. 1, E). The top of the bowl is turned outward. The eye does not seem to be round, but somewhat triangular, the rounded apex being directed ventrally. It is 22 millimeters in length (antero-posteriorly), 15 millimeters high (dorso-ventrally), and 12 millimeters from the base to the outer side. The stalk of the eye is 9 millimeters in diameter, but only 2 or 3 millimeters long.

The edge of the eye is produced into a flange ventrally and laterally, but not dorsally. The round aperture in the outer face of the eye is usually spoken of as the pupil and leads into the cavity of the eye lined by the retina, there being no lens or any medium of refraction in the eye. The sea water has free ingress to or egress from the cavity of the eye. The pupil is about 2 millimeters in diameter. From the ventral side of the pupil a groove leads across the face of the eye to its ventral edge. The posterior edge of the groove projects over the groove to the opposite side, transforming this into a tubular channel.

Usually the edges and the center of the face of the eye are slightly raised, leaving a depression between them. Except for a few almost microscopic depressions of the surface, the face and sides of the eye are quite smooth. The outer epithelium of the eye is composed of long, slender ciliated cells. The groove on the face of the eye is lined with a similar epithelium. Von Hensen suggests that a constant stream of water may be driven through it, keeping the pupil clean, and preventing the entrance of foreign bodies into the eye.

The membrane forming the outer face of the eye is quite thin: 1 millimeter thick at the edges, it gradually becomes thinner until the pupil is reached, where it is scarcely thicker than writing paper.

The sides of the eye are much thicker than the outer face, and they increase in thickness as they approach the stalk. The dorsal side is about 1.5 millimeters in thickness; the ventral side is double this thickness. The capsule of the eye is composed for the most part of connective tissues; a little muscular tissue is also present.

In longitudinal section the cavity of the eye is oval with a blunt outer and somewhat pointed inner pole. The wall of the outer portion of the cavity is of an intense black color. This black area is approximately circular. The side and back walls are of a light gray color, the line of demarkation between the black and gray portions of the wall being very sharp. The difference in color is caused by the fact that in the posterior portion of the cavity the retina bears rods which hide the pigment, while the rods are absent on the anterior portion of the retina.

I follow Haller's account of the structure of the retina. The retina is about 1 millimeter in thickness at the posterior side of the cavity, gradually becoming thinner as it passes anteriorly. The branches of the optic nerve spread out in a thin fibre layer immediately beneath the retinal epithelium.

The epithelial layer of the retina is composed of two kinds of cells. The first are columnar cells, having a width equal to about one-eighth of their height. The nucleus lies in the upper end of the lower third of the cell. Fine pigment granules lie in the cell above the nucleus, but rarely below it.

The second kind of retinal cells are much more slender than the first, almost thread-like in shape. The nucleus usually lies at the beginning of the upper third of the cell. The pigment granules are larger than in the broader cells, and often are so large compared with the width of the cell body as to be arranged like a string of beads. They also frequently extend below the nucleus. The broad and fine cells alternate regularly. The pigment does not extend quite to the upper end of the cell, nor often into the lower third of the cell. Thus the pigment forms a dark band which is very noticeable in sections of the eye.

The rod layer which covers the gray portion of the retina is composed of slender rods of equal size. The rods are about three times as long as the retinal cells. Each rod is composed of an axial cord which stains deeply in carmine, and of a lightly staining cortex.

The epithelium of the retina is separated from the nerve-fibre layer by a thick basement membrane, through which the nerve fibres penetrate and enter the retinal cells. The nerve fibres enter the broad retinal cells just above the nucleus. The bases of the fine retinal cells are continuous with nerve fibres.

RHINOPHORE. (Figs. 21 and 22.)

Between the stalk of the eye and the projecting posterior edge of the cephalic sheath is an organ, probably olfactory, which has lately been compared with the rhinophore of certain Gastropoda, and to which this name is applied. It is a small pyramidal protuberance of the side of the head, located on a horizontal line with the lower edge of the stalk of the eye. The body of the eye projects over the rhinophore, completely hiding it when the Nautilus is not viewed from below. The posterior side of the rhinophore is produced into a finger-like process of about the same height as the pyramidal base; the whole is 8 or 10 millimeters in height. The process is not annulated and is "not retractile" (Willey, 1897, 1), and bears no resemblance nor relation to the digital tentacles. It may be well to speak of this as the tentacle of the rhinophore. Just dorsal to the tentacle is a pit 6 millimeters in depth and 2 millimeters in diameter (the dorsal pit). On the anterior side of the base of the tentacle is the opening of another pit, narrower but much deeper than the dorsal pit. This is the fossa of the rhinophore. It is 10 or 12 millimeters in depth, extending into the tissues of the head in a line directed inward and downward, except as the last 2 or 3 millimeters of the tube turns sharply forward. The base of the fossa is near the otocyst, and Keferstein thinks that this is what Macdonald mistook for the otocystic canal. From just within the external opening the fossa is continued upward in the center of the tentacle nearly to its tip.

The walls of the fossa are much folded longitudinally and are lined by a single-layered ciliated epithelium of slender columnar cells. Among these are many cells which remind one strongly of the olfactory cells in some of the vertebrata.

The middle portion of these cells is swollen, forming a large, spherical, clear body which is distinguishable in sections viewed under low powers. The proximal and distal ends of the cells seem to be exceedingly slender and thread-like. These cells are limited to the walls of the fossa. The epithelium of the dorsal pit is like that of the outer surface of the rhinophore.

A large nerve appears to leave the anterior side of the cerebral ganglion just under the point of union of the cerebral and optic ganglia, and, lying close to the fossa, extend to the tip of the tentacle of the rhinophore.

The body of the rhinophore is composed for the most part of dense elastic connective tissue, though in the base of the organ are some muscles.

Keferstein describes the tentacle of the rhinophore as "ein zungenförmiger Lappen . . . der wie eine Klappe die Mündung seines Axenkanals schliessen kann." In preserved specimens the tentacle frequently is folded down over the mouth of the fossa, but this is apparently due to its being pressed upon the eye, so that the tentacle is probably in an unnatural position.

OTOCYSTS.

The otocysts of *Nautilus pompilius* lie upon the front side of the cartilage immediately back of the pedal ganglia, and near the junction of the latter with the cerebral and pleurovisceral ganglia. They are ovate in form, measuring about 3.5 millimeters in the direction of their long diameter. The end of the auditory nerve spreads out over the surface of the otocyst.

The otocyst is a thin walled sac almost completely filled by an immense number of elliptical crystals packed closely together. The crystals vary in thickness between 0.0011 and 0.0066 millimeter, and in length from 0.0033 to 0.014 millimeter. The crystals are composed of calcium carbonate, giving characteristic chemical and light reactions. They all have the shape which would be assumed by a perfect crystal of dog-tooth spar if all its angles were rounded. Very

frequently cases of the twinning of two or more crystals are seen. In instances where two crystals are twinned the angle between their axis is usually 78°, any divergence from this angle being quite small, so far as observed. When twinned the ends of each crystal are as perfect as in single crystals. The union of two or several crystals forms the cross and star-shaped bodies, "etc." mentioned by MACDONALD.

CARTILAGE. (Fig. 40.)

In the region of the bases of the digital tentacles is a large and strong cartilage which affords a firm place of attachment for the major muscles of the body. It is composed of a central portion which OWEN has termed the body, from each side of which a pair of processes project dorsally (the cephalic processes) and ventrally (the infundibular processes). The cartilage slants from above downward and forward, the ends of the cephalic processes reaching dorsally to the body wall of the nuchal region immediately back of the hood and in front of the crura of the funnel, while the infundibular processes extend into the funnel through the inner wall of which they show as white lines.

The greatest width of the cartilage is 3 centimeters, the length between the tips of the processes is 4.75 centimeters. The infundibular processes have a length of 2.5 centimeters, the cephalic processes a length of 1 centimeter.

The cephalic processes are round and end squarely. The muscles of the digital tentacles, the labial tentacles, and the spadix are attached to their anterior faces. The shell muscles find an attachment upon their posterior faces.

The infundibular processes are much broader than the cephalic as well as thinner and nearly flat. Their broad anterior faces are turned somewhat inward as well as upward. These faces are slightly concave, while the outer and posterior faces are slightly convex. The tissues of the anterior portion of the funnel are attached to the lower portion of the anterior faces, while the muscles of the posterior portion and of the crura of the funnel are attached to the posterior faces of the infundibular processes. The pedal ganglia lie against the upper portions of the anterior faces of the infundibular processes, while the pleurovisceral ganglia are supported by the median processes of the body of the cartilage. The body of the cartilage is bent downward and backward in the middle, forming a sharp reentrant angle anteriorly and a projecting point posteriorly. From the upper portions of the anterior side of the body of the cartilage a pair of small processes project toward the median line, the median processes (m. p.). The muscles of the buccal mass, the inferior labial lobe or VAN DER HOEVEN'S organ, and the levator muscles of the funnel, are attached to the body of the cartilage. The points of attachment of the latter muscles are marked by the dotted lines at l. i. in Fig. 40.

The body of the cartilage is penetrated by two veins on each side. These enter widely separated upon the anterior side, but leave the cartilage close together upon the posterior side, the cavities of the cartilage containing the veins opening here into a common depression. The upper veins (v) come from the region of the base of the tentacles; the lower veins (v') come from the anterior portion of the funnel. In the central part of the cephalic process is a small cavity which extends nearly to its tip and communicates with the cavity containing the vein from the cephalic region.

SUMMARY.

It may be a convenience if the additions to our knowledge of the anatomy of *Nautilus pompilius* presented in the foregoing pages are briefly summarized. The principal result aimed at has been to unite the numerous isolated observations on Nautilus in a coherent account which will at least have the advantage of accessibility.

It has been found that the digital tentacles have a regular arrangement, few variations from which exist.

The nerve of each tentacle possesses accumulations of ganglion cells about its periphery corresponding to each of the annulations of the outer portion of the tentacle. The inner projecting side of each segment of the digital tentacles is covered by a peculiar epithelium, which

there is some reason to consider as sensory. This portion of the segment is also provided with a peculiar musculature which enables it to act as an adhesive organ of considerable power.

The evidence renders it probable that the lamellated organ upon the inferior labial lobe of the female is composed of a number of modified cirri. Between the lamellæ are peculiar pits, lined by an epithelium which seems to be sensory.

Van der Hoeven's organ of the male is shown to be the homologue of the inferior labial lobe of the female. Its lamellæ correspond to the lamellæ and cirri of the inferior labial lobe. Van der Hoeven's organ is largely glandular; its activity may be periodic. Among the gland cells in all parts of the organ are scattered great numbers of sensory cells of a peculiar character. These seem to correspond to the sensory cells observed upon the inferior labial lobe of the female. It is to be noted, however, that in the latter organ the sensory cells are concentrated, but in the former scattered. The inferior labial lobe is provided with a quite complex special musculature. A similar musculature is possessed by Van der Hoeven's organ.

The second cirrus of the spadix bears a set of glands hitherto undescribed. The structure of the large slime gland upon the outer surface of the spadix sheath is described. A similar gland is found in a less developed condition upon the outer side of the sheath of the antispadix. The spadix possesses a powerful muscle, extending from its base across the cephalic sheath.

The ocular tentacles are proven by their innervation to be members of the digital series, modified for a sensory function. Upon the inner side of the nerve, within the ocular tentacles, is an accessory nerve composed of many bundles of nerve fibers, which enter the primary nerve as they pass toward the central nervous system. The ocular tentacles possess "breaking planes," i. e., planes where the tissues are somewhat discontinuous, and along which the tentacles break with great ease.

Attention is called to the fact that the position of the organs of the pallial complex of Nautilus has been incorrectly figured and described by all authors except Joubin. The arrangement of these organs differs from that found in the Dibranchiata, and approaches that found in many Gastropoda. The gills, anus, preanal and interbranchial papillæ, pericardial and renal pores, and the nidamental gland are situated upon the inner surface of the mantle. The paired reproductive orifices are situated upon the body wall within the mantle cavity.

There does not yet seem to be sufficient evidence to warrant our calling certain papillæ near the bases of the gills *osphradia*. Both dissections and serial sections of the papillæ in question have failed to show the special innervation required; other observers also seem to be a little less than sure of the presence of special nerves to these papillæ.

The funnel is composed of two essentially different portions, the anterior part being fibrous, the posterior portion muscular. The crura of the funnel are so formed that they can, by a fanning motion, cause respiratory currents through the mantle chamber, and possibly currents strong enough for the progression of the animal.

The visceral portion of the body wall is thin and non-muscular. It contains a nervous plexus. It is attached to the shell by three aponeurotic bands proceeding from the ends of the shell muscles. The dorsal and posterior ventral bands limit the septum-forming portion of the body wall. A sharp backward projection of the dorsal aponeurotic band corresponds to a depression in the face of each septum in the younger half or two-thirds of the shell.

Aside from minor additions in the description of the anatomy of the digestive tract as a whole, the muscles of the buccal mass are described and figured. They are found to form a quite highly developed system.

The renal organs are found within the mantle and in the reverse position from that described by earlier authors.

Willey's sketches and my own dissections have been combined to form a nearly complete account of the arterial circulation.

Some previously undescribed nerves have been followed to their terminations, especially the nerves of the ocular tentacles, of Van der Hoeven's organ, and of the spadix and antispadix.

The ocular nerves are branches of a nerve supplying digital tentacles as well. The nerves of Van der Hoeven's organ correspond to the nerves of the inferior labial lobe in all particulars. The otocystic nerve arises from the cerebral ganglion.

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PLATE I.

FIG. 1.—A Nautilus seen from the right side, the right half of the shell having been cut away.

AV, anterior ventral aponeurotic band.
C, cirrus of a digital tentacle.
Csh, cephalic sheath, composed of the fused sheaths of digital tentacles.
CR, crus of funnel.
DM, dorsal portion of mantle.
E, eye.
F, funnel.
Ho, hood.
I, involution of shell.
O′, preocular tentacle.
O″, postocular tentacle.
PV, posterior ventral aponeurotic band.
S, living chamber of shell.
Si, siphon of shell.
Sl, siphuncle of body.
SM, area of attachment of shell muscle.
Sp, lat-formed septum.
VM, ventral portion of mantle. This is free from the body from the edge as far back as the anterior ventral aponeurotic band.

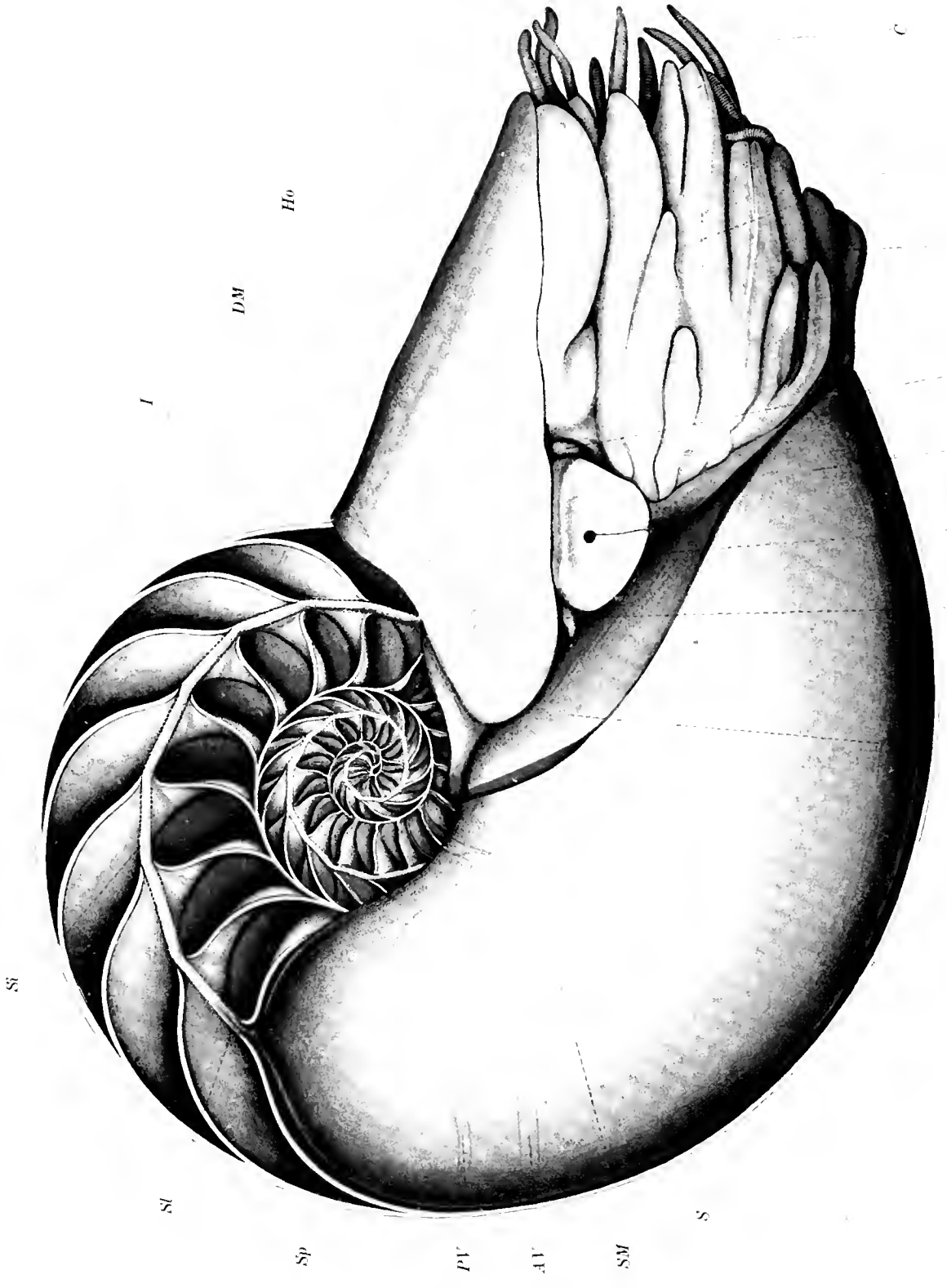


Fig. 1.

PLATE II.

FIG. 2.—View of the dorsal side of a Nautilus removed from its shell.

CR, crescentic ridge on the posterior face of the hood

DA, dorsal aponeurotic band

DM, dorsal portion of mantle. The index line points to a depression in the dorsal side of the body into which fits the involution of the shell.

DT^2, second digital tentacle.

E, eye.

HoA, auricle of hood.

HoC', HoC, cirri of tentacles composing the hood.

O', preocular tentacle

Si, base of siphuncle.

X, backwardly projecting point of dorsal aponeurotic band, which is evidently the cause of the small backward projections near the dorsal edges of the septa, shown in Fig. 1.

y, constriction of the siphuncle where it passes through a septum.

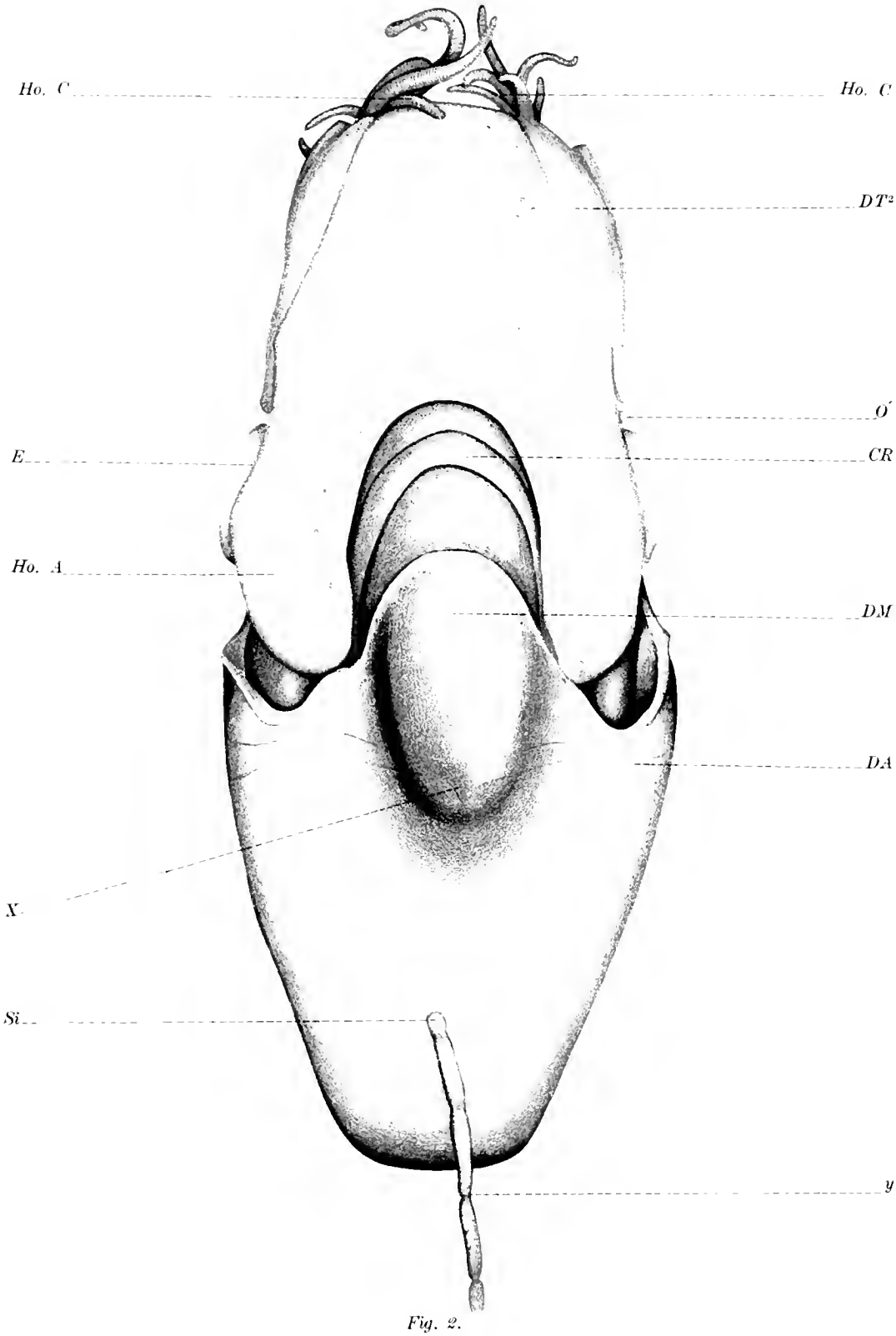


Fig. 2.

PLATE III.

FIG. 3.—Male viewed from the ventral surface; the mantle has been turned back over the posterior end of the body, exposing its inner surface and the organs contained in the mantle chamber.

A, anus.
DT, digital tentacles, composing the cephalic sheath.
E, eye.
F, tunnel.
IP, interbranchial papilla.
O″, postocular tentacle
P, penis.
PA, preanal papilla
PP, pericardial pore.
RA, anterior renal pore.
RP, posterior renal pore.

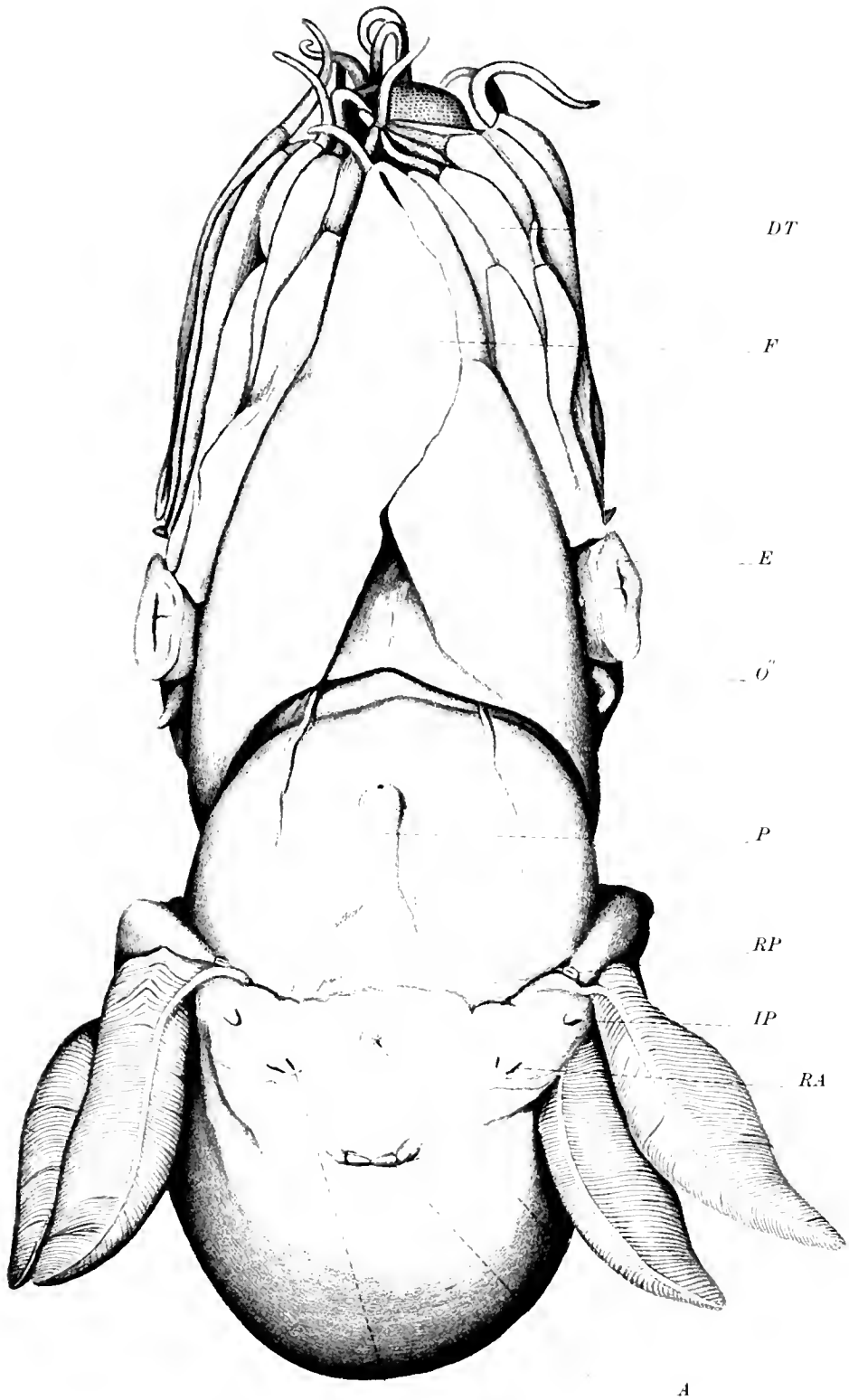


Fig 3

PLATE IV.

FIG. 4.—Mantle chamber of female viewed from the ventral side. The mantle has been turned back over the posterior end of the body.

B, raised and overlapping border of the nidamental gland.
BV, branchial vein of the anterior gill.
F, base of funnel.
GA, anterior gill.
GP, posterior gill.
LM, lateral portion of mantle.
N, nidamental gland.
OV, protruding end of oviduct; oviducal papilla.
PA, preanal papillæ.
SM, shell muscle.
VM, ventral portion of mantle.
Y, thickened portion of mantle between the inturned ends of the nidamental gland.

FIG. 5.—Cephalic region of female viewed from the dorsal side. The hood has been slit open along the median line to show the arrangement of the labial lobes and tentacles.

B, buccal mass.
CR, crescentic ridge upon the posterior face of the hood.
DM, dorsal portion of the mantle.
Ho, hood.
L, lamellated organ upon the center of the inferior labial lobe. The fan-like cirrus-bearing portions of the lobe are seen at the sides of the lamellated organ.
SLL, superior labial lobe.

FIG. 6.—Funnel, opened and viewed from the ventral side.

C, infundibular portions of the cartilage showing through the integument of the dorsal wall of the funnel.
CR, crus of funnel.
L, ligamentous band of the integument extending from the posterior edge of the funnel backward over the surface of the shell muscle.
M, shell muscle,
V, valve of funnel

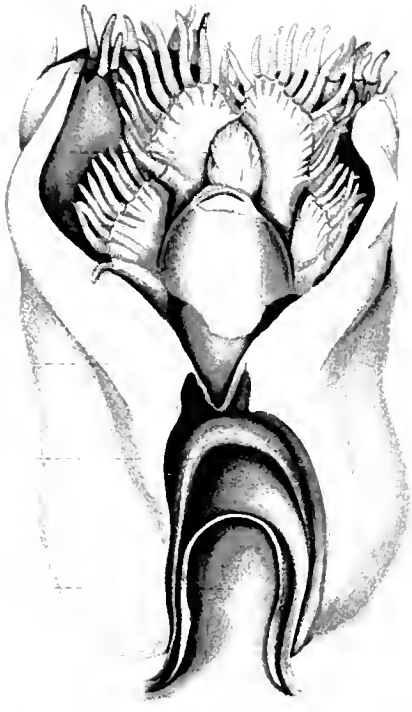


Fig. 5.

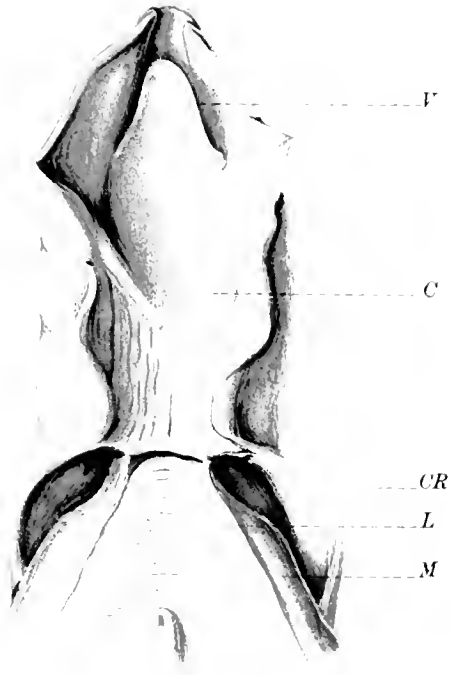


Fig. 6.

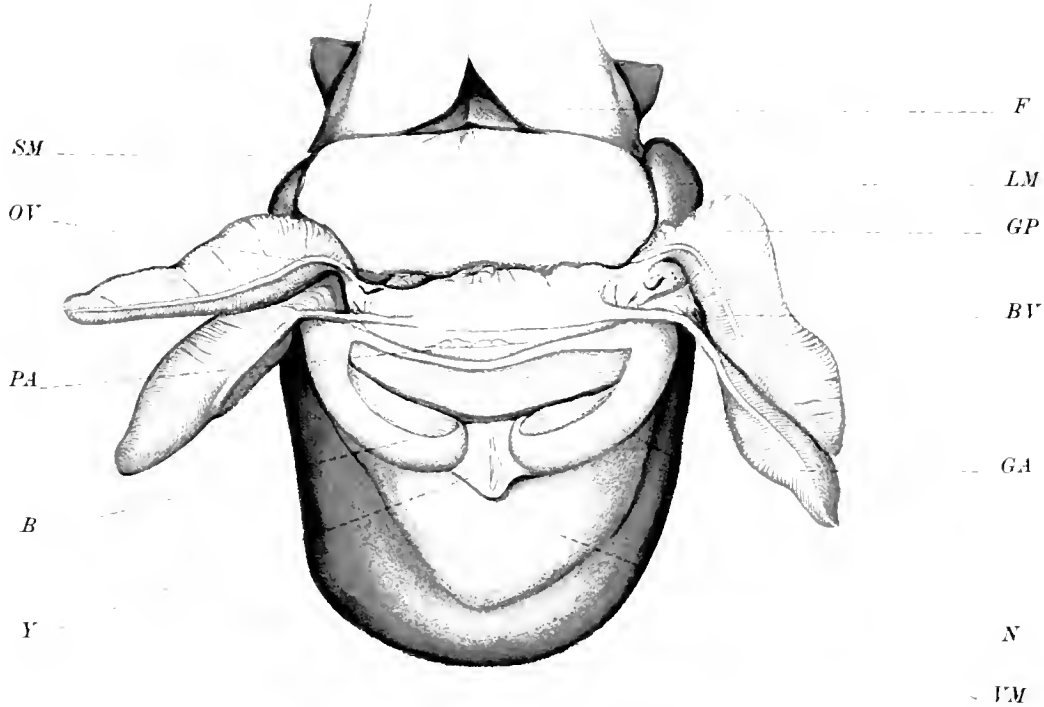


Fig. 4.

PLATE V.

Fig. 7.—Male, viewed from the dorsal surface. The hood, mantle, and body wall have been cut open in the median line in order to show the mouth parts, the haemocœl, and the cœlom, with their contained organs.

Ao, aorta.
ASp, antispadix.
B, buccal mass.
BM, buccal membrane, cut open dorsally to show the tips of the jaws.
BW, wall of the posterior portion of the body.
CR, crescentic ridge upon the posterior face of the hood.
DBR, dorsal buccal retractor muscle.
DM, dorsal portion of the mantle cut open and folded down.
DT, digital tentacles.
GL, genital ligament.
Ho, hood.
L, L, lobes of the liver, covered by the haemocœlic membrane.
Oe, œsophagus, lying in the haemocœl.
S, siphuncle.
SLL, superior labial lobe.
Sp, spadix.
St, stomach.
T, testis.
UJ, upper jaw.
VM, ventral portion of mantle.
X, junction of the haemocœlic membrane and body wall along the line of the dorsal aponeurotic band.

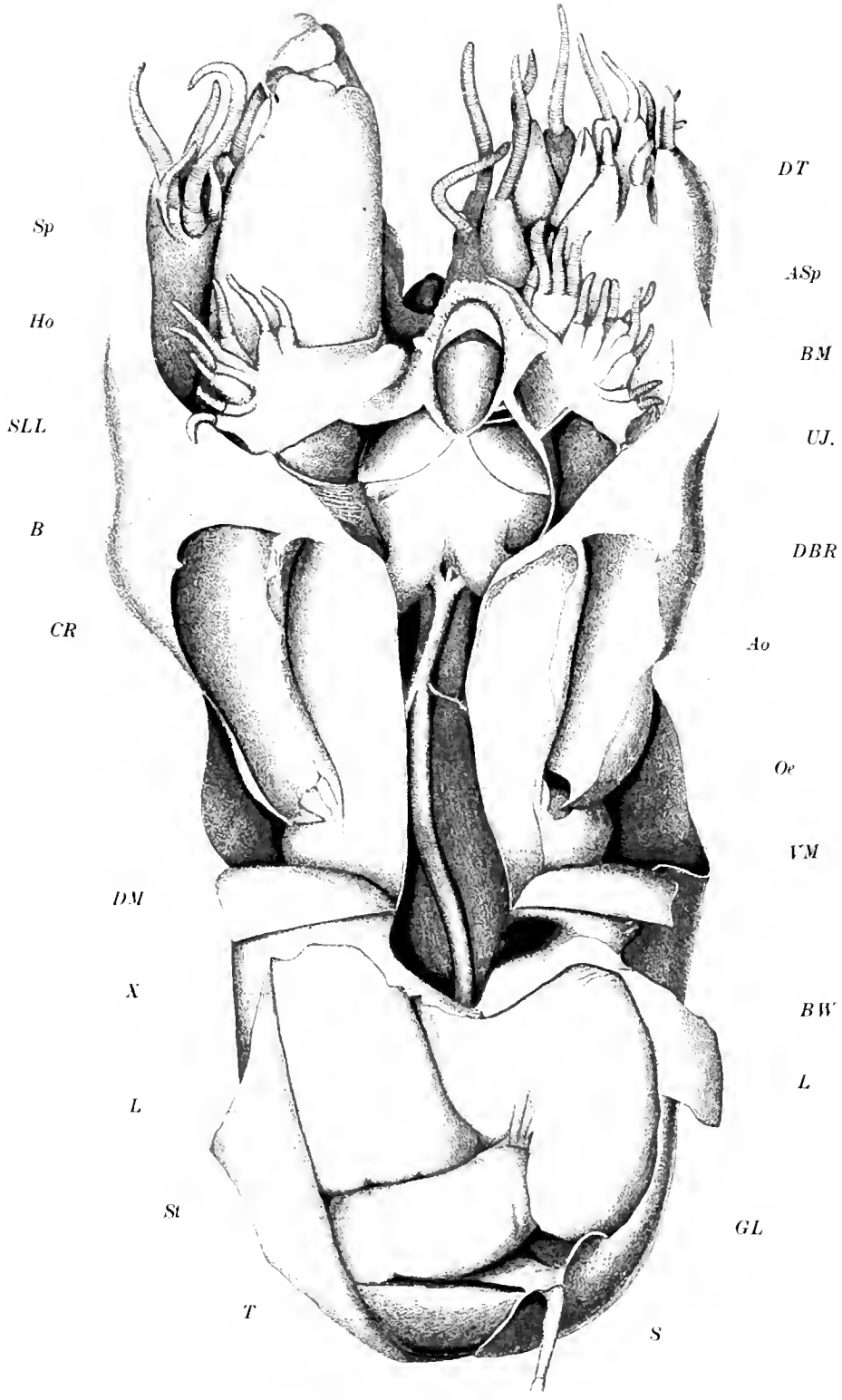


Fig. 7.

PLATE VI.

Fig. 8.—Ventral view of Van der Hoeven's organ. × 2.

L, vertical laminæ.

N, nerve.

VF, vertical fissure.

W, wall of the pocket, or atrium, into which the anterior end of the organ projects cut from its attachment to the organ and folded to one side.

1, 2, 3, muscles of the organ.

Fig. 9.—Longitudinal section of Van der Hoeven's organ, taken through the median vertical fissure. (The ventral side is uppermost.) × 2.

G, G, glandular portion of the organ.

HF, horizontal fissure.

L, horizontal laminæ.

Fig. 10.—Cross section of Van der Hoeven's organ taken just back of the middle of the organ. (The ventral side is uppermost.) × 2.

Fig. 11.—Shell of *Nautilus pompilius*. ½ natural size.

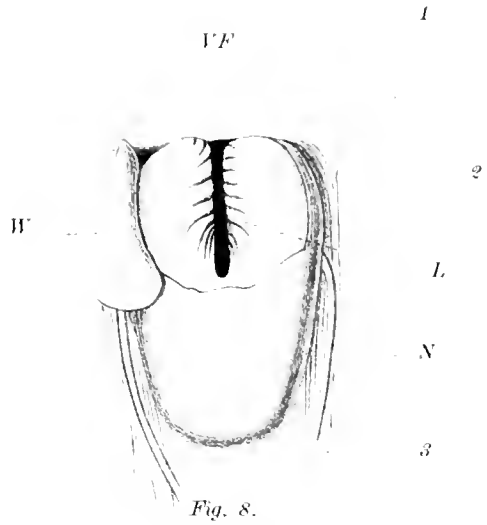


Fig. 8.

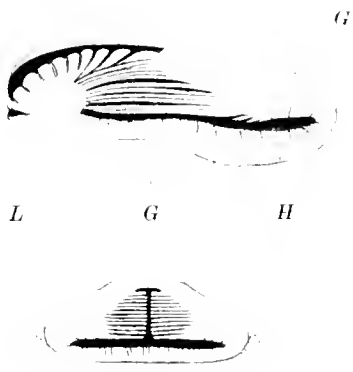


Fig. 10.

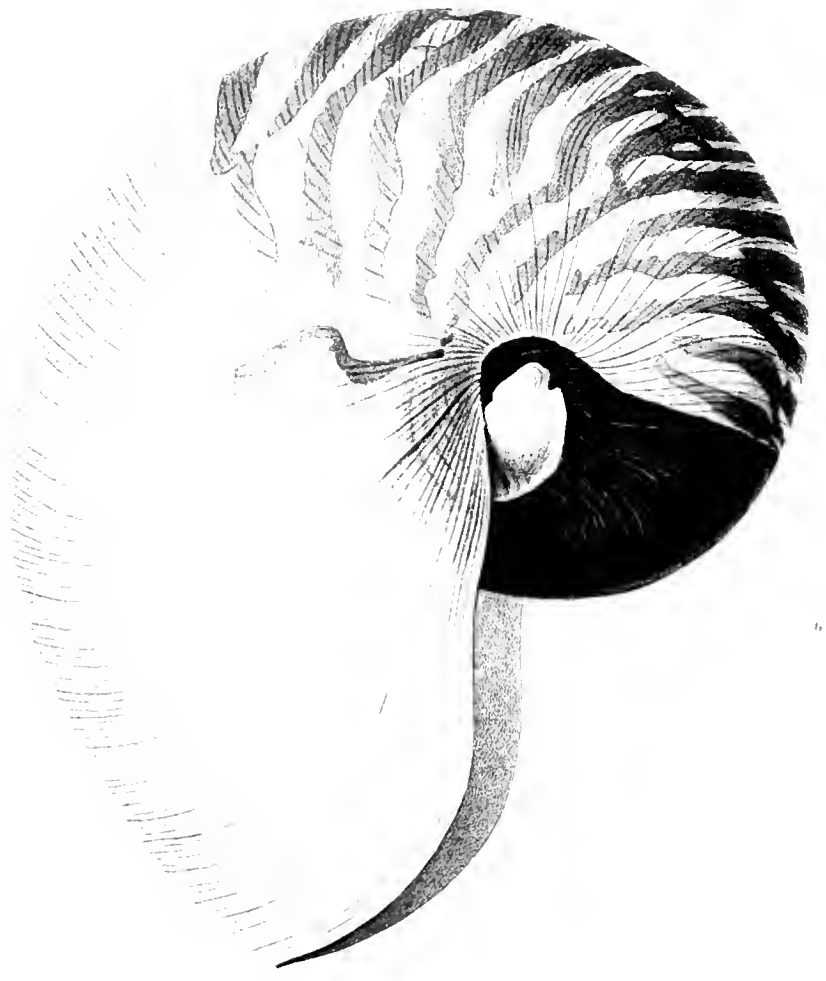


Fig. 11.
Shell.

PLATE VII.

FIG. 12.—Antispadix, viewed from the outer side. Nearly twice natural size.
G, slime gland upon the sheath of the antispadix.
F, projecting flap of the sheath, partly covering the fourth tentacle.
4, fourth tentacle.

FIG. 13.—Spadix, viewed from the inner side. The loose integument covering its base has been cut away. Natural size.
1, first cirrus.
2, second cirrus.
3, third cirrus.

FIG. 14.—Spadix, viewed from the outer side. Natural size.
G, slime gland of the sheath.
SH, line along which the integument has been cut away to expose the base of the spadix.
1, first cirrus.
2, second cirrus.
3, third cirrus.
4, fourth cirrus, nearly covered by the projecting flap of the spadix sheath.

FIG. 15.—First cirrus of the spadix. Nearly natural size.

FIG. 16.—Second cirrus of the spadix, viewed from the ventral side. Natural size.

FIG. 17.—Third cirrus of the spadix, viewed from the dorsal side. Natural size.

FIG. 18.—Third cirrus of the spadix, viewed from the ventral side. Natural size.

FIG. 19.—Fourth cirrus of the spadix. Natural size.

FIG. 20.—Lamellated organ upon the median portion of the inferior labial lobe of the female, viewed from the dorsal side. Twice natural size.

FIG. 21.—Rhinophore, viewed from the anterior side. × 3.
DP, aperture of the dorsal pit.
F, aperture of the fossa.

FIG. 22.—Longitudinal section of the rhinophore passing through the fossa and the tentacle.
a, nerve.
b, c, portions of the fossa. c is near the opening of the fossa to the exterior. The section does not extend to the closed central end of the fossa. The heavy outer line indicates the extent of the external epithelium. Only as much of the rhinophore as is bounded by this line extends beyond the surface of the body.

FIG. 23.—Cross section through the middle of a gill. × 2.
1, branchial vein.
2, branchial artery.
3, stem of gill.
4, respiratory membrane of leaflet.
5, supporting portion of leaflet.

FIG. 24.—Lamellated region upon the inner surface of the cephalic sheath of the female, just back of the ventral notch, which forms an organ for receiving the spermatophore. Below the lamellated region the tip of the funnel is seen; at the sides, some of the most ventral digital tentacles. Twice natural size.

FIG. 25.—Spermatophore *in situ* upon the lamellated receiving region. Natural size.

FIG. 26.—Base of the inferior labial lobe of the female, seen from the dorsal side. × 2.
1, 1′, levator muscles.
2, 2′, approximator muscles.
3, 4, 3′, 4′, lateral retractor muscles.
5, dorsal median retractor muscle.

Fig. 13.

Fig. 14.

Fig. 18.

Fig. 17.

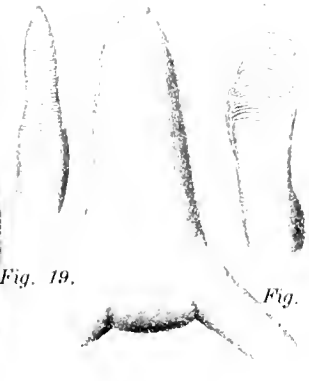


Fig. 19.

Fig. 16.

Fig. 15.

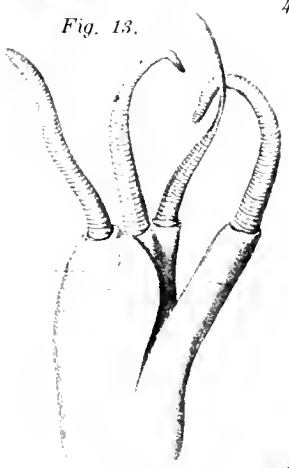
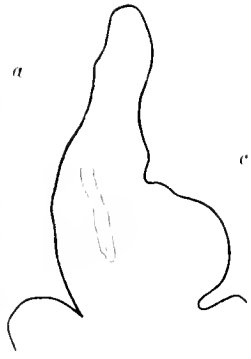


Fig. 12.

Fig. 21.

Fig. 23.



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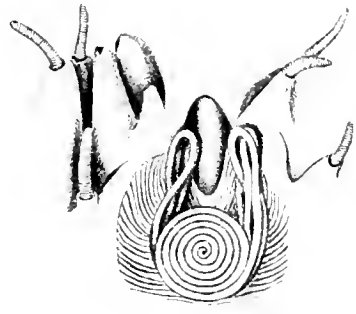


Fig. 22.

Fig. 25.

Fig. 24.

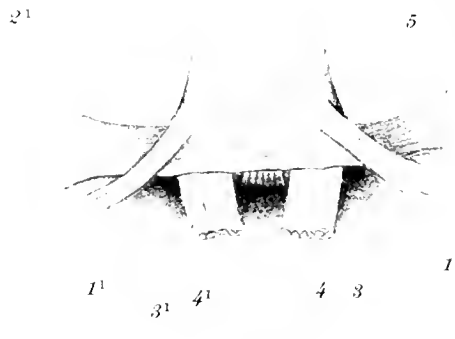


Fig. 26.

PLATE VIII.

FIG. 27.—Dorsal view of the digestive organs. Natural size.

Ao, dorsal aorta, dividing into innominate and buccal arteries.
B, buccal mass.
C, C, posterior columellar arteries.
Coe, cœcum.
GL, gastric ligament.
H, hepatic artery.
I', first loop of the intestine around the cœcum.
I², posteriorly directed portion of the second loop of the intestine.
I³, anteriorly directed portion of the second loop of the intestine.
IA, intestinal artery.
IL, intestinal ligament.
L, L, left lobes of the liver.
L', L', right lobes of the liver.
Oe, œsophagus (proventriculus).
PA, anterior proventricular artery.
PN, PN, pallio-nuchal arteries.
PP, posterior proventricular artery.
St, stomach.

FIG. 28.—Dorsal view of the buccal mass, the buccal membrane and enveloping muscular membrane being cut in the median dorsal line and opened. × 2.

Ao, aorta, dividing into innominate and buccal arteries.
BM, buccal membrane.
CG, cerebral ganglion, giving off nerves to the buccal mass.
DLR, dorso-lateral buccal retractor muscles.
DR, dorsal buccal retractor muscle.
LJ, tip of lower jaw.
LJ', posterior portion of the outer flange of the lower jaw.
LM, levator muscle of the buccal mass.
M, mandibular muscle.
MM, enveloping muscular membrane.
N, nerves to the buccal membrane.
Oe, œsophagus.
UJ, upper jaw.
X, buccal membrane, passing onto the base of the superior labial lobe.

FIG. 29.—The buccal mass turned upward and backward so as to show its ventral surface and the dorsal surface of Van der Hoeven's organ. Natural size.

FIG. 30.—Side view of the upper jaw. × 2.

FIG. 31.—View of the inner surface of half of the lower jaw, cut in order to show the small inner flange. × 2.

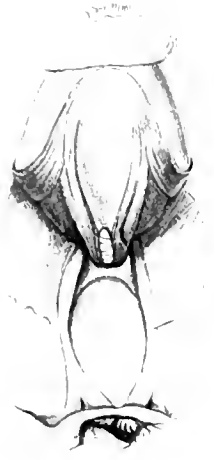


Fig. 29.

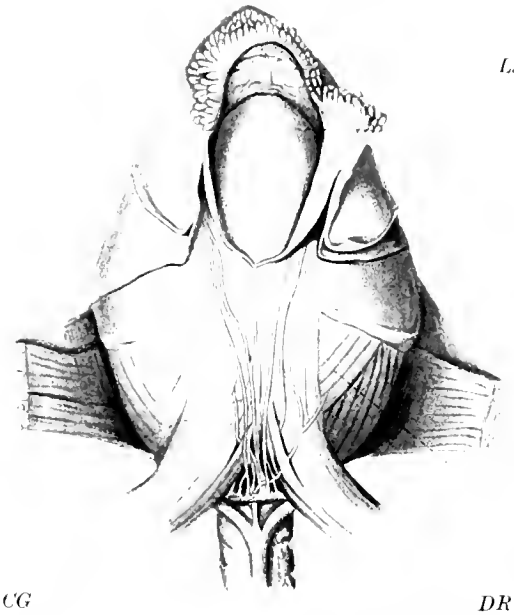


Fig. 28.

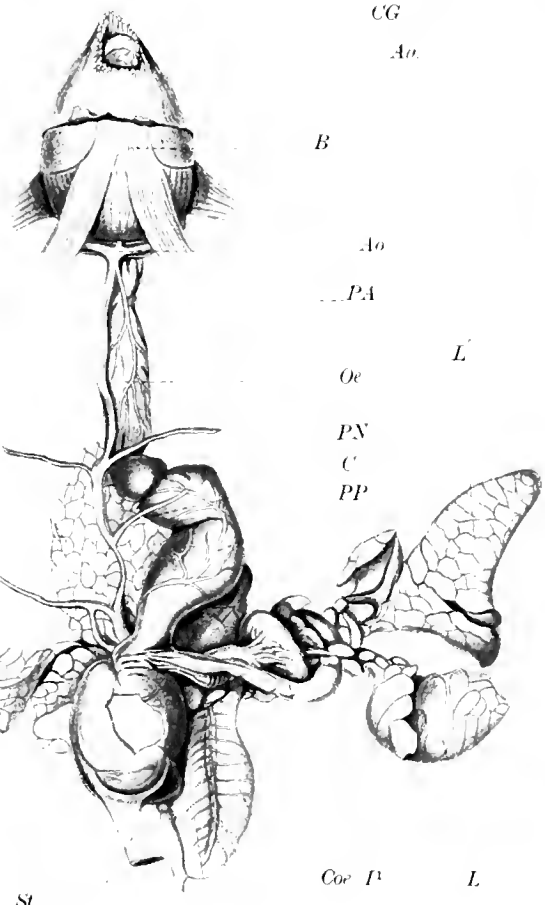


Fig. 27.

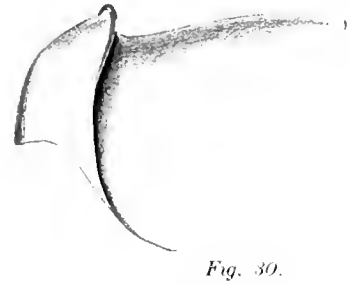


Fig. 30.
upper jaw.

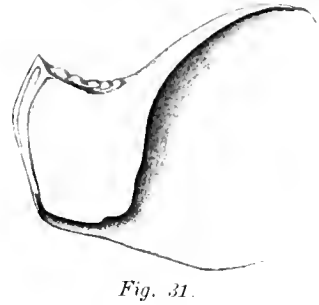


Fig. 31.

PLATE IX.

FIG. 32.—Alimentary canal opened along the dorsal side. Natural size.
AP, anterior prelingual process.
BM, buccal membrane.
C, cœcum, showing its projecting lamellæ.
HD, openings of the hepatic ducts into the cœcum.
LJ, lower jaw.
MM, mandibular muscle.
Oe, œsophagus.
PP, posterior prelingual process.
Pr, proventriculus.
R, radula.
Re, rectum.
S, saccular posterior portion of the stomach.
SO, salivary pore.
SP, salivary process.
T, tentacles of the stomach.
Tn, tongue.
UJ, upper jaw.
V, vestibule.
X, apparently permanent ridges of the œsophagus.
1, 1, intestinal ridge.
2, intestinal ridge.
3, 3, intestinal ridge.
4, foliaceous ridge.

FIG. 33.—Ventral view of the buccal mass, a portion of its muscular membrane having been folded back. × 2.
BG, buccal ganglion.
BM, buccal membrane, cut and turned forward over the tip of the jaw.
LJ, outer flange of the lower jaw.
LM, levator muscle of the buccal mass.
M, mandibular muscle; this ends ventrally along the edge of the upper jaw.
MM, muscular membrane of the buccal mass.
N^1, outer cerebro-buccal connective.
N^2, inner cerebro-buccal connective.
Oe. M, membrane surrounding the base of the œsophagus and connecting with the membrane surrounding the central nervous system.
OM, part of the membrane stretched between the ventral buccal retractors.
Ph. G, pharyngeal ganglion.
RL, ligament of the radular sac.
RS, radular sac.
VBR, ventral buccal retractor muscle.
1, retractor of the anterior prelingual process.
2, retractor of the posterior prelingual process.
3, 3, unpaired muscle, forked posteriorly, going to the posterior prelingual process.
4, muscle extending into the posterior prelingual process, and also to the portion of the tongue anterior to the upwardly directed part of the radular sac.
5, muscle to the anterior portion of the tongue.
6, muscle to the membrane covering the projection of the upper jaw.
7, muscle to the dorsal surface of the radular sac.
8, Muscle which probably plays a share, at least, in the opening of the jaws.
9, origins of muscles 1, 2, 7, upon the inner surface of the muscular membrane.

FIG. 34.—Dorsal view of the buccal mass, the enveloping muscular membrane having been cut along the median line. The view is also somewhat from behind. × 2.
A, branches of the superior mandibular artery penetrating the mandibular muscles.
BM, buccal membrane, also slit open dorsally.
LJ, tip of lower jaw.
M, mandibular muscle.
MM, muscular membrane of the buccal mass.
Oe, œsophagus, swollen at one place by food which remained in it when the animal died.
UJ, tip of the upper jaw.
UJ′, posterior edge of the inner flange of the upper jaw.

FIG. 35. The radular sac and the lingual muscles of one side exposed and viewed from the ventral side. × 2.
EL, external lingual muscle.
EL′, cut end of the external lingual muscle.
IL, internal lingual muscle.
LP, lingual protractor muscle.
R, radular muscle.
R′, cut end of the radular muscle.
Ra, radula.
RS, radular sac.
S, septum extending from the dorsal median line of the tongue to the muscular membrane just above the radular sac, which has been cut away from the exposed side of the preparation.
T, tendinous area where the lingual muscles join.
X, division of the septum.
Y, point of the upper jaw to which the lingual protractor is attached.

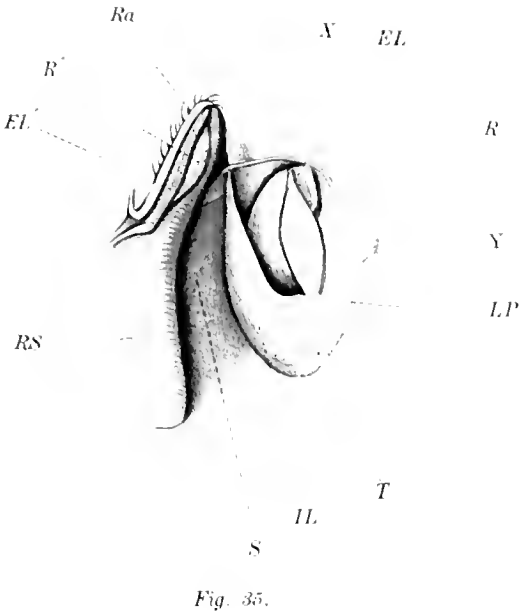


Fig. 35.

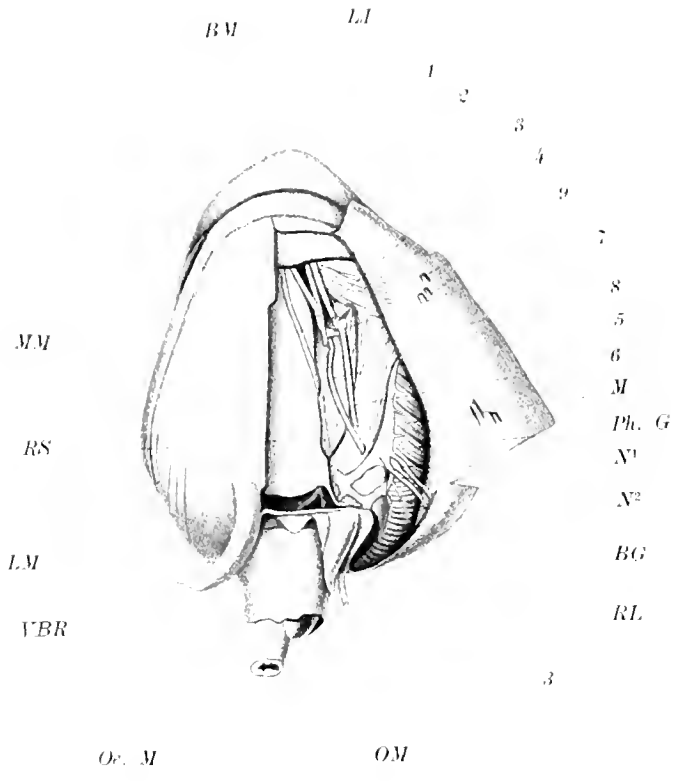


Fig. 33.

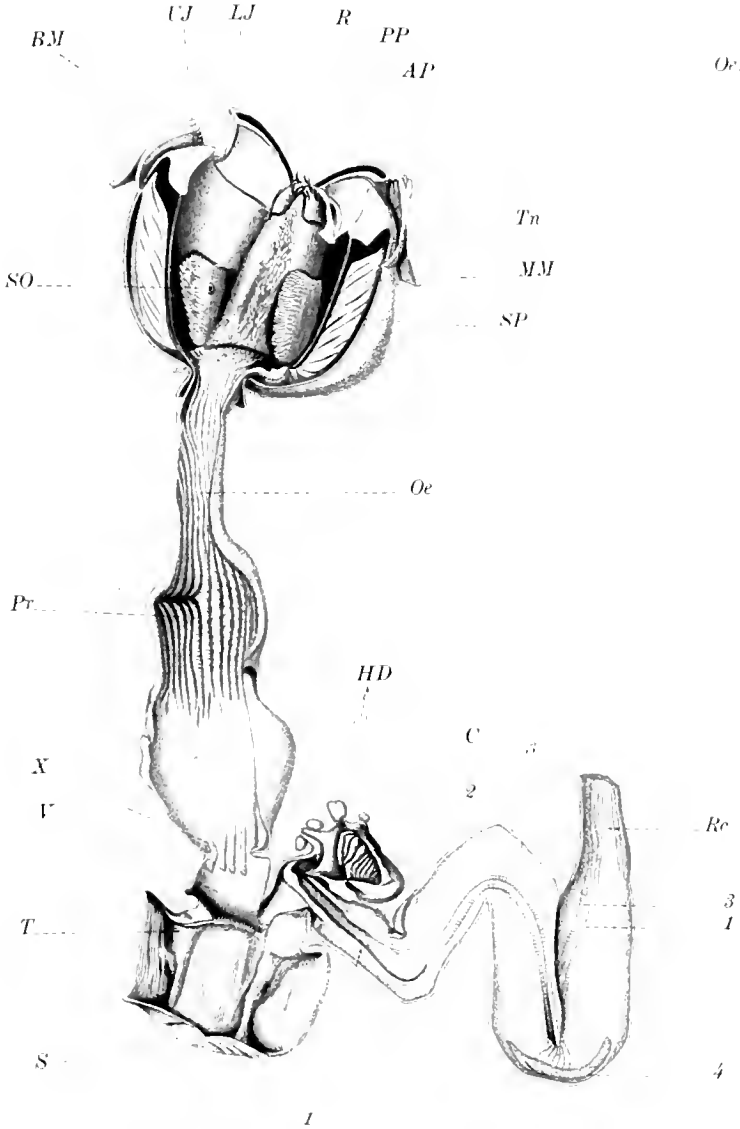


Fig. 32.

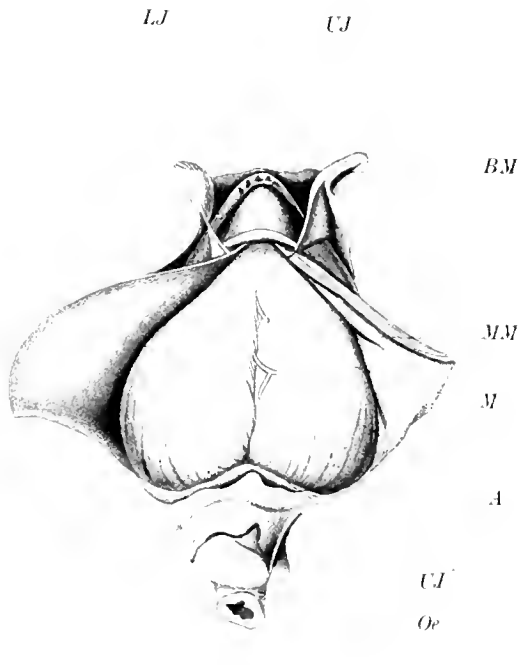


Fig. 34

PLATE X.

Fig. 36.—The ventral portion of the body wall is cut open and reflected to show the pericardial chamber. Natural size.

a. br. v., anterior branchial vein; in this case collapsed and not forming an auricular expansion.

a. p. g., anterior pericardial gland. The one to the left lies naturally; the one on the right has been turned upward to show the anterior branchial vein.

H, heart, enfolded by the pallio-visceral ligament. The septal artery runs over its ventral surface, suspended by a mesentery-like fold of the pallio-visceral ligament, and through the posterior viscero-pericardial aperture.

j, junction of the body wall and the pallio-visceral ligament posteriorly.

l, ligament from the ventral edge of the posterior renal sac extending along the body wall.

p. a., pallial artery.

p. br. v., posterior branchial vein, partly expanded.

p. p. g., posterior pericardial gland.

p. v. a. b., posterior ventral aponeurotic band.

p. v. l., pallio-visceral ligament. The three apertures through it by which the pericardial and genital divisions of the cœlom are put in communication are at either side of and behind the heart.

p. v-p. ap., posterior viscero-pericardial aperture.

pyr. s., pyriform sac.

r. s., anterior wall of the right posterior renal sac.

Fig. 37.—Renal appendages from the posterior wall of one of the renal sacs. × 2.

Fig. 38.—Male genital organs viewed from above and in front. The anterior portion is represented as dissected from the body wall. Natural size.

ac. gl., accessory gland surrounding the vas deferens.

ao, aorta, passing upward from the heart at the back of the hæmocœlic membrane.

g. l., genital ligament.

gas. l., gastric ligament.

I, intestine, cut at the middle of the second loop.

Il., intestinal ligament.

P. ap., external opening of the penis.

P. l., left tube of the penis.

P. r., right tube of the penis.

p-v. l., pallio-visceral ligament at its attachment to the posterior side of the heart.

pyr. ap., external aperture of the pyriform sac.

pyr. s., pyriform sac.

r., rectum.

sep., septum dividing the spermatophore sac.

sp. s., spermatophore sac.

S. V., seminal vesicle.

T. ap., aperture of testis.

T. g., face of the testis which is pressed against the stomach.

T. l., face of the testis which is pressed against the liver.

v. d.¹, proximal thin-walled portion of the vas deferens.

v. d.², commencement of the thick-walled portion of the vas deferens, which extends from this point to the seminal vesicle.

x, thickening of the tissues of the genital ligament extending from the root of the siphuncle.

y, tunic of the accessory gland carried upon the back of the testis.

Fig. 39.—Female genital organs viewed from in front and above. The anterior portion of the ovary rests upon the pallio-visceral ligament. The heart and auricles show through the viscero-pericardial apertures. Natural size.

ao. aorta.

ex. ap., external aperture of the oviduct.

g. l., attachment of the genital ligament to the posterior body wall.

gas. l., gastric ligament.

I., intestine.

Il., intestinal ligament.

l a., line along which the hæmocœlic membrane is attached ventrally.

l. v-p. ap., left anterior viscero-pericardial aperture.

Ov., ovary.

Ov. ap., aperture of the ovary slightly pulled away from the inner aperture of the oviduct.

ovid., thin-walled portion of the oviduct.

ovid. ap., inner aperture of the oviduct.

ovid. pap., plaited, freely projecting tip of the oviduct, the ovidneal papilla.

p. au., posterior auricle.

pyr. ap., opening of the pyriform sac into the mantle cavity.

pyr. s., pyriform sac.

r. l., ligament attaching the rectum to the pallio-visceral ligament.

r. v-p. ap., right anterior viscero-pericardial aperture.

s., nodule in the genital ligament at the root of the siphuncle.

Fig. 40.—Cartilage viewed from the anterior side. Natural size.

c., cephalic process.

i., intermandibular process.

l. i., point of attachment of the levator of the funnel.

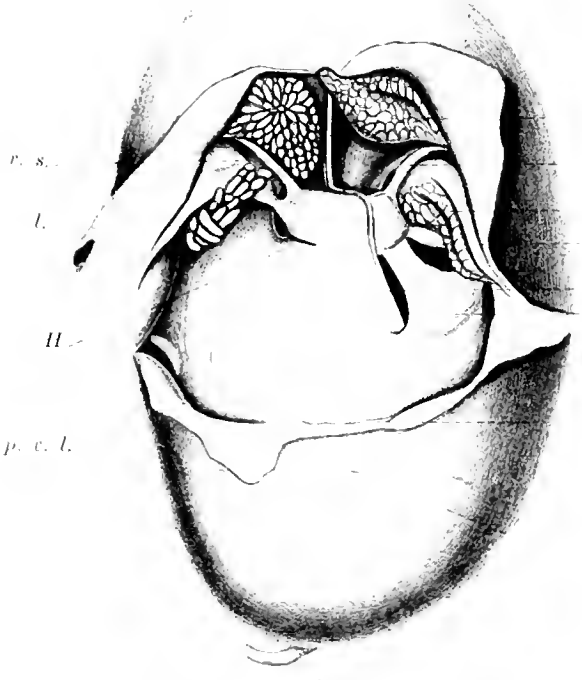
m. p., median process of the body of the cartilage.

v, v', holes through the cartilage occupied by veins.

Fig. 39.

Fig. 38.

p. a.



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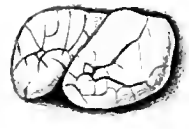

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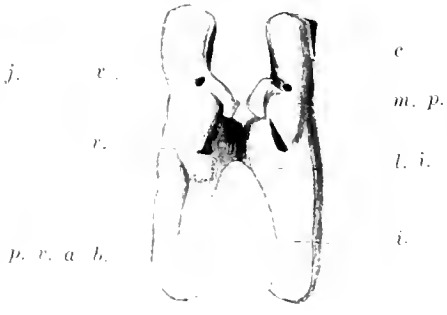

Fig. 40.

PLATE XI.

FIG. 41.—Nervous system, dissected and viewed from the dorsal side. × 2.

1, nerve to mandibular muscle.
2, pharyngeal commissure.
3, nerves to mandibular muscle.
4, pharyngeal ganglion.
5, outer cerebro-buccal connective.
6, inner cerebro-buccal connective.
7, right nerve of the inferior labial lobe.
8, infundibular nerve.
9, nerves to digital and superior labial tentacles.
10, large nerve innervating hood and digital tentacles.
11, nerve of postocular tentacle; the other branch of this nerve innervates the preocular tentacle and the posterior portion of the hood, and sometimes digital tentacles.
12, cerebral ganglion.
13, pleuro-visceral ganglion.
14, nerves to shell muscle and the body wall.
15, nerve to the walls of the vena cava, in this case springing from the visceral nerve, 22.
16, Nerves to the spermatophore sac and the genital duct.
17, nerve seeming to go to the posterior wall of the anterior renal sac.
18, nerve seeming to go to the posterior wall of the posterior renal sac.
19, posterior branchial nerve.
20, anterior branchial nerve.
21, nerve to the wall of the vena cava, in this case arising directly from the pleuro-visceral ganglion.
22, visceral nerve.
23, nerves from the outer end of the cerebral ganglion to the posterior portion of the hood.
24, base of the optic nerve, which may be a ganglion.
25, portion of the optic nerve in the stalk of the eye.
26, branches of the optic nerve in the capsule of the eye.
27, nerves proceeding from the cerebral ganglion to the dorsal side of the buccal mass, some being distributed to the mandibular muscles, but most passing to the papillæ on the edge of the buccal membrane.
28, pedal ganglion.
29, pedal commissure.
30, nerve proceeding to the base of the spadix, and there ending in an enlargement from which several fine nerves go to the tissues of the spadix.
31, nerve to œsophagus.
32, buccal ganglion.
33, buccal commissure.
34, nerve to salivary gland.
35, ganglion of inferior labial lobe (or Van der Hoeven's organ).

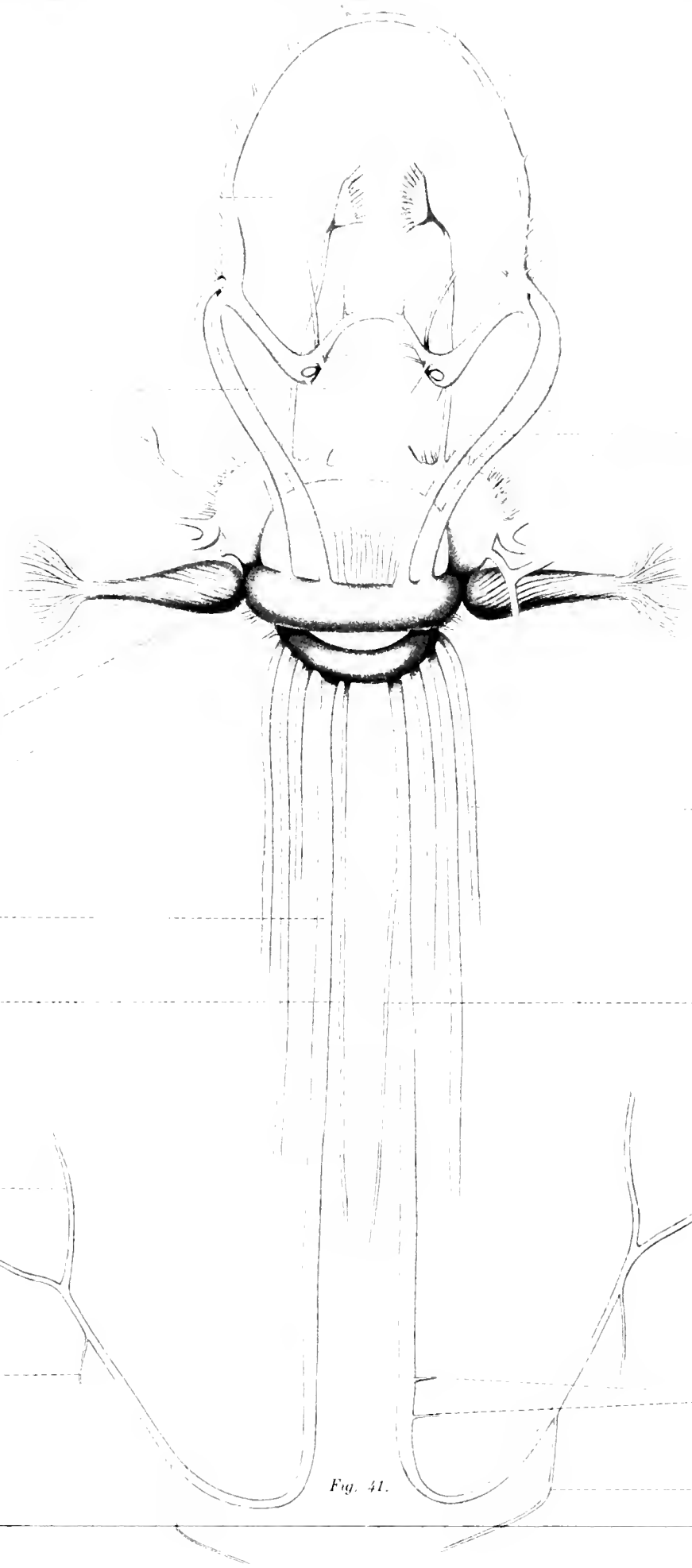
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Fig. 41.

PLATE XII.

Fig. 42.—Central tooth of the radula

Fig. 43.—First lateral tooth of the radula.

Fig. 44.—Second lateral tooth of the radula.

Fig. 45.—Third lateral tooth of the radula.

Fig. 46.—Fourth lateral tooth of the radula.

Fig. 47.—Fifth lateral tooth of the radula.

Fig. 48.—Sixth lateral tooth of the radula.

Fig. 49.—Cross section of a digital tentacle. C. L. × 15.

C, cirrus.

SH, sheath.

Fig. 50.—Longitudinal section of the tip of a digital tentacle. C. L. × 20.

A, artery.

G, G, annular grooves between ridges.

LM, fasciculi of longitudinal muscles.

N, nerve.

R, suctorial ridge.

SH, tip of sheath of cirrus.

T, transverse muscle layer.

V, vein.

Fig. 44

Fig. 46.

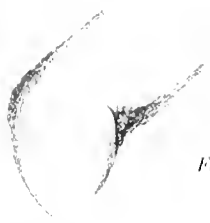


Fig. 48.

Fig. 43.

Fig. 42.

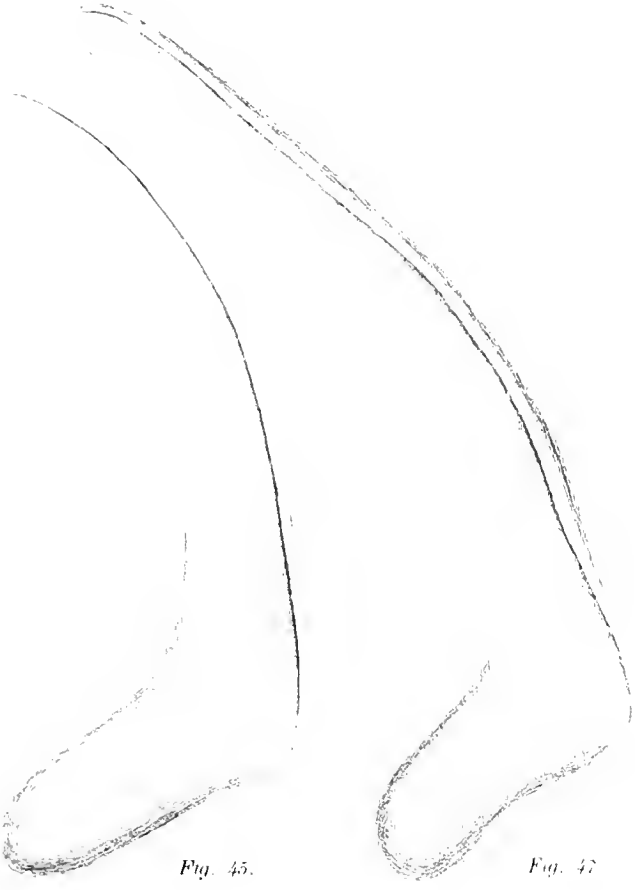


Fig. 45.

Fig. 47

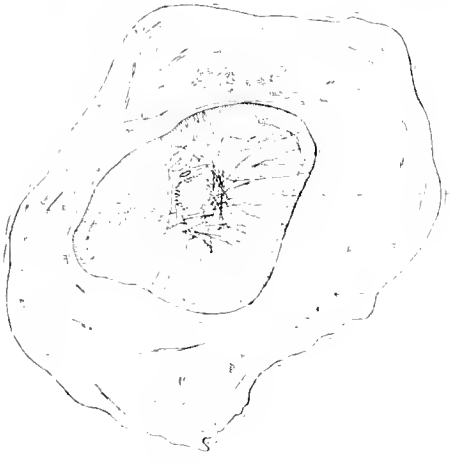


Fig. 49.

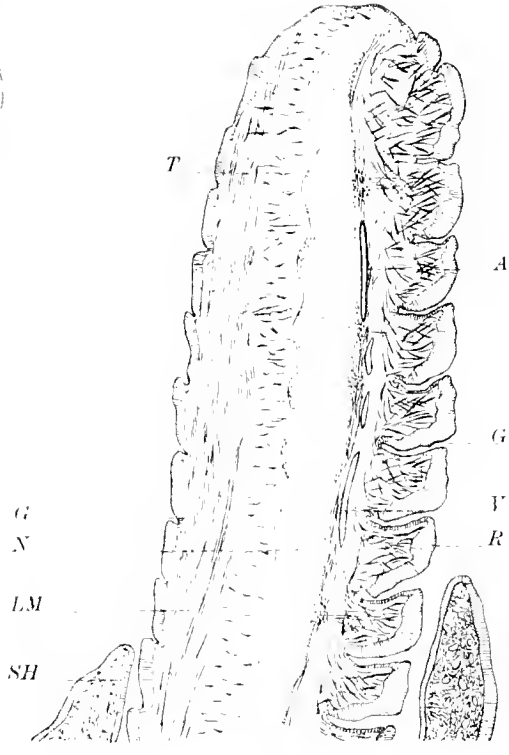


Fig. 50.

PLATE XIII.

FIG. 51. Cross section of a cirrus of the superior labial group of a male. C. L. — 20.

A, artery.

CM, circular muscle layer.

E, thickened epithelium of the inner (sensorial) surface of the annular ridge.

LM, radially arranged longitudinal muscles.

LM′, outer layer of longitudinal muscles.

N, nerve.

OM, oblique muscle layer.

RM, radiating transverse muscle fibres inside the projecting portion of the annular ridge.

TM, transverse muscle fibres surrounding the nerve and radiating outward between the longitudinal muscles.

V, vein.

FIG. 52. Longitudinal section of the tip of the first cirrus of the spadix. C. L. — 14.

N, nerve.

TM, alternating layers of transverse muscle fibres.

V, vascular corium of the tip of the cirrus.

FIG. 53. Cross section of the first cirrus of the spadix. C. L. — 7.

A, artery.

N, nerve.

V, V, veins.

FIG. 54. Cross section of the fourth cirrus of the spadix. C. L. — 14.

FIG. 55. Longitudinal section of a gland of the second cirrus of the spadix. C. L. — 60.

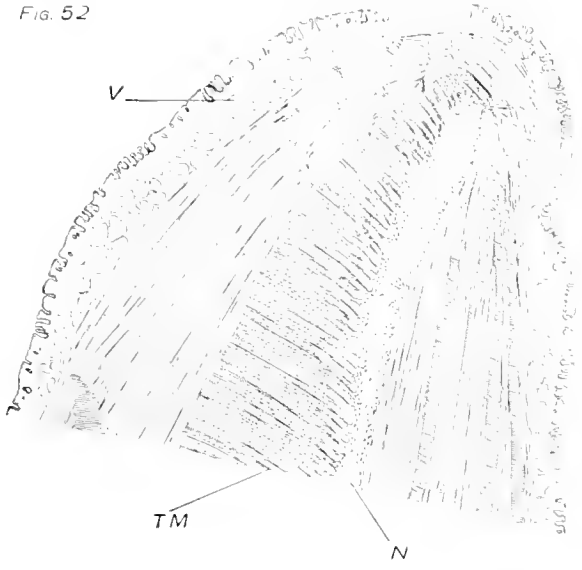
U, epithelium of the dorsal surface of the cirrus.

G, secretory epithelium.

L, lumen of gland.

N, neck of gland.

FIG. 52



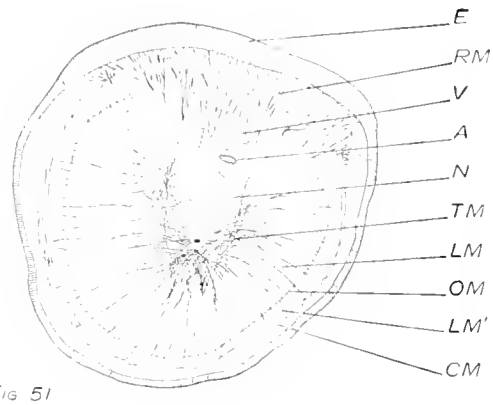


FIG 51

FIG 54

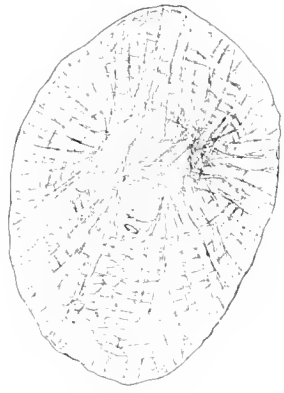


FIG 53

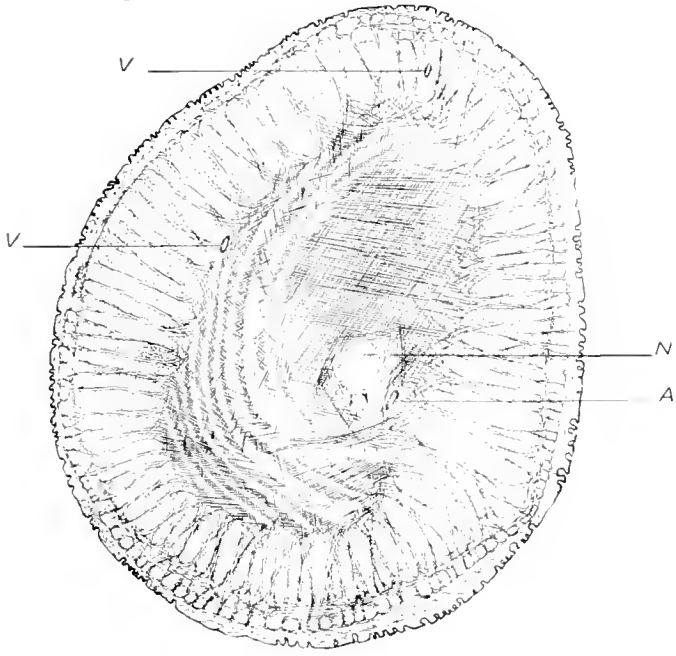
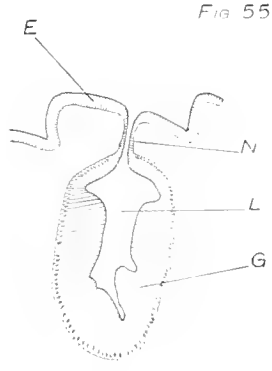


FIG 55



L. E. Griffin, Del.

PLATE XIV.

FIG. 56.—Slightly oblique cross section of the second cirrus of the spadix. C. L. × 12.

A, artery.

G, gland.

GL, layer of glands.

N, nerve.

V, vein.

FIG. 57.—Section through the slime gland on the sheath of the spadix perpendicular to the surface. C. L. × 20.

A, a single cell of the glandular epithelium highly magnified. Camera lucida outline. Magnification about 400 diameters.

FIG. 58.—Longitudinal section of the tip of the fourth cirrus of the spadix. C. L. × 10.

N, nerve.

V, vascular sinuses of the body of the cirrus.

V′, vascular sinuses in the ridges upon the outer side of the cirrus.

FIG. 59.—Slightly oblique cross section of the third cirrus of the spadix. C. L. × 14.

A, artery.

Cr, crypt, with projecting tongue. By following the series of sections shown by each row of crypts the manner in which the tongue projects from the wall of the crypt may be made out.

CrL, layer of crypts.

V, vein.

FIG. 60.—Longitudinal section of the tip of the third cirrus of the spadix. C. L. × 8.

Cr, crypt.

N, nerve.

FIG 56

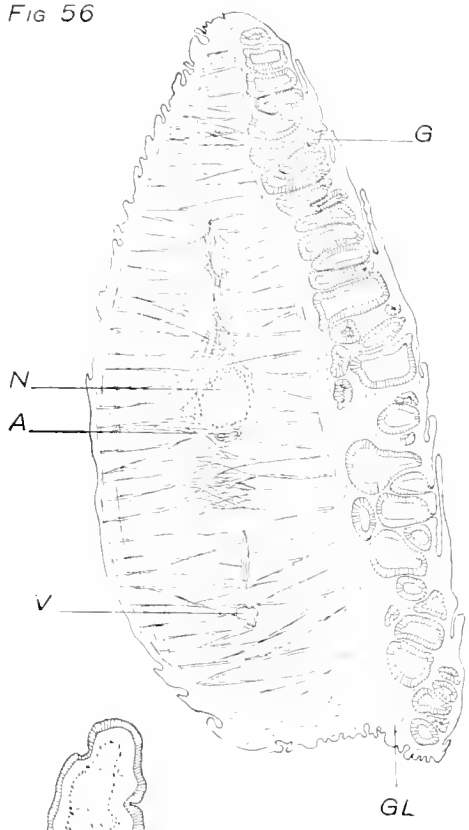
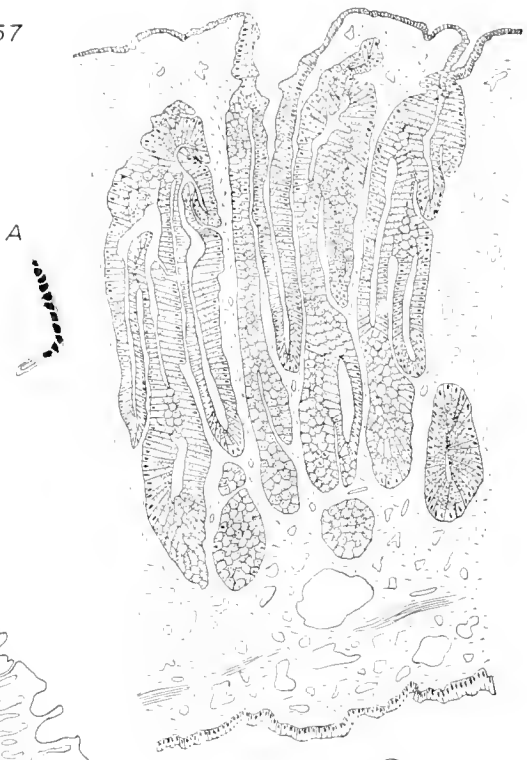


FIG 57



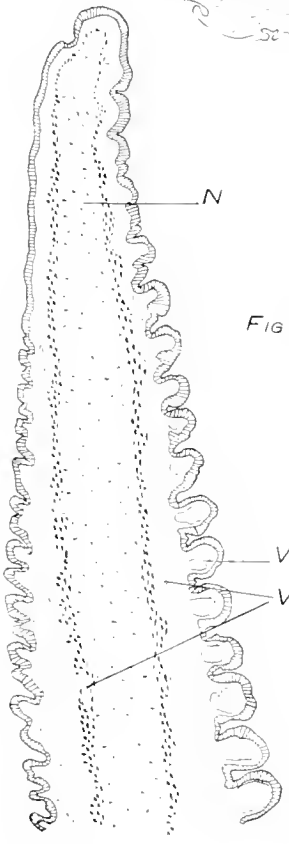


FIG 58

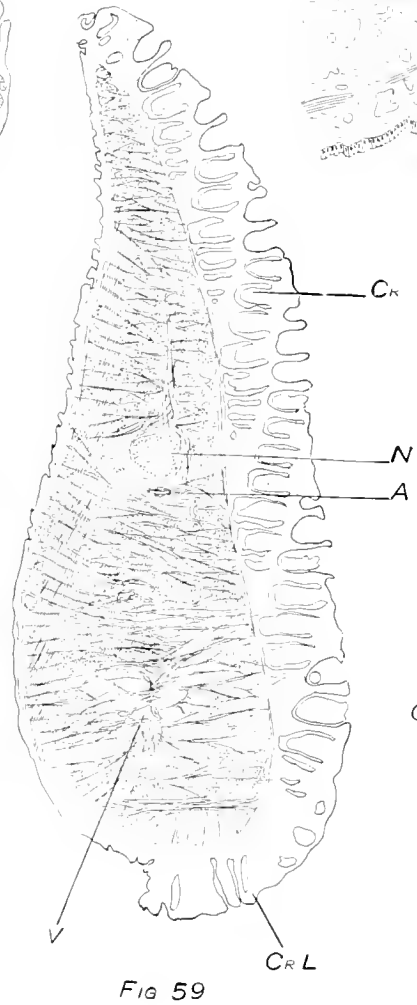


FIG 59

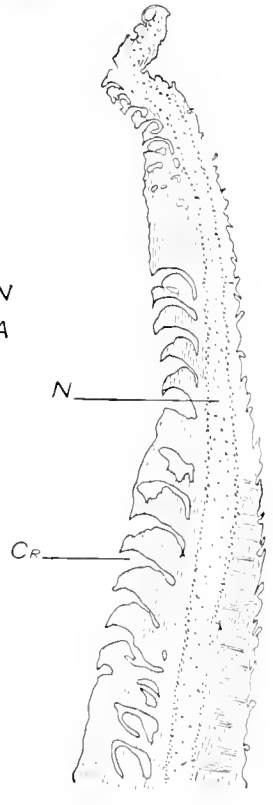


FIG. 60

L. E. Griffin, Del.

PLATE XV.

FIG. 61.—Longitudinal section of the tip of the second cirrus of the spadix. C. L. × 14.

G, gland.

N, nerve.

FIG. 62.—Longitudinal section through a crypt and its tongue of the third cirrus of the spadix. C. L. × 35.

FIG. 63.—Longitudinal section of the base of the preocular tentacle. C. L. × 20.

N, nerve trunk.

N′, nerve bundles running along the anterior side of the nerve trunk.

FIG. 64.—Longitudinal section of the tip of the preocular tentacle. C. L. × 20.

A, artery.

CG, ciliated groove on anterior side.

G, groove on posterior side.

N, nerve.

n, branch nerve to the peripheral portion of the tentacle.

R, ridge on anterior side of tentacle.

V, vein.

X, breaking plane.

FIG. 65.—Slightly oblique cross section of the preocular tentacle about 6 millimeters from its tip. C. L. × 35.

CG, ciliated groove between the upper and lower projecting ridges, R and R′.

N, nerve.

N′, nerve bundles running along anterior side of nerve.

R, base of projecting ridge.

R′, upwardly projecting portion of the next lower ridge.

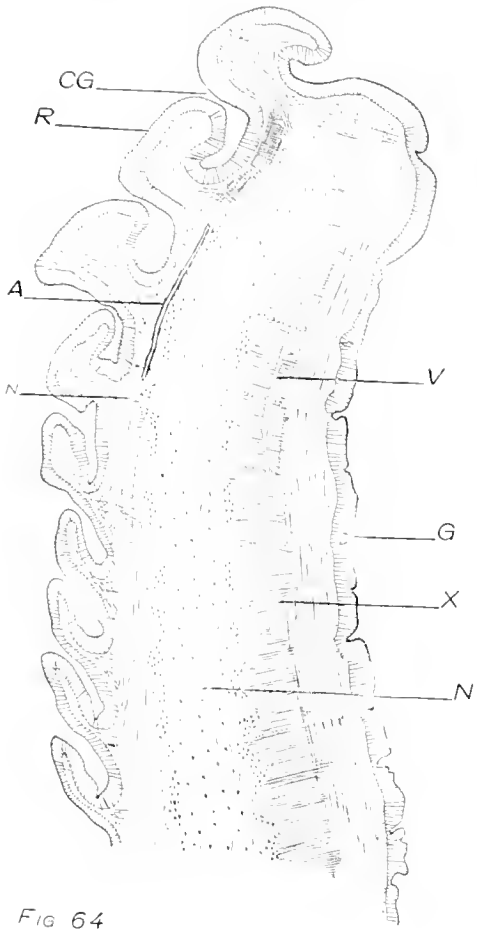


FIG. 64

FIG. 65

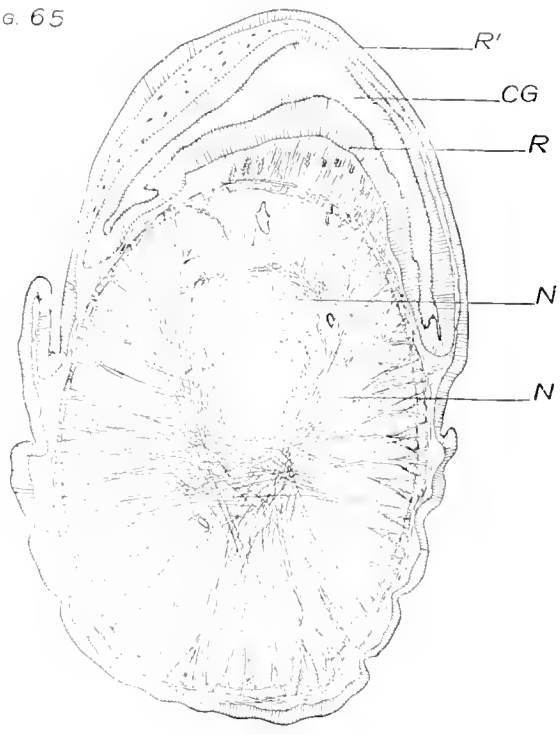


FIG. 62

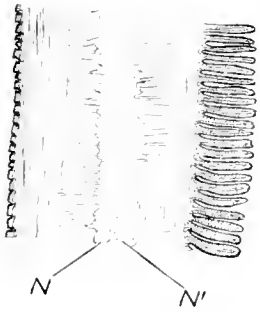


FIG. 63

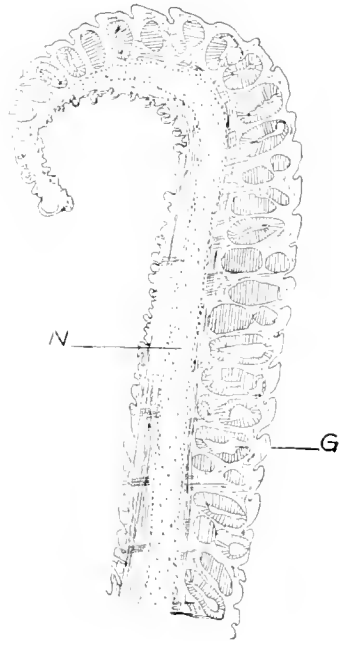


FIG 61

PLATE XVI.

FIG. 66.—Cross section through the middle of Van der Hoeven's organ. C. L. × 8.

D, dorsal surface.

A, atrium.

G, G, G, glandular portions of the organ.

Gn, ganglion.

HF, horizontal fissure.

L, lamina.

N, nerves to the lamina.

SH, wall of the atrium.

VF, vertical fissure

FIG. 67. Longitudinal section of a gland of Van der Hoeven's organ. C. L. × 35.

FIG. 68.—Cross section of gland tubules of Van der Hoeven's organ. C. L. × 35.

FIG. 69.—Section of the mantle through the bases of the preanal papillæ. C. L. × 12.

G, G, glands.

IM, inner surface of mantle.

O, opening of gland.

OM, outer surface of mantle.

P, P, bases of the preanal papillæ.

FIG. 70. Cross section of the salivary gland. C. L. × 20.

A, artery.

BS, blood sinus of salivary process.

N, nerve.

O, opening from the central cavity of the gland to the pharyngeal cavity.

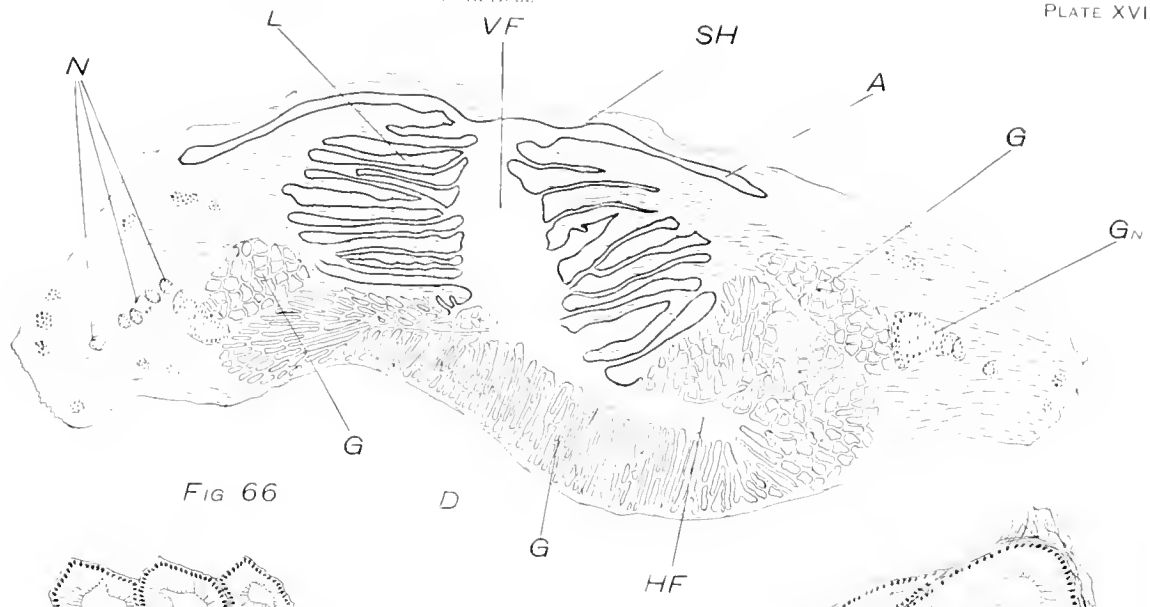


FIG 66

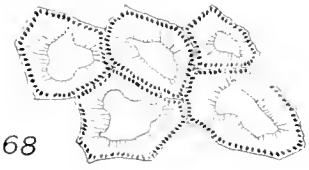


FIG 68

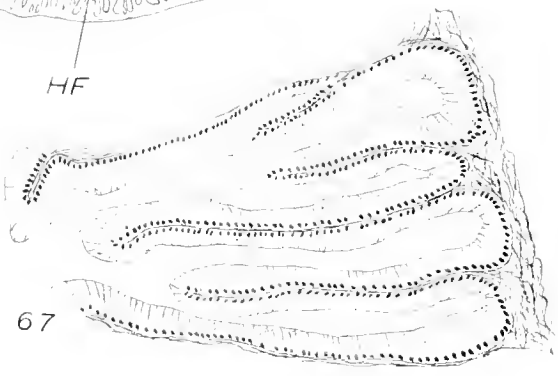


FIG 67

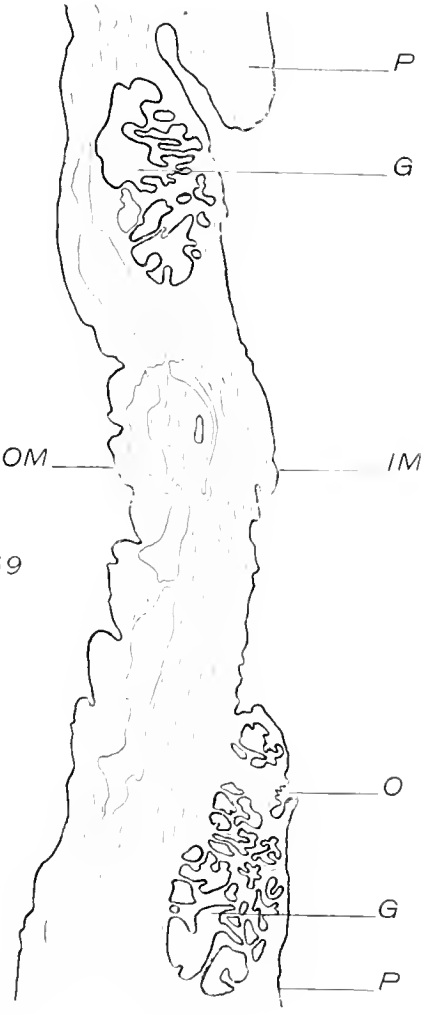


FIG. 69

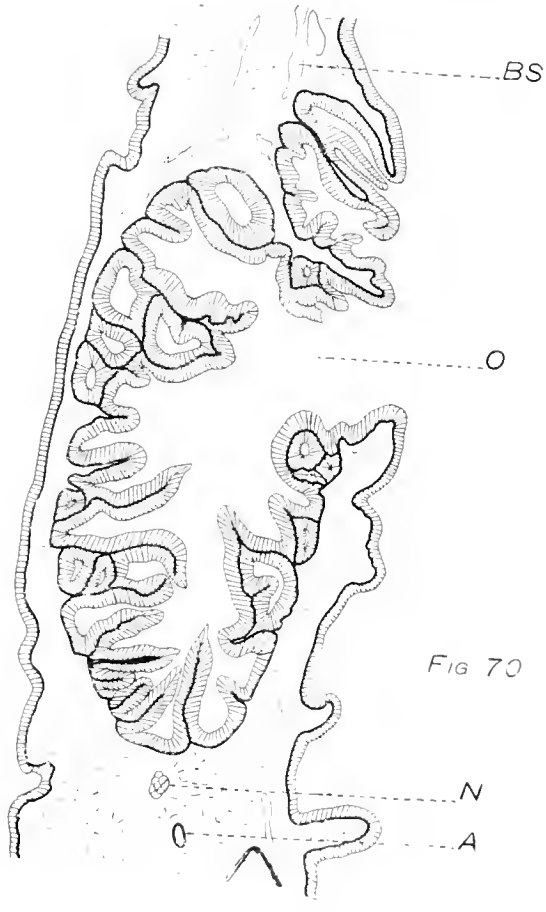


FIG 70

PLATE XVII.

FIG. 71.—Cross section of the nerve of a digital tentacle. Borax carmine and Lyons blue stain. The ganglion cells in red.

FIG. 72.—Epithelium of the inner side of an annular ridge of a digital tentacle. Also two isolated epithelial cells from the inner surface of the ridge.

FIG. 73.—Section of the secretory epithelium from a gland of Van der Hoeven's organ. The secretory cells had separated from the submucosa, revealing the sensory cells which lie between them. As the section was somewhat oblique, the outer ends of the cells are not shown.

Fig. 71.

Fig. 72.

Fig. 73.

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AN EXPERIMENTAL INQUIRY REGARDING THE NUTRITIVE VALUE OF ALCOHOL.

BY

W. O. ATWATER AND F. G. BENEDICT.

Presented to the Academy by JOHN S. BILLINGS.

CONTENTS.

APPENDIX.

AN EXPERIMENTAL INQUIRY REGARDING THE NUTRITIVE VALUE OF ALCOHOL.

BY W. O. ATWATER AND F. G. BENEDICT.

INTRODUCTION.

The present report gives the details of a number of metabolism experiments with men, in which the effects of diet with and without alcohol have been compared.[a] The details of a number of digestion experiments, which form part of the same investigations, have also been included.

PURPOSE OF THE EXPERIMENTS.

The main purpose of the experiments has been to get light upon the effects of alcohol in the diet, with especial reference to the question of its nutritive value.

Food is used in the body to build and repair tissue and to furnish energy. Only the nitrogenous compounds (protein) of the food serve the first purpose; they also serve as a source of energy, but the main supply of energy is obtained from the fats and carbohydrates. The fuel ingredients may be burned at once or may be stored for future use.

Alcohol contains no nitrogen and therefore can not build or repair tissue; it is rather to be classed with the fats and carbohydrates, and if it has any food value, this must be as a fuel. It does not appear to be stored for any considerable time, but is disposed of soon after it is taken into the body.

Alcohol, however, differs from the protein, fats, and carbohydrates of food materials in that it may exert, and when taken in large enough doses does exert, an indirect action upon the brain and nerves and through them upon the nutritive and other processes to which the general term metabolism is applied. In this way its actual value may be either increased or diminished according as it aids or hinders digestion, or either accelerates or retards metabolism. We have then to consider not only its direct action as nutriment for the supply of energy, but also its indirect action upon the metabolism and utilization of other food. In the experiments here

[a] The inquiry was undertaken at the instance of the Committee of Fifty for the Investigation of the Drink Problem. The experimental work was done in the chemical laboratory of Wesleyan University. A large share of the expense was borne by the committee of fifty although contributions were also received from the Elizabeth Thompson and Bache funds and from private individuals. The experiments were parallel with others of similar character, which are conducted under the auspices of the United States Department of Agriculture. These latter experiments form a part of a general inquiry regarding the food and nutrition of man, which is authorized by Congress and prosecuted in different parts of the United States. The special inquiry into the nutritive action of alcohol was made possible by the generosity of Wesleyan University, which offered to the committee of fifty the use of laboratory and other facilities that have been made available to the Department of Agriculture and the Storrs Experiment Station for nutrition inquiries.

The investigation has been pursued with the active cooperation of a number of gentlemen, including especially Mr. A. P. Bryant, under whose direction the computations of the results have been made, and Mr. A. W. Smith, Dr. O. F. Tower, and Dr. J. F. Snell, all of whom have been intimately associated with the elaboration of the apparatus and methods. Mr. Smith and Dr. Snell served as subjects in several of the experiments reported beyond, though the subject of the larger number was Mr. E. Osterberg.

The details of the experiments without alcohol and of two of those with alcohol, Nos. 7 and 10, have been published in bulletins of the United States Department of Agriculture as stated beyond.

described the indirect action of alcohol has been studied only in so far as (1) through its influence upon the secretion of digestive juices or otherwise it has tended to increase or diminish the proportion of the other food digested, or (2) it has increased or decreased the metabolism of other food or body material.

The ulterior effects of alcohol do not come within the scope of this particular inquiry, which is limited to its use by the body as nutriment.

THE QUESTIONS ACTUALLY STUDIED.

It appears then that whatever value alcohol may have for nutriment must depend upon its ablity to serve as fuel for furnishing energy to the body. Accordingly the main question proposed for study is this: What is the value of alcohol for fuel and how does it compare in this respect with sugar, starch, fats, and other nutrients of ordinary food materials? A collateral question is the effect of alcohol upon the proportions of nutrients digested from the food with which it was taken.

Experimental research has shown several ways in which the ingredients of ordinary food and body material serve as fuel. They are oxidized in the body; in the oxidation, their potential energy becomes kinetic and is thus made useful to the body; part of this kinetic energy appears as heat; another part appears as muscular work; in yielding energy by its own oxidation, food protects the material of the body and of other food from consumption. We have then to consider how alcohol compares with the ordinary fuel ingredients of the food in these ways.

It is clear that the main problem is that of the metabolism of energy in the body. Accordingly, while the experiments here described bear upon the use of alcohol in each of the ways just mentioned and upon collateral topics also, the fundamental question studied has been this: To what extent is the energy of alcohol transformed and utilized in the body like the energy of the nutrients, especially the fats and carbohydrates, of ordinary food materials?

In studying these questions we go down to one of the fundamental principles of material science. The plan of the whole inquiry is based upon the principle that the chemical and physical changes which take place in the body, and to which the general term metabolism is applied, occur in obedience to the laws of the conservation of matter and energy. That the law of the conservation of matter applies within the living organism, no one would question. It might seem equally certain that the metabolism of energy within the body takes place in accordance with the law of the conservation of energy. In experiments with men in the respiration calorimeter described beyond, the close agreement between the income and the outgo of energy in the body, under various conditions of work and rest, may be regarded as practically demonstrating that the law holds in the living organism. Such demonstration had, indeed, been approximated by earlier investigations, notably those of Rubner with dogs.

APPARATUS AND METHODS OF INQUIRY.

The experiments here described were made with a respiration calorimeter especially devised for research of this kind. The apparatus serves to measure the materials received and given off by the body, including the products of respiration, and is thus a "respiration apparatus." It also serves to measure the heat given off by the body and hence is a form of calorimeter. To indicate this twofold purpose it is called a "respiration calorimeter." The apparatus and methods of its use have been described elsewhere;[a] a brief description will suffice here.

[a] In the following bulletins of the Office of Experiment Stations of the United States Department of Agriculture: No. 44, Report of Preliminary Investigations on the Metabolism of Nitrogen and Carbon in the Human Organism with a Respiration Calorimeter of Special Construction, by W. O. Atwater, Ph. D., C. D. Woods, B. S., and F. G. Benedict, Ph. D.; No. 63, Description of a New Respiration Calorimeter and Experiments on the Conservation of Energy in the Human Body, by W. O. Atwater, Ph. D., and E. B. Rosa, Ph. D., pp. 94; No. 69, Experiments on the Metabolism of Matter and Energy in the Human Body, by W. O. Atwater, Ph. D., and F. G. Benedict, Ph. D., with the cooperation of A. W. Smith, M. S., and A. P. Bryant, M. S., pp. 112; No. 109, Further Experiments on the Metabolism of Matter and Energy in the Human Body, by W. O. Atwater, Ph. D., and F. G. Benedict, Ph. D., with the cooperation of A. P. Bryant, M. S., A. W. Smith, M. S., and J. F. Snell, Ph. D.

The chamber of the apparatus is so arranged that a man may spend a number of days in comparative comfort within it. It is lighted by a window, and is furnished with a folding chair, table, and bed, and, when the experiment involves muscular work, with a stationary bicycle also. The chamber is ventilated by a measured current of air, samples of which are taken for analysis before it enters and after it leaves the chamber. In this way the products of respiration are determined. Provision is also made for weighing, sampling, and analyzing all the food and drink, and the solid and liquid excreta as well. By comparing the chemical elements and compounds received by the body in food, drink, and inhaled air with those given off in the solid, liquid, and gaseous forms by the intestines, kidneys, lungs, and skin, it is possible to strike a balance between the total income and the total outgo of matter in the man's body. This serves as the measure of the metabolism of matter in the body.

In addition to this the metabolism of energy is also studied. To this end it is necessary to determine the potential energy of the food and drink taken into the body and of the solid and liquid excreta given off by the body, as well as the amounts of energy given off in the form of heat, external muscular work, and otherwise. The measurements of the potential energy of the food and excreta are made with the bomb calorimeter.[a] The determination of the heat given off from the body is made by certain arrangements in connection with the respiration calorimeter. A current of water passing through a special coil of pipes suspended in the chamber absorbs the heat that is generated within it, and by measuring the quantity of water that passes through the coil and its rise in temperature the amount of heat absorbed may be determined. To this is added the latent heat of the water vaporized within the chamber.

So delicate are the measurements of temperature that the observer sitting outside and recording the changes every two or four minutes immediately detects a rise or fall of even one one-hundredth of a degree in the temperature of the inner copper wall or of the air inside the chamber. If the man inside rises to move about, the increase in the heat given off from his body with this muscular work shows itself in a rise of temperature which is immediately detected.

In the work experiments the subject spends a certain portion of each day in muscular exercise upon an apparatus arranged as an ergometer, by which the amount of muscular work done may be measured. The ergometer consists of a stationary bicycle connected with a dynamo by which the power which the rider applies to the pedals, and which is not changed to heat by the friction of the machine, is converted into an electric current, which is passed through an electric lamp and is in turn changed to heat. The ergometer is arranged to measure the amount of muscular work done, in terms of heat, by determinations of the amount of energy converted into heat by friction and the amounts of electric current generated and changed to heat.

From the energy of food, drink, solid and liquid excretory products, and body material stored or lost the net income of energy may be computed. The net outgo is measured by the apparatus. By comparing these the balance of income and outgo of energy is found.

The data obtained as explained above, taken in connection with what is known of the physiological processes that go on in the body, give more accurate information than can be otherwise obtained regarding the ways in which the food is used in the body and the quantities of food ingredients that are needed to supply the demands of the body for the various purposes of work and rest and the comparative nutritive value of different food materials.

ACCURACY OF APPARATUS AND METHODS.

Two methods of testing the accuracy of the apparatus are employed. By one method known amounts of heat are generated electrically within the chamber, and the heat is measured by the apparatus. In this way its accuracy as a calorimeter only is tested. By the second method known amounts of ethyl alcohol of known purity and composition are burned completely within the chamber, and the amounts of water, carbon dioxide, and heat resulting from the combustion of alcohol are determined by the apparatus. In this way its accuracy both as a respiration apparatus and as a calorimeter is tested. In the average of five electrical tests the amount of heat

[a] For description of the bomb calorimeter see U. S. Dept. Agr., Office Expt. Stations, Bul. 21, pp. 120–126, and Storrs Conn. Experiment Station Report, 1897, p. 190.

measured by the calorimeter was 100.01 per cent of the amount generated by the electric current. The averages of the results obtained in seventeen alcohol tests are summarized in the following table:

Summary of results of tests in which alcohol was burned in the calorimeter.

	Carbon dioxide.	Water.	Heat.
	Grams.	*Grams.*	*Calories.*
Amount required	19,239.8	12,264.4	64,554.1
Amount found	19,206.9	12,379.1	64,513.3
	Per cent.	*Per cent.*	*Per cent.*
Ratio of amount found to amount required	99.8	[a]100.9	99.9

[a] After the completion of the later experiments a slight leak was found in the "valve box" through which the outgoing air current passed on its way to and from the "freezers," and by which water, condensed on the outside, may have entered. There is every reason to believe that the quantity of water actually found was thus made too large by a fraction of 1 per cent. In the average of the first nine experiments the amount of water found was 100.6 per cent of that required. As an alcohol check test was generally made between each two metabolism experiments or series of experiments we have a means of knowing when the leak began to effect the results and the amount of the error introduced. See Bulletin 109 of the Office of Experiment Stations, above referred to.

The results thus indicate that the respiration calorimeter is an instrument of precision and that the determinations of carbon dioxide, water, and heat produced within the chamber of the respiration calorimeter are sufficiently accurate for experiments with the living subject.

THE EXPERIMENTS.

GENERAL PLAN.

For the subjects of the experiments men were selected who were in good health, had apparently normal digestion, and did not find the confinement in the chamber uncomfortable. A diet was chosen which provided materials as palatable and in as much variety as was consistent with convenient preparation, and with accurate sampling and analysis. The quantity and composition of the diet were generally such as to maintain the body nearly in nitrogen and carbon equilibrium under the conditions of the experiment, whether of work or of rest. In 13 of the experiments the diet included alcohol.

The alcohol amounted in general to about 72 grams (2½ ounces) a day, or as much as would be contained in a bottle of claret or 3 or 4 glasses of whisky. In most cases pure (ethyl) alcohol, but in some whisky or brandy was used. It was mixed with either water or coffee, and was given in 6 small doses, 3 with meals and the rest at regular intervals between, in order to avoid as far as possible any effect upon the nerves. The alcohol supplied not far from 500 calories of energy. In the experiments without external muscular work, the total energy of the diet was about 2,500 calories, so that the alcohol furnished one-fifth of the total energy. In the experiments in which the man was engaged in more or less active muscular work, the total energy of the food was larger, averaging about 3,900 calories, so that the alcohol furnished between one-seventh and one-eighth of the total energy of the diet.

In order that the subject might become accustomed to the diet and reach approximate nitrogen equilibrium with it before the experiment proper began, a preliminary digestion experiment of at least 3 days immediately preceded the metabolism experiment. Any change of diet found desirable or necessary was made during this period, and the preliminary experiment was continued until nitrogen equilibrium was supposed to be more or less nearly reached. In most cases the preliminary experiment continued 4 days. During this period the subject was, in general, engaged in his customary occupation, but conformed his muscular activity more or less to that of the coming experiment. Thus if it was to be a work experiment, he rode a bicycle or walked a considerable distance each day. If it was to be a rest experiment, he avoided all unnecessary exercise. For supper on the last day of this preliminary digestion experiment

about .3 of a gram of lampblack was taken in a gelatin capsule with the food, in order to mark the separation of the feces of the preliminary experiment from those of the metabolism experiment proper. The subject entered the chamber about 7 o'clock on the evening of the last day of the preliminary digestion period and retired about 11 o'clock. At about 1 o'clock in the morning the heat measurements were begun.

The night sojourn in the chamber sufficed to get the temperature of the apparatus and its contents of carbonic acid and water into equilibrium, so that accurate measurements might begin at 7 o'clock on the first morning of the experiment proper. In some cases the experiment continued only 4 days; in other cases the experimental period consisted of 6 or 9 successive days spent within the apparatus, the entire period being divided into 3 experiments of 2 or 3 days each with changes in the diet as hereafter explained. The determinations of carbon dioxide, water vapor, and heat were made in 6-hour periods, so that complete data for an experiment showed the total amounts of these compounds given off from the body during the periods ending at 1 p. m., 7 p. m., 1 a. m., and 7 a. m. of each day of the experiment. As noted beyond, the urine was also collected and its nitrogen content determined for corresponding periods.

The daily routine of the subject within the chamber was indicated by a programme made up before the beginning of the experiment. A copy of the programme was furnished to the subject, who followed it with reasonable closeness, and other copies were posted in convenient places outside the apparatus for the benefit of those who had the experiments in charge.

Much care was necessarily taken in preparing the food materials selected for the diet and in taking samples for analysis. With the exception of milk and alcohol, the proper quantity of each kind of food, either for each meal or for the whole day, was put up in glass jars before the experiment began; and materials which might spoil during the course of the experiment, such as bread and meat, were thoroughly sterilized.

Special arrangements were made by which the mixed milk from a definite number of select cows was supplied for each experiment. But even with this precaution, the milk was not entirely uniform in composition from day to day.

The handling of the alcohol was much simpler. A quantity sufficient for several experiments was procured and analyzed, and the proper amounts were drawn each day as needed.

As stated above, the separations of the feces for each experiment were made by means of lampblack. The total feces for each experiment were analyzed, and the average per day used in the computations of results. It was assumed that when the food and exercise were so nearly uniform the undigested residues and metabolic products would not vary greatly from day to day, and such irregularities as might occur would hardly affect the average for an experiment.

The urine was collected in 6-hour periods, and the amount, specific gravity, and nitrogen determined for each period. Aliquot portions of the urine of the 6-hour periods were taken for preparation of a composite sample for the day, and in like manner aliquot portions of the composite sample of urine for each day were taken for the preparation of a sample for the whole experiment or series of experiments. The nitrogen and heat of combustion were determined in the urine for each day and in the composite for the whole experiment. The carbon and hydrogen were determined in the composite sample of urine for the whole experiment or series of experiments, and were divided among the different days in proportion to the amount of nitrogen.[a]

THE MEN WHO SERVED AS SUBJECTS OF THE EXPERIMENTS.

Three different men, E. O., A. W. S., and J. F. S., have served as subjects in these experiments. Each of these, when not sojourning in the apparatus, was engaged in work connected with the investigations. E. O. was a general assistant in the chemical laboratory, a Swede by birth, who had been a number of years in this country; he was 32–33 years old, and weighed about 155 pounds. Since boyhood he had been accustomed to the moderate use of alcoholic beverages. A. W. S. was a physicist, a native of New England, 25 years old, and weighed

[a] For further explanation, see U. S. Dept. Agr., Office Exp. Stations, Bul. 69, pp. 21 and 35.

about 155 pounds. J. F. S. was a chemist, a Canadian by birth, 29 years old, and weighed about 150 pounds. The last two had always been total abstainers. The subjects were weighed without clothing.

SYMPTOMS OBSERVED IN EXPERIMENTS WITH ALCOHOL.

In deciding upon the daily amount of alcohol and its division into doses, the purpose was to give the subjects as much as they could well take without apparent nervous disturbance. As above stated, the quantity of absolute alcohol, about 72 grams per day, was divided into 6 nearly equal doses, of which 3 were taken with the meals and 3 between meals. It supplied about one-fifth of the total energy of the diet in the rest experiments and about one-seventh in the work experiments. On one or two occasions J. F. S. experienced a slight tingling in the ears immediately after drinking the alcohol. On one occasion E. O. complained of a slight feeling of dullness. On one occasion A. W. S. thought he experienced a very slight dizziness. Otherwise neither one was at any time aware of any especial effect of the alcohol upon the sensations in any way. With the exception of the tingling in the ears noticed by J. F. S., it is not certain that any of the symptoms referred to were due to the alcohol.

As regards the effect of alcohol upon the body temperature and pulse rate in these experiments there is little to be said. The only observations made were those by the subjects themselves, and the difficulty of accurately determining one's own normal pulse rate is well known. The observations of temperature were made with a clinical thermometer in the mouth or axilla by the usual method, which of course does not show the exact average internal temperature of the body. The data obtained with E. O. and A. W. S. were not sufficiently accurate and numerous to be decisive. The observations by J. F. S. were made at frequent intervals and with considerable care. The results imply a slightly decreased body temperature and increased pulse rate in the experiments with alcohol diet as compared with those with ordinary diet, but the differences are not large.

The data as observed are recorded in the tables in the appendix.

GENERAL DESCRIPTIONS OF INDIVIDUAL METABOLISM EXPERIMENTS.

The data of the experiments with alcohol are given in detail in the appendix beyond. The results are summarized, and brief descriptions of the experiments are given on the following pages. The results of these experiments are here compared with those of similar experiments without alcohol, the details of which are published elsewhere, as indicated in Table 1, which follows.

LIST OF METABOLISM EXPERIMENTS WITH AND WITHOUT ALCOHOL, AND GROUPING FOR COMPARISON.

Of the metabolism experiments with men in the respiration calorimeter, 13 had for one of their objects the study of the nutritive value of alcohol. The details of 11 of these are given in the present report; those of 2 others have been published elsewhere. These 13 experiments are compared with a like number made with the same men, but without alcohol in the diet. Table 1 gives a list of these 26 experiments, with grouping for comparison and references to publications in which the details may be found.

TABLE 1.—*List of the experiments, and grouping for comparison of results with and without alcohol.*

	Group.	No.	Date.	Duration.	Subject.	Nature of the experiment.		Protein in food.	Energy in food.	Place of publication of details.
						Rest or work.	Ordinary or alcohol diet.			
				Days.				*Grams.*	*Calories.*	
More strictly comparable.	A	9	Jan. 10–14, 1898	4	E. O.	Rest	Ordinary	119	2,717	[a]
		10	Feb. 15–19, 1898	4	do	Rest	Alcohol	123	2,769	[a]
	B	24	Mar. 19–22, 1899	3	do	Rest	Ordinary	124	3,061	[b]
		22	Mar. 13–16, 1899	3	do	Rest	Alcohol	124	3,044	[c]
	C	26	Feb. 14–17, 1900	3	J. F. S.	Rest	Ordinary	100	2,490	[b]
		28	Feb. 20–23, 1900	3	do	Rest	do	99	2,489	[b]
		27	Feb. 17–20, 1900	3	do	Rest	Alcohol	99	2,491	[c]
	D	11	Mar. 22–26, 1898	4	E. O.	Work	Ordinary	124	3,862	[b]
		12	Apr. 12–16, 1898	4	do	Work	Alcohol	121	3,891	[c]
	E	29	Mar. 16–19, 1900	3	J. F. S.	Work	Ordinary	100	3,487	[b]
		31	Mar. 22–25, 1900	3	do	Work	do	100	3,495	[b]
		30	Mar. 19–22, 1900	3	do	Work	Alcohol	99	3,458	[c]
	F	32	Apr. 20–23, 1900	3	do	Work	Ordinary	101	3,487	[b]
		34	Apr. 26–29, 1900	3	do	Work	do	100	3,493	[b]
		33	Apr. 23–26, 1900	3	do	Work	Alcohol	100	3,486	[c]
Less strictly comparable.	G	13	Nov. 8–11, 1898	3	E. O.	Rest	Ordinary	117	2,596	[b]
		14	Dec. 20–24, 1898	4	do	Rest	do	94	2,513	[b]
		7	June 8–12, 1897	4	do	Rest	Alcohol	104	2,462	[a]
	H	5	May 4–8, 1897	4	do	Rest	Ordinary	119	2,655	[a]
		15	Jan. 16–18, 1899	2	do	Rest	Alcohol	109	2,653	[c]
		16	Jan. 18–20, 1899	2	do	Rest	do	109	2,653	[c]
		17	Jan. 20–22, 1899	2	do	Rest	do	109	2,653	[c]
	I	21	Feb. 12–15, 1899	3	A. W. S.	Rest	Ordinary	97	2,264	[b]
		18	Feb. 6–8, 1899	2	do	Rest	Alcohol	97	2,776	[c]
		19	Feb. 8–10, 1899	2	do	Rest	do	97	2,776	[c]
		20	Feb. 10–12, 1899	2	do	Rest	do	97	2,776	[c]

[a] U. S. Dept. Agr., Office Expt. Stations, Bul. 69, on "Experiments on the Metabolism of Matter and Energy in the Human Body," by W. O. ATWATER, F. G. BENEDICT, and Associates.

[b] U. S. Dept. Agr., Office Expt. Stations, Bul. 109, on "Further Experiments on Metabolism of Matter and Energy, 1898–1900," by ATWATER, BENEDICT, and Associates.

[c] The present memoir.

The experiments are divided into groups, each group including experiments with and without alcohol, but made with the same subject. In some groups there are only two experiments, one with alcohol and one with ordinary diet; in others there are more than one experiment either with or without alcohol.

More and less strictly comparable experiments.—In the first 6 groups, A to F, inclusive, the experiments with and without alcohol were practically duplicates in duration, muscular activity, and amounts of protein and energy in the diet, the main difference being that a part of the fats and carbohydrates of the ordinary diet, enough to supply in general about 500 calories of energy, was replaced by the isodynamic amount of alcohol. In the 3 groups, G to I, which include a number of the earlier experiments, those with and without alcohol were not so nearly duplicates. In some instances the difference was unintentional, and was due to a difficulty in obtaining food materials of like composition at different times. In these cases it was not found practicable to complete the analyses long enough in advance of the experiments to insure uniformity of diet as regards amounts of protein and energy. Later, means were devised for putting up food materials in considerable quantities and preserving them by canning or cold storage, so that the amounts of protein and energy in the diet were made more nearly the same in experiments separated by longer or shorter intervals of time. Accordingly the experiments of groups A to F are designated as more directly comparable and those of Groups G to I as less directly comparable.

Order of arrangement of experiments with and without alcohol.—In these experiments two different orders of arrangement have been observed. By one plan the experiments with and without alcohol are separated by a longer or shorter interval, and in each case the experiment proper, during which the subject is in the respiration calorimeter, is preceded by a preliminary period during which he is outside the chamber but has the same or nearly the same diet and exercise. The experiments of Groups A, B, D, G, and No. 5 of Group H belong to this class. Each of these experiments has continued in the majority of cases for 8 days, the first half being devoted to the preliminary and the other half to the actual experimental period. In some instances, however, the preliminary period was only 3 days. One object of the preliminary period has been to bring the body as nearly into nitrogen equilibrium as practicable. The attempts to secure nitrogen equilibrium by this means have not, on the whole, been successful, a circumstance to which more especial attention is called beyond.

By the other plan the experiments with and without alcohol follow one another without interruption, thus making really successive periods of a single experiment, or successive experiments of a series. Each such series is preceded by a preliminary experiment, during which the man is not in the chamber, but receives, at least during the latter part of the period, the same diet as in the experiment proper. At the end of the preliminary period the man enters the chamber and remains there during the several periods of the experiments proper. The transitions from one diet to another are thus immediate. The experiments of Groups C, E, F, and I and Nos. 15, 16, and 17 of Group H were of this sort. Since, however, No. 15 was preceded by a preliminary period, and the only differences between Nos. 15, 16, and 17 were in the kind of alcoholic beverage—commercial alcohol, whisky, and brandy—these might be considered one experiment of the first kind.

Each plan has its advantages and disadvantages. A reason for this is found in the fact that alcohol in moderate quantities appears to have, with some persons, especially with those unaccustomed to its use, a special effect upon nitrogen metabolism. It seems probable that this is exercised through the nervous system, that it may for a short time tend to increase the excretion of nitrogen, but that it is, in some cases at any rate, only temporary, and disappears after a few days when the permanent effect manifests itself. Accordingly, there is a disadvantage in the second plan, in which the alcohol experiment proper is not preceded by a preliminary period with alcohol diet, in that the persistent effect of the alcohol may not become manifest during the first days of its use in the experiment. Whether, when, or how much this factor may influence a given experiment it is difficult to say.

On the other hand, there is a disadvantage in the first plan in that, as the experiments with and without alcohol are not consecutive, the body may, during the interval between them, become changed in its capacity or tendency to respond to the different diets. The second plan has the corresponding advantage that differences in the observed results in two consecutive periods might be more clearly due to the diet and less influenced by changes in bodily condition; but here, again, we are dealing with uncertainties.

To some it might seem that the best test of the effect of alcohol upon nitrogen metabolism would be found in experiments on the first plan, while others would consider those on the second plan more trustworthy. To the writers it seems that experiments on both plans are desirable. Of course the most desirable plan of all would be to continue the experiments through periods long enough to make sure that the normal action of the alcohol appears, and to alternate the alcohol periods with periods without alcohol. This plan has been followed successfully in experiments upon the special question of the protection of protein by alcohol, as explained in the discussion of this subject beyond.

GROUP A. EXPERIMENTS NOS. 9 AND 10. REST EXPERIMENTS WITH ORDINARY DIET AND WITH ALCOHOL DIET.

The 2 experiments in this group were planned to compare the effects of ordinary diet with those of alcohol diet when the subject did as little mental and muscular work as practicable. The subject, E. O., was the same as in a number of other experiments. The amounts of nutrients

and energy per day in the diet in both experiments were such as previous observation and experiment with the same subject had indicated to be sufficient but not excessive. Experiment No. 10 was as exact a duplicate as possible of experiment No. 9, except that part of the fats and carbohydrates of the ordinary diet of No. 9 were taken out and were replaced in No. 10 by an amount of alcohol that was practically isodynamic with the fats and carbohydrates for which it was substituted, as explained below.

The preliminary digestion experiment preceding metabolism experiment No. 9 began with breakfast January 6, 1898, and continued 4 days. During this preliminary period the subject was engaged in his usual occupation as laboratory janitor, save that he had as little muscular exercise as practicable. His diet was essentially the same as during the period of actual experiment in the calorimeter.

The subject entered the respiration chamber on the evening of January 9, and experiment No. 9 began at 7 a. m. on January 10 and continued until 7 a. m. January 14. During this period within the chamber his occupation consisted of reading, writing, etc., but with very little muscular or mental activity. The diet furnished 120 grams of protein and 2,717 calories of energy per day.

Between the close of experiment No. 9 and the beginning of No. 10 there was an interval of about 4 weeks, in which the subject was engaged in his usual occupation as laboratory assistant. The preliminary digestion period of No. 10 began with breakfast February 11, 1898, and continued 4 days. The subject had as little muscular exercise as practicable aside from his regular occupation. The diet during the preliminary period was practically the same as during the experiment proper.

The subject entered the respiration chamber in the evening of February 14, and the experiment proper began at 7 a. m. February 15 and continued 4 days. The diet of the experiment, which furnished 123 grams of protein and 2,709 calories of energy per day, differed from the diet of experiment No. 9 in that about 37 grams of fat and 45 grams of carbohydrates, supplying 520 calories of energy, were taken out of the ordinary diet and were replaced by 80 grams of commercial alcohol with 90.6 per cent or 72.5 grams of absolute alcohol, having a heat of combustion of 512 calories. Thus, the amount of alcohol was very nearly isodynamic with the amounts of fats and carbohydrates which it replaced, and the total amounts of protein and energy were practically the same in the diets of both experiments.

The following table summarizes the results of these two experiments. Detailed data of the experiments will be found in Bulletin 69 of the Office of Experiment Stations of the United States Department of Agriculture.

TABLE 2.—*Summary of results of metabolism experiments Nos. 9 and 10.*

[Quantities per day.]

	Protein.	Fat.	Carbohydrates.	Alcohol.	Nitrogen.	Carbon.	Energy.
Experiment No. 9.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
In total food	119.6	69.0	341.8	.....	19.1	261.6	2,717
In available food	111.7	64.9	329.7	.....	17.8	235.6	2,426
Actually metabolized	115.3	46.7	(329.7)	.....	18.4	223.6	2,277
Heat measured	.....	.....	.....	.....	.....	.....	2,309
Gain (+) or loss (−) to body	−3.6	+18.2	.....	.....	−0.6	−12.0	+149
Experiment No. 10.							
In total food	123.5	31.6	297.4	72.5	19.8	253.3	2,709
In available food	114.9	27.9	288.4	71.4	18.4	227.5	2,427
Actually metabolized	121.8	6.7	(288.4)	71.4	19.5	214.9	2,268
Heat measured	.....	.....	.....	.....	.....	.....	2,283
Gain (+) or loss (−) to body	−6.9	+21.2	.....	.....	−1.1	+12.6	+159

GROUP B. EXPERIMENTS NOS. 24 AND 22, WITH NO. 23 FOR COMPARISON. REST EXPERIMENTS WITH ORDINARY DIET AND WITH ALCOHOL.

The experiments of this group are a series of 3 carried out with E. O. in March, 1899. The purpose was to compare the effects of alcohol with those of sugar upon the metabolism of nitrogen and especially of carbon and energy, when the subject had little muscular or mental activity. During this series the subject remained in the calorimeter 9 days and 10 nights without intermission, and each experiment continued 3 days and nights. The plan of the experiments was to give the subject a diet consisting of a so-called basal ration which was the same in all 3 experiments, and a supplemental ration which was different in each experiment. The basal ration given was as large as the average of the rations that had been used in the previous experiments with the same subject. It furnished 123 grams of protein and 2,535 calories of energy per day. The supplemental ration consisted of alcohol in experiment No. 22 and sugar in experiment No. 24, each in quantity sufficient to furnish a little over 500 calories per day, as explained below. In experiment No. 23 the basal ration alone was given.

The preliminary digestion experiment continued 4 days, beginning with breakfast on March 9, the lampblack for the separation of the feces having been taken with the supper the night before. During this preliminary period the subject was engaged in his usual occupation as laboratory assistant, but had as little muscular exercise as practicable. For 3 days of this preliminary experiment the subject lived on the basal ration alone. On the fourth day 79.2 grams of commercial ethyl alcohol, with 90.9 per cent or 72 grams of absolute alcohol, were added to the diet. The alcohol was taken by the subject in coffee infusion, the total amount for the day being divided into 6 portions, one being taken at each meal and the other 3 portions between meals.

The subject entered the respiration chamber on the evening of March 12, and experiment No. 22 began at 7 o'clock in the morning of March 13 and continued until 7 a. m. March 16. During this experiment the diet consisted of the basal ration, supplemented each day by 72 grams of alcohol, as stated above. This amount of alcohol added 509 calories per day to the energy of the basal ration.

Experiment No. 23 began at 7 a. m. on March 16 and continued until 7 a. m. March 19. The diet in this experiment consisted of the basal ration alone without the alcohol, but at the request of the subject with the addition of a small amount of horseradish to add flavor to the diet.

Experiment No. 24 began at 7 a. m. March 19 and continued until 7 a. m. March 21. The diet in this experiment consisted of the basal ration and the horseradish, supplemented each day by 130 grams of cane sugar in the form of rock candy. The daily ration of candy was given to the subject each morning with breakfast, and he ate it as he felt disposed during the day. This amount of sugar added 515 calories per day to the energy of the basal ration, a similar amount to that added by the alcohol in experiment No. 22.

The following table summarizes the results of experiments Nos. 22 and 24. The results of No. 23 are also included, although they are not strictly comparable with either 22 or 24, because removal of the alcohol without replacement by any other material reduced the energy of the diet by about 500 calories. Detailed data of No. 22 will be found in the Appendix, pp. 330 to 342, and those of Nos. 23 and 24 will be found in Bulletin 109 of the Office of Experiment Stations.

TABLE 3.—*Summary of results of metabolism experiments Nos. 24, 25, and 23.*

[Quantities per day.]

	Protein.	Fat.	Carbohydrates.	Alcohol.	Nitrogen.	Carbon.	Energy.
Experiment No. 24.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
In total food	123.6	68.8	408.6	.....	19.8	299.7	3,061
In available food	115.4	64.4	403.7	.....	18.5	277.4	2,809
Actually metabolized	113.7	4.7	(403.7)	.....	18.2	230.9	2,238
Heat measured	.....	.....	.....	.....	.....	.....	2,272
Gain (+) or loss (−) to body	+1.7	+59.7	.....	.....	+0.3	+46.5	+571
Experiment No. 23.							
In total food	123.6	68.8	278.6	.....	19.8	244.9	2,546
In available food	116.6	65.1	272.6	.....	18.7	234.6	2,432
Actually metabolized	118.2	56.2	(272.6)	.....	19.0	228.5	2,216
Heat measured	.....	.....	.....	.....	.....	.....	2,176
Gain (+) or loss (−) to body	−1.6	+8.9	.....	.....	+0.3	+6.1	+75
Experiment No. 22.							
In total food	123.2	68.8	276.1	72.0	19.8	279.8	3,044
In available food	116.2	65.1	270.1	69.8	18.7	256.5	2,777
Actually metabolized	114.8	2.4	(270.1)	69.8	18.5	207.8	2,180
Heat measured	.....	.....	.....	.....	.....	.....	2,258
Gain (+) or loss (−) to body	−1.4	+62.7	.....	.....	+0.2	+48.7	−597

GROUP C. EXPERIMENTS NOS. 26, 28, AND 27. REST EXPERIMENTS WITH ORDINARY DIET AND WITH ALCOHOL DIET.

The series of experiments forming this group was carried out with J. F. S. in February, 1900. The purpose of the experiments was to obtain data concerning the relative power of isodynamic quantities of alcohol, sugar, and butter to replace one another in the diet, when the subject was at rest. During this series the subject remained in the calorimeter 9 days and 10 nights, and each experiment continued 3 days and nights. The diet consisted of a basal ration furnishing approximately 100 grams of protein and 1,982 calories of energy per day, which was uniform in all 3 experiments, and a supplemental ration which was differed in the several experiments, being butter in No. 26, alcohol in No. 27, and sugar in No. 28, the amount of each used being sufficient to furnish about 500 calories of energy.

The preliminary digestion experiment began with breakfast on February 10, and continued 4 days. During this preliminary period the diet consisted of the basal ration supplemented by 63.5 grams of butter, furnishing 0.1 of a gram of nitrogen and 508 calories of energy; thus making a total of 100 grams of protein and 2,490 calories of energy in the daily diet.

The subject entered the respiration chamber on the evening of February 13, and experiment No. 26 began at 7 a. m. February 14, and continued 3 days. During this experiment the diet consisted of the basal ration supplemented by fat in the form of butter, as in the preliminary digestion experiment.

Experiment No. 27 began at 7 a. m. February 17, and continued 3 days. During this experiment the diet consisted of the basal ration supplemented by 79.5 grams of commercial ethyl alcohol with 90.6 per cent or 72 grams of absolute alcohol supplying 509 calories of energy per day, so that during this experiment the daily diet furnished 99 grams of protein and 2,491 calories of energy. The alcohol was administered in sweetened water, and the mixture was consumed in 6 portions during the day, 3 with meals and 3 between meals.

Experiment No. 28 began at 7 a. m. February 20, and continued 3 days. The diet during this experiment consisted of the basal ration supplemented by 28 grams of sugar daily in the form of rock candy. The daily ration during this experiment thus furnished 99 grams of protein and 2,889 calories of energy. The total amount of rock candy for the day was supplied to the subject with his breakfast, and he ate it from time to time during the day according to his taste.

The major portion of it was consumed at about the hours at which the alcohol had been taken in the previous experiment.

The following table summarizes the results of these 3 experiments. Detailed data of experiment No. 27 will be found in the Appendix, pages 342 to 353, and those of experiments Nos. 26 and 28 in Bulletin 109 of the Office of Experiment Stations.

TABLE 4.—*Summary of results of metabolism experiments Nos. 26, 28, and 27.*

[Quantities per day.]

	Protein.	Fat.	Carbohydrates.	Alcohol.	Nitrogen.	Carbon.	Energy.
Experiment No. 26.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
In total food	99.6	94.8	247.2	.....	15.9	233.2	2,490
In available food	92.7	92.0	240.5	.....	14.8	212.8	2,256
Actually metabolized	96.2	67.6	(240.5)	.....	15.4	196.1	2,043
Heat measured	.....	.....	.....	.....	.....	.....	2,085
Gain (+) or loss (−) to body	−3.5	+24.4	.....	.....	−0.6	+16.7	+213
Experiment No. 28.							
In total food	98.6	40.3	375.2	.....	15.8	245.8	2,489
In available food	90.8	36.3	369.9	.....	14.6	224.9	2,249
Actually metabolized	95.3	14.5	(369.9)	.....	15.3	210.7	2,067
Heat measured	.....	.....	.....	.....	.....	.....	2,079
Gain (+) or loss (−) to body	−4.5	+21.8	.....	.....	−0.7	+14.2	+182
Average Nos. 26, 28.							
In total food	99.1	67.6	311.2	.....	15.9	239.5	2,490
In available food	91.8	64.2	305.2	.....	14.7	218.8	2,253
Actually metabolized	95.8	41.1	(305.2)	.....	15.3	203.4	2,055
Heat measured	.....	.....	.....	.....	.....	.....	2,082
Gain (+) or loss (−) to body	−4.0	+23.1	.....	.....	−0.6	+15.4	+198
Experiment No. 27.							
In total food	98.6	40.3	247.2	72.0	15.8	229.5	2,491
In available food	91.6	38.2	240.1	71.1	14.7	208.9	2,264
Actually metabolized	97.6	20.0	(240.1)	71.1	15.7	198.3	2,125
Heat measured	.....	.....	.....	.....	.....	.....	2,123
Gain (+) or loss (−) to body	−6.0	+18.2	.....	.....	−1.0	+10.6	+139

GROUP D. EXPERIMENTS NOS. 11 AND 12. WORK EXPERIMENTS WITH ORDINARY DIET AND WITH ALCOHOL DIET.

The two experiments in this group were similar to those in Group A, except that those in Group A were rest experiments, while those in Group D were work experiments; that is, they were planned to compare the effects of ordinary diet and of alcohol diet when the subject was engaged in active muscular work. The subject, E. O., was the same in both groups. The work in these experiments was performed on the bicycle ergometer described on page 237.

The ordinary diet in experiment No. 11 furnished 124 grams of protein and 3,862 calories of energy per day. The amount of protein was nearly the same as in No. 9, but in order to supply energy for muscular work the amount of energy in No. 11 was made to exceed considerably that in No. 9 by an increase in the amount of fats and carbohydrates in the diet.

The preliminary period of this experiment began with breakfast, March 18, 1898, and continued 4 days. During this time the subject was engaged in his usual occupation, and took a considerable amount of exercise each day walking or riding a bicycle. On the evening of March 21 he entered the respiration chamber, and the experiment proper began at 7 a. m. March 22, and continued until 7 a. m. March 26.

Experiment No. 12 was intended to be as exact a duplicate as possible of experiment No. 11, except that some of the sugar, starch, and fat was taken out of the diet and replaced by an isodynamic amount of alcohol. The alcohol diet of this experiment furnished 121 grams of protein and 3,891 calories of energy per day, as compared with 124 grams of protein and 3,862

calories of energy per day in the ordinary diet of experiment No. 11. In consideration of the difficulties in planning and regulating the diet so as to furnish exactly a definite quantity of protein or energy, the agreement of the two diets in regard to amount of protein per day is very satisfactory.

In order to obtain a palatable diet in experiment No. 12, considerably more fat was furnished than in experiment No. 11, consequently the carbohydrates (sugars and starches) had to be reduced more than would be required for their replacement by the amount of alcohol used. The fat was increased by 30 grams, corresponding to about 285 calories of energy, and the carbohydrates were decreased by 189 grams, corresponding to about 770 calories. In the place of the materials left out of the diet 80 grams of commercial alcohol, with 90.5 per cent or 72.4 grams of pure ethyl alcohol, furnishing 512 calories of energy, were given each day. In this way the energy of the alcohol diet of experiment 12 was made to agree very satisfactorily with that of the ordinary diet of experiment No. 11.

The preliminary period of this experiment began with breakfast on April 8, 1898, and continued 4 days, during which the subject took considerable exercise in addition to his regular occupation. The diet during the preliminary period was the same as during the metabolism experiment proper. The subject entered the chamber on the evening of April 11; metabolism experiment No. 12 began at 7 a. m. April 12, and continued until 7 a. m. April 16.

The following table summarizes the results of these 2 experiments. Detailed data of experiment No. 12 will be found in the Appendix, pages 291 to 305; those of No. 11 in Bulletin 109 of the Office of Experiment Stations:

TABLE 5.—*Summary of results of metabolism experiments Nos. 11 and 12.*

[Quantities per day.]

	Protein.	Fat	Carbohydrates	Alcohol.	Nitrogen.	Carbon.	Energy.
Experiment No. 11.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
In total food	124.1	129.1	484.6	.....	19.8	373.5	3,862
In available food	110.0	120.1	472.2	.....	17.6	340.6	3,510
Actually metabolized	113.0	159.8	(472.2)	.....	18.1	372.6	3,901
Heat measured	.....	.....	.....	.....	.....	.....	3,932
Gain (+) or loss (−) to body	3.0	39.7	.....	.....	−0.5	−32.0	−391
Experiment No. 12.							
In total food	120.6	158.5	296.1	72.4	19.3	344.8	3,891
In available food	112.8	152.0	290.4	70.9	18.0	319.6	3,614
Actually metabolized	113.8	184.2	(290.4)	70.9	18.2	344.7	3,922
Heat measured	.....	.....	.....	.....	.....	.....	3,927
Gain (+) loss (−) to body	−1.0	−32.2	.....	.....	−0.2	−25.1	−308

GROUP E. EXPERIMENTS NOS. 29, 31, AND 30. WORK EXPERIMENTS WITH ORDINARY DIET AND WITH ALCOHOL DIET.

The series of experiments forming this group was carried out in March, 1900. They were made with the same subject, J. F. S., as in Group C, and for the same purpose, namely, to study the relative replacing power of isodynamic quantities of alcohol, sugar, and fat. During this series the subject remained in the calorimeter 9 days and 10 nights without intermission, and each experiment in the series continued 3 days and nights. The experiments in Group E differ from those in Group C, however, in that the subject worked for 8 hours each day upon the bicycle ergometer, described on page 237. As in the previous series of experiments referred to, there was a basal ration which was the same and a supplemental ration which was different in each of the 3 experiments. The basal ration was planned to furnish approximately the same amount of protein as in the series in Group C, with the addition of about 1,000 calories of energy per day in order to furnish the extra energy required for the performance of the external muscular work and the general increase of bodily activity. It furnished about 100 grams of protein and from 2,949 to 2,984 calories of energy per day in the different experiments.

The preliminary digestion experiment began with breakfast March 12, 1900, and continued 4 days. The diet during this period consisted of the basal ration supplemented by cane sugar, as in experiment No. 29.

The subject entered the respiration chamber on the evening of March 15, and experiment No. 29 began at 7 a. m. March 16, and continued 3 days. During this experiment the diet consisted of the basal ration supplemented by 128 grams of cane sugar furnishing 507 calories of energy per day, as in the preliminary digestion period; the whole diet furnishing daily 100 grams of protein and 3,487 calories of energy. The daily amount of sugar in the form of rock candy was supplied to the subject each morning at breakfast, and he ate it at intervals during the day according to his taste.

Experiment No. 30 began at 7 a. m. March 19, immediately at the close of experiment 29. The diet in this experiment consisted of the basal ration supplemented by 79.5 grams of commercial alcohol containing 90.6 per cent or 72 grams of pure ethyl alcohol in place of the sugar of experiment No. 29. The alcohol supplied 509 calories of energy, and the whole ration in this experiment furnished 99 grams of protein and 3,458 calories of energy per day. The commercial alcohol used in this experiment was added each day to 795.5 grams of water sweetened with 25 grams of sugar from the basal ration. The total mixture, 900 grams, was divided into 6 portions which were taken with meals and between meals, as in other alcohol experiments.

Experiment No. 31 began at 7 a. m. on the morning of March 22, and continued 3 days. The diet in this experiment consisted of the basal ration supplemented by 63.5 grams of butter in place of the alcohol in the previous experiment. The butter furnished nearly 1 gram of protein and 511 calories of energy, so that the whole ration furnished 101 grams of protein and 3,495 calories of energy per day. The butter was consumed at meals with the rest of the diet.

The following table summarizes the results of these 3 experiments. Detailed data of experiment No. 30 will be found in the Appendix, pages 354 to 366, and those of experiments Nos. 29 and 31 will be found in Bulletin 109 of the Office of Experiment Stations.

TABLE 6.—*Summary of results of metabolism experiments Nos. 29, 31, and 30.*

[Quantities per day.]

	Protein.	Fat.	Carbohydrates.	Alcohol.	Nitrogen.	Carbon.	Energy.
Experiment No. 29.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
In total food	100.1	106.0	470.7	.....	16.0	333.6	3,487
In available food	94.8	103.0	464.6	.....	15.2	314.1	3,260
Actually metabolized	99.8	126.8	(464.6)	.....	16.0	334.9	3,515
Heat measured	.....	.....	.....	.....	.....	.....	3,589
Gain (+) or loss (−) to body	−5.0	−23.8	.....	.....	−0.8	20.8	−255
Experiment No. 31.							
In total food	100.9	160.8	342.7	.....	16.1	321.5	3,495
In available food	95.8	158.1	336.7	.....	15.3	302.5	3,275
Actually metabolized	98.1	174.0	(336.7)	.....	15.6	315.8	3,439
Heat measured	.....	.....	.....	.....	.....	.....	3,420
Gain (+) or loss (−) to body	−2.3	15.9	.....	.....	−0.3	−13.3	−164
Average 29 and 31.							
In total food	100.5	133.4	406.7	.....	16.0	327.6	3,491
In available food	95.3	130.6	400.7	.....	15.2	308.3	3,268
Actually metabolized	99.0	150.5	(400.7)	.....	15.8	325.4	3,477
Heat measured	.....	.....	.....	.....	.....	.....	3,505
Gain (+) or loss (−) to body	−3.7	−19.9	.....	.....	−0.6	−17.1	−209
Experiment No. 30.							
In total food	99.2	104.2	340.9	72.0	15.9	315.5	3,458
In available food	94.9	102.1	336.2	71.2	15.2	296.6	3,242
Actually metabolized	108.0	119.1	(336.2)	71.2	17.3	316.5	3,479
Heat measured	.....	.....	.....	.....	.....	.....	3,470
Gain (+) or loss (−) to body	−13.1	−17.0	.....	.....	−2.1	−19.9	−237

GROUP F. EXPERIMENTS NOS. 32, 34, AND 33. WORK EXPERIMENTS WITH ORDINARY AND WITH ALCOHOL DIET.

The series of experiments forming this group was made in April, 1900. The plan of the experments in this series was as nearly as possible a duplicate of that of the experiments forming Group E, the chief difference being that in the series in Group E the basal ration was supplemented in the first experiment by sugar, in the second by alcohol, and in the third by butter, whereas in the series in Group F the butter was used in the first experiment, alcohol in the second, and sugar in the third. Both series were work experiments in which the same subject, J. F. S., spent 8 hours each day working on the bicycle ergometer. In each series the subject remained 9 successive days within the calorimeter, and the whole investigation was divided into 3 experiments of 3 days each, the different experiments being distinguished from each other by changes in the supplemental ration. The basal ration in this series furnished 100 grams of protein and about 2,977 calories of energy per day. The amount of energy in the basal ration varied slightly in the successive experiments of the series, because of slight differences in the composition of the milk.

The preliminary digestion experiment began with breakfast April 16 and continued 4 days. The diet consisted of the basal ration supplemented with fat in the form of butter, as in experiment No. 32.

The subject entered the respiration chamber on the evening of April 19 and experiment No. 32 began at 7 a. m. April 20 and continued 3 days. The diet consisted of the basal ration supplemented by 63.5 grams of butter, furnishing 1 gram of protein and 510 calories of energy. The butter was consumed at meals with the rest of the diet. The total diet in this experiment supplied 101 grams of protein and 3,487 calories of energy per day.

Experiment No. 33 began at 7 a. m. April 23 and continued 3 days. The diet in this experiment consisted of the basal ration, supplemented by 79.5 grams of commercial alcohol with 90.6 per cent, or 72 grams, of absolute alcohol, furnishing 509 calories of energy. The commercial alcohol was added each day to 795.5 grams of water sweetened with 25 grams of sugar, making 900 grams of a mixture which was divided into six portions (see p. 292), the larger of which were taken at meals and the smaller between meals and before retiring. The total diet in this experiment furnished 100 grams of protein and 3,486 calories of energy per day.

Experiment No. 34 began at 7 a. m. April 26 and continued 3 days. The diet consisted of the basal ration supplemented by 128 grams of cane sugar, furnishing 507 calories of energy. The daily amount of sugar was supplied to the subject each morning in the form of rock candy, which he ate at intervals during the day according to his taste. The total diet in this experiment furnished 100 grams of protein and 3,493 calories of energy per day.

The following table summarizes the results of these 3 experiments. Detailed data of experiment No. 33 will be found in the Appendix, pages 366 to 378, and those of experiments Nos. 32 and 34 in Bulletin 109 of the Office of Experiment Stations:

TABLE 7.—*Summary of results of metabolism experiments Nos. 32, 34, and 33.*

[Quantities per day.]

	Protein.	Fat.	Carbohydrates	Alcohol.	Nitrogen.	Carbon.	Energy.
Experiment No. 32.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
In total food	100.5	151.6	353.9	.....	16.1	320.0	3,487
In available food	93.1	147.2	344.5	.....	14.9	296.4	3,226
Actually metabolized	98.1	182.1	(344.5)	.....	15.7	325.6	3,573
Heat measured	.....	.....	.....	.....	.....	.....	3,565
Gain (−) or loss (−) to body	−5.0	−34.9	.....	.....	0.8	−29.2	−347
Experiment No. 34.							
In total food	99.7	99.3	477.9	.....	16.0	335.7	3,493
In available food	92.4	94.4	470.1	.....	14.8	312.5	3,241
Actually metabolized	104.3	129.4	(470.1)	.....	16.7	345.4	3,629
Heat measured	.....	.....	.....	.....	.....	.....	3,587
Gain (−) or loss (−) to body	11.9	−35.0	.....	.....	−1.9	−32.9	−388

TABLE 7.—*Summary of results of metabolism experiments Nos. 32, 34, and 33*—Continued.

	Protein.	Fat.	Carbohydrates.	Alcohol.	Nitrogen.	Carbon.	Energy.
Average Nos. 32 and 34.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
In total food	100.1	125.5	415.9	.....	16.0	327.8	3,490
In available food	92.8	120.8	407.3	.....	14.8	304.4	3,234
Actually metabolized	101.3	155.8	(407.3)	.....	16.2	335.5	3,601
Heat measured							3,576
Gain (+) or loss (−) to body	−8.5	−35.0	.....	.....	−1.4	−31.1	−367
Experiment No. 33.							
In total food	99.7	99.3	355.0	72.0	16.0	319.6	3,486
In available food	92.4	95.0	346.9	71.3	14.8	295.7	3,227
Actually metabolized	108.2	133.4	(346.9)	71.3	17.3	333.3	3,669
Heat measured							3,632
Gain (+) or loss (−) to body	−15.8	−38.4	.....	.....	−2.5	−37.6	−442

GROUP G. EXPERIMENTS NOS. 13, 14, AND 7. REST EXPERIMENTS WITH ORDINARY AND WITH ALCOHOL DIET.

While the 3 experiments in this group are all rest experiments and all with the same subject, E. O., the ordinary experiments and the alcohol experiments were not planned to be exact duplicates of each other, and are therefore less exactly comparable than those in preceding groups. For the sake of comparison with the alcohol experiment, No. 7, however, 2 ordinary experiments, Nos. 13 and 14, were chosen in which the average of the amounts of protein and energy in the daily diet in the 2 experiments was practically the same as in the alcohol experiment. Since these experiments were made with the same subject and under conditions somewhat similar, the results may be compared in studying the effect of alcohol on metabolism.

Experiment No. 13 was intended to be as nearly as possible a duplicate of experiment No. 9. The ordinary diet in experiment No. 13 furnished 117 grams of protein and 2,596 calories of energy per day, which was 2 grams of protein and 121 calories of energy less than in No. 9. The preliminary period of No. 13 began with breakfast November 8, 1898, and continued 4 days, during which the subject had as little muscular exercise as practicable outside of his regular occupation as laboratory assistant. He entered the chamber on the evening of November 7, and the experiment proper began at 7 a. m. November 8. It was intended that the experiment should continue 4 days, but on the fourth day a leak occurred in the ventilating air pipe at such a point that the results for that day were destroyed; consequently the experiment is recorded as a 3-day experiment. While this was a rest experiment in general character, the subject was not so quiet throughout the experimental period as he had been in earlier and was in later similar experiments.

Experiment No. 14 was carried out under much the same conditions as No. 13, with the exception that in No. 14 the amount of protein in the diet was reduced from 117 to 94 grams per day, and the energy from 2,596 to 2,513 calories per day. The preliminary digestion experiment began with breakfast December 17, 1898, and continued 3 days. The subject entered the apparatus on the evening of December 19, and the experiment proper began at 7. a. m. December 20 and continued 4 days.

The average of the amounts of protein and energy in the daily diet of the 2 ordinary experiments, 13 and 14, was 105 grams of protein and 2,555 calories of energy.

The alcohol diet in experiment No. 7 furnished 104 grams of protein and 2,462 calories of energy per day. The diet in this experiment included 80 grams of commercial alcohol, with 90.6 per cent, or 72.5 grams, of pure ethyl alcohol, which furnished 512 calories of energy per day. The preliminary digestion experiment began with breakfast June 4, 1897, and continued 4 days. The subject entered the chamber on the evening of June 7, and the experiment proper began at 7 p. m. June 8 and continued 4 days.

The following table summarizes the results of these experiments. Detailed data of experiment No. 7 will be found in Bulletin 69, and those of Nos. 13 and 14 in Bulletin 109 of the Office of Experiment Stations:

TABLE 8.—*Summary of results of metabolism experiments Nos. 13, 14, and 7.*

[Quantities per day.]

	Protein.	Fat.	Carbohydrates.	Alcohol.	Nitrogen.	Carbon.	Energy.
Experiment No. 13.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
In total food	117.1	87.8	270.2	.....	18.7	245.8	2,596
In available food	110.2	81.6	265.0	.....	17.6	219.6	2,298
Actually metabolized	121.9	54.7	(265.0)	.....	19.5	205.2	2,112
Heat measured	.....	.....	.....	.....	.....	.....	2,151
Gain (+) or loss (−) to body	11.7	+26.9	.....	.....	−1.9	+14.4	+186
Experiment No. 14.							
In total food	94.4	82.5	289.8	.....	15.1	239.0	2,513
In available food	89.0	78.8	286.6	.....	14.2	219.4	2,289
Actually metabolized	101.4	54.4	(286.6)	.....	16.2	207.3	2,131
Heat measured	.....	.....	.....	.....	.....	.....	2,193
Gain (+) or loss (−) to body	−12.4	+24.4	.....	.....	−2.0	−12.1	+158
Average, experiments Nos. 13–14.							
In total food	105.8	85.2	280.0	.....	16.9	242.4	2,555
In available food	99.6	80.2	275.8	.....	15.9	219.5	2,294
Actually metabolized	111.7	54.5	(275.8)	.....	17.8	206.3	2,122
Heat measured	.....	.....	.....	.....	.....	.....	2,172
Gain (+) or loss (−) to body	−12.0	+25.7	.....	.....	−1.9	+13.2	+172
Experiment No. 7.							
In total food	104.4	68.2	190.4	72.5	16.7	218.6	2,462
In available food	98.8	65.8	186.6	69.5	15.8	197.1	2,230
Actually metabolized	110.8	80.1	(186.6)	69.5	17.7	214.5	2,434
Heat measured	.....	.....	.....	.....	.....	.....	2,394
Gain (+) or loss (−) to body	−12.0	−14.3	.....	.....	−1.9	−17.4	−204

GROUP H. EXPERIMENTS NOS. 5, 15–17. REST EXPERIMENTS WITH ORDINARY DIET AND WITH ALCOHOL DIET.

The experiments in Group H were all rest experiments with the same subject, E. O. One purpose of the 3 experiments with alcohol diet (Nos. 15–17) was to compare the effect of alcohol when taken in different forms, as commercial alcohol, whisky, or brandy. The experiment with ordinary diet (No. 5) has been chosen for comparison with the 3 experiments with alcohol diet for the reason that, while the amount of protein was somewhat larger in the former than in the latter, the amount of energy was practically the same in both diets. The experiments in this group are less comparable than those in Groups G and I because of differences in the circumstances under which the experiments were made. Experiment No. 5 was the first of the series of metabolism experiments in which the determinations of income and outgo of both matter and energy were made. The diet in this experiment was more varied than that in some of the later experiments, and the methods of sampling were not satisfactory, which will account in part for the unusually wide discrepancies between the theoretical values for income and those actually found for outgo of energy. On the other hand, experiments Nos. 15–17 were made at a later period when the apparatus and the methods of experimenting were much improved.

The preliminary period of experiment No. 5 began April 27, 1897, and continued 8 days, instead of 4 days as usual, because unexpected circumstances delayed the starting of the experiment proper. The subject entered the calorimeter at about 9 o'clock on the evening of May 3 and the experiment proper began at 7 a. m. May 4, and continued 4 days. The diet in this experiment furnished 119 grams of protein and 2,655 calories of energy per day.

Each of the 3 experiments, Nos. 15–17, was of 2 days' duration, and one followed the other without intermission and without the subject leaving the respiration chamber, so that in a way

they constitute one long experiment. No attempt was made to obtain a separation of the feces for the different experiments. The usual separations, however, were made, the first between the preliminary digestion experiment and the beginning of metabolism experiment No. 15, and the second at the close of experiment No. 17. The diet in these experiments consisted of a basal ration which was the same in all 3 experiments, supplemented by alcohol in the form of pure ethyl alcohol in experiment No. 15, by alcohol in the form of whisky in experiment No. 16, and by alcohol in the form of brandy in experiment No. 17. The total diet including the alcohol furnished 109 grams of protein and 2,653 calories of energy per day.

The preliminary digestion experiment began January 12, 1899, and continued 4 days as usual. During this preliminary experiment the subject received the basal ration, and in addition to this 72.5 grams of absolute ethyl alcohol, which was administered daily in coffee infusion sweetened with 45 grams of sugar.

The subject entered the respiration chamber on the evening of January 15 and experiment 15 began at 7 a. m. January 16. During this experiment he received the basal ration supplemented by 79.8 grams of 90.9 per cent commercial alcohol, or 72.5 grams of absolute ethyl alcohol, in 775.2 grams of coffee infusion, the whole of which was sweetened with 45 grams of cane sugar. There was 900 grams of the mixture which sufficed for the whole day. This was taken at 6 intervals, the larger portions being consumed with the meals and the smaller portions between meals and just before retiring.

Experiment No. 16 began at 7 a. m. January 18, and continued 2 days. The diet in this experiment consisted of the basal ration supplemented by 158.3 grams of whisky, with 45.8 per cent, or 72.5 grams, of absolute alcohol. This was mixed with 696.7 grams of water sweetened with 54 grams of sugar, and the whole divided into 6 doses and taken as before. The mixture was made with water rather than with coffee infusion, because it was thought the objection might be raised that the coffee might perhaps, to some extent, counteract the effect of the alcohol. The whisky, sugar, and water were furnished to the subject, who mixed them at the usual hours within the apparatus. The amount of alcohol found in the air current was larger during this experiment than during the one preceding it, suggesting that some alcohol may have been volatilized as the whisky was poured into the drinking cup and mixed with the water. The mixing was therefore done outside the apparatus in the next experiment, and the alcohol in the air current was again less than in No. 16.

Experiment No. 17 began at 7 a. m. January 20, and continued 2 days, during which the subject received the basal ration supplemented by 143.8 grams of brandy, with 50.4 per cent, or 72.5 grams, of absolute alcohol, per day. This amount was added to 711.2 grams of water and 45 grams of sugar, making a total of 900 grams of the mixture, which was administered in 6 portions, as in the previous experiments.

The following table summarizes the results of these 4 experiments. Detailed data of experiments Nos. 15–17 will be found in the Appendix, pages 305 to 317; those of No. 5 will be found in Bulletin 69 of the Office of Experiment Stations:

TABLE 9.—*Summary of results of metabolism experiments Nos. 5 and 15–17.*

[Quantities per day.]

	Protein.	Fat.	Carbohydrates.	Alcohol.	Nitrogen.	Carbon.	Energy.
Experiment No. 5.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
In total food	119.1	94.7	275.5	.....	19.1	248.9	2,655
In available food	108.8	89.0	269.1	.....	17.4	223.5	2,384
Actually metabolized	113.0	96.8	(269.1)	.....	18.1	231.7	2,482
Heat measured	.....	.....	.....	.....	.....	.....	2,379
Gain (+) or loss (−) to body	4.2	−7.8	.....	.....	0.7	−8.2	−98
Experiment No. 15.							
In total food	108.9	39.9	276.9	72.5	17.4	245.7	2,653
In available food	103.8	36.9	272.4	71.0	16.6	226.1	2,426
Actually metabolized	97.8	33.1	(272.4)	71.0	15.6	220.0	2,357
Heat measured	.....	.....	.....	.....	.....	.....	2,362
Gain (+) or loss (−) to body	+6.0	+3.8	.....	.....	+1.0	+6.1	+69

TABLE 9.—*Summary of results of metabolism experiments Nos. 5 and 15–17*—Continued.

[Quantities per day.]

	Protein.	Fat.	Carbohydrates.	Alcohol.	Nitrogen.	Carbon.	Energy
Experiment No. 16.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
In total food	108.9	39.9	276.9	72.5	17.4	245.7	2,653
In available food	103.8	36.9	272.4	70.4	16.6	225.9	2,424
Actually metabolized	96.6	31.9	(272.4)	70.4	15.5	218.3	2,336
Heat measured							2,332
Gain (+) or loss (−) to body	+7.2	+5.0			+1.1	+7.6	+88
Experiment No. 17.							
In total food	108.9	39.9	276.9	72.5	17.4	245.7	2,653
In available food	103.8	36.9	272.4	71.0	16.6	226.1	2,427
Actually metabolized	97.8	25.9	(272.4)	71.0	15.6	214.5	2,289
Heat measured							2,276
Gain (+) or loss (−) to body	+6.0	−11.0			+1.0	−11.6	+138
Average, Nos. 15, 16, and 17.							
In total food	108.9	39.9	276.9	72.5	17.4	245.7	2,653
In available food	103.8	36.9	272.4	70.8	16.6	226.0	2,426
Actually metabolized	97.4	30.3	(272.4)	70.8	15.6	217.6	2,327
Heat measured							2,323
Gain (+) or loss (−) to body	+6.4	+6.6			+1.0	+8.4	+99

GROUP 1. EXPERIMENTS NOS. 21 AND 18–20. REST EXPERIMENTS WITH ORDINARY AND WITH ALCOHOL DIET.

The series of experiments comprising this group was carried out in February, 1899. The purpose of the experiments with alcohol diet in this series was the same as that of experiments 15–17, namely, to determine whether there is any difference in the effect of alcohol when taken in different forms. Experiments Nos. 18–20 were somewhat similar in plan to Nos. 15–17, but were made with a different subject, A. W. S. The subject remained in the calorimeter 9 days without intermission. During the first 6 days of this period the 3 alcohol experiments, Nos. 18–20, were made, each of 2 days' duration, as in experiments 15–17. These were followed by one experiment, No. 21, of 3 days, in which the diet contained no alcohol.

As in the preceding series, the diet in experiments 18–21 consisted of a basal ration which was the same in all the experiments, and a supplemental ration which was different in each. This basal ration furnished 97 grams of protein and 2,264 calories of energy per day. In experiments Nos. 18–20 the basal ration was supplemented by commercial alcohol, whisky, and brandy, respectively, the quantity of each used being sufficient to furnish 72.5 grams of absolute alcohol per day, with a heat of combustion of 512 calories. The total diet in the alcohol experiments furnished 97 grams of protein and 2,776 calories of energy per day. In experiment No. 21 the alcohol was omitted, and the diet consisted of the basal ration alone.

The preliminary digestion experiment began with breakfast February 2, and continued 4 days. During this period the diet was the same as in experiment No. 18, and consisted of the basal ration and the alcohol in the form of commercial spirits, which was administered in coffee infusion, sweetened with sugar.

The subject entered the respiration chamber on the evening of February 5, and experiment No. 18 began at 7 a. m. February 6, and continued 2 days. In this experiment the diet consisted of the basal ration, supplemented by 79.8 grams of commercial alcohol, with 90.9 per cent, or 72.5 grams, of absolute alcohol. The commercial spirits was mixed with 775.2 grams of coffee infusion, sweetened with 45 grams of cane sugar. The whole mixture made 900 grams, which was divided into 6 portions, the larger of which were taken with meals, and the smaller between meals and just before retiring.

Experiment No. 19 began at 7 a. m. February 8, and continued 2 days. The diet in this experiment consisted of the basal ration, supplemented by 158.3 grams of whisky, with 45.8 per cent, or 72.5 grams, of absolute alcohol. The whisky was mixed with 696.7 grams of water,

sweetened with 45 grams of cane sugar, the whole mixture forming 900 grams, which was administered as in experiment No. 18.

Experiment No. 20 began at 7 a. m. February 10, and continued 2 days, during which the diet consisted of the basal ration, supplemented by 143.8 grams of brandy, with 50.4 per cent, or 72.5 grams, of absolute alcohol. The brandy was mixed with 711.2 grams of water, sweetened with 45 grams of cane sugar. The whole mixture amounted to 900 grams, which was administered in 6 portions as in the previous experiments.

Experiment No. 21 began at 7 a. m. February 12, and continued 3 days. The diet in this experiment consisted of the basal ration alone, without alcohol. The results of this experiment are here given in comparison with 3 alcohol experiments because it was a part of the same series and followed the alcohol experiments without intermission and without the subject leaving the respiration chamber. The results are hardly comparable with those of the alcohol experiments, however, since by the omission of the alcohol from the diet the amount of energy per day was reduced nearly one-fifth, while the amounts of protein, fats, and carbohydrates remained the same.

The following table summarizes the results of these 4 experiments. Detailed data of experiments Nos. 18–20 may be found on pages 317 to 330 in the Appendix. Those of No. 21 may be found in Bulletin 109 of the Office of Experiment Stations.

TABLE 10.—*Summary of results of metabolism experiments Nos. 18, 19, and 20.*

[Quantities per day.]

	Protein.	Fat.	Carbohydrates.	Alcohol.	Nitrogen.	Carbon.	Energy.
Experiment No. 21.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
In total food	96.9	72.4	250.1	.....	15.5	215.2	2,264
In available food	90.4	68.4	246.1	.....	14.5	195.4	2,038
Actually metabolized	96.0	93.3	(246.1)	.....	15.4	217.4	2,304
Heat measured	.....	.....	.....	.....	.....	.....	2,279
Gain (+) or loss (−) to body	−5.6	−24.9	.....	.....	−0.9	−22.0	−266
Experiment No. 18.							
In total food	96.9	72.4	250.1	72.5	15.5	253.0	2,776
In available food	90.4	68.4	246.1	69.5	14.4	232.0	2,532
Actually metabolized	102.6	43.3	(246.1)	69.5	16.4	219.3	2,367
Heat measured	.....	.....	.....	.....	.....	.....	2,485
Gain (+) or loss (−) to body	−12.2	+25.1	.....	.....	−2.0	−12.7	+168
Experiment No. 19.							
In total food	96.9	72.4	250.1	72.5	15.5	253.0	2,776
In available food	90.4	68.4	246.1	69.9	14.5	233.5	2,550
Actually metabolized	90.4	33.3	(246.1)	69.9	14.5	206.6	2,220
Heat measured	.....	.....	.....	.....	.....	.....	2,279
Gain (+) or loss (−) to body	.....	+35.1	.....	.....	.....	−26.9	−330
Experiment No. 20.							
In total food	96.9	72.4	250.1	72.5	15.5	253.0	2,776
In available food	90.4	68.4	246.1	69.7	14.5	233.5	2,549
Actually metabolized	88.2	47.3	(246.1)	69.7	14.1	216.2	2,339
Heat measured	.....	.....	.....	.....	.....	.....	2,303
Gain (+) or loss (−) to body	2.2	+21.1	.....	.....	+0.4	−17.3	+210
Average of 18, 19, and 20.							
In total food	96.9	72.4	250.1	72.5	15.5	253.0	2,776
In available food	90.4	68.4	246.1	69.7	14.5	233.0	2,544
Actually metabolized	93.7	41.3	(246.1)	69.7	15.0	214.1	2,308
Heat measured	.....	.....	.....	.....	.....	.....	2,357
Gain (+) or loss (−) to body	3.3	+27.1	.....	.....	0.5	−18.9	+236

DIGESTION EXPERIMENTS.

The data of the metabolism experiments above described include statistics of the amounts of nutrients consumed in the food and excreted in the feces. The difference between these amounts represents the so-called digestible or available nutrients.[a] The amount of each nutrient thus made available divided by the amount in the corresponding food is here taken as the coefficient of availability.

Each metabolism experiment, therefore, includes a digestion experiment; furthermore, each metabolism experiment or series of experiments was preceded by a digestion experiment, generally of 4 days' duration, during which the subject was outside the respiration calorimeter, but had the same diet, and as nearly as convenient the same amount of muscular exercise, as in the metabolism experiment. We thus have for each metabolism experiment or series of metabolism experiments two corresponding digestion experiments. While the chief object of the preliminary experiment was to bring the body into approximate nitrogen equilibrium, the results, as bearing upon the availability of the food, are of importance.

The portions of protein, fat, carbohydrates, and ash not made available are eliminated in the feces. The unavailable alcohol is eliminated through the kidneys, lungs, and skin, and was determined in these experiments according to the method described beyond (p. 258).

In what has been said about the availability of the different nutrients in food no reference has been made to the availability of the energy. While it is commonly believed that all of the energy of the available fats and carbohydrates is capable of use by the body, all of the energy of the protein can not be so utilized. The nitrogen of the available protein is eliminated from the body in the form of urea, uric acid, and similar compounds, carrying with them a certain amount of energy. From the results of a considerable number of determinations of the ratio of the heat of combustion of urine to the available protein it has been found that for each gram of the latter there is lost in the urine an average of 1.25 calories of energy. This amount must therefore be deducted from the energy of the available food in order to obtain the available energy of the available protein. This is done by multiplying the number of grams of the latter by 1.25, and deducting the product from the difference between the total energy in the food and that in the feces. The difference gives the amount of available energy, which, divided by the total energy in the food consumed, gives the coefficient of availability of the energy.[b]

The proportions of the different nutrients digested and made available in any given case depend upon the diet and the individual. So far as concerns the diet, the availability may vary with (1) the kinds, (2) the amounts of food materials, (3) the method of preparation, and (4) the accessories, including condiments, beverages, etc., and with the rest, alcoholic beverages. The same diet may be differently digested by different individuals or by the same individual under different conditions of health, physical activity, and nervous strain.

The details of the digestion experiments with alcohol diet are given in Tables CV to CXVIII of the Appendix.

Table 11 compares the availability of food in diets with and without alcohol and the availability of the same diet with the same persons outside and inside the respiration chamber. In the first case the principal difference is that of diet, the alcohol being the chief factor; in the second case the differences are those of the physical and mental condition of the individual. The discussion of the effect of alcohol upon availability of the nutrients of the diet is given on pages 256 to 258, beyond.

[a] For further discussion see page 256 beyond, and Repts. Storrs (Conn.) Agr. Exp. Sta., 1896, p. 163, and 1897, p. 154.

[b] For further discussion of this subject see Atwater and Bryant, Rept. Storrs (Conn.) Agr. Exp. Sta., 1899, p. 96. See also discussion by W. O. Atwater in Bul. 99 of the U. S. Dept. Agr., Office of Experiment Stations, Proceedings of the Association of American Agricultural Colleges and Experiment Stations, 1900, p. 112.

TABLE 11.—*Summary of coefficients of availability of nutrients and energy in preliminary and calorimeter periods and with ordinary and alcohol diet.*

	Protein.	Fat	Carbohydrates	Energy
Experiments with E. O.				
	Per cent.	*Per cent.*	*Per cent.*	*Per cent.*
Ordinary diet, average 6 experiments	92.4	93.8	97.9	90.6
Alcohol diet, average 5 experiments	94.2	93.5	97.9	91.1
Preliminary period, average 12 experiments	92.5	93.7	97.7	90.7
Calorimeter period, average 12 experiments	93.2	94.1	97.9	90.9
Experiments with J. F. S.				
Ordinary diet, average 6 experiments	93.4	95.8	98.1	92.7
Alcohol diet, average 3 experiments	93.8	96.2	97.9	93.0
Preliminary period, average 4 experiments	92.1	95.8	97.2	91.4
Calorimeter period, average 4 experiments	93.8	97.2	97.7	92.4
Average 12 experiments with ordinary food	92.9	94.7	98.0	91.7
Average 8 experiments with alcohol	94.0	94.5	97.9	91.8
Average 16 preliminary periods	92.4	94.2	97.6	90.9
Average 16 calorimeter periods	93.3	94.9	97.8	91.3

DISCUSSION OF THE RESULTS OF THE EXPERIMENTS.

The special purpose of the experiments summarized on the preceding pages, in so far as they have had to do with the nutritive action of alcohol, has been the study of the metabolism of the energy of alcohol and its consequent value for fuel as compared with isodynamic amounts of carbohydrates and fats. Incidentally, its effects upon digestion, the completeness of its oxidation, and its action in protecting body fat and protein from oxidation have also been observed. The more important results may be discussed under the following topics:

1. Effect of alcohol upon the digestion of food.
2. Proportions of alcohol oxidized and unoxidized.
3. Metabolism of the energy of alcohol.
4. Protection of body material by alcohol.
   a. Protection of body fat.
   b. Protection of body protein.
5. Effect of alcohol upon the radiation of heat from the body.
6. Alcohol as a source of heat in the body.
7. Alcohol as a source of muscular energy.

EFFECT OF ALCOHOL UPON THE DIGESTION OF FOOD.—DIGESTIBILITY VERSUS AVAILABILITY OF NUTRIENTS.

The term digestibility as applied to food has several meanings, which are not clearly distinguished in popular usage. It commonly refers to either the ease with which a given food material is digested, or the time required for the process, or the extent to which the material "agrees" or "disagrees" with different persons, or its effects upon bodily comfort and health. These factors depend largely upon individual peculiarities, vary widely with different persons and with the character of the food, and are difficult to measure.

The term digestibility is also used to designate the quantity or proportion of the food or of each of its different ingredients—protein, fats, carbohydrates, and mineral matters—actually digested and absorbed in the passage of the food through the digestive tract. Only this latter factor of digestibility is considered in these experiments. To determine what amount of each nutrient is actually digested it is necessary to know the quantity that is taken into the body in food and the quantity that has escaped digestion and is excreted in the feces. The latter quantity is not easily determined, however, because the feces contain, besides those portions of the food that have

resisted the action of the digestive juices, other materials, the so-called metabolic products, which are mainly the residues of the digestive juices, and which are not easily separated from the undigested portion of the food. For this reason it is difficult to determine the actual digestibility of food or of its several ingredients.

The availability of the food or of the several ingredients, however, may be more accurately determined. By availability is here meant the quantity or proportion that can be used for the building and repair of tissue and the yielding of energy. The metabolic products, although derived originally from the digested food, are not used for either building material or fuel, and hence are not available in the sense in which the word is here employed. They may, therefore, be included with the undigested residue of the food and the small quantities of intestinal epithelium and other materials which make up the rest of the feces, and the amounts of available nutrients may be found by subtracting from the total ingredients of the food the total corresponding ingredients in the feces. These have often been called the digestible rather than the available nutrients, but the distinction here made is quite important.

The availability of the ingredients as thus determined is usually expressed by the percentage of the total amount of each in the food. This percentage is called the coefficient of availability. In the following table, which is a summary of a more detailed table given in the Appendix, the coefficients of availability of the protein, fats, and carbohydrates of the ordinary diet are compared with those of the alcohol diet, as actually found in the experiments. The average coefficients of availability of the nutrients of food as found in 93 experiments[a] with healthy men with ordinary diet under various conditions of work and rest are appended in the table for comparison.

TABLE 12.—*Coefficients of availability of food in the averages of experiments with and without alcohol.*

Kind and number of experiments	Coefficients of availability.			
	Protein.	Fat.	Carbohydrates.	Energy.
Experiments more directly comparable.				
	Per cent.	*Per cent.*	*Per cent.*	*Per cent.*
Without alcohol, Nos. 9, 11, 26 and 28, 29 and 31, 32 and 34	92.6	94.9	97.9	91.8
With alcohol, Nos. 10, 12, 27, 31, 33	93.7	94.6	97.8	92.1
Experiments less directly comparable.				
Without alcohol, Nos. 5, and 13 and 14	92.6	94.1	98.1	90.3
With alcohol, Nos. 7 and 15 to 17	95.0	94.4	97.3	91.3
Average of other observations	93.0	95.0	98.0	[a] 92.3

[a] Availability of energy based upon average proportions and amounts of nutrients found in dietaries of 38 families of farmers, mechanics, and professional men and 15 college boarding clubs in different parts of the United States. See article by A. P. BRYANT on "Some Results of Dietary Studies." Yearbook U. S. Dept. Agriculture, 1898, p. 439.

It thus appears that the alcohol had little appreciable effect upon the availability of the other ingredients of the diet; the coefficients of availability of the nutrients of the ordinary food were practically the same with and without alcohol as part of the diet. The protein appears to have been slightly more available when the diet contained alcohol. The differences, especially in the more comparable experiments, are less than might be found with different subjects using the same ordinary food, or with the same subject using the same food at different times and under different conditions.

The conclusion from the results of these experiments would be to the effect that alcohol in moderate amounts tended to increase very slightly the availability of the nutrients of the diet, especially of the protein. In view, however, of the fact that there are often marked differences in the availability of the same diet with different persons and with the same person at different

[a] See ATWATER and BRYANT, Availability and Fuel Value of Food Materials, Rept. Storrs (Conn.) Expt. Sta., 1899, p. 73.

times, even this conclusion should be held with a degree of reserve. While it is statistically valid for these experiments, the extent to which it would be true in general experience is by no means certain.

PROPORTIONS OF ALCOHOL OXIDIZED AND UNOXIDIZED.

The difference between the amount of alcohol taken into the body in food and the amount given off unoxidized by the kidneys, lungs, and skin is taken as the amount oxidized in the body. For the determination of the amounts not oxidized in the body quantitative examination was made of the several excretory products for the presence of alcohol. No similar examination of the feces for alcohol was practicable; but, as it has been found in other experiments[a] that no alcohol was excreted through this channel, even when considerable quantities were ingested, it was here assumed that the feces would contain no appreciable amount of the alcohol taken with the food.

The alcohol eliminated by the kidneys would, of course, be found in the urine; that given off by the lungs and skin in the "drip" water collected from the surface of the system of cooling tubes, or it might pass out of the chamber as vapor in the air current and be condensed in the "freezers," in which a large part of the water is collected from the outgoing air, or it might even pass through the freezers as vapor and be ultimately absorbed in concentrated sulphuric acid in an apparatus arranged for the purpose.

The determinations of the amounts of alcohol given off from the body unoxidized in experiment No. 7 were made according to the method described by Bodländer.[b] This method, however, does not give results sufficiently accurate when the amounts of alcohol are as small as were found in these experiments. In the latter experiments a modification[c] of this method was used, which has been shown to give very satisfactory results in the determination of extremely small quantities of alcohol.

The urine, drip water, and freezer water were distilled several times in order to separate the alcohol and other volatile and readily oxidizable organic matters and to obtain them in a more concentrated form. The amount of organic matter (here designated as reducing material) in the distillates was then determined by the method mentioned above. The amount of reducing material in the air current was estimated by passing the outgoing air through bulbs containing concentrated sulphuric acid, and determining the amount of reducing material in the acid. The total amount of reducing material thus determined in the various excretory products was calculated as alcohol.

Other investigators[d] have found evidence that such reducing materials are excreted by the body when no alcohol was ingested. In several experiments in which alcohol did not form part of the diet, examinations of respiratory and excretory products were made the same as when alcohol was given, and reducing materials were found to be present.[e] The average amount found in these experiments without alcohol was, therefore, deducted from the total amount determined in the experiments with alcohol and the difference taken as alcohol excreted, as shown below:

Alcohol ingested and excreted unoxidized.

Alcohol ingested, average 13 experiments	grams..	72.3
Reducing material in excretory products:		
When alcohol was ingested, average 13 experiments	grams..	1.6
When no alcohol was ingested, average 6 experiments	do....	.3
Alcohol excreted	grams..	1.3
Total alcohol metabolized	do....	71
Do	per cent..	98.2

[a] See Bodländer in Arch. Physiol., Pflüger, 32 (1883), p. 424.

[b] Loc. cit.

[c] See Benedict and Norris on "The Determination of Small Quantities of Alcohol," Jour. Am. Chem. Soc., 20 (1898), p. 299.

[d] Dupré, Proc. Roy. Soc. (London), 20 (1871–72), 268. See also Billings, Mitchell, and Bergey on "The composition of expired air and its effect upon animal life." Smithsonian Contributions to Knowledge, XXIX (1895), No. 989.

[e] See Table CXXI in the Appendix.

From Table CXXII in the Appendix it will be observed that the quantities of alcohol eliminated by the lungs, skin, and kidneys varied from 0.7 to 2.7 grams, and averaged 1.3 grams per day. These quantities correspond to a range of from 1 per cent to 3.7 per cent and an average of 1.9 per cent of the total amount of alcohol ingested. We consider, therefore, that in general when alcohol is taken in small doses not more than 2 per cent is given off unoxidized, and the results of the later experiments indicate that this figure is really too large. Accordingly, the coefficient of availability of alcohol is taken as 98 per cent.

Comparing this with the coefficients of availability of protein, fat, and carbohydrates in the diet with alcohol, as given in the Table 12, p. 257, it appears that the coefficient of availability of alcohol in these experiments was practically the same as that of the carbohydrates and larger than those of fats and protein of ordinary food. That is to say, it was found that 2 per cent or less of the total alcohol ingested in these experiments was given off unoxidized by the lungs and skin, while on the average about 2 per cent of the carbohydrates, 5 per cent of the fats, and 7 per cent of the protein of the ordinary diet appeared to be excreted unoxidized.

The conclusion is that in these experiments the alcohol was more completely consumed than are the nutrients of ordinary mixed diet.

METABOLISM OF THE ENERGY OF ALCOHOL.

It was stated above that the experiments with men in the respiration calorimeter had shown a very close agreement between the income and outgo of energy in the body, and that this was regarded as practically a demonstration that the law of the conservation of energy holds in the living organism. Up to April, 1900, the results of 30 such experiments had been obtained. These covered, all told, 93 days; they were made with 4 different subjects, under various conditions of diet and occupation. When the figures for individual days or for individual experiments are considered, there appears to be more or less disagreement between the figures for income and those of outgo energy, though the differences are inside the natural range of error in such physiological experiments. When the results of all the experiments are averaged together, however, the differences counterbalance each other, and the daily income, 2,718 calories, is found to be practically identical with the daily outgo, 2,716 calories. This agreement is in accordance with the law of the conservation of energy, and thus confirms the belief that this law governs the metabolism of energy in the living organism.

In 13 of the 30 experiments referred to alcohol formed a part of the diet. The results of these experiments compared with those without alcohol imply very clearly that the law of the conservation of energy holds as well with the diet containing alcohol as with the ordinary diet. This may be seen from Table 13, which epitomizes the more detailed statistics given in Table CXX in the Appendix, and compares the averages of the results of the rest and the work experiments in which alcohol formed part of the diet with those of similar experiments without alcohol. Both those experiments that are strictly comparable and those less comparable, as explained on a preceding page, are here included.

TABLE 13.—*Metabolism of energy. Averages of results of experiments with ordinary and with alcohol diet.*

Experiments with and without alcohol.	Energy of net income.[a]	Energy of outgo measured as—		
		Heat.	Muscular work.	Total.
MORE DIRECTLY COMPARABLE.				
Rest experiments.	*Calories.*	*Calories.*	*Calories.*	*Calories.*
Without alcohol: Nos. 9, 24, 26, and 28	2,190	2,221	.....	2,221
With alcohol: Nos. 10, 22, 27	2,191	2,221	.....	2,221
Work experiments.				
Without alcohol: Nos. 11, 29 and 31, 32 and 34	3,660	3,451	220	3,671
With alcohol: Nos. 12, 30, 33	3,690	3,461	215	3,676

[a] Estimated energy of material actually oxidized in the body.

TABLE 13.—*Metabolism of energy. Averages of results of experiments with ordinary and with alcohol diet*—Continued.

Experiments with and without alcohol.	Energy of net income.[a]	Energy of outgo measured as—		
		Heat.	Muscular work.	Total.
MORE DIRECTLY COMPARABLE—continued.				
Average of rest and work experiments.				
	Calories.	*Calories.*	*Calories.*	*Calories.*
Without alcohol	2,925	2,836	[b](110)	2,946
With alcohol	2,941	2,841	[b](108)	2,949
LESS DIRECTLY COMPARABLE.				
Rest experiments.				
Without alcohol: Nos. 13 and 14, 5, 21	2,302	2,277	.....	2,277
With alcohol: Nos. 7, 15 to 17, 18 to 20	2,356	2,358	.....	2,358
Average of all above experiments.				
Without alcohol	2,717	2,650	[b](73)	2,723
With alcohol	2,746	2,680	[b](72)	2,752

[a] Estimated energy of material actually oxidized in the body.

[b] In this average the muscular work of the work experiments is distributed over both the work and the rest experiments, which is of course not strictly logical.

The energy of net income given in the table above represents the energy of the material actually oxidized in the body, as determined from the energy of the food, of the excretory products, and of the body material stored or lost. The energy of outgo is that given off from the body in the form of heat and external muscular work, as measured by the apparatus. According to the law of the conservation of energy, the income and the outgo must be equal. From the comparisons given in the table above it will be seen that, whether the diet did or did not contain alcohol, the outgo was sometimes greater and sometimes less than the income, but the difference in every case was far within the range of variation to be expected in physiological experiments of such nature as these, so that the results may be considered as showing practical agreement. If we counterbalance the variations by averaging the experiments in which alcohol formed part of the diet and those without alcohol, we get the following results:

Daily income and outgo of energy with and without alcohol.

Diet.	Energy of material oxidized in the body.	Energy given off by the body.
	Calories.	*Calories.*
Average 13 experiments, without alcohol	2,717	2,723
Average 13 experiments, with alcohol	2,746	2,752

When the diet contained no alcohol, the energy of the proteids, fats, and carbohydrates burned in the body, averaging 2,717 calories per day, was practically identical with the energy given off by the body in the form of heat, or heat and (the heat equivalent of) external muscular work, averaging 2,723 calories per day. When alcohol formed part of the diet the total energy of the proteids, fats, and carbohydrates burned in the body, added to the energy of the alcohol, averaged 2,746 calories per day, and the energy given off as heat, or heat and external muscular work, averaged 2,752 calories per day. The total kinetic energy of outgo is equal to the total potential energy of income, whether it be with ordinary diet alone, or with ordinary food and alcohol.

To these results there can be but one interpretation. The energy which was latent or potential in the alcohol was wholly transformed in the body, was actually given off from the body, and was exactly recovered as heat or heat and muscular work. Otherwise, how did the body

dispose of the energy of the alcohol, and from what other source did it get an exactly equal amount to replace it?

The conclusions, therefore, are:

1. The law of the conservation of energy obtained with the alcohol diet as with the ordinary diet.

2. The potential energy of the alcohol oxidized in the body was transformed completely into kinetic energy, and appeared either as heat, or as muscular work, or both. To this extent, at any rate, it was used like the energy of the protein, fats, and carbohydrates of the food.

THE PROTECTION OF BODY MATERIAL BY ALCOHOL.

General considerations. Previous experiments and their explanation.—The belief was formerly quite general that alcohol has a specific pharmacodynamic action in retarding the metabolism of body material, both fat and proteid. As much of the earlier experimenting implied that alcohol in moderate quantities tends to "prevent waste" or "conserve the tissues," and its oxidation in the body was not understood, this effect was naturally attributed to its action as a drug. Later, as the functions of the nonnitrogenous nutrients of food came to be better understood, and the fact that alcohol is oxidized as they are in the body became fully established, the view has become common that its effect in retarding or protecting metabolism is to be explained by a nutritive rather than a pharmacodynamic action—that, in other words, it tends, by its own oxidation, to prevent the oxidation of other materials. This latter function of alcohol, however, has been denied on two grounds:

1. The increased circulation of the blood through the peripheral capillaries and the fall of body temperature which follows the ingestion of alcohol have led to the theoretical inference that the energy supplied to the body by the oxidation of the alcohol is lost by the extra radiation of heat it causes, so that it can not do the work of the fats and carbohydrates in protecting food or body material from consumption. This ground, however, is hardly tenable since, as shown beyond, the fall of body temperature with ordinary doses is very small, and the amount of extra heat radiated is only a fraction of that supplied by the alcohol.

2. The other ground for doubting the power of alcohol to protect body material from consumption is that of direct experiment. That it may protect fat is generally conceded, but there are a number of reliable experiments on record in which the replacement of the carbohydrates and fats of a ration by alcohol has been followed by an increased elimination of nitrogen. This has been explained by the assumption that alcohol tends to increase rather than diminish the catabolism of protein in the body. On the other hand there is a considerable amount of experimental evidence to the effect that alcohol may and at times does serve as a protector of protein.

As explained in a review of the experimenting upon this subject[a] it seems to us that the conflicting results may be explained by the hypothesis of two opposing tendencies of alcohol, the one pharmacodynamic and the other nutritive. This view makes the former a specific, and sometimes, if not always, temporary action of alcohol, by which it increases the catabolism of protein, while the latter action is that resulting from its oxidation. According as the latter or the former action predominates the alcohol may protect protein or fail to do so. In favor of this theory is the fact that it explains and harmonizes the results of previous experimenting and those of our own experiments also.

In considering the efficiency of alcohol for the protection of body fat and protein it is important to distinguish between two questions. Does alcohol protect these materials at all? Is it equal in protecting power to the isodynamic amount of fats or of carbohydrates, or of a mixture of the two? The comparisons in these experiments are between nearly isodynamic amounts of alcohol and the other ingredients.

[a] Report of Physiological Subcommittee of Committee of Fifty for the Investigation of the Liquor Problem, Boston, Houghton, Mifflin & Co. (In press at the time of this writing.) See also a more detailed review of the subject by Rosemann. Der Einfluss des Alkohols auf den Eiweissstoffwechsel; Arch. f. d. ges. Physiol., Bd. 86, 1901, pp. 307–503.

The evidence of the experiments here reported.—Although the present experiments were not planned for the study of these particular questions, they throw some light upon them. The details, in their bearing upon the protection or nonprotection of body protein and fat, are brought together in Table CXX in the appendix, and the average results are summarized in Table 14 herewith, which shows the amounts of available protein and energy of the diet and the amounts of protein and fat gained or lost by the body in the experiments with and without alcohol.

TABLE 14.—*Comparison of gains and losses of protein and fat in experiments with and without alcohol.*

Experiments compared	Serial numbers of experiments	Total number of days.	Average per day			
			Available food		Gain + or loss −	
			Protein.	Energy.	Protein.	Fat
MORE DIRECTLY COMPARABLE.						
A and B:						
E. O., rest—			*Grams.*	*Calories.*	*Grams.*	*Grams.*
Average, 2 experiments without alcohol.	9, 24	7	114	2,618	− 1.0	−39.0
Average, 2 experiments with alcohol	10, 22	7	116	2,602	− 2.8	−42.0
D:						
E. O., work—						
1 experiment without alcohol	11	4	110	3,510	− 3.0	−39.7
1 experiment with alcohol	12	4	113	3,614	− 1.0	−32.2
A, B, and D:						
E. O., rest and work—						
Average, 3 experiments without alcohol.	9, 24, 11	11	112	2,915	− 1.6	−12.7
Average, 3 experiments with alcohol	10, 22, 12	11	115	2,939	− 2.2	−17.2
C:						
J. F. S., rest—						
Average, 2 experiments without alcohol.	(26, 28)	6	92	2,253	− 4.0	+23.1
1 experiment with alcohol	27	3	92	2,264	− 6.0	−18.2
E and F:						
J. F. S., work—						
Average, 4 experiments without alcohol.	(29, 31), (32, 34)	12	95	3,251	− 6.1	−27.5
Average, 2 experiments with alcohol	30, 33	6	94	3,235	−14.5	−27.7
C, E, and F:						
J. F. S., rest and work—						
Average, 6 experiments without alcohol.	(26, 28), (29, 31), (32, 34).	18	94	2,918	− 5.4	10.6
Average, 3 experiments with alcohol	27, 30, 33	9	93	2,911	−11.6	12.4
A to F (Group I):						
E. O. and J. F. S., rest and work—						
Average, 9 experiments without alcohol.	9, 24, 11, (26, 28), (29, 31), (32, 34).	29	103	2,917	− 3.5	1.1
Average, 6 experiments with alcohol	10, 22, 12, 27, 30, 33	20	104	2,925	− 6.9	− 2.4
LESS DIRECTLY COMPARABLE.						
G, H, and I (Group II):						
E. O. and A. W. S., rest—						
Average, 4[a] experiments without alcohol.	(13, 14), 5, 21	14	100	2,239	− 7.3	2.3
Average, 7[a] experiments with alcohol	7, (15, 16, 17), (18, 19, 20)	16	98	2,400	− 3.0	− 6.5
AVERAGE OF ALL THE ABOVE EXPERIMENTS.						
A to I (Group III):						
E. O., J. F. S., and A. W. S., rest and work—						
Average, 13 experiments (3 with work) without alcohol.	(13, 14), (26, 28), (29, 31), (32, 34), 5, 9, 11, 21, 24.	43	102	2,691	− 4.8	− 0.1
Average, 13 experiments (3 with work) with alcohol.	7, (15, 16, 17), (18, 19, 20), 10, 12, 22, 27, 30, 33.	36	102	2,750	− 5.6	− 3.8

[a] When two or more similar experiments are grouped together, the group is counted as 1 experiment in drawing the average. Experiments thus treated are put in parenthesis in the second column; thus, (15 to 17).

The grouping in Table 14 is on the same basis as in the corresponding tables in the preceding pages and in the Appendix.

When the fuel value of the diet is in excess of the needs of the body, the latter often, though not always, increases its store of material. Sometimes this increase is in the form of protein, sometimes fat, and sometimes both protein and fat. When the body requires energy in excess of that supplied by the food, it will draw upon its previously accumulated store of fat or protein, or both, for fuel. Along with the gains and losses of protein and fat are changes in the carbohydrates (glycogen), but the total quantity of these substances in the tissues is relatively small. The present methods of experimenting do not suffice for accurate measurement of the changes of glycogen, and it is commonly left out of account in discussions such as that in which we are now engaged.

PROTECTION OF BODY FAT.

The figures for the individual experiments in Table CXX of the Appendix show in some cases a larger gain or smaller loss of fat without alcohol than with it; in other cases the results are reversed. When, however, the experiments are grouped together and the averages with and without alcohol are compared, it is clear that, except where the differences in fuel value of the diet were considerable, the differences of fat balance are hardly large enough to be of consequence. Taking the experiments altogether, the figures of the tables, and especially those of Table 14, show slight gains in fat both with and without alcohol, but the gain is slightly larger with the alcohol. Thus in Group I, in which the experiments are more directly comparable, the average gain in 9 experiments without alcohol is 1.1 grams, in 6 with alcohol 2.4 grams, making a difference in favor of the alcohol of 1.3 grams. In the less directly comparable experiments there is an average difference of 8.8 grams, and in Group III with all the experiments there is an average of 3.9 grams in favor of the alcohol. It is also to be noted that in general the total energy of the rations with the alcohol average somewhat larger than in those without alcohol. The figures for differences just cited are brought out more clearly in Table 17, beyond, in the discussion of the utilization of energy in the experiments with and without alcohol. The comparison as there made in detail shows on the whole an advantage of the ordinary diet over that with alcohol, though the difference is very small, indeed.

A direct indication of the fat-protecting power of alcohol is found in the series of experiments with E. O., Nos. 22, 23, 24. These were practically three successive periods of 3 days each. In all there was a basal ration with 116 grams available protein and 2,290 calories of available energy. To this ration was added—in the first experiment, alcohol; in the second, nothing; in the third, sugar. The alcohol and sugar each furnished about 500 calories of energy. With the alcohol there was a daily gain of 63 grams of fat; with the basal ration this was reduced to 9 grams; with the sugar it rose again to 60 grams per day. With the sugar there was a gain of 1.7 and with the alcohol a gain of 1.4 grams, while with the basal ration alone there was a loss of 1.6 grams of protein. Leaving this slight gain or loss of protein out of account, the net gain of fat with the alcohol above that in the basal ration was 54 grams, which would make very nearly 500 calories. The net gain of fat with sugar was 51 grams. In this particular case, therefore, with isodynamic quantities of sugar and alcohol, the gain of fat was practically the same with both.

An even more striking illustration of the fat-protecting power of alcohol is found in experiments Nos. 18–21, with A. W. S. as summarized on page 329 beyond. When alcohol was added to a basal ration of ordinary food, the body gained fat at the rate of 21–35 grams per day; but when the giving of alcohol was stopped and the body had only the basal ration, it lost 25 grams of fat per day.

A clearer demonstration of the power of alcohol to protect fat from consumption would be hardly possible than that given in the experiments with E. O. and A. W. S., just cited.

We thus have two kinds of tests of the power of alcohol as compared with that of isodynamic amounts of carbohydrates and fats of the food for the protection of body fat. In every individual case the protecting power of the alcohol is manifest. In some instances it is slightly inferior and in others it is slightly superior in this respect, and on the average it is just about equal to the nutrients which it replaced.

So far as we are aware these are the only experiments in which the power of alcohol to protect fats has been determined by direct quantitative tests. While there are numerous experiments on record which have seemed to indicate that alcohol has this power, we have found none which seem to us to imply the opposite.[1] Fortunately this question, which is one of no little importance, thus seems to be so clearly settled as to require no further discussion. Such is not the case with the similar question regarding the power of alcohol to protect protein from consumption.

PROTECTION OF BODY PROTEIN.

As regards the protection of body protein by alcohol, the results of the experiments are variable, but on the whole the catabolism of protein, as measured by the amount of nitrogen excreted by the kidneys, was slightly larger in the experiments with than in those without alcohol. In discussing the effect of alcohol upon protein metabolism, we must consider the variations from day to day in the amount of nitrogen excreted in the urine when alcohol forms a part of the diet, and compare them with the variations in similar experiments in which alcohol is not included in the diet. The data of the daily eliminations of nitrogen by the different subjects in experiments with and without alcohol are summarized in Table CXXIII in the Appendix.

What especially concerns us here is the influence of the substitution of alcohol for a portion of the ordinary food upon the gain or loss of body protein. As this seems to depend largely upon the individual, it will be well to discuss the experiments with the three subjects separately.

Experiments with E. O.—With this subject there was a marked tendency to excrete more nitrogen in the urine on either the day before or the day after he entered the respiration chamber. This tendency was as noticeable in the experiments without as in those with alcohol. This variation in nitrogen excretion is independent of either the character of the food or the activity of the subject, and appears to be due to a psychic cause that is little understood. Since this variation was often much larger than any which could be attributed to the alcohol, we hesitate to assign to the latter any definite and uniform effect upon the metabolism of nitrogen.

It is to be noted that there is no experiment with E. O. in which an alcohol diet immediately preceded or followed a diet furnishing the same amount of energy from ordinary food materials without alcohol. There are, however, a number of separate experiments which may be compared, as is done in Table 15.

TABLE 15.—*Experiments with E. O.—Gains and losses of body protein and fat with and without alcohol.*

Experiments.	Total number of days.	Average per day			
		Available food		Gain (+) or loss (−).	
		Protein	Energy.	Protein.	Fat.
MORE DIRECTLY COMPARABLE.					
Rest experiments.					
		Grams.	*Calories.*	*Grams.*	*Grams.*
Without alcohol, Nos. 9, 24	7	114	2,618	−1.9	+39.0
With alcohol, Nos. 10, 22	7	116	2,602	−2.8	+42.0
Work experiments.					
Without alcohol, No. 11	4	110	3,510	−3.0	−39.7
With alcohol, No. 12	4	113	3,614	−1.0	−32.2
Rest and work experiments.					
Without alcohol, Nos. 9, 24, 11	11	112	2,915	−1.6	+12.7
With alcohol, Nos. 10, 22, 12	11	115	2,939	−2.2	+17.2

[1] See review of experiments on the effects of alcohol on the metabolism of carbon in the report of the Committee of Fifty referred to on page 261.

TABLE 15.—*Experiments with E. O.—Gains and losses of body protein and fat with and without alcohol*—Continued.

Experiments	Total number of days.	Average per day			
		In available food		Gain (+) or loss (−).	
		Protein.	Energy.	Protein.	Fat.
LESS DIRECTLY COMPARABLE.					
Rest experiments.					
		Grams.	*Calories.*	*Grams.*	*Grams.*
Without alcohol, Nos. 13, 14[a]	7	99	2,294	−12.0	−25.7
With alcohol, No. 7	4	99	2,230	−12.0	−14.3
AVERAGE OF ALL ABOVE.					
Without alcohol	18	109	2,760	− 4.2	+16.0
With alcohol	15	111	2,762	− 4.6	− 9.4

[a] Nos. 13 and 14 averaged as one experiment.

In the less directly comparable experiments Nos. 13 and 14 are grouped together as one, since the average quantities of protein and energy are the same as in No. 7. The details, however, show that while the quantities of energy in the rations were the same in both, No. 13 had 110 and No. 14 only 89 grams of protein. Nevertheless the results as regards gain or loss of body material were almost identical. In each there was a loss of 12 grams of protein and in No. 13 there was a gain of 27 grams and in No. 14 a gain of 24 grams of fat. The experiments were 40 days apart. We lay especial stress upon this circumstance, because it illustrates the futility of drawing final conclusions from a single experiment. In each of these cases the metabolism experiment was preceded by a period of 4 days with similar diet while the subject was outside the calorimeter, but in neither case was nitrogen equilibrium obtained. Neither one of these experiments, therefore, could be taken as a basis for conclusion as to the quantity of protein required for either nitrogen equilibrium or constant elimination of nitrogen. A special reason for citing them here with No. 7 is that they were made with the same subject as the other experiments of the table.

The chief reliance is to be placed upon the more directly comparable experiments. In those in which the subject was at rest, the alcohol ration furnished 2 grams more protein and 16 less calories of energy per day than the nonalcohol ration. There was a larger loss of protein by 1.8 grams and a larger gain of fat by 3 grams with the alcohol. These differences are all very small, but in so far as they go they imply that the alcohol was somewhat less efficient as a protector of protein than the fats and carbohydrates which it replaced. In the work experiments the alcohol ration supplied 3 grams more of protein and 104 calories more of energy than the other. With both there was a loss of protein, the amount being 3 grams per day without and 1 gram per day with alcohol; but since the alcohol ration furnished 3 grams of protein more than the other, there remains a deficit of 1 gram of protein per day against the alcohol ration as compared with that without alcohol, and that notwithstanding the larger fuel value of the diet. Here again the alcohol ration is slightly inferior in protein protecting power.

Taking the rest and work experiments together, the alcohol rations, with an average of 3 grams of protein and 24 calories of energy per day more than the nonalcohol ration, show a greater loss of protein by 0.6 gram per day. On the other hand there is a slightly larger average gain of fat with the alcohol.

If we reckon the less comparable experiments in the general average, we have 111 grams of protein with alcohol as against 109 grams without it, while the quantities of energy are the same in both rations. The average loss of protein is 0.4 gram greater and the gain of fat 5.6 grams less with the alcohol; but of course much less stress is to be laid upon the less comparable experiments.

On the whole it is clear that in these experiments with this subject the alcohol was not as efficient as isodynamic quantities of fats and carbohydrates in protecting protein. Notwithstanding

the energy of the alcohol was actually larger than that of the fats and carbohydrates which it replaced, it did not equal them in protecting power. The difference is the more striking because of the slightly larger average quantities of protein in the alcohol rations. On the other hand, the differences between the amounts of protein and energy in the alcohol as compared with the nonalcohol experiments are so slight as to imply only a slight inferiority of the alcohol in the protection of protein.

While the alcohol was not isodynamically equal to the carbohydrates and fats in protecting power, it would be going very far to deny that the experiments imply a positive protecting action. Not only were the differences in favor of the protecting power of the carbohydrates and fats as compared with the alcohol very small, but the quantity of energy supplied by the alcohol was large. To claim that the alcohol has no protecting power would be to assume that the same reduction of fats and carbohydrates in the rations without any replacement by alcohol would have resulted in no greater differences in protein protection. This is in the highest degree improbable.

In this connection the results of experiments Nos. 22, 23, 24 above referred to are worthy of consideration. With the normal ration, plus alcohol, there was a gain of 1.4 grams of protein and 63 grams of fat per day; but when, in the period immediately following, the alcohol was removed, there was a loss of 1.6 grams of protein and a gain of only 9 grams of fat.

Experiments with A. W. S.—With this subject we have but one series of rest experiments. This consisted of a preliminary period of 4 days, followed by four experimental periods, during which the subject was in the respiration chamber. Throughout the preliminary and experimental periods there was a uniform basal ration of ordinary food, supplying about 90 grams of protein and 2,040 calories of energy. To this was added, in the preliminary period of 4 days, commercial alcohol, furnishing about 500 calories of energy. The nitrogen in the urine during the successive days was 12.2, 16, 19, 16.4 grams; that is to say, there was a marked increase of protein catabolism during the whole period. The first three experiments proper were of 2 days each. In the first of these periods commercial alcohol, in the second whisky, and in the third brandy was added to the basal rations, the quantities being sufficient to furnish the same amount, about 500 calories, of energy. The daily quantities of nitrogen in the urine were 17.4, 15.4, 14.7, 14.2, 13.8, and 14.4 grams; that is to say, the rise in nitrogen excretion continued through the first day of the first period; thereafter it fell. During the fourth period of 3 days the basal ration was given without the alcohol. The nitrogen excretion was 14.5, 16.2, 15.4 grams, thus showing an increase again. The natural inference is that with this subject, who had always been an abstainer, the rise in nitrogen excretion at first was due to the alcohol. The very evident fall after the fifth day implies that the action of alcohol in increasing the nitrogen was transitory, and that it had passed away at the end of the third period. The increase of nitrogen excretion in the fourth period was apparently due to the reduction of the ration by the removal of the alcohol.

The average gains and losses of protein and fat for the separate periods may be tabulated as follows:

Period	Days.	Alcohol added to basal ration.	Gain (+) or loss (−) grams per day.	
			Protein.	*Fat.*
First	2	Commercial alcohol	−12	+25
Second	2	Whisky	− 0	+35
Third	2	Brandy	+ 2	+21
Fourth	3	None	3	−25

We thus have a gradual change from a loss of nitrogen to equilibrium and positive gain with the alcohol, and on its removal a positive loss. With the fat there is a constant gain with the alcohol and marked loss on its removal.

While it would be unwise to generalize from a single series of experiments, the indications here point clearly toward three conclusions: (1) The alcohol at first caused an increase of

nitrogen metabolism and loss of body protein, but this effect was temporary; (2) thereafter the alcohol protected body protein; (3) the alcohol protected fat throughout.

Experiments with J. F. S.—With the third subject there was opportunity to observe the immediate effect produced upon nitrogen metabolism by the substitution of alcohol for a part of the ordinary nutrients of the diet. Three series of experiments were made. Each included three periods of 3 days each. In each series the subject received the same basal ration throughout, but in addition thereto enough of either butter, sugar, or alcohol to furnish about 500 calories. In the first series the subject was at rest, and the order of addition was butter, alcohol, sugar. In the second series the subject was at work and received a larger diet, the order being sugar, alcohol, butter. The third series was similar in all respects to the second except that the order was butter, alcohol, sugar.

These experiments were thus better adapted than any of those previously discussed to show the immediate effect of the substitution of alcohol for other nutrients in the diet, and in each case it will be seen that this substitution resulted in a loss (or an increased loss) of body protein, which loss continued through the 3 days of the alcohol period. The subject was unused to alcoholic beverages, and from what has already been said such a loss of protein during the first few days of the alcohol diet was to be expected from the results of other similar experiments. Whether this loss would have ceased on continuing the alcohol diet, as seems to have been the case with A. W. S., the experiments do not show.

Experiments with J. F. S.—Gains and losses of body protein and fat with and without alcohol.

Experiments.	Total days.	Averages per day.			
		In available food.		Gain (+) or loss (−).	
		Protein.	Energy.	Protein.	Fat.
Rest experiments.					
		Grams.	*Calories.*	*Grams.*	*Grams.*
Without alcohol, Nos. 26, 28	6	92	2,253	4.0	−23.1
With alcohol, No. 27	3	92	2,264	− 6.0	+ 18.2
Work experiments.					
Without alcohol, Nos. 29, 31, 32, 34	12	95	3,251	− 6.1	−27.5
With alcohol, Nos. 30, 33	6	94	3,255	−14.5	−27.7
Average of all above.					
Without alcohol	18	94	2,918	5.4	−10.6
With alcohol	9	93	2,911	− 11.6	−12.4

Thus all of the experiments with this subject would indicate clearly that for periods of 3 days the alcohol was inferior to either fat or carbohydrates as a protector of protein. It should be stated, also, that the loss of body protein with the alcohol was greater than the figures in the table would indicate, for the nitrogen elimination of the period preceding the alcohol was in each case slightly increased by the entrance of the subject into the respiration chamber, while that of the period following the alcohol is increased by the lag in the excretion of the extra nitrogen metabolized under the influence of the alcohol. The lag would, of course, likewise prevent the effect of the alcohol from becoming fully apparent in the first day of the alcohol period. Hence a better idea of the actual effect of the alcohol would probably be obtained by omitting from consideration the first day of each period. The average elimination of nitrogen thus becomes, in the fore periods, 15.5 grams, in the alcohol periods, 17.1 grams, and in the after period, 15.5 grams per day, showing a difference in favor of the ordinary nutrients of 1.6 grams of nitrogen, or 10 grams of protein instead of 6.2 grams, as shown in the preceding table.

It is also noticeable that the loss of body protein under the influence of alcohol was larger with this subject when at work than when at rest. The difference is not great and may be

simply accidental. It might, however, be interpreted as indicating that the subject worked to better advantage on the ordinary diet than on the diet of which a part was alcohol. This would accord with the conclusions drawn by Chauveau from experiments on dogs[a] and by Parkes from extended observations on marching soldiers and workingmen.[b]

Summary.—In interpreting these experiments two things are to be considered. One is that the differences between the amounts of nitrogen excreted with and without alcohol are generally very small. The other is that there is good ground for the belief that with persons little accustomed to the use of alcohol it may have a tendency to increase nitrogen metabolism, which may counteract, to greater or less extent, the tendency to protect protein, though, with some persons at least, this action appears to be temporary. The results with the individual subjects may be briefly recapitulated as follows:

With E. O., who was accustomed to the use of moderate quantities of alcoholic beverages, the protein protecting power of the alcohol was apparent, but seemed to be somewhat inferior to that of fats and carbohydrates.

With A. W. S., an abstainer, there was an increase of nitrogen excretion during the first days after the beginning of the alcohol diet, with a resulting loss of body protein, but this action ceased after 5 or 6 days, and thereafter the alcohol apparently protected protein, though the experiments do not show how its efficiency in this respect compared with that of the carbohydrates and fats.

With J. F. S., who was also an abstainer, there was, in each case, an increase of nitrogen excretion and loss of body protein during the 3-day periods in which the alcohol replaced fat or sugar. There was thus a marked inferiority of alcohol in protecting power. The result is similar to that observed with A. W. S. during the first days with alcohol, but the experiments do not show what the effect of continuing the alcohol diet would have been, and they are, therefore, not decisive.

Taking the results of all the experiments together, it may be said that—

1. They offer no evidence to imply that alcohol can not protect protein, though they imply in some cases it may, at least for a time, fail to do so.

2. On the other hand, they give very marked indications of its protein protecting power.

3. They imply clearly that in this respect it was in some cases nearly or quite equal and in others decidedly inferior to the isodynamic amounts of carbohydrates and fats which it replaced.

Other experiments upon the protection of protein by alcohol.—It is clear that the experiments above described are not conclusive regarding the action of alcohol in protecting protein from consumption. They were not planned for the study of this subject. To make the results decisive the alcohol periods should be long enough to eliminate the more or less temporary action of alcohol as a drug; the available energy of the ration of the nonalcohol periods should equal in some cases the total available energy of the alcohol ration, while in other cases it should equal only that of the ordinary food of the alcohol ration, and finally, the experiments should be repeated with different persons and under different conditions. These facts we did not fully understand when the experiments were begun, nor would it have been practicable with the means at our disposal to make such experiments with men in the respiration calorimeter as would be needed for the comprehensive study of the question. Experiments of from twenty to thirty consecutive days seem necessary for the most satisfactory results. For a man to spend so long a time in the respiration chamber of our apparatus would be, to say the least, very tedious, and the cost of such experiments, in labor and money, would have exceeded our available resources. Fortunately, the results obtained by a number of other investigators, while our experiments were being made and since, have done much to clarify the situation as regards the effects of alcohol upon protein metabolism.

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[a] Compt. rend. Acad. d. Sc. Par. 132, pp. 65 and 110.

[b] Proc. Roy. Soc. 20 (1871–72), 402, and monograph "On the issue of a spirit ration during the Ashantee campaign, 1874," etc. London, 1875.

Referring to the above-named reviews of the subject,[a] and especially to that of Rosemann for details and references to the original memoirs, it will suffice here to summarize the results. It appears that:

1. A large number of early experiments have brought conflicting results, some implying the protection of protein by alcohol; others the opposite. Of the former class those of Mogilianski are of especial interest. Of the latter those of Miura, made under the direction of Van Noorden, and those of Schmidt and of Schoeneseiffen, under the direction of Rosemann, have been much quoted. The general plan of experimenting followed by these three investigators consisted in giving the subject an ordinary diet for a time and observing the nitrogen balance. Thereafter, during a period of four to six days, alcohol was used. In Miura's case the alcohol was substituted for carbohydrates in a diet which had been adequate for maintaining nitrogen equilibrium; but with the alcohol the excretion of nitrogen increased and the body lost nitrogen. With Schmidt, alcohol was added to a diet with which nitrogen equilibrium had been maintained; the alcohol did not diminish the excretion of the nitrogen and the equilibrium continued. With Schoeneseiffen, alcohol was added to an inadequate diet with which there was loss of nitrogen; the loss continued with the alcohol.

These experiments have furnished the chief basis for the contention that alcohol can not protect protein. In Miura's case the increase of nitrogen excretion with the alcohol was as large, and, indeed, in one instance very slightly larger, than when the carbohydrates were removed and no alcohol was used in their place. Miura, and after him Rosemann and others, inferred that alcohol was unable to protect protein from disintegration, and went so far as to ascribe to it a positive disintegrating action and to apply to it the term "proteid poison."

2. Neumann, in 1899, made experiments on a similar plan, save that the alcohol period was continued for sixteen days, during which part of the fat of the normal diet was replaced by alcohol. He found that during the first four days of the alcohol period there was no evidence of protein protection; the nitrogen excretion was increased and was as large as during another period when the ordinary ration was reduced and no alcohol was used in its place. Thereafter the nitrogen excretion diminished, and during the remaining twelve days of the alcohol period it was the same as with the normal ration. When the alcohol was removed and nothing substituted the excretion of nitrogen increased as before. Neumann concludes that in his own case the failure of the alcohol to protect protein at first was probably due to a specific though temporary action by which it tended to increase the disintegration of protein so that the tendency to protein protection was counteracted. Later this special action disappeared and the protecting action came into full play.

Neumann's interpretation of his experiments was questioned by Rosemann, who has been a most vigorous opponent of the theory that alcohol can protect protein, and a keen critic of the experiments which have seemed to favor this view. He maintained the disintegrating, but questioned the protecting action of the alcohol, alleging defects in the plans of Neumann's experiments. Neumann, without replying, repeated his experiments in such ways as to meet Rosemann's objections, and found conclusive evidence of the protecting power of the alcohol, these later results being published early in 1900. In 1901, Chotzen, working under the direction of Rosenfeld, and in 1901, Clopatt, each published results of inquiries which agreed with Neumann's. Meantime Rosemann made several series of experiments of his own, the outcome of which, to his surprise, clearly demonstrated the protecting power of alcohol, and confirmed the views maintained by Neumann. He has taken the pains to prepare an extensive summary of the experimenting in this field,[b] in which he assents fully to the interpretation placed by Neumann, Rosenfeld, Chotzen, and Clopatt upon their experiments; believes that the protection of protein is shown by other experiments, as those of Mogilianski; considers it fully demonstrated by his own experiments; and

[a] Rosemann interprets two of our experiments, Nos. 7 and 10, the only ones then published, as not showing the protection of protein; an interpretation from which we should not dissent, since No. 7 was exceptional, and two experiments could hardly suffice for the establishment of the principle.

[b] See page 261.

comes to the definite conclusion that alcohol has a twofold influence upon the metabolism of protein, as previously suggested by Neumann. He is inclined to believe, with Neumann, that the disintegrating action is most apt to occur with persons little accustomed to the use of alcohol, and is of short duration, while in its action as a protector of protein it is analogous to the carbohydrates and fats, its influence being due to the utilization of its energy by the body. According to this view, the results obtained by Miura and others, in whose experiments the alcohol periods continued only from four to six days, are explained by the disintegrating action of the alcohol, which counteracted the protecting action, so that the resultant effect was an apparent failure of the alcohol to protect protein. With Neumann the alcohol periods continued after this disintegrating action ceased, and showed the more permanent protecting influence. The fact that in a number of the experiments the protecting influence was manifested from the start is explained by the absence or only partial action of the disintegrating tendency.

We have, then, a clearly defined theory regarding the influence of alcohol upon proteid metabolism. This theory assumes two different kinds of action of alcohol. In the one it is a direct protector of protein, and serves the body as food; in the other it tends to disintegrate protein, and acts as a drug. The belief in the first action follows as a corollary from the oxidation of alcohol in the body and the transformation of its energy. In undergoing these changes alcohol is similar to sugar, starch, and fat, which, by their own oxidation and consequent supply of energy to the body are able to protect the constituents of the food and of the body, including protein, from oxidation. That alcohol may and does protect protein is abundantly demonstrated by the experiments above cited.

The disintegrating influence of alcohol upon protein is less definitely proven. The theory is little more than a convenient hypothesis for explaining the failure of alcohol, under some circumstances, to protect protein. It is the only satisfactory hypothesis which has thus far been suggested. It is all the easier to accept because of the considerations that the breaking up of protein compounds in the body seems to be influenced, in some unexplained way or ways, by the nervous system, and this latter in turn is influenced by alcohol. In our own experiments, for instance, the excretion of nitrogen is apparently affected at times by the mental condition of the subject.

In large enough doses alcohol has a paralyzing effect, and may thus reduce general metabolism to a minimum and cause coma or even death. There is no proof that it can not, on the other hand, increase proteid metabolism.

The positive proof of the disintegrating action of alcohol upon protein is limited in amount. The experimental demonstration must be sought in cases in which more protein is broken down with alcohol than without it, the ration of ordinary food being otherwise the same in both cases. We have been able to find only three cases on record in which the amount of protein thus broken down with alcohol apparently exceeded by more than 0.1 gram of nitrogen per day the amount broken down without alcohol. They are discussed in the review above referred to. The first was in one of Miura's experiments, in which the excess with alcohol amounted to 0.5 gram of nitrogen (3.2 grams of protein) per day during an alcohol period of four days. The second was in one of Neumann's experiments, in which the excess during the first four days of an alcohol period of ten days was 0.9 gram of nitrogen per day. During the remaining six days of the same period the nitrogen excretion was less by 1.5 grams per day than in the corresponding period without alcohol. The third was in an experiment by Clopatt. During the first six days of an alcohol period of twelve days the nitrogen excretion exceeded that of a corresponding period without alcohol by 2 grams per day. During the remaining six days of the same alcohol period the nitrogen excretion was less by 1.4 grams per day than it was without alcohol.

It seems to the writers that in view of the unavoidable irregularities in the nitrogen balance in such experimenting these data are insufficient to demonstrate the disintegrating action of alcohol, but, taken in connection with the need of an explanation for the occasional failure of alcohol to protect protein, they make the theory plausible.

Sources of uncertainty in this kind of experimenting.—One point which has hardly received the attention it deserves in discussions of this kind is the uncertainty of the nitrogen balance in any given case as a measure of the actual influence of a given condition upon nitrogen metabolism. This has been emphasized elsewhere in the present memoir (see pp. 393 and 394). Differences which look large in a table of figures are often far inside the unavoidable variations in actual experimenting.

Even when the differences are significant the interpretation may be erroneous. A striking illustration of the danger of such error is found in the current discussion of the question we are now considering. For a number of years past writers upon this subject have insisted most positively that alcohol, instead of being a protector of protein, is a protein poison. This theory is based almost wholly upon the experiments of Miura, Schmidt, and Schoeneseiffen. The experiments of Neumann, Rosenfeld-Chotzen, Clopatt, and Rosemann, not to speak of others, including our own, have shown that this theory was wrong and have given us a very plausible hypothesis to explain why it was wrong.

We can not insist too strongly upon the danger of drawing positive conclusions from figures for nitrogen balance as a measure of protein protection by either alcohol or sugar or starch or fat. Certainty comes only with careful planning and execution and manifold repetition of experiments.

Incidentally, it is to be noted that the excretion of nitrogen in the urine is not necessarily an exact measure of the amount of proteid broken down in short periods, since the time between the disintegration of the protein and the appearance of the nitrogen in the urine, the so-called nitrogen lag, varies widely. The longer the experimental period the less the error from this source.

Finally, there is the unsettled question as to how much of the protein metabolized is that of food and how much comes from organized tissue.

Final conclusions regarding the influence of alcohol upon protein metabolism.—The experiments and considerations above cited seem to us to warrant the following conclusions:

1. The power of alcohol to protect the protein of food or body tissue, or both, from consumption is clearly demonstrated. Its action in this respect appears to be similar to that of the carbohydrates and fats; that is to say, in its oxidation it yields energy needed by the body, and thus saves other substances from oxidation. In this way alcohol serves the body as food. Just how moderate quantities of alcohol compare with isodynamic amounts of sugar, starch, and fat in the power to protect protein from catabolism is not yet settled. Apparently it is in some cases equal, in others inferior, to these substances. It is by no means certain that the fats and carbohydrates are always equal to each other in this power.

2. Alcohol appears also to exert at times a special action as a drug. In large quantities it is positively toxic, and may retard or even prevent metabolism in general and proteid metabolism in particular. In small doses it seems at times to have an opposite influence, tending to increase the disintegration of protein. This action, though not conclusively demonstrated, is very probable. It offers a satisfactory explanation for the occasional failure of alcohol to protect protein, the assumption being that the two tendencies counteract each other. The only justification for calling alcohol a proteid poison is found in this disintegrating tendency. This pharmacodynamic action of alcohol appears to be temporary and most apt to occur with people little accustomed to its use. The circumstances under which such action occurs can not now be fully defined.

Influence of coffee upon protein metabolism in these experiments.—In some of these experiments alcohol was administered with coffee, in others with water. It might be thought that the presence of the coffee would interfere with the action of the alcohol.[a] The figures give no support for this view, as is shown in the following tabular statement.

[a] See Woodbury and Egbert, A Physiologic Consideration of the Food Value of Alcohol, Jour. Am. Med. Asso., Mar. 31, 1900.

Elimination of nitrogen in presence and absence of coffee.

[Quantities per day.]

Kind and number of experiments	Days.	Nitrogen.			
		In food.	In feces.	In urine.	Gain (+) or loss (−) to body.
		Grams.	*Grams.*	*Grams.*	*Grams.*
I. With coffee:					
Average 4 experiments with alcohol [10, 12, 18, 22]	13	18.6	1.2	18.2	−0.8
Average 4 experiments without alcohol [9, 11, 21, 24]	14	18.6	1.5	17.5	−0.4
Increase (+) or decrease (−) with alcohol		0	−0.3	−0.7	0.4
II. Without coffee:					
Average 5 experiments with alcohol [(19, 20), 27, 30, 33]	13	15.8	1.0	16.1	−1.3
Average 7 experiments without alcohol [21, (26, 28), (29, 31), (32, 34)]	21	15.9	1.0	15.7	−0.8
Increase (+) or decrease (−) with alcohol		−0.1	0	−0.4	0.5
Increase (+) or decrease (−) in presence of coffee		**+0.1**	**−0.3**	**−0.3**	**−0.1**
III. Direct comparison, alcohol with and without coffee:					
Experiments 15, 17, 18, alcohol given with coffee	6	16.5	0.9	16.0	−0.4
Experiments 16, 19, 20, alcohol given without coffee	6	16.5	1.0	14.9	−0.6
Increase (+) or decrease (−) in presence of coffee		**0**	**−0.1**	**−1.1**	**−1.0**

This table comprises all of the experiments that are directly comparable. The experiments in which the alcohol was given with coffee are averaged together and compared with the corresponding nonalcohol experiments, and the figures in the third line of category I show the effects of alcohol in presence of coffee. Under II a similar comparison is made of the experiments in which no coffee was given, the third line of figures here showing the effects of alcohol when taken alone. By subtracting the third line of figures under II from the corresponding figures under I we obtain values which may be taken as showing the influence of the coffee. A more direct comparison of results with and without coffee is given under III, but the number of experiments compared is necessarily smaller, and therefore individual variations have relatively much greater weight. While the differences which could be attributed to the coffee are probably within the limits of experimental error, it would seem that if there is any effect it is to increase rather than to retard proteid metabolism.

EFFECT OF ALCOHOL UPON THE RADIATION OF HEAT FROM THE BODY.

A current theory maintains that although alcohol supplies heat to the body it also increases the radiation of heat from the body, so that much or all the energy it supplies is wasted.

This theory is based upon two kinds of evidence, which are well attested and make it very plausible. One is the distension of the blood vessels which cause the flush of the skin when alcohol is taken. The other is the lowering of the temperature of the body after the ingestion of alcohol, which is shown by many of experiments and is explained by the loss of heat.

Some writers even go so far as to claim that the extra heat radiation due to the distension of the peripheral vessels is greater than the heat supply from the oxidation of the alcohol. According to this view, alcohol, instead of being a source of energy, is a cause of its loss to the body.

The difficulty with the theory is the exaggeration of the influence of small quantities of alcohol in increasing heat radiation. While the temperature of the body has been found to fall considerably after the ingestion of large doses of alcohol, and especially under exposure to great cold, the effect of ordinary doses is slight and often imperceptible.

In the experiments here described the determinations of body temperature were made with an ordinary clinical thermometer in the mouth and axilla, as elsewhere stated. This method,

which is the one ordinarily followed, does not give results as accurate as are to be desired. In some of the earlier experiments, especially with E. O., the observations are of doubtful value. Steps have been taken in this laboratory to devise a thermometer and method of observation which will show more accurately the variations of internal temperature of the body.[a] Meanwhile, as may be seen from the detailed figures, it is clear that the observations do not imply that the bodily temperatures with and without alcohol were greatly different. This agrees with the results of other observations.[b]

The alcohol used in these experiments was equivalent to about 72 grams of absolute alcohol per day taken in 6 doses. This is about the amount contained in an ordinary bottle of wine with 10 per cent alcohol or 3 or 4 glasses (6 or 8 ounces) of whisky.

If we use our own observations and the others just referred to as a basis, it would seem that the fall of body temperature produced by such amounts of alcohol might ordinarily range from nothing to one-half of a degree centigrade. The heat which the body of an average man would have to lose in order to reduce the temperature one-half of a degree might be roughly calculated as follows:

We may take the weight of the body of the average man at 148 pounds, or 67 kilos. The specific heat of the body is not exactly known, but may be estimated at 0.83. On this base a fall of temperature of one-half of a degree centigrade would correspond to ½ (67 x 0.83), or about 28 calories. Of the 72 grams of alcohol, 98 or 99 per cent, or between 70 and 71 grams, would be burned in the body, and would yield at 7.1 calories per gram about 500 calories of heat. By this estimate, if the 72 grams of alcohol were taken in one dose and caused a lowering of the body temperature by one-half of a degree, the 28 calories of heat wasted in the extra radiation due to the alcohol would be one-eighteenth the amount supplied by its combustion.

This method of calculating the amount of heat which the body must lose in order to produce a given fall of temperature is hardly correct. It would be so if we had to do only with a fixed amount of heat at the outset and a fixed amount of loss. But, as a matter of fact, the body is constantly gaining heat from the oxidation of material from within and constantly losing not only by outward radiation, but in other ways, as in the exhalation of air and water, vapor in respiration, in the excretions of the kidneys and intestine, and in the evaporation of water from the skin. The actual temperature depends upon the income and outgo of heat. The income depends upon the material oxidized in the body. The outgo is regulated to a greater or less extent by processes which are not fully understood, but in which the nervous system is the important agency.

Experimental inquiries.—Meanwhile we may consider the experimental evidence bearing directly upon the question of the radiation of heat with and without alcohol.

In a series of experiments by Reichert with dogs the effect of alcohol on the radiation of heat was tested.[c] The experimental periods were, however, only 5 or 6 hours each, and there was no complete comparison of the effects of different diets. The rate of heat radiation and the change of body temperature were carefully observed. The results implied a probable but at most very small increase of heat radiation as the result of administering alcohol.

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[a] F. G. Benedict and J. F. Snell, Eine neue Methode um Körpertemperaturen zu messen. Archiv. f. d. ges. Physiologie 88, p. 492 (1901).

[b] The results of the most reliable observations are well summarized by Pembrey (Schaefer's Physiology, I, 820) in the following statements:

"Various observers have found that alcohol taken in ordinary quantities as a beverage causes a slight depression, generally less than half a degree, in the temperature of healthy men. On the other hand, poisonous doses may cause a fall of 5° or 6°—in fact, many of the lowest temperatures recorded in man have been observed in drunken persons exposed to cold. See Davy, *Phil. Trans.*, London, 1850, p. 444; Lichtenfels and Fröhlich, *Denkschriften d. k. Akad. d. Wissensch.*, Wien, 1852, Bd. iii, Abth. 2, S. 131; Lallemand, Perrin, and Duroy, 'Du rôle de l'alcool et des anesthésiques dans l'organisme,' Paris, 1860; Ogle, *St. George's Hosp. Rep.*, London, 1866, vol. i, p. 233; Ringer and Rickards, *Lancet*, London, 1866, vol. ii, p. 208; Cuny Bouvier, *Arch. f. d. ges. Physiol.*, Bonn, 1869, Bd. ii, S. 370; Godfrin, 'De l'alcool, son action physiologique, ses applications thérapeutiques,' 1869; Weckerling, *Deutsches Arch. f. klin. Med.*, Leipzig, 1877, Bd. xix, S. 317; Zuntz, *Fortschr. d. Med.*, Berlin, 1887; Geppert, *Arch. f. exper. Path. u. Pharmakol.*, Leipzig, Bd. xxii, 36; Parkes and Wollowicz, *Proc. Roy. Soc. London*, 1870, vol. xviii, p. 362, found that alcohol in ordinary quantities had no effect on the temperature of a healthy man."

Therapeutic Gazette, February, 1900.

The experiments with men in the respiration calorimeter here described give extended data regarding both the consumption of fuel and the radiation of heat. The details are summarized in Table CXX in the appendix. The final outcome is simple and may be illustrated by two cases, Groups A and D. In each there were two experiments, practically alike, save that one was with ordinary diet and the other with a diet in which part of the fats and carbohydrates were replaced by alcohol as above described. In Group A the subject was at rest, i. e., doing no external muscular work. The potential energy of the material burned in the body and the amounts of heat given off in calories were practically the same, as is shown by the figures herewith. The differences in the results without and with alcohol are entirely within the limits of ordinary variation:

Comparison of energy of material metabolized and heat given off per day in rest experiments with and without alcohol.

Diet	Energy of material burned.	Energy given off by the body as heat.
	Calories.	*Calories.*
Without alcohol, experiment No. 9	2,277	2,309
With alcohol, experiment No. 10	2,268	2,283

If the alcohol had caused increased radiation of heat, more heat would have been given off from the body and more fuel would have been required, and naturally more would have been burned in the alcohol experiment than in the other. Such, however, was not the case.

In the experiments of Group B the man was engaged for eight hours a day in active muscular work, driving a stationary bicycle. The amount of work was such that he burned enough fuel to yield in all 3,900 calories, and, as the food did not supply enough, he used up some of his store of body fat. The results of such experimenting imply that when the body has not enough food for its support and is forced to draw upon its reserve capital, it uses the materials economically. The energy given off from the body was in two forms—heat and external work. This work was practically the same in both experiments and is reckoned with the heat in the energy given off.

Comparison of energy of material metabolized and heat given off per day in work experiments with and without alcohol.

Diet.	Energy of material burned.	Energy given off by the body as heat and muscular work.
	Calories.	*Calories.*
Without alcohol, experiment No. 11	3,901	3,922
With alcohol, experiment No. 12	3,932	3,927

Here again there was slightly more fuel burned per day with alcohol than without, though the difference was small, while the amount of heat given off was practically the same in the one case as the other. So far as the disposal of the energy is concerned, the figures imply that alcohol was used as economically as the fat, sugar, and starch which it replaced, and that it caused no increased radiation of heat.

We have, all told, 13 experiments with alcohol, covering 36 days. For purposes of comparison these have been grouped, as already explained (p. 241), with 13 experiments without alcohol, covering 43 days.

The subject in 5 of these groups, E. O., was a man who had been long accustomed to the moderate use of alcoholic beverages. The subjects in the other four groups, A. W. S. and J. F. S., were two men who had always been total abstainers.

The results are summarized in the table herewith, which is condensed from Table CXX of the appendix. The first column gives the figures for energy for material actually oxidized. The figures in the second column show the relation between the averages of experiments with alcohol

and those without alcohol, the latter being taken as a basis (100 per cent). The corresponding values for total and proportional energy measured as heat in the two classes of experiments are shown in the last two columns of the table. Thus, in the average of all the experiments without alcohol the energy of the material actually oxidized was 2,717 calories. In the average of all the experiments with alcohol it was 2,746 calories. The latter was 101.1 per cent of the former.[a]

TABLE 16.—*Comparison of energy of material oxidized and heat given off in experiments with and without alcohol.*

[Averages per day.]

	Energy of material oxidized.		Heat given off.[b]	
EXPERIMENTS MORE DIRECTLY COMPARABLE.				
Average of work and rest experiments.	*Calories.*	*Per cent.*[c]	*Calories.*	*Per cent*
Without alcohol (9 experiments)	2,925	100.0	2,946	100.0
With alcohol (6 experiments)	2,941	100.5	2,949	100.1
EXPERIMENTS LESS DIRECTLY COMPARABLE.				
Average of rest experiments.				
Without alcohol (4 experiments)	2,302	100.0	2,277	100.0
With alcohol (7 experiments)	2,356	102.4	2,358	103.5
AVERAGE OF ALL ABOVE EXPERIMENTS.				
Groups A–I.				
Without alcohol (13 experiments)	2,717	100.0	2,723	100.0
With alcohol (13 experiments)	2,746	101.1	2,752	101.1

There was slightly more fuel burned and more heat given off from the bodies of the men when they had alcohol in their diet than when they had the same amount of protein and energy in a diet without alcohol, but with conditions otherwise similar. The differences, however, were very small: in the more directly comparable experiments the excess of fuel burned with the alcohol diet, as measured in calories, was only five parts and that of heat given off only one part in 1,000. In the less directly comparable experiments the differences were larger, but still small.

The quantities of total food were generally below rather than above the requirements of the body, especially in the work experiments, as may be seen from Table CXX of the Appendix. The general results of experiment imply that under such circumstances the body makes economical use of its food and its reserve supply of material. The fact, therefore, that under these conditions the oxidation of material and radiation of heat were so nearly the same with the rations with and without alcohol add still greater force to the comparison.

The conclusion is that in these experiments, with three different men at rest and at work, when 72 grams of alcohol per day taken in six doses and furnishing 500 calories of energy replaced the isodynamic amounts of fats and carbohydrates, the alcohol caused no considerable increase in the amount of heat radiated from the body.

If the alcohol in these experiments had all been taken at one dose, it might have caused the cutaneous vessels to dilate, stimulated the sweat glands (?), and increased the circulation, and thus increased the heat radiation. If there had been enough to cause the ordinary symptoms of intoxication, and especially if it had sufficed to induce the comatose condition for which the expression "dead drunk" is used, and if the men had at the same time been exposed to severe

[a] A difference so small as this is well inside the range of unavoidable error in single experiments. It is only where a large number of such experiments are averaged that differences of one or two parts in one hundred could probably be regarded as significant.

[b] Including heat equivalent of external muscular work in the work experiments.

[c] Of amount oxidized without alcohol.

cold, the production of heat in the body might have been retarded, and the radiation increased so as to lower the body temperature by several degrees.

RAPIDITY OF COMBUSTION OF ALCOHOL IN THE BODY.

There is a popular impression that alcohol is burned in the body much more rapidly than ordinary food, and that in consequence not only is the energy resulting from its oxidation wasted, but derangements of bodily functions may result from the rapid combustion of the alcohol. The exact grounds for the belief or nature of the supposed disturbances we have not seen distinctly stated. Nevertheless, as the impression prevails to some extent, at least among physicians and physiologists, it seems to demand consideration.

Leaving out of account the unsettled question as to how soon after the ingestion of the alcohol its oxidation begins, the main problem is the rate of oxidation. If it is especially rapid, either one of two results may follow. The oxidation of other materials may go on as usual, in which case the total production of carbon dioxid and heat will be abnormally large; or the oxidation of other substances may be diminished so as to compensate for more or less of the oxidation of the alcohol, in which case the rate of production of carbon dioxid and heat may be little, if any, larger than without the alcohol. The natural test will be found in the measurement of these rates of production. So far as we are aware no adequate tests of this character have thus far been made.

In examining the literature of the subject we have not succeeded in finding any experimental proof that the rate of elimination of carbon dioxid or heat from the body is materially increased or decreased by moderate quantities of alcohol. Satisfactory tests would involve the measurement by short periods, as, for instance, hour by hour. Our own experiments were not planned for this purpose, and the measurements were made generally in six-hour periods. There was nothing in the observations to imply that the rate of production of either carbon dioxid or heat was materially increased either immediately after the ingestion of the alcohol or later.

Part of the heat given off from the body is carried away in water vapor given off from the lungs and skin, but the larger portion finds its way to the water current, by which it is carried out of the chamber. The rate of flow of this current and its rise of temperature in passing through the chamber thus measure the rate of evolution of heat from the body other than that carried away by water vapor.

The observations of rate of flow and rise in temperature are made every few minutes, and thus show the rate of evolution of the larger portion of the heat.

We have taken the pains to calculate the evolution of heat for hourly periods for three series of experiments, in which the alcohol diet and ordinary diet were compared, viz, Nos. 22–24, 26–28, 29–31. The calculations, however, have been limited to the night periods between 7 p. m. and 7 a. m., because the evolution of both carbon dioxid and heat is much more regular by night than by day, and any disturbance, such as might be caused by the rapid oxidation of alcohol, would be more easily detected in comparing the figures for the experiments with and without alcohol during the night periods.

The results of these comparisons are negative. There are practically no more irregularities or indications of disturbance in the alcohol than in the nonalcohol experiments. There is nothing in the figures which seems to us to indicate any appreciable tendency toward increase of heat production during the first, second, or third hour after the ingestion of the alcohol. The figures are, indeed, so destitute of such indications as to hardly warrant their printing.

We are therefore led to the conclusion that in these experiments either the alcohol was not suddenly or rapidly oxidized, or if there was such rapid oxidation, there was a corresponding decrease in the oxidation of carbohydrates, fats, or protein.

It is interesting to note that this conclusion accords with the other observations, viz, those of the total heat production and the economy of the use of energy in the rations with or without alcohol. All of these imply that the alcohol, carbohydrates, and fats simply replaced one another as sources of energy: that as either was oxidized the others were proportionately spared.

ALCOHOL AS A SOURCE OF HEAT IN THE BODY.

In the rest experiments the heat given off from the body was equivalent to the total potential energy of the materials oxidized. This was as true in the experiments in which alcohol made part of the diet as in those with ordinary food exclusively. The alcohol must therefore have contributed its full quota of heat as truly as did the starch or fat, and all its potential energy was converted into heat within the body.

In the work experiments the same principle applies, and it follows that unless all the potential energy of the alcohol was converted directly into that of external muscular work part must have been converted into heat within the body. But the total energy of external muscular work was at most the equivalent of 280 calories, while the energy of the alcohol was about 500. Even if all the external work was done at the expense of the alcohol, there would remain 220 calories which must have been transformed into heat within the body. But it is extremely improbable that the alcohol supplied all and the ordinary food none of the energy of external work. In so far, therefore, as the latter came from the ordinary food, more than 220 of the 500 calories of the alcohol must have reached the form of heat within the body.

We have to do here with the question: Of the total energy which was potential in the alcohol and was made kinetic by its oxidation, how much was transformed directly into heat and how much was first changed to the energy of muscular and other bodily work, internal and external, and was afterwards transformed into heat? This involves two fundamental problems. One is the still unsettled physiological question as to whether the production of muscular energy in general is or is not a direct transformation of potential into mechanical energy. The other is the more specific question as to whether the energy of alcohol is like that of the ordinary nutrients of food in its transformation into muscular energy. Both will be referred to beyond in the discussion of alcohol as a source of muscular energy. Meanwhile it is safe to say that:

1. Unless all the potential energy of the alcohol was transformed directly into the energy of internal work in the rest experiments or into that of internal and external work in the work experiments, a supposition that seems highly improbable, part must have been transformed directly into heat in the body.

2. Whether the potential energy was first transformed into muscular energy or not, the whole in the rest experiments and part at any rate in the work experiments reached the form of heat within the body.

The conclusion is that in all these experiments alcohol was a source of heat for the body.

ALCOHOL AS A SOURCE OF MUSCULAR ENERGY.

General considerations.—The question whether or not the energy of alcohol is used for muscular work is not yet definitely answered. The experiments thus far made do not provide means for tracing the energy of the alcohol through the changes it undergoes in the body, and finding how much of it becomes muscular energy. Nor is it easy to devise such experiments. The difficulty is that the potential energy of the alcohol is transformed along with that of other materials oxidized, and there is no known way of separating the kinetic energy which comes from the alcohol from that which is supplied by the carbohydrates or fats or protein. While there is no evidence of any differences between the energy from the several sources, the absolute proof that no such differences exist is not yet at hand.

Back of this is the more fundamental question as to how muscular energy is produced. Concerning this two theories are held. One is that part of the potential energy of the food and body material oxidized is converted directly into the mechanical energy exerted by the muscle. The other is that the contraction of the muscle, by which its work is done, is due to heat. According to this view, practically all of the potential energy is first transformed into heat and a part afterwards appears as muscular energy. If the second view is correct, it is hard to see how the heat derived from the oxidation of the alcohol should be in any way different from

the rest of the heat. If the muscular energy is the first product of the transformation of potential energy, it is conceivable that there might be some attribute of alcohol which would prevent its potential energy from being changed into mechanical energy. But there is nothing in the results of experiment to imply any such difference between alcohol on the one hand, and sugar, starch, or fat on the other. The case regarding the transformation of energy is like that just referred to regarding the use of the energy after it is transformed. There is no evidence of any difference between alcohol and other nutrients in either respect, but there is no proof that the difference does not exist.

The most satisfactory method of study of this question as to whether alcohol can be a source of the mechanical energy exerted by the muscles is by measuring the amounts of different substances metabolized and the amounts of muscular work done, and thus getting light upon the comparative efficiency of the several substances as parts of a diet for muscular work.

If the experiment could be made with lean meat and alcohol in such a way that the body could obtain no other fuel than alcohol and protein, and the energy of the internal and external muscular work should be found to exceed that of the protein, it would be clear that the rest of the muscular energy must come from the alcohol. But as yet we have no means for measuring the internal work, and it would probably be difficult to find a man who could do much external work day after day on such a diet without drawing upon the store of material in his body.

For the present, therefore, we are limited to experiments in which other fuel is burned with the alcohol, and our conclusions must depend upon measurements of (1) the energy supplied by each kind of fuel, (2) the energy given off from the body, and (3) the amount of muscular work performed.

Here again we meet a difficulty, namely, that of measuring the muscular work. We have to do with two kinds of work, external and internal. The external work is that which is performed outside of the body, as, for instance, the power which a man riding a bicycle applies to the pedals. This is capable of quite accurate measurement. Such measurements were made in the experiments here described. By internal work is meant that of circulation, respiration, digestion, etc. Thus a not inconsiderable amount of energy must be used for the muscular contractions of the heart by which the blood is pumped out through the arteries and back from the veins. It is held by some physiologists that a large portion of the total energy supplied by the food is used for this internal physiological work. At present no exact method is known for measuring the internal work of the body. It is transformed into heat before it leaves the body and in the experiments with the respiration calorimeter it is collected and measured as part of the total heat given off. But this total heat includes also the heat which was produced in the body and not used for muscular work, and no way has yet been found to distinguish between the heat which has and that which has not been used, and to measure the two quantities of heat separately.

We know from measurements of the external muscular work that it represents at most a fraction, and generally a small fraction of the total energy transformed. It may be that in the case of a man doing a large amount of muscular labor this external work added to the internal work would account for the larger part of the total energy transformed in the body.

The measurements of income of energy from the oxidation of ordinary nutrients and alcohol and of outgo of energy in the different forms of heat and external muscular work therefore do not answer the specific question as to how much of the energy provided by the alcohol is used for either internal or external muscular work, or both.

Economy of utilization of the energy of the rations with and without alcohol.—We may nevertheless get some light on the question by putting it in another way: Is the total energy of the ration used as economically when part of it is supplied by alcohol as when the whole comes from ordinary food? The question may be approached in two ways, (1) by considering the differences in the amounts of available energy in the diets with and without alcohol, and comparing these with the energy in the body protein and fat gained or lost in the two cases, and (2) by

comparing the energy of material actually oxidized in parallel experiments with and without alcohol. The principles here involved may be explained as follows:

The energy needed and used by the body.—The body requires and uses a certain amount of energy. This amount is larger when the man is at work and smaller when he is at rest. The larger the amount of energy used, the more material will be metabolized to furnish it. If the available nutrients of the food exceed the amounts metabolized, the excess will be stored in the body. Assuming the store of carbohydrates to remain constant, the body will gain protein or fat or both. Translating this last statement from terms of material to terms of energy, if the available energy of the food exceeds the energy metabolized, the amount of energy in the body will be increased by the storage of energy in protein or fat. On the other hand, if the available energy of the food does not supply the demand, the lack will be made up by drafts upon body protein or fat. We thus have two measures of the energy used by the body. One is the gain or loss of body protein and fat with a given amount of available energy in the food. The other is the total energy metabolized whether it be more or less than the available energy of the food.

Economy of utilization of energy.—We have distinguished between the energy needed and that actually metabolized. If the body uses the energy economically it does not metabolize more than it needs. But it does not always make the most economical use of either material or energy. If it has more food than it needs, it may use this wastefully. Part of the excess of material, at times perhaps the whole, may be stored for future use, but often more or less of the excess is simply consumed and the energy wasted. On the other hand, if the food only equals the demand, and especially if it falls short and body material has to be drawn upon, the body will probably make economical use of the energy of both food and body material. This was the case in the experiments now under discussion. When the men were at rest the food supplied but little more, and when they were at work it supplied less, than was actually needed. In these experiments, therefore, the two measures just referred to, namely, the energy of body material gained or lost and the total energy metabolized, show how much the body uses when the energy is economically utilized.

To state the case in another way, either the energy of material gained or lost with the given diet, or the energy of the total material oxidized, gives a measure of the energy actually employed for economical use. These quantities can be expressed in calories.

Comparative economy of energy of different materials.—This brings us to the question at issue. Is the energy of alcohol equal, superior, or inferior in value to that of carbohydrates or fats or other nutrients of ordinary food as part of a diet for rest or for muscular work? Will a calorie of energy from alcohol go as far, farther, or not as far as a calorie from sugar, starch, fat, or protein in meeting the actual needs of the body? The answer is to be sought in the experiments in which a diet of ordinary food is compared with a diet containing alcohol, the total available protein and energy of the food and the other conditions being the same in both experiments. The test will be found in the gains or losses of body protein and fat, and in the total energy metabolized in the two experiments. Any differences in either of these factors, to wit, (1) gains or losses of body material, or (2) energy metabolized, provided they are outside the limits of experimental error, must be attributed to the diet; that is to say, the alcohol in the diet. If the body gains or loses the same amount of material, or if it metabolizes the same amount of energy with both diets, a calorie of energy from one is equal to a calorie of energy from the other, and as a source of energy the alcohol is equal to the isodynamic amount of the carbohydrates or fats which it replaces. If the gain of material is less or the loss more, or if the total energy metabolized is larger with the alcohol, the latter is inferior as a source of energy, and vice versa.

Experimental results.—Table 17 shows the differences between the available energy of the food in experiments with and without alcohol and the corresponding differences between the energy of body material gained or lost in the same experiments. The figures in the fourth and sixth columns are computed from those in the third and fifth, respectively, using the factor 5.65 for the energy of one gram of protein, and 9.54 for that of one gram of fat.

TABLE 17.—*Comparison of gains and losses of body protein and fat, and transformation of energy in experiments with and without alcohol.*

[Quantities per day.]

Groups, kind, and number of experiments.	Available in food.		Gain (+) or loss (−) in body material.				(*g*)
	(*a*) Protein.	(*b*) Energy.	(*c*) Protein.	(*d*) Energy of protein, $c \times 5.65$	(*e*) Fat.	(*f*) Energy of fat, $e \times 9.54$	Energy of material oxidized, $b-(d+f)$.
I. More directly comparable:	*Grams.*	*Calories.*	*Grams.*	*Calories.*	*Grams.*	*Calories.*	*Calories.*
9 experiments without alcohol	103	2,917	− 3.5	−19	+ 1.1	+ 11	2,925
6 experiments with alcohol	104	2,925	− 6.9	−39	+ 2.4	+ 23	2,941
Increase (+) or decrease (−) with alcohol	**+ 1**	**+ 8**	**− 3.4**	**−20**	**+ 1.3**	**+ 12**	**+16**
II. Less directly comparable:							
4 experiments without alcohol	100	2,239	− 7.3	−41	− 2.3	− 22	2,302
7 experiments with alcohol	98	2,400	− 3.0	−17	− 6.5	− 61	2,356
Increase (+) or decrease (−) with alcohol	**2**	**+161**	**+ 4.3**	**+24**	**− 8.8**	**+ 83**	**+54**
III. Average of I and II:							
13 experiments without alcohol	102	2,691	− 4.8	−25	− .1	− 1	2,717
13 experiments with alcohol	102	2,750	− 7.1	−40	+ 3.8	− 36	2,746
Increase (+) or decrease (−) with alcohol	**0**	**+ 59**	**− 2.3**	**−15**	**+ 3.9**	**+ 37**	**−33**
Work and rest experiments of Group I:							
Work experiments compared—							
5 experiments without alcohol	100	3,337	− 5.1	−27	−31.5	−301	3,660
3 experiments with alcohol	100	3,361	−10.0	−56	−29.2	−278	3,690
Increase (+) or decrease (−) with alcohol	**0**	**− 24**	**− 4.9**	**−29**	**− 2.3**	**+ 23**	**− 30**
Rest experiments compared—							
4 experiments without alcohol	106	2,496	− 2.0	−11	+33.7	+317	2,190
3 experiments with alcohol	108	2,489	− 3.8	−21	+34.1	+319	2,191
Increase (+) or decrease (−) with alcohol	**+2**	**− 7**	**− 1.8**	**− 10**	**+ .4**	**+ 2**	**− 1**

The bold-face figures in the last line of each group in the columns for protein and fat give the gain or loss of material and energy in the alcohol experiments as compared with those without alcohol. The plus sign indicates greater gain and the minus sign greater loss with the alcohol than without it.

So far as the available (digestible) nutrients of the food are concerned, the quantities of protein are about the same and the quantities of energy slightly larger with alcohol than without it, but with the body material, on the other hand, there was generally a little larger loss of protein and a little larger gain or smaller loss of fat in the experiments with alcohol.

The figures in the last column represent the energy of material actually oxidized; that is, the total energy metabolized in the two classes of experiments. The full-face figures show by the + sign the excess of energy metabolized with the alcohol diet. The values are found by deducting the algebraic sum of the calories of energy gained or lost in protein and fat from the total available energy of the food as indicated by the letters and formulæ in the column headings. Thus in the first group we have an excess of $+8-(-20+12)=16$ calories of total energy metabolized in the alcohol as compared with the nonalcohol experiments. The same result is found by comparing the total quantities of energy metabolized, namely, 2,925 without and 2,941 with alcohol. The variations in the amounts of body material gained or lost and in the amounts of energy metabolized in the two classes of experiments may be due to either of three causes:

1. Such experimental errors as irregularities in the daily absorption of the food from the alimentary canal, or variations in the amounts of carbohydrates in the body which are here assumed to be constant from morning to morning, or from experiment to experiment, or small errors in the estimates of gains or losses of protein and fat from the gains or losses of nitrogen

and carbon. These errors are hardly avoidable, but on the whole they appear to counterbalance one another so that their effect is eliminated in the averages of a considerable number of experiments.

2. Differences in the activity of the subjects in the two classes of experiments. These differences are not easy to avoid. The man in the chamber may make more muscular effort on one day than on another in taking down his bed in the morning and in setting it up at night, or he may move about more in caring for the food and excretory products and weighing himself and the absorbers. In the work experiments there may be differences in the external muscular work despite the best efforts to make the amounts constant from day to day. These differences in muscular activity, though small, may affect the metabolism of matter and energy.

3. The energy furnished by the alcohol may not be as efficient, calorie for calorie, in meeting the demands of the body as the energy from the materials which it replaces. It is hardly to be supposed that the experimental errors in categories (1) and (2) will be considerable. It is still less probable that they will be so concentrated in either the alcohol or nonalcohol experiments as to materially affect the average results. If, therefore, the differences between the figures for the experiments of the two classes are large and reasonably constant, it would seem fair to attribute them to differences in the actual value of the alcohol as compared with isodynamic amounts of fats and carbohydrates.

The figures of Table 17 show differences to the disadvantage of the alcohol. The differences are, however, mainly within the range of experimental error.[a]

In the more directly comparable experiments (Group I) the conditions with and without alcohol were closely similar. In Group II there were not inconsiderable differences between the amounts of protein and energy in the diet, in the number of subjects, in the number of experiments, and in the amounts of muscular exercise. These differences do not, in our judgment, destroy the value of the comparisons in Group II, though they do make the differences in result less decisive. The results of Group II are, therefore, valuable as confirming those of Group I.

Gains and losses of body material as indicative of the relative effectiveness of alcohol.—The differences in the gains or losses of protein and fat in the experiments with alcohol as compared with the others are slightly to the disadvantage of the alcohol. They thus imply that, calorie for calorie, the energy furnished to the body by the alcohol was less effective than that furnished by the carbohydrates and fats. These differences may be due to experimental errors, but even if they are wholly charged to the alcohol they make it only slightly inferior to the nutrients which it replaces. The inferiority is found only in the work experiments; in the rest experiments there is practically no difference between the alcohol and the ordinary nutrients in effectiveness.

Amounts of energy metabolized as indicative of the relative effectiveness of alcohol.—The results here are similar to those found in the comparison of gains or losses of material. This is to be expected, since the two measures are really different expressions of the same fundamental fact. In the rest experiments the results with and without alcohol are practically identical. The inferiority of the alcohol is limited to the work experiments.

Energy of material metabolized in work experiments with and without alcohol.—In the work experiments more material was oxidized than the food supplied, and the deficiency was made up by drafts upon the previously accumulated store of body protein and fat. Under these circumstances the body may be supposed to use the energy economically so as to make the drafts upon

[a] The differences between the results with and without alcohol are in all cases small. Considering them from the ordinary mathematical standpoint, they are, of course, noticeable; but in such physiological experimenting as this the unavoidable errors of individual experiments are considerable, and it is only when a large number of such experiments are averaged that differences of one or two parts in one hundred could properly be regarded as significant. Indeed, in this whole discussion there is danger of being misled by the figures in the tables unless one constantly recalls the fact that the range of unavoidable variation is wide. When, however, the averages of large numbers of experiments show a constant difference on one side or the other, it may be permissible to use such differences for conclusions and generalizations. On the whole, it might seem that in these experiments the results were sufficiently numerous to imply a slight inferiority of the alcohol in respect to the economy of the use of energy; but this inference rests upon the rather questionable assumption of the absolute equality of all conditions other than the presence or absence of alcohol in the diet.

its capital as small as practicable. It would therefore seem that the amounts of material oxidized in the experiments with the two kinds of diet would give a somewhat critical test of the power of the body to utilize the energy of alcohol, either directly for muscular work or indirectly to save the energy of other materials for that work. We may, then, determine the relative efficiency of the alcohol in supplying energy in these experiments by comparing the amounts of energy in material oxidized. If the amounts are the same with and without alcohol the inference is that the energy of the alcohol was utilized as effectively, so far as simply the economy of energy is concerned, as that of the fats and carbohydrates; but if more energy is metabolized with the alcohol we must conclude that it is inferior as a source of energy in a diet for muscular work. We may take, for instance, the pair of experiments Nos. 11 and 12, in which the man was at hard work. (See Table CXX, p. 390.) His body used, in No. 11, with ordinary diet, 3,901 calories of energy per day. The food digested and absorbed from the diet supplied 3,510 calories, and the body burned enough of its previously accumulated material, protein and fat, to supply the lacking 391 calories.

In the corresponding alcohol experiment, No. 12, enough of the fats, sugar, and starch of the previous diet to furnish about 500 calories of energy was taken out and replaced by sufficient alcohol to furnish approximately the same amount, 500 calories. It happened that the total energy in the alcohol ration was about 30 calories the larger. Furthermore, the availability of the food proved to be slightly larger, so that the whole available energy of the alcohol ration was 3,614 calories. The amount of work done and the other conditions were practically the same as in the previous experiment. The body transformed 3,922 calories and in order to do so drew enough from its own store to furnish 308 calories.

According to these figures the body burned a trifle more material in the alcohol experiments than in the others—enough to furnish 3,922 instead of 3,901 calories of energy. But the alcohol diet furnished, with the alcohol, a somewhat larger amount of total energy, and furthermore a somewhat larger proportion of the nutrients of the ordinary food was digested, so that the body had 104 calories more of available energy. The fact that it drew 83 calories less from its previously stored material in this experiment than in No. 11 indicates that it used its energy economically. In each of these two cases the daily amount of external muscular work measured was equivalent to not far from 200 calories. In the first experiment all of this came from ordinary food. It may be that in the second experiment likewise it all came from the reduced supply of the ordinary food, and that none of the energy actually transformed into muscular work came from the alcohol. There is, however, no reason to suppose that the body made any distinction between the energy from the alcohol and that from the other fuel, and even if it did so it made just as good use of the energy of the alcohol to meet its other needs as it did of the energy of the ordinary nutrients.

The test of the comparative economy of the two diets so far as concerns the supply of energy is found in the amount of energy of material oxidized. This was 20 calories, or about 0.6 per cent the larger in the alcohol diet. This is far inside the limit of experimental error. Indeed, the quantity of energy given off from the body as measured by the respiration calorimeter was 5 calories larger with the ordinary than with the alcohol diet. (See Table CXX of the Appendix.) Of course such differences have practically no significance in physiological experimenting.

The results of the experiments in their bearing upon the subject are summarized herewith:

Average amounts of energy in material oxidized.

[Calories per day.]

Groups.	Experiments.	Ordinary diet.	Alcohol diet.
I	A–C.. More directly comparable, rest	2,190	2,191
	D–F.. More directly comparable, work	3,664	3,694
	A–F.. More directly comparable, all	2,927	2,942
II, G–I ..	Less directly comparable, rest	2,302	2,356
III, A–I ..	All above	2,719	2,747

It appears that in the more directly comparable experiments the energy of material oxidized averaged the same where the subjects were at rest, but was about 1 per cent larger with the alcohol when they were at work. In the less directly comparable experiments, in all of which the subjects were at rest, the average was larger by about 2 per cent with the alcohol diet. This is perhaps no more than was to be expected with the slight differences in the conditions of the experiments.

In this method of comparison by amounts of material and energy oxidized, as in the previous method, the differences were too small to be taken into account in individual experiments, but appearing as they do in the average of a number of experiments they are not without significance. The conclusion is that the energy of the alcohol diet was slightly less economically used than that of the ordinary diet, especially in the work experiments. This implies that the energy of the alcohol itself was less economically utilized than that of the fats and carbohydrates, but the differences are so small as to be of little or no practical consequence.

Relative effectiveness of alcohol expressed in percentages.—In the work experiments of Group I 3,664 calories were metabolized with the ordinary, and 3,694 with the alcohol ration. The relative costs of maintaining the body with the two rations were thus 3,664 : 3,694 = 100 : 100.8 or 99.2 : 100; the difference of 30 calories being 0.8 per cent. Assuming the difference to be due wholly to the inferiority of the alcohol ration, its effectiveness, calorie for calorie, would be 99.2 per cent of that of the ordinary ration, so far as the energy is concerned.

The alcohol supplied 500 calories of energy, of which the 30 calories would represent 6 per cent. If we charge the deficit wholly to the alcohol, the latter would be, calorie for calorie, 6 per cent less effective than the fats and carbohydrates it replaced. In other words, the effectiveness of the alcohol as a source of energy in the ration for muscular work in this case would be 94 per cent of that of the isodynamic amounts of carbohydrates and fats.

Calculated in these ways the effectiveness of the alcohol ration as compared with the ordinary ration, and that of the alcohol as compared with carbohydrates and fats in the experiments of Groups I–III, would be as follows:

Percentages of effectiveness of energy.

Groups.	Experiments. Classification.	Energy of alcohol ration as compared with energy of ordinary ration.	Energy of alcohol as compared with energy of carbohydrates and fats.
		Per cent.	*Per cent.*
I	More directly comparable	99.5	97.0
II	Less directly comparable	97.7	89.2
III	Average of I and II	99.0	94.4
I	Rest experiments	100.0	99.8
I	Work experiments	99.2	94.0

Summary.—The conditions and results of these experiments and the inferences here drawn from them regarding alcohol as a source of muscular energy may be briefly summarized:

1. We have here experiments with ordinary diet compared with other experiments in which the conditions were similar except that carbohydrates and fats sufficient to supply 500 calories of energy of the 2,200–3,600 calories in the daily ration were replaced by the isodynamic amount (about 72 grams) of alcohol, the latter being taken in six doses. The conditions of work and rest were very nearly the same in the corresponding experiments, with and without alcohol.

2. The amounts of material and energy transformed in the experiments with alcohol were very nearly the same as in the corresponding ones without alcohol. Where the ration was insufficient to meet the needs of the body, and it had to draw upon its store of fat and protein to supply the lacking energy, the drafts were practically the same with the ordinary as with the alcohol diet, so far as concerns the energy of the body material drawn upon.

3. The utilization of the energy of the whole ration was slightly less economical with the alcohol than with the ordinary diet, especially when the subjects were at hard muscular work,

but the difference in favor of the ordinary food was very small indeed, hardly enough to be of practical consequence. From this it follows that the energy of the alcohol was utilized very nearly or quite as well as that of the other fuel ingredients which it replaced.

4. That the alcohol contributed its share of energy for muscular work is a natural hypothesis and very probable, but not absolutely proven. The hypothesis that the energy of the alcohol was not so used, is not called for as an explanation of any fact observed in these experiments.

It should not be forgotten that the desirability of alcohol as part of a diet for muscular work is not decided by the narrower questions here discussed. There is a very essential difference between the transformation of the potential energy of alcohol into the mechanical energy of muscular work and the advantage or disadvantage of alcohol in the diet of people engaged in muscular labor. Even with the small doses in these experiments there were indications that the subjects worked to slightly better advantage with the ordinary rations than with the alcohol. The results of practical tests on a large scale elsewhere coincide with those of general observation in implying that the use of any considerable quantity of alcoholic beverages as part of the diet for muscular labor is generally of doubtful value and often positively injurious.[a] Aside from the question of the power of alcohol to protect protein and fat and supply energy to the body for various useful purposes, there are the far weightier considerations of the general effect of alcohol upon the muscular and especially the nervous system and upon health and welfare. Upon these most serious hygienic, economical, and ethical problems the experiments here reported throw no special light.

[a] For a summary of results of experiments upon various phases of this subject by different investigators, see article by Prof. J. H. Abel in the Report of the Physiological Subcommittee of the Committee of Fifty for the Investigation of the Drink Problem. (See page 261 of this memoir.)

SUMMARY OF PLAN AND RESULTS OF THE EXPERIMENTS.

Purpose, subjects, and method.—The purpose of the experiments, so far as the physiological action of alcohol is concerned, was primarily to get light upon the ways by which its potential energy is transformed and utilized in the body, but attention was also given to the effects of alcohol upon the digestion of the food taken with it, the proportions of alcohol that were oxidized and escaped oxidation, and its effects upon the metabolism of carbon and nitrogen and the gain and loss of fat and protein in the body.

The subjects were three young, healthy, active men who were ordinarily engaged in rather light work; one was a laboratory assistant, one a physicist, and one a chemist in the chemical laboratory of Wesleyan University, where the experiments were made. The first, E. O., a Swede by birth, had been accustomed from his youth to drink small quantities of alcoholic beverages; the other two, A. W. S. and J. F. S., had always been abstainers.

The results of experiments with ordinary diet were compared with those of experiments in which part of the fats and carbohydrates of the ordinary food were replaced by the isodynamic amount, about 72 grams (2½ ounces) of absolute alcohol, generally in the form of commercial alcohol, though in one experiment brandy and in another whisky was used. The amount of alcohol was about as much as would be supplied in a bottle of claret, or 6 ounces of whisky, or 5 ounces of brandy.

The ordinary diet consisted of meat, milk, bread, cereals, butter, sugar, and the like, with, in some cases, coffee. The quantities were such as had been found to be sufficient, or nearly so, for meeting the demands of the body under the conditions of the experiments, whether of rest or muscular work. The methods of preparation were such as to make the food palatable to the subject.

During the metabolism experiments proper the subjects were in the chamber of the respiration calorimeter, where they remained during periods varying from 4 to 9 days. The sojourn was made comfortable and the conditions seemed to be normal. Each metabolism experiment or series of experiments in the respiration chamber was preceded by a period during which the subject had essentially the same diet and nearly the same amount of muscular exercise outside the chamber. In these preliminary experiments the amounts, composition, and heats of combustion of the food, feces, and urine were determined. In the metabolism experiments the determinations include besides these the water and carbon dioxide of the incoming and outgoing air current by which the chamber was ventilated, the heat given off from the body, and, in the work experiments, the heat equivalent of the muscular work done. In the alcohol experiments the determinations were made of the small amounts of alcohol excreted by the kidneys, lungs, and skin.

Accordingly the data of the metabolism experiments show the income and outgo of the body as expressed in terms of (a) nitrogen, carbon, and hydrogen; (b) water, protein, fats, carbohydrates, and mineral matters; (c) potential energy of food and unoxidized excreta, and (d) kinetic energy of heat given off from the body and external muscular work performed. The accuracy of the apparatus and method were assured by burning alcohol within the chamber measuring the amounts of carbon dioxide, water, and heat produced. Such tests were made generally between each two experiments or experimental series. Taking the theoretical amounts at 100, the average amounts found were carbon dioxid, 99.6; water, 100.6; heat, 99.9.

In the so-called "rest" experiments the subject had no more muscular exercise than was involved in dressing and undressing, weighing himself, arranging his folding bed, chair, and table,

and caring for the food and solid and liquid excreta. His diversion was found in reading, writing, and occasional conversation by telephone with persons outside. In the "work" experiments the subject engaged in the active muscular exercise of riding a stationary bicycle for eight hours or thereabouts per day. The wheel of the bicycle was belted to a dynamo connected with an electric lamp, so that the muscular power which was applied to the pedals was converted partly into heat by friction but mainly into electrical energy and then into heat. The apparatus was calibrated so as to serve as an ergometer for measuring the external muscular work.

In interpreting the results in their bearing upon the physiological action of alcohol, it should be particularly noted that the whole amount of alcohol ingested per day was small and that furthermore it was taken in 6 doses, 3 with meals and 3 between meals. The object of the experiments was to study the action of alcohol under conditions calculated to secure the minimum of influence upon the nervous system. With such small doses, the equivalent of a glass of wine each, and thus distributed, two of the subjects were able to detect practically no sensible effect of the alcohol, while the third, J. F. S., felt nothing more than at times a slight "tingling" in the ears. There was in some cases an apparent though slight quickening of pulse rate, but practically no lowering of body temperature was observed. In such freedom from nervous disturbance it was believed that the normal nutritive action would be best observed.

There is the more reason for emphasizing this last point, because in the majority of the published experiments with men and animals for the study of the effects of alcohol the quantities of the latter have been much larger. Doses of 1 to 1½ grams per kilogram of body have commonly been considered small, and those of 2 to 3 grams per kilogram have been common and generally taken on an empty stomach. Often the amounts have been such as to cause the symptoms of drunkenness. In our experiments, on the other hand, the whole amount per day was only about 1 gram per kilogram body weight; the individual doses were only about one-sixth of a gram per kilogram, and half of them were taken with meals. This fact doubtless accounts for a not inconsiderable share of the difference between the results of our experiments and those found by a number of other investigators.

While the quantities of alcohol were small, the energy sufficed to make about one-fifth of the total energy of the diet in the "rest," and one-seventh of the total energy of the diet in the "work" experiments.

It is to be especially noted that these experiments were not made to test the effects of alcohol upon muscular or nervous activity or power, nor do they lead to any conclusions regarding the effects of alcohol when taken habitually or in large quantities.

The observed results.—The results, as shown by the statistics of the experiments, may be briefly stated as follows:

1. The quantities of alcohol eliminated by the lungs, skin, and kidneys varied from 0.7 to 2.7 grams, and averaged 1.3 grams per day (see p. 258). This corresponds to an average of 1.9 per cent of the whole alcohol ingested. Accordingly over 98 per cent of the ingested alcohol was oxidized in the body. There is, however, reason to believe that 99 per cent would more nearly represent the proportion actually oxidized.

2. The experiments give data for comparing the availability and fuel value of alcohol with those of the nutrients of ordinary food. The word "availability" as here applied to the ordinary nutrients, expresses the proportion which is digested and made available for the building and repair of tissue and the yielding of energy. This proportion is the difference between the total amount and that excreted by the intestine. In like manner the available alcohol would be the difference between the total amount ingested and the amount excreted by the lungs, skin, and kidneys, practically none being excreted by the intestine. The available energy of the ordinary nutrients is the total energy (heat of oxidation) less that of the material unoxidized. For fats, carbohydrates, and alcohol it is the heat of oxidation of the total available material. For the protein it is the same, less the heat of oxidation of the unoxidized residue excreted by the kidneys. The available energy is taken as the measure of the fuel value. The following table compares the coefficients of availability and the fuel values of the protein, fats, and carbohydrates of ordinary

diet, as found by a considerable number of experiments,[a] with those of the alcohol as shown by the experiments here reported.

TABLE 18.—*Comparison of availability (digestibility) and fuel values of nutrients of food in ordinary diet with those of alcohol.*

	Heat of combustion per gram.	Coefficients of availability—		Fuel values.			
		Of material.	Of energy.	Referred to available material.		Referred to total material.	
				Per gram.	Per pound.	Per gram.	Per pound.
	Calories.	*Per cent.*	*Per cent.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*
Protein	5.65	92	70	4.4	2,000	4.0	1,820
Fats	9.40	95	95	9.4	4,260	8.9	4,040
Carbohydrates	4.10	97	97	4.1	1,860	4.0	1,820
Alcohol	7.07	98	98	7.1	3,210	6.9	3,140

The isodynamic values of alcohol, carbohydrates, and fats are thus in the ratios of 6.9 : 4 : 8.9, and 1 gram of alcohol would be isodynamic with 1.73 grams carbohydrate or 0.78 gram of fats of ordinary food materials.

3. The proportions of food and of the several kinds of nutrients digested and made available for use in the body were practically the same in the experiments with and those without alcohol in the diet. The only difference worthy of mention was in the proportions of protein made available. These were very slightly larger with the alcohol, but the difference was too small to be of practical consequence. In all the experiments, both those with and those without alcohol, the results agree very closely with those commonly found in digestion of food in ordinary mixed diet by healthy men.

4. The potential energy of the alcohol was transformed into kinetic energy in the body as completely as that of the ordinary nutrients. The income and outgo of energy were equal in the experiments without alcohol; the same was true in the experiments with alcohol. In all the experiments the body obeyed the law of conservation of energy.

5. With the exception of the energy of the external muscular work in the work experiments, all of the energy of the food, including that of the alcohol, left the body as heat, and must therefore have been transformed into heat within the body. Part of this total energy must have been used for the internal mechanical (muscular) work; the energy thus used was therefore transformed into heat before leaving the body.

6. The radiation of heat from the body was very slightly greater with the alcohol diet than with the ordinary diet, but the difference was extremely small—enough to make only about 1 per cent of the whole energy metabolized and not over 6 per cent of the energy of the alcohol.

7. The efficiency of alcohol in the protection of body fat from consumption was very evident. The losses of fat were no larger and the gains no smaller with the alcohol diet than with the corresponding diet without alcohol. In this respect there was no indication of any considerable difference between the alcohol and the nearly isodynamic amounts of fats and carbohydrates which it replaced. This was the case in all the experiments.

8. The efficiency of the alcohol in protecting body protein was evident, but it was not fully equal in this respect to the isodynamic amounts of the ordinary nutrients. The results, however, were not the same with the different subjects. With E. O., who had been accustomed to use alcoholic beverages, the differences between the alcohol diet and the ordinary diet in their apparent effects upon nitrogen metabolism were small. The figures showed a slightly larger output of nitrogen with the alcohol, but the differences were not large enough to be of especial significance. With A. W. S., who was unaccustomed to alcohol, its use in the place of other

[a] See discussion of this subject by W. O. ATWATER and A. P. BRYANT in the Report of the Storrs (Conn.) Experiment Station for 1899, from which the figures for ordinary nutrients in the table are taken.

nutrients resulted, at first, in an increased excretion of nitrogen in the urine and inferentially a greater catabolism of protein, but after 5 or 6 days the output of nitrogen fell to what seemed to be the amount with ordinary diet, and when the alcohol was removed and diet thus reduced there was an increase in the output. These results implied that the alcohol at first failed to protect protein but was afterwards able to do so. There was, however, but one series of experiments with this subject. With J. F. S., also an abstainer, the alcohol periods covered only 3 days, during which there was in each case an increased nitrogen catabolism. On the whole these experiments accord with the belief that with some persons, especially those who are not accustomed to the use of alcohol, it may fail to protect protein; but this action is temporary and the more permanent influence is to protect protein.

9. That a part of the potential energy of the alcohol was transformed into the kinetic energy of muscular work these experiments do not prove, though they make it highly probable. They imply that, so far as the utilization of the total energy of the diet was concerned, there was a slight advantage in economy in favor of the ordinary as compared with the alcohol diet, especially when the subjects were at hard muscular work, but the difference was inside the limits of experimental error and too small to be of practical consequence. On the average it was less than 1 per cent of the total energy and hardly reached 5 per cent of the energy of the alcohol. From this it follows that the energy of the alcohol was utilized nearly if not quite as well as that of the fats, sugar, and starch which it replaced.

10. We repeat that there is a very essential difference between the transformation of the potential energy of alcohol into the kinetic energy of heat, or of either internal or external muscular work, and the usefulness or harmfulness of alcohol as a part of ordinary diet. Regarding this latter question the experiments bring no more evidence than they do regarding the influence of alcohol upon the nervous system or its general effect upon health and welfare.

APPENDIX.

The details of the experiments described above are set forth in the following pages, and include:

1. Kinds of experimental data and methods for obtaining them.
2. Statistical details of metabolism experiments with alcohol.
3. Statistical details of digestion experiments with alcohol.
4. Tabular summaries.

A list of the experiments, with groupings for comparison, may be found in Table 1, on page 241 of the first part of this report. As there explained, the metabolism experiments here described in detail were made with alcohol as a part of the diet. They are compared with similar experiments without alcohol, which have been described in detail elsewhere. Each metabolism experiment or series of metabolism experiments with or without alcohol not only included a digestion experiment, but was also preceded by such an experiment. The data of these digestion experiments are also given beyond. The experiments without alcohol and two of those with alcohol have been described in detail elsewhere. In several instances the results are here summarized with the details of the alcohol experiments.

DATA.—EXPERIMENTAL METHODS.

METABOLISM EXPERIMENTS.

The larger part of the statistics of the metabolism experiments have to do with the income and outgo of material and energy.

Experimental data of income.—These include statistics of the kinds, amounts, composition, and potential energy of food and drink, the volume of the ventilating current of air entering the chamber and the amount of carbon dioxide and water in that air. The food for each experiment was selected before the experiment began and the desired amounts for different meals were placed in suitable jars, as described on page 239. Such of the analytical determinations as were necessary for the control of the diet, in order to insure the desired amount of protein and energy, were made previous to the beginning of the experiment.

Experimental data of outgo.—These include statistics of the amount, composition, and heat of combustion of the unoxidized materials of feces and urine, the quantity of carbon dioxid and water in the air leaving the chamber, and the total energy given off by the body in the form of heat and external muscular work.

Apparatus and general methods of inquiry.—The respiration calorimeter and method of its use have been described in detail in publications referred to on page 236.[a] The methods of analysis of food, feces, and urine were, in the main, those adopted by the Association of Official Agricultural Chemists,[b] but with certain modifications which have been developed in this laboratory.[c] The heats of combustion were determined by use of the bomb calorimeter.[d]

[a] Bulletins 44, 63, 69, and 109 of the Office of Experiment Stations of the U. S. Dept. Agr.

[b] See Bulletin 46, revised, of the Division of Chemistry, U. S. Dept. Agr.

[c] See U. S. Dept. Agr., Office of Experiment Stations, Bul. 44, p. 22; Bul. 69, p. 18, and Report of Storrs (Conn.) Expt. Sta., 1891, p. 47. The methods for the determination of carbon and hydrogen in use in this laboratory are described in detail by F. G. Benedict in Elementary Organic Analysis, The Chemical Publishing Co., on page 51 of which the apparatus is pictured.

[d] The bomb calorimeter and accessory apparatus used have been described by W. O. Atwater and associates in Bulletin 21 of the Office of Experiment Stations of the U. S. Dept. Agr., p. 123, and in the Reports of the Storrs (Conn.) Expt. Sta., 1894, p. 133, and 1897, p. 199.

Further descriptions of experimental methods are given in connection with the descriptions of experiment 12, beyond.

Composition of food materials and feces.—The figures for the analyses of the food materials and feces of the alcoholic experiments here described are given in Tables I and II.

TABLE I.—*Composition of food materials used in metabolism experiments Nos. 12, 15, 16, 17, 18, 19, 20, 22, 27, 30, and 33.*

Laboratory No.	Food material.	Experiment No.	Nitrogen.	Carbon.	Hydrogen.	Water.	Protein (N × 6.25).	Fat.	Carbohydrates.	Ash.	Heat of combustion per gram determined.
			Per ct.	*Per ct.*	*Per ct.*	*Per ct.*	*Per ct*	*Per ct.*	*Per ct.*	*Per ct.*	*Calories.*
2860	Beef cooked	12	4.38	17.85	2.61	65.3	27.4	5.6	.....	2.5	2.000
3009	.....do	15–17	4.17	15.24	2.29	69.2	26.1	2.6	.....	2.2	1.682
3022	.....do	18–20	4.46	16.57	2.54	66.7	27.9	2.6	.....	2.1	1.827
3027	.....do	22	5.59	23.57	3.37	56.6	34.9	6.1	.....	1.0	2.633
3176	.....do	27	5.41	19.55	2.70	62.5	33.8	2.8	.....	.9	2.198
3186	.....do	30	5.72	20.89	2.99	60.3	35.7	3.0	.....	1.0	2.327
3205	.....do	33	5.13	18.55	2.66	64.5	32.1	2.8	.....	1.0	2.075
2858	Ham, deviled	12	2.93	36.10	5.45	41.4	18.3	36.4	.....	4.0	4.366
2861	Butter	12	.08	63.81	10.14	10.9	.5	86.4	.....	2.2	7.906
3003	.....do	15–17	.19	61.90	10.40	10.3	1.2	86.0	.....	2.5	7.959
3021	.....do	18–20	.21	66.23	10.55	8.7	1.3	87.5	.....	2.5	8.178
3029	.....do	22	.17	69.16	10.52	9.5	1.1	86.8	.....	2.6	8.027
3177	.....do	27	.26	65.02	10.02	9.9	1.6	85.9	.....	2.6	8.002
3187	.....do	30	.20	65.11	10.44	9.2	1.3	86.3	.....	3.2	8.048
3206	.....do	33	.20	65.58	10.37	8.4	1.3	87.6	.....	2.7	8.210
2857	Milk, whole	12	.49	6.57	1.00	87.5	3.1	4.5	4.2	.7	.798
3024	.....do	18–20	.51	7.03	.94	86.6	3.2	4.4	5.0	.8	.782
3190	.....do	30	.64	8.00	1.20	85.0	4.0	5.4	4.8	.8	.900
3201	.....do	33	.66	8.22	1.24	85.1	4.1	5.2	4.8	.8	.904
3006	Milk, skimmed	15–17	.65	4.61	.66	89.5	4.1	.1	5.5	.8	.468
3031	.....do	22	.58	4.11	.59	90.7	3.6	.1	4.8	.8	.409
3179	.....do	27	.67	4.63	.63	90.0	4.2	.3	4.7	.8	.462
2842	Maize breakfast food	12	1.88	44.39	6.49	4.9	11.8	8.2	73.4	1.7	4.437
3004	Cereal, parched	15–22	1.82	41.39	6.17	6.1	11.4	.6	80.4	1.5	4.056
3168	.....do	27	1.87	42.20	5.94	5.6	11.7	1.7	79.1	1.9	4.136
3193	.....do	30–33	1.92	42.72	6.30	4.1	12.0	1.4	80.5	2.0	4.202
2859	Bread	12	1.51	27.27	3.92	40.4	9.4	1.0	48.1	1.1	2.663
2968	.....do	15–20	1.27	27.33	4.11	41.7	7.9	2.8	46.3	1.3	2.710
3032	.....do	22	1.27	28.05	3.98	46.4	7.9	3.4	47.0	1.3	2.889
3180	.....do	27	1.42	27.76	3.99	39.3	8.9	1.6	48.9	1.3	2.803
3192	.....do	30	1.50	29.14	4.30	36.5	9.4	2.0	50.8	1.3	2.931
3204	.....do	33	1.38	28.27	4.30	37.8	8.6	2.5	49.8	1.3	2.869
3181	Gingersnaps	27, 30	1.00	44.32	6.61	4.1	6.2	8.3	79.8	1.6	4.434
3207	.....do	33	.88	43.87	7.20	3.7	5.5	7.2	81.6	2.0	4.434
3069	Horse-radish	17	.20	4.50	.60	89.3	1.3	.2	8.3	.9	.380
	Sugar	(a)	.....	42.10	6.48	.....	.....	.....	100.0	.....	3.960
	Alcohol	(b)	.....	52.17	13.05	.....	.....	.....	.....	.....	7.069

[a] Used in all the experiments. [b] As pure ethyl alcohol.

TABLE II.—*Composition of feces in metabolism experiments Nos. 12, 15, 16, 17, 18, 19, 20, 22, 27, 30, and 33.*

Laboratory No.		Experiment No.	Nitrogen.	Carbon.	Hydrogen.	Water.	Protein (N × 6.25).	Fat.	Carbohydrates.	Ash.	Heat of combustion per gram determined.
			Per ct.	*Per ct.*	*Per ct.*	*Per ct.*	*Per ct.*	*Per ct.*	*Per ct.*	*Per ct.*	*Calories.*
2863	Feces	12	1.35	13.05	1.85	74.1	8.4	7.0	6.1	4.4	1.473
3008	.....do	15–17	1.57	14.85	2.07	68.3	9.8	5.6	8.6	7.7	1.675
3033	.....do	18–20	1.62	14.03	1.94	72.6	10.1	6.3	6.3	4.7	1.571
3035	.....do	22	1.59	14.44	2.07	69.3	9.9	5.2	8.5	7.1	1.610
3184	.....do	27	1.53	12.26	1.10	69.5	9.6	2.9	9.7	8.3	1.335
3196	.....do	30	1.43	13.53	1.89	71.2	8.9	4.5	9.8	5.6	1.487
3210	.....do	33	1.37	13.22	1.92	71.0	8.5	5.0	9.4	6.1	1.452

TABLE III.—*Composition of materials not included in Tables I and II used in connection with digestion experiments.*

Laboratory No.	Material.	Digestion experiment No.	Nitrogen.	Water.	Protein.	Fat.	Carbohydrates.	Ash.	Heat of combustion per gram. (determined.)
			Per cent.	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Calories.*
2845	Milk	47	0.50	90.48	3.13	0.10	5.52	0.77	402
2846	....do	48	.53	90.36	3.31	.11	5.45	.77	414
2856	....do	51	.53	85.88	3.31	5.00	5.07	.74	865
3005	....do	80	.64	80.44	3.98	.06	5.66	.86	467
2809	Feces	41	1.89	71.44	11.79	5.38	6.63	4.76	1,564
2810	....do	42	1.81	70.96	11.30	4.95	7.63	5.16	1,530
2847	....do	47	1.48	73.37	9.28	3.84	9.08	4.43	1,349
2848	....do	48	1.57	71.01	9.83	4.15	10.21	4.80	1,445
2862	....do	51	1.47	70.32	9.20	7.56	7.42	5.50	1,598
3007	....do	80	1.68	62.69	10.53	7.17	12.03	7.58	2,068
3034	....do	83	1.75	68.75	10.93	5.68	7.60	7.04	1,568

Composition of coffee infusion.—Coffee infusion was prepared by pouring boiling water over ground coffee and straining the infusion thus obtained. The nitrogen was determined in this infusion and found to amount to about 0.004 grams per liter—quantities too small to be taken into account. The coffee infusion is therefore reckoned simply as so much water.

STATISTICAL DETAILS OF METABOLISM EXPERIMENTS.

The details of the methods of conducting the experiments and of computing the results, as well as the statistical tables in which these results are presented, will be advantageously given in connection with the description of one of the experiments. For this purpose we select No. 12, which is the first in consecutive order of those here described in detail.

EXPERIMENT NO. 12—WORK WITH ALCOHOL DIET.

Subject.—E. O., laboratory assistant, 31 years of age and weighing, without clothing, about 71 kilograms (157 pounds).

Occupation during experiment.—Work 8 hours a day upon a stationary bicycle belted to a small dynamo, thus making an ergometer as described on page 237. The voltage was measured and the current passed through resistance within the apparatus and thus transformed into heat and measured with the heat given off by the subject. Previous calibration showed the amount of work done in driving the bicycle.

Duration.—Preliminary period 4 days, beginning with breakfast April 8, 1898, and experiment proper 4 days, beginning at 7 a. m. April 12 and ending at 7 a. m. April 16. The subject entered the respiration chamber on the evening of April 11 and thus spent 5 nights and 4 days within the calorimeter.

Diet. Ordinary food furnishing 121 grams of protein and 3,379 calories of energy, and in addition 72.4 grams of alcohol furnishing 512 calories of energy, making the total energy of the diet 3,891 calories. The alcohol was added to a sweetened coffee infusion. It was taken in 6 doses, 3 with the meals and the other 3 between meals and just before retiring. The coffee infusion was prepared in the usual manner, care being taken to keep that given to the subject free from particles of coffee. To 690 grams of infusion were added 50 grams of sugar and 80 grams of commercial ethyl alcohol containing 90.63 per cent absolute alcohol. The 80 grams of commercial alcohol thus contained 72.4 grams of absolute alcohol and 7.5 grams water. The diet was practically the same during both the preliminary digestion experiment and the metabolism experiment proper. The kinds and amounts of different food materials taken at each meal and the amounts of coffee infusion and water consumed at different times during the day are shown herewith.

Diet in metabolism experiment No. 12.

FOOD

	Breakfast.	Dinner.	Supper.	Total.
	Grams.	*Grams.*	*Grams.*	*Grams.*
Beef	75	100	.....	175
Deviled ham	.....	.....	50	50
Butter	25	40	30	95
Whole milk	250	260	390	900
Bread	75	100	125	300
Maize breakfast food	60	.....	.....	60
Sugar	20	.....	[a]50	[a]70
Alcohol	.....	.....	.....	[b]72.4

DRINK.

Time	Amount.	
	Coffee infusion with alcohol and sugar.[c]	Water.
	Grams.	*Grams.*
Breakfast	175	200
10.20 a. m	150	200
12.30 p. m	.....	200
Dinner	175	.....
3.50 p. m	125	200
Supper	175	.....
10 p. m	130	200
Total	930	1,000

[a] Including 50 grams used in coffee infusion and alcohol.
[b] Added to coffee infusion and taken as indicated below.
[c] Made by adding 80 grams of 90.5 per cent commercial alcohol and 50 grams sugar to 800 grams coffee infusion. The mixture then contained 807.5 grams water, 72.4 grams absolute alcohol and 50 grams sugar.

Daily routine.—In order to make the conditions of the experiment on the different days as nearly uniform as practicable a daily programme was drawn up and one copy was given to the subject within the respiration chamber while others were posted outside for the use of those carrying on the details of the experiment. The routine in experiment No. 12 was as follows:

Daily program—Metabolism experiment No. 12.

7.00 a. m	Rise, pass urine, collect drip, weigh absorbers, weigh self stripped and dressed.	1.50 p. m	Begin work.
		3.50 p. m	Stop work, rest 10 minutes, drink alcohol, drink 200 grams water.
7.45 a. m	Breakfast, drink 200 grams water.	4.00 p. m	Begin work.
8.20 a. m	Begin work.	6.00 p. m	Stop work.
10.20 a. m	Rest 10 minutes, drink alcohol, drink 200 grams water.	6.30 p. m	Supper, change underclothes, weigh self stripped and dressed.
10.30 a. m	Begin work.	7.00 p. m	Pass urine, collect drip, weigh absorbers.
12.30 p. m	Stop work, drink 200 grams water.		
1.00 p. m	Pass urine, collect drip, weigh absorbers.	10.00 p. m	Take cover off food aperture, drink 200 grams water, retire.
1.15 p. m	Dinner.	1.00 a. m	Pass urine.

The subject weighed himself, with and without clothing, at about 7 a. m. and 7 p. m. each day of the experiment. He observed his pulse rate, after intervals of rest, and took his body temperature from time to time by means of a registered clinical thermometer. The body temperatures were measured *sub lingua*. We do not think that great reliance can be placed upon observations for either pulse rate or temperature when made by the subject upon himself under such conditions.

A hygrometer inside the chamber was observed two or three times each day in order to give data concerning the amount of water vapor within the calorimeter, but the figures are not used in the final computations of results.

These statistics noted by the subject within the calorimeter are recorded in a diary, together with any other information which he thinks may be of value in interpreting the results of the experiment.

The main facts in the diary of experiment No. 12 are shown in Table IV.

Table V recapitulates the record of work done on the ergometer. It is much less than would be required to propel a bicycle the number of miles indicated by the cyclometer.

TABLE IV.—*Summary of diary—Metabolism experiment No. 12.*

Date and time	Weight of subject.		Pulse rate per minute.	Temperature.	Hygrometer.	
	Without clothes.	With clothes.			Dry bulb.	Wet bulb.
	Kilograms.	*Kilograms.*		*F.*	*C.*	*C.*
Apr. 12, 7.00 a. m.	70.92	75.09	64	98.4	21.5	16.4
12, 12.40 p. m.			68	98.8	21.8	18.6
12, 7.00 p. m.	71.72	75.38				
12, 9.45 p. m.			77	98.3	21.5	18.0
13, 7.00 a. m.	71.09	74.82	56	96.1	21.4	17.4
13, 12.40 p. m.			68	98.8	21.5	18.8
13, 6.30 p. m.	71.40	74.96				
13, 9.45 p. m.			71	98.4	21.5	18.0
14, 7.00 a. m.	70.56	74.19	58	97.0	21.4	17.0
14, 12.40 p. m.			70	99.0	21.4	18.8
14, 6.30 p. m.	70.98	74.50				
14, 9.45 p. m.			73	98.5	21.5	17.8
15, 7.00 a. m.	70.47	73.98	57	97.2	21.3	16.8
15, 12.40 p. m.			72	97.0	21.7	19.0
15, 7.00 p. m.	71.12	74.51				
15, 9.45 p. m.			74	99.0	21.5	17.8
16, 7.00 a. m.	70.31	73.98	60	96.4	22.0	18.4

TABLE V.—*Record of work done—Metabolism experiment No. 12.*

Date and time.	Cyclometer reading.[a]	Number of miles.	Actual duration of work.	Rate.	Heat equivalent.
			Mins.	*Watts.*	*Calories.*
Apr. 12, 7.00 a. m.	641				
		41	120	31	107.1
12, 10.20 a. m.	600				
		41	120		
12, 12.30 p. m.	559				
		38	120	28	96.7
12, 3.50 p. m.	521				
		39	120		
12, 6.00 p. m.	482				
13, 8.20 a. m.	480				
		40	120	31	107.1
13, 10.20 a. m.	440				
		40	120		
13, 12.30 p. m.	400				
		41	120	30	103.7
13, 3.50 p. m.	359				
		40	120		
13, 6.00 p. m.	319				
14, 8.20 a. m.	316				
		35	120	29	100.2
14, 10.20 a. m.	281				
		39	120		
14, 12.30 p. m.	242				
		36	120	27	93.2
14, 3.50 p. m.	206				
		36	120		
14, 6.00 p. m.	170				

[a] The cyclometer was reversed.

TABLE V.—*Record of work done—Metabolism experiment No. 12*—Continued.

Date and time.	Cyclometer reading.[a]	Number of miles.	Actual duration of work.	Rate.	Heat equivalent.
			Mins.	*Watts.*	*Calories.*
Apr. 15, 8.20 a. m	168				
		36	120		
15, 10.20 a. m	132			30	103.7
		39	120		
15, 12.30 p. m	93				
		36	120		
15, 3.50 p. m	57			26	89.3
		23	120		
15, 5.30 p. m	34				
	.....	600	1,920	.....	801.0

[a] The cyclometer was reversed.

Food and excreta.—The weight, composition, and heat of combustion of the food and feces in this experiment are shown in Tables VI and VII. The weights of the different elements and compounds are computed by use of the values for percentage composition of the different materials as shown in Tables I and II:

TABLE VI.—*Weight, composition, and heat of combustion of foods—Metabolism experiment No. 12.*

Laboratory No.	Food material.	Weight per day.	Water.	Protein.	Fat.	Carbohydrates.	Nitrogen.	Carbon.	Hydrogen.	Heat of combustion.
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
2860	Beef	175.0	114.3	47.9	9.8	.....	7.67	31.24	4.57	350
2858	Deviled ham	50.0	20.7	9.2	18.2	.....	1.47	18.05	2.73	218
2861	Butter	95.0	10.4	.5	82.1	.....	.08	60.62	9.63	751
2857	Whole milk	900.0	787.5	27.6	40.5	37.8	4.41	59.13	9.00	718
2859	Bread	300.0	121.2	28.3	3.0	144.3	4.53	81.81	11.76	799
	Maize breakfast food	60.0	2.9	7.1	4.9	44.0	1.13	26.67	3.90	266
	Sugar	70.0	.....	.....	.....	70.0	.....	29.47	4.54	277
	Total	1,650.0	1,057.0	120.6	158.5	296.1	19.29	306.99	46.13	3,379
	Alcohol	72.4	.....	.....	.....	.....	.....	37.77	9.45	512
	Total	.....	.....	.....	.....	.....	19.29	344.76	55.58	3,891

TABLE VII.—*Weight, composition, and heat of combustion of feces—Metabolism experiment No. 12.*

Laboratory No.		Weight.	Water.	Protein.	Fat.	Carbohydrates.	Nitrogen.	Carbon.	Hydrogen.	Heat of combustion.[a]
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
2862	Total, four days	370.0	274.2	31.1	25.9	22.6	5.00	48.29	6.85	545
	Average per day	92.5	68.6	7.8	6.5	5.7	1.25	12.07	1.71	136

The separations between the feces from the food consumed during the experiment and those from the food consumed before and after were made by means of charcoal, as described on page 239. Inasmuch as separations made in this way are at the best not as satisfactory as might be desired, no attempt was made to determine the excreta from the food on different days of the experiment. It is assumed that, when the food and exercise are so nearly uniform, the undigested residues and metabolic products would not vary a great deal from day to day. Even if there were irregularities from day to day they would hardly be large enough to affect very greatly the average for the whole experiment.

The amount, specific gravity, and nitrogen of the urine for the different 6-hour periods during the experiment are shown in Table VIII, and the carbon, hydrogen, water, and energy of

the daily urine in Table IX. The urine was also collected during the preliminary period of 4 days and during 12 hours following the experiment. Aliquot portions (from one-half to two-thirds) in these 6-hour periods were taken for the preparation of a composite sample of the urine for the day, and in like manner aliquot portions (about one-eighth of the total weight of urine) of the composite sample of the urine for 24 hours were taken for the preparation of a composite sample for the whole period of the experiment. The nitrogen was determined in the urine for each day and in the composite for 4 days of the experiment. The quantities of nitrogen eliminated each day, as determined from the 6-hour periods and from the composite sample for the day, do not always agree exactly. Such discrepancies may be due in part to small errors in the sampling of the composites, in part to errors in the amount of urine measured out for analysis, and in part to errors in the analyses. Samples were measured out for analyses in a calibrated 5-c. c. pipette, and it is possible that differences in the amount delivered from time to time might introduce slight errors in the results. It is assumed, where discrepancies exist, that the values obtained from the 6-hour periods are the more accurate, and these latter are consequently used in the estimation of the nitrogen balance.

It is difficult to evaporate urine to dryness without more or less decomposition of urea to ammonium carbonate, and consequent loss of energy. Accordingly, no attempt was made to determine the solid matter in the urine of individual days, but a portion of the composite sample for the experiment was dried according to the manner described on page 239 and the residue used for the determination of carbon, hydrogen, and heat of combustion. The heat of combustion is also determined in the composite samples of the fresh urine each day, as explained above. The precautions taken to avoid error through loss of nitrogen, carbon, and energy during the process of drying of the urine have been described in the publication referred to on page 239.

The nitrogen is determined in the fresh urine from day to day, but in order to obtain an approximate measure of the amount of carbon and hydrogen in the urine on the successive days of the experiment some computations are necessary. In making these computations it is assumed that the ratio of nitrogen to carbon, hydrogen or water-free substance will be the same for each individual day as for the 4 days. Thus, the amount of nitrogen in the urine of the first day of the experiment was 17.62 grams, and that for the whole experiment 71.86 grams. The carbon for the whole experiment was found by actual determinations to be 49.15 grams. The computations for the amount of carbon in the urine for the first day would then be as follows: $71.86 : 49.15 :: 17.62 : x\ (= 12.05)$. This method of estimating the carbon and hydrogen in the urine on the different days is manifestly more accurate than would be the case if the total quantity of carbon and hydrogen in the urine for the experiment were divided by the number of days, as is done in estimating the daily excretion through the feces. We know that the quantities of nitrogen and carbon in the urine vary from day to day, and have an accurate measure of the variation of the nitrogen, and, since the variation in the nitrogen must involve variations in the amount of carbon united with this nitrogen in the form of urea and allied compounds, it does not seem inappropriate to take the variations in the nitrogen as a measure of the corresponding variations in the carbon. Of course, there may be varying quantities of non-nitrogenous compounds in the urine from day to day, which would render the above method of estimation more or less inaccurate. It is probable, however, that the variations in nitrogen give the fairest measure of the variations in carbon and hydrogen. As a matter of fact, it has been found that the heat of combustion varies in close relation to the nitrogen. Of course, the results for the experiment as a whole are not affected by the subdivisions of the amounts for the individual days.

TABLE VIII.—*Amount, specific gravity, and nitrogen of urine by 6-hour periods—Metabolism experiment No. 12.*

Date.	Period.	Amount.	Specific gravity.	Nitrogen.	
1898.		*Grams.*		*Per cent.*	*Grams.*
Apr. 12–13	7 a. m. to 1 p. m.	309.4	1.026	1.18	3.64
	1 p. m. to 7 p. m.	349.0	1.030	1.51	5.28
	7 p. m. to 1 a. m.	247.6	1.027	1.90	4.70
	1 a. m. to 7 a. m.	187.0	1.030	2.14	4.00
	Total	1,093.0			17.62
	Total by composite	1,093.0	1.028	1.64	
13–14	7 a. m. to 1 p. m.	316.7	1.025	1.40	4.42
	1 p. m. to 7 p. m.	455.4	1.029	1.29	5.89
	7 p. m. to 1 a. m.	276.4	1.027	1.84	5.07
	1 a. m. to 7 a. m.	286.0	1.028	2.00	5.73
	Total	1,334.5			21.11
	Total by composite	1,334.5	1.028	1.59	
14–15	7 a. m. to 1 p. m.	243.6	1.024	1.14	2.78
	1 p. m. to 7 p. m.	386.3	1.024	1.24	4.78
	7 p. m. to 1 a. m.	285.4	1.025	1.72	4.91
	1 a. m. to 7 a. m.	154.3	1.030	2.06	3.18
	Total	1,069.6			15.65
	Total by composite	1,069.6	1.025	1.48	
15–16	7 a. m. to 1 p. m.	320.5	1.024	1.39	4.45
	1 p. m. to 7 p. m.	326.0	1.026	1.32	4.30
	7 p. m. to 1 a. m.	333.3	1.028	1.65	5.49
	1 a. m. to 7 a. m.	160.3	1.028	2.02	3.24
	Total	1,140.1			17.48
	Total by composite	1,140.1	1.026	1.51	
	Total for 4 days, by periods	4,637.2			71.86
16	7 a. m. to 1 p. m.	325.8		.73	2.38

TABLE IX.—*Daily elimination of carbon, hydrogen, water, and energy in urine—Metabolism experiment No. 12.*

Date.	Amount.	Carbon.		Hydrogen.		Water.		Heat of combustion.	
								Per gram.	Total.
1898.	*Grams.*	*Per ct.*	*Grams.*	*Per ct.*	*Grams.*	*Per ct.*	*Grams.*	*Calories.*	*Calories.*
Apr. 12 to 13	1,093.0	.....	12.05	.....	3.30	.....	1,025.9	0.112	123
13 to 14	1,334.5	.....	14.44	.....	3.95	.....	1,254.1	.108	145
14 to 15	1,069.6	.....	10.70	.....	2.93	.....	1,010.0	.115	123
15 to 16	1,140.1	.....	11.96	.....	3.27	.....	1,073.6	.114	130
Total	4,637.2	1.06	49.15	29	13.45	94.1	4,363.6	(.112)	[a]521

[a] The heat of combustion of the urine was determined in the composite sample for each day and in the total composite for four days. The total heat of combustion of the urine for the experiment, as determined in the latter sample, was 0.112 calorie per gram, or a total of 519 calories.

Carbon dioxid and water of respiration and perspiration.—The determinations of carbon dioxid and water in the ventilating air current in this experiment are shown in Tables XI and XII, which follow. Table X gives the total amounts of carbon dioxid and of water in the air of the chamber at the close of each period and the gain or loss during the period. Differences in the amounts in the chamber at the beginning and end of a given period—"residual" amounts, as they are here termed—indicate whether the ventilating air current has removed more or less carbon dioxid and water than was actually exhaled by the subject during the corresponding period. For instance, if a change from rest to work is made during a given period, the quantities of carbon dioxid and water given off will be increased, and the air remaining in the chamber at the end of the period will contain a larger amount of these products than was present in the air of the chamber at the beginning. This increase must be added to the amount actually

found in the ventilating air current in order to obtain the actual amount exhaled during the interval. On the other hand when the transition is made from a period of considerable activity to one of rest, there is a gradual diminution of the quantity of residual carbon dioxid and water in the air of the chamber. This residual carbon dioxid is carried out in the ventilating air current during the period, but was actually given off during some preceding period. The total amount measured must, therefore, be diminished by the difference in the quantities of residual carbon dioxid at the beginning and end of the period. Furthermore, with the increased water content of the air consequent upon increased muscular work, the amount of water accumulated by condensation upon the water system or "absorbers" may be gradually increased. Indeed, the amount of water thus condensed in periods of active work is apt to be so large that a portion gradually drips from the troughs or shields beneath the water system into the "drip flasks" suspended at the end of the shields. This water is called "drip." The weight of the water system or absorbers also increases through the condensation of moisture which does not run off into the drip. On the other hand, with the change from work to rest, the weight of the absorbers diminishes because of evaporation of some of the moisture condensed thereon during the previous period.

In order to determine the actual amount of carbon dioxid and water vapor in the air of the chamber at the close of each period, samples of the air are drawn and the quantities of carbon dioxid and water determined. At the same time the absorbers are weighed and the drip collected. The data thus obtained, shown in Table X, serve for correcting the amounts of carbon dioxid and water found in the ventilating air current, as shown in Tables XI and XII beyond.

In experiment No. 12 drip was not weighed at the end of each period, but was poured into a bottle and the total amount for each 24 hours passed out at the close of the day and weighed. We have, therefore, no measure of the amount of drip in the different periods. It is altogether improbable that the amount was uniform from period to period, but in lack of any indication as to how it should be subdivided, the amounts have been apportioned equally among the four periods of the day. While this may introduce some error in individual periods, it does not affect the accuracy of the figures for the whole day.

TABLE X.—*Comparison of residual amounts of carbon dioxid and water in the chamber at the beginning and end of each period and the corresponding gain or loss—Metabolism experiment No. 12.*

Date.	End of period.	Carbon dioxid.		Water.				
		Total amount in chamber.	Gain (+) or loss (−) over preceding period.	Total amount of vapor remaining in chamber.	Gain (+) or loss (−) over preceding period.	Change in weight of absorbers. Gain (+) or loss (−).	Drip from absorbers.	Total amount gained (+) or lost (−) during period.
1898.		*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Apr. 12–13..	7 a. m.	29.3	.....	40.7	.....	.....	.....	.....
	1 p. m.	93.6	+64.3	58.4	−17.7	−286	191.5	495.2
	7 p. m.	71.5	22.1	57.6	− .8	166	191.6	24.8
	1 a. m.	31.4	−40.1	56.6	− 1.0	− 34	191.6	156.6
	7 a. m.	30.5	.9	51.2	− 5.4	− 34	191.6	152.2
	Total	.....	1.2	.....	−10.5	− 52	766.3	828.8
13–14..	1 p. m.	99.5	+69.0	61.9	−10.7	−112	298.0	420.7
	7 p. m.	79.0	20.5	64.9	− 3.0	− 9	298.0	292.0
	1 a. m.	31.4	−47.3	57.6	− 7.3	− 25	297.9	265.6
	7 a. m.	26.9	− 4.8	51.8	− 5.8	− 25	297.9	267.1
	Total	.....	− 3.6	.....	− .6	− 53	1,191.8	1,245.4
14–15..	1 p. m.	88.2	+61.3	60.2	− 8.4	− 77	251.3	336.7
	7 p. m.	74.4	13.8	63.8	− 3.6	11	251.3	265.9
	1 a. m.	25.1	−49.3	56.0	− 7.8	− 81	251.2	162.4
	7 a. m.	27.1	− 2.0	50.7	− 5.3	− 81	251.2	164.9
	Total	.....	− .2	.....	− 1.1	74	1,005.0	929.9

TABLE X.—*Comparison of residual amounts of carbon dioxid and water in the chamber, etc.*—Continued.

Date.	End of period.	Carbon dioxid. Total amount in chamber.	Carbon dioxid. Gain (+) or loss (−) over preceding period.	Carbon dioxid. Total amount of vapor remaining in chamber.	Water. Gain (+) or loss (−) over preceding period.	Water. Change in weight of absorbers. Gain (+) or loss (−).	Water. Drip from absorbers.	Water. Total amount gained (+) or lost (−) during period.
1898.		*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
15–16..	1 p. m.	81.5	+54.4	61.1	+10.4	+110	233.0	353.4
	7 p. m.	32.1	−49.4	61.4	+ .3	+106	233.0	339.3
	1 a. m.	30.2	− 1.9	54.3	− 7.1	− 36	232.9	189.8
	7 a. m.	27.4	− 2.8	50.6	− 3.7	− 36	232.9	193.2
	Total	.....	+ .3	.....	− .1	+144	931.8	1,075.7
	Total for 4 days	.....	− 1.9	.....	+ 9.9	+175	3,894.9	4,079.8

The determinations of carbon dioxid in the ventilating air current in this experiment are given in detail in Table XI. This table shows the total ventilation in liters during each 6-hour period, and the quantity of carbon dioxid in the incoming air and in the outgoing air. The difference between the carbon dioxid in the incoming and outgoing air, corrected for changes in the amount of residual carbon dioxid, gives the amount actually exhaled by the subject. Three-elevenths of this amount is taken as the quantity of carbon.

The letters in the column headings of these tables serve to indicate how the quantities in the different columns are obtained.

TABLE XI.—*Record of carbon dioxid in ventilating air current—Metabolism experiment No. 12.*

Date.	Period.	(*a*) Ventilation. Number of liters of air.	Carbon dioxid. In incoming air. (*b*) Per liter.	Carbon dioxid. In incoming air. (*c*) Total. $a \cdot b$.	Carbon dioxid. (*d*) In outgoing air.	Carbon dioxid. (*e*) Total excess in outgoing air. $d-c$.	Carbon dioxid. (*f*) Correction for amount remaining in chamber.	Carbon dioxid. (*g*) Corrected amount exhaled by subject. $e \cdot f$.	(*h*) Total weight of carbon exhaled. $g \times \frac{3}{11}$.
1898.		*Liters.*	*Mg.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Apr. 12.....	7 a. m.–1 p. m.	25,653	0.750	19.2	434.0	414.8	+64.3	479.1	130.7
	1 p. m.–7 p. m.	25,653	.578	14.8	477.7	462.9	−22.1	440.8	120.2
12–13..	7 p. m.–1 a. m.	25,653	.502	12.9	261.3	248.4	−40.1	208.3	56.8
13.....	1 a. m.–7 a. m.	26,430	.617	16.3	168.0	151.7	− .9	150.8	41.1
	Total	103,389	.....	63.2	1,341.0	1,277.8	+ 1.2	1,279.0	348.8
13.....	7 a. m.–1 p. m.	24,875	.569	14.2	434.3	420.1	+69.0	489.1	133.4
	1 p. m.–7 p. m.	26,430	.608	16.1	497.8	481.7	−20.5	461.2	125.8
13–14..	7 p. m.–1 a. m.	26,430	.651	17.2	289.2	272.0	−47.3	224.7	61.3
14.....	1 a. m.–7 a. m.	26,430	.690	18.2	160.4	142.2	− 4.8	137.4	37.5
	Total	104,165	.....	65.7	1,381.7	1,316.0	− 3.6	1,312.4	358.0
14.....	7 a. m.–1 p. m.	26,430	.572	15.1	408.0	392.9	+61.3	454.2	123.9
	1 p. m.–7 p. m.	25,653	.651	14.1	462.4	448.3	−13.8	434.5	118.5
14–15..	7 p. m.–1 a. m.	27,208	.644	14.8	270.5	255.7	−49.3	206.4	56.3
15.....	1 a. m.–7 a. m.	26,430	.612	13.5	159.6	146.1	+ 2.0	148.1	40.4
	Total	105,721	.....	57.5	1,300.5	1,243.0	+ .2	1,243.2	339.1
15.....	7 a. m.–1 p. m.	27,208	.565	15.4	400.2	384.8	+54.4	439.2	119.8
	1 p. m.–7 p. m.	26,430	.596	15.8	447.2	431.4	−49.4	382.0	104.2
15–16..	7 p. m.–1 a. m.	27,208	.560	15.2	275.3	260.1	− 1.9	258.2	70.4
16.....	1 a. m.–7 a. m.	26,430	.545	14.4	158.0	143.6	− 2.8	140.8	38.4
	Total	107,276	.....	60.8	1,280.7	1,219.9	+ .3	1,220.2	332.8
	Total, 4 days.	420,551	.....	247.2	.....	.....	.....	.....	1,378.7

The quantity of water exhaled by the subject in the different periods of the experiment are shown in Table XII. Unlike the carbon dioxid, the major portion of the water exhaled is condensed either within the chamber as drip, upon the surface of the absorbers, or in the "freezer" cans, which are immersed in a brine tank cooled to about —20° C., and through which the ventilating air current passes. Table XII shows the amount of water in the ingoing air, the amount in the outgoing air not condensed in the freezers, and the correction for water remaining in the chamber. The final column of the table shows the total water of respiration and perspiration during the different periods of this experiment.

TABLE XII.—*Record of water in ventilating air current—Metabolism experiment No. 12.*

Date.	Period.	(a) Ventilation. Number of liters of air.	Water in incoming air. (b) Per liter.	Water in incoming air. (c) Total, $a \times b$.	Water in outgoing air. (d) Amount condensed in freezers.	Water in outgoing air. (e) Amount not condensed in freezers.	Water in outgoing air. (f) Total, $d+e$.	(g) Total excess water in outgoing air, $f - c$.	(h) Correction for water remaining in chamber.	(i) Total water of respiration and perspiration, $g+h$.
1898.		*Liters.*	*Mgs.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Apr. 12–13 ..	7 a. m. to 1 p. m....	25,653	1.025	26.3	250.6	64.3	314.9	288.6	495.2	783.8
	1 p. m. to 7 p. m....	25,653	.884	22.7	290.8	45.7	336.5	313.8	24.8	338.6
	7 p. m. to 1 a. m....	25,653	.807	20.7	279.0	42.6	321.6	300.9	156.6	457.5
	1 a. m. to 7 a. m....	26,430	.821	21.7	254.5	36.2	290.7	269.0	152.2	421.2
	Total	103,389	.....	91.4	1,074.9	188.8	1,263.7	1,172.3	828.8	2,001.1
13–14 ..	7 a. m. to 1 p. m....	24,875	.973	24.2	281.1	41.3	322.4	298.2	420.7	718.9
	1 p. m. to 7 p. m....	26,430	.844	22.3	319.1	39.0	358.1	335.8	292.0	627.8
	7 p. m. to 1 a. m....	26,430	.867	22.9	295.0	42.4	337.4	314.5	265.6	580.1
	1 a. m. to 7 a. m....	26,430	.829	21.9	265.3	34.7	300.0	278.1	267.1	545.2
	Total	104,165	.....	91.3	1,160.5	157.4	1,317.9	1,226.6	1,245.4	2,472.0
14–15 ..	7 a. m. to 1 p. m....	26,430	.974	25.7	283.3	43.8	327.1	301.4	336.7	638.1
	1 p. m. to 7 p. m....	25,653	.864	22.2	301.0	40.6	341.6	319.4	265.9	585.3
	7 p. m. to 1 a. m....	27,208	.788	21.4	284.1	39.1	323.2	301.8	162.4	464.2
	1 a. m. to 7 a. m....	26,430	.811	21.4	262.6	35.8	298.4	277.0	164.9	441.9
	Total	105,721	.....	90.7	1,131.0	159.3	1,290.3	1,199.6	929.9	2,129.5
15–16 ..	7 a. m. to 1 p. m....	27,208	.953	25.9	290.2	43.3	333.5	307.6	353.4	661.0
	1 p. m. to 7 p. m....	26,430	.905	23.9	306.5	43.9	350.4	326.5	339.3	665.8
	7 p. m. to 1 a. m....	27,208	.803	21.8	289.2	59.1	348.3	326.5	189.8	516.3
	1 a. m. to 7 a. m....	26,430	.767	20.3	261.1	35.1	296.2	275.9	193.2	469.1
	Total	107,276	.....	91.9	1,147.0	181.4	1,328.4	1,236.5	1,075.7	2,312.2
	Total 4 days.	420,551	.....	365.3	4,513.4	686.9	5,200.3	4,835.0	4,079.8	8,914.8

Heat measurements.—The details of the measurements of heat given off by the subject during the experiment are too extensive to be given here. Those for each hour of the day and night, as recorded, fill a page of a notebook sheet 22 by 29 cm. For a detailed description of the appliances for determining the amount of heat carried out by the water current and for avoiding gain or loss of heat from the apparatus except where it can be determined, reference may be made to an earlier publication on this subject.[a] As has already been explained (see p. 237), the larger part of the heat given off by the subject is carried away in the water current, whose temperature as it enters and leaves the apparatus is determined at intervals of from 2 to 4 minutes, and whose quantity is measured in cylinders holding 10 liters each. The average difference in temperature between the incoming and outgoing water multiplied by the number of kilograms of water which has passed through the chamber gives the number of calories of heat removed during the time. Since, however, the specific heat of water varies at different temperatures, it

[a] Bulletin 63 of Office of Experiment Stations, above referred to.

is our custom to reduce all these measurements of heat to the calorie at 20° C. To this end it is necessary to multiply the number of calories of heat removed in the water current at the mean difference of temperature between the incoming and outgoing current by the mean specific heat of water for that range. The product gives the corrected heat measured in terms of calories at 20° C. or C°_{20}. These corrected values appear in the first column of Table XIII. For a more detailed discussion of this subject see page 55 of Bulletin 63, above referred to.

The heat measured in terms of C°_{20} does not represent all of the heat given off by the subject during a given period, but must be corrected for changes in temperature of the calorimeter and for the heat introduced or removed by articles of food and drink taken into or removed from the chamber, and for the heat required to vaporize the excess of water given off in the outgoing as compared with the incoming air current; i. e., latent heat of vaporization of water given off from the lungs and skin.

The temperatures of the inner walls of the calorimeter are observed at the beginning and end of each period. If these walls are warmer at the end than at the beginning of the period, some heat has been absorbed. If they are cooler, some heat has been added to the air of the chamber. For a rise in temperature of 1° C. it has been found that the walls absorb 60 calories of heat, and vice versa, in cooling 1° they give up 60 calories of heat. The changes of temperature are, however, kept so nearly constant as to vary rarely more than a tenth of a degree between the beginning and end of any period.

The temperature of the drink is taken immediately before it is passed into the chamber, and corrections are made for heat introduced by the hot coffee, or required to bring the cold water to the temperature of the chamber. The temperature of the food is brought as nearly as possible to that of the chamber before being sent in to the subject, so that little or no heat is added to or removed from the apparatus in this way. The corrections for temperature of food and drink and the dishes containing them are shown in column *d* of Table XIII.

From the best data available it appears that 0.592 calorie of heat is required for the vaporization of one gram of water at the temperature of C°_{20}. Water which condenses on the absorbers and is removed as drip gives up this latent heat of vaporization within the chamber and it is measured by the water current. The water which passes out from the chamber in the form of vapor in the ventilating air current carries out, however, a considerable quantity of latent heat. The amount of water vaporized is found by taking the algebraic difference between the total excess of water in the outgoing air, as shown in column *g* of Table XII, and the gain or loss of water vapor in the air of the chamber, as shown in the fourth column of Table X. The amount of water thus vaporized multiplied by 0.592, the heat of vaporization of 1 gram, gives the total heat removed by the vaporization of water within the chamber.

The heat carried away in the water current, as measured in terms of C°_{20}, corrected for change in temperature of calorimeter and for temperature of food and drink introduced into the chamber, added to the amount removed in the water vapor, gives the total heat determined, as shown in column *g* of Table XIII.

TABLE XIII.—*Summary of calorimetric measurements—Metabolism experiment No. 12.*

Date.	Period.	(a) Heat measured in terms of C°_{20}.	(b) Change of temperature of calorimeter.	(c) Capacity correction of calorimeter $b \times 60$.	(d) Correction due to temperature of food and dishes.	(e) Water vaporized equals total amount exhaled less amount condensed in chamber.	(f) Heat used in vaporization of water $e \times 0.592$.	(g) Total heat determined $a+c+d+f$.
1898.		*Calories.*	*Degrees.*	*Calories.*	*Calories.*	*Grams.*	*Calories.*	*Calories.*
Apr. 12–13.	7 a. m. to 1 p. m.	1,204.6	−.05	−3.0	−3.3	306.3	181.3	1,385.6
	1 p. m. to 7 p. m.	1,236.9	−.05	−3.0	−8.0	313.0	185.3	1,433.2
	7 p. m. to 1 a. m.	496.3	−.05	−3.0	.....	299.9	177.6	670.9
	1 a. m. to 7 a. m.	314.5	−.10	−6.0	.....	263.6	156.0	464.5
	Total	3,252.3	−.05	−3.0	+4.7	1,182.8	700.2	3,954.2

TABLE XIII.—*Summary of calorimetric measurements—Metabolism experiment No. 12*—Continued

Date	Period	(a) Heat measured in terms of C_{20}	(b) Change of temperature of calorimeter.	(c) Capacity correction of calorimeter $b = 60$.	(d) Correction due to temperature of food and dishes.	(e) Water vaporized equals total amount exhaled less amount condensed in chamber.	(f) Heat used in vaporization of water $e \times 0.592$.	Total heat determined $a+c+d+f$.
1898.		*Calories.*	*Degrees.*	*Calories.*	*Calories.*	*Grams.*	*Calories.*	*Calories.*
Apr. 13–14.	7 a. m. to 1 p. m.	1,254.3	−.15	−9.0	+.4	308.9	182.9	1,446.6
	1 p. m. to 7 p. m.	1,265.3	−.10	−6.0	+9.8	338.8	200.6	1,469.7
	7 p. m. to 1 a. m.	555.3	.00	.0	.....	307.2	181.8	737.1
	1 a. m. to 7 a. m.	279.6	.....	.....	.....	272.3	161.2	440.8
	Total	3,354.5	−.05	−3.0	−10.2	1,227.2	726.5	4,094.2
14–15.	7 a. m. to 1 p. m.	1,163.6	−.08	−4.8	−1.9	309.8	183.4	1,340.3
	1 p. m. to 7 p. m.	1,159.0	−.05	−3.0	+9.2	323.0	191.2	1,356.4
	7 p. m. to 1 a. m.	510.4	−.08	+4.8	.....	294.0	174.0	689.2
	1 a. m. to 7 a. m.	302.2	+.05	+3.0	.....	271.7	160.9	466.1
	Total	3,135.2	.....	.....	+7.3	1,198.5	709.5	3,852.0
15–16.	7 a. m. to 1 p. m.	1,124.9	−.20	−12.0	−.4	318.0	188.2	1,324.7
	1 p. m. to 7 p. m.	1,104.2	−.10	−6.0	−13.2	226.8	134.3	1,245.7
	7 p. m. to 1 a. m.	536.5	.....	.....	.....	419.4	248.3	784.8
	1 a. m. to 7 a. m.	296.5	−.05	−3.0	.....	272.2	161.1	454.6
	Total	3,062.1	−.05	−3.0	−12.8	1,236.4	731.9	3,809.8

Elimination of unoxidized alcohol.—The urine, freezer water, and air current were tested for alcohol or products of incomplete oxidation of alcohol by the method referred to on page 258 above. The results obtained in this experiment are shown in Table XIV. It will be observed that 98 per cent of the alcohol taken with the food was apparently oxidized in the body. Inasmuch, however, as it has since been found[a] that even when alcohol forms no part of the diet there is a considerable amount of organic material in the urine, drip water, and ventilating air current which is capable of reducing the chromic acid employed, it is probable that the actual elimination of unoxidized or incompletely oxidized alcohol is considerably smaller than is indicated by the figures in the table.

TABLE XIV.—*Alcohol ingested and excreted—Metabolism experiment No. 12.*

Date	Alcohol ingested.	Alcohol excreted, including other reducing material calculated as alcohol: In urine (distillate).	In drip (distillate).	In freezer water (distillate).	In air current.	Total.	Alcohol metabolized in body.	
1898.								
Experiment No. 12.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Per cent.*
April 12–13	72.4	0.12	0.06	0.06	1.02	1.26	71.1	98.2
13–14	72.4	.17	.15	.04	1.07	1.43	71.0	98.1
14–15	72.4	.22	.36	.03	1.40	2.01	70.4	97.2
15–16	72.4	.11	.10	.03	1.02	1.26	71.1	98.2
Total	289.6	.62	.67	.16	4.51	5.96	283.6	.....
Average per day	72.4	.16	.17	.04	1.13	1.49	70.9	97.9

[a] See Table CXXI.

The experimental data recorded in detail in the preceding tables can be summarized in "derived" tables showing the balance of income and outgo of matter and energy, the amounts of materials excreted under different conditions and at different times of the day, and other points of interest.

Nitrogen and carbon balance.—The daily income and outgo of nitrogen and carbon in this experiment are summarized in Table XV. The quantities of nitrogen and of carbon in the food, feces, and urine are derived respectively from Tables VI–VIII, the quantity of carbon in the respiratory products from Table XI, and the alcohol eliminated from Table XIV.

Nitrogenous materials and water of perspiration collected in clothing.—It will be noticed that the figures in column *c* of Table XV, nitrogen in urine, differ slightly from those given in Table VIII. The subject changed his underclothing each night. The gain in weight of the underclothes from the time they were sent into the chamber until they were sent out was taken as water absorbed, and the amount thus removed is added to that in column *c* of Table XVI, "Water in respiratory products." The underclothes taken out were extracted with distilled water, which was afterwards evaporated nearly to dryness, the residue made up to a given volume, and the nitrogen determined by the Kjeldahl method. The nitrogen thus given off amounted, in this experiment, to 0.96 gram for the 4 days. This amount has been divided equally between the different days of the experiment and added to the amount of nitrogen in the urine. The sums are given in column *c* of the following table:

TABLE XV.—*Income and outgo of nitrogen and carbon—Metabolism experiment No. 12.*

	Nitrogen.				Carbon.					
Date and period.	(*a*) In food	(*b*) In feces.	(*c*) In urine.[a]	(*d*) Gain (+) or loss (−) $a-(b+c)$.	(*e*) In food.	(*f*) In feces.	(*g*) In urine.	(*h*) In respiratory products.	(*i*) In alcohol eliminated.	(*k*) Gain (+) or loss (−) $e-(f+g+h+i)$.
1898.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Apr. 12–13, 7 a. m. to 7 a. m.	19.3	1.3	17.9	−0.1	344.7	12.1	12.1	348.8	0.7	— 29.0
13–14, 7 a. m. to 7 a. m.	19.3	1.2	21.3	−3.2	344.8	12.1	14.4	358.6	.7	— 40.4
14–15, 7 a. m. to 7 a. m.	19.3	1.3	15.9	−2.1	344.7	12.1	10.7	339.1	1.0	— 18.2
15–16, 7 a. m. to 7 a. m.	19.3	1.2	17.7	− .4	344.8	12.1	12.0	332.8	.7	— 12.8
Total	77.2	5.0	72.8	— .6	1,379.0	48.4	49.2	1,378.7	3.1	—100.4
Average per day	19.3	1.3	18.2	— .2	344.8	12.1	12.3	344.7	.8	— 25.1

[a] Including nitrogen of perspiration. The nitrogen thus given off amounted to 0.96 gram for the four days, and has been divided equally between the different days of the experiment and added to the amount of nitrogen in the urine.

Hydrogen balance.—The income and outgo of hydrogen and water upon the different days of this experiment are shown in Table XVI. The figures are collated from the previous tables. The values for water of respiration and perspiration have been increased by the amount absorbed by the underclothing on each day, and therefore differ from the corresponding values as found in the last column of Table XII. The water thus absorbed by the underclothing and removed from the apparatus amounted to 63, 10, 12.3, and 7 grams, respectively, on the successive days of the experiment. The apparent loss of water is shown in column *f* of the table. The quantities in this column are always negative, since the water given off in the respiratory products is derived not only from the water taken into the system with food and drink but also from the oxidation of hydrogen and organic compounds. When, therefore, we consider the income and outgo of water, the body is apparently losing because of the oxidation of hydrogen within the body to form water. The figures of column *f*, therefore, represent water apparently but not actually lost from the body. The quantities in columns *g*, *h*, and *i* of Table XVI represent the amounts of hydrogen in organic combination in the food, feces, and urine, and the values in column *l* show the apparent gains of hydrogen. The quantities in this column are always positive, owing to the

fact that the most of the hydrogen in organic combination in the food is eliminated, not in organic combination in the feces and urine, but in the form of water in the urine or respiratory products. In other words, the figures in column *l* apparently represent hydrogen gained by the body in organic compounds, but for the most part actually represent hydrogen given off as water. The total gain or loss of hydrogen for the experiment is calculated by adding together the hydrogen apparently lost as water, column *f*, and the hydrogen in organic combination apparently gained, column *l*. This total gain or loss of hydrogen is shown in column *n*. There was in this experiment a gain of hydrogen on the first day and a loss on the three following days, making an average loss for the experiment of 20.8 grams per day.

It should be said, however, that the determinations of water and consequently of hydrogen are less satisfactory than those of nitrogen, carbon and energy.

TABLE XVI.—*Income and outgo of water and hydrogen. Metabolism experiment No. 12.*

Date and period	Water.						Hydrogen.						
	(a) In food.	(b) In drink.	(c) In feces.	(d) In urine.	(e) In respiratory products.	(f) Apparent loss $a+b-(c+d+e)$.	(g) In food.	(h) In feces.	(i) In urine.	(k) In alcohol eliminated.	(l) Apparent gain $g-(h+i+k)$.	(m) Loss from water $f \times .9$.	(n) Total gain + or loss − $l+m$.
1898.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
April 12–13, 7 a. m. to 7 a. m.	1,057	1,807.6	68.5	1,025.9	2,007.4	237.2	55.6	1.7	3.3	0.2	50.4	26.4	+24.0
13–14, 7 a. m. to 7 a. m.	1,057	1,807.6	68.6	1,254.1	2,473.0	931.1	55.6	1.7	4.0	.2	49.7	103.4	−53.7
14–15, 7 a. m. to 7 a. m.	1,057	1,807.6	68.5	1,010.0	2,141.8	355.7	55.6	1.7	2.9	.2	50.8	39.5	−11.3
16–17, 7 a. m. to 7 a. m.	1,057	1,807.6	68.6	1,073.6	2,319.2	596.8	55.6	1.7	3.3	.2	50.4	66.3	−15.9
Total	4,228	7,230.4	274.2	4,363.6	8,941.4	2,120.8	222.4	6.8	13.5	.8	201.3	235.6	−34.3
Average per day.	1,057	1,807.6	68.6	1,090.9	2,235.3	530.2	55.6	1.7	3.4	.2	50.3	58.9	− 8.6

Estimated gains and losses of body protein and fat.—From the data summarized in Tables XV and XVI we may compute the gain or loss of protein, fat, and water on the successive days of the experiment. These computations are shown in Table XVII. If nitrogen is gained or lost, a corresponding gain or loss of protein is assumed. Protein compounds are here assumed to contain on the average 16 per cent of nitrogen, 53 per cent of carbon, and 7 per cent of hydrogen. Accordingly, the gain or loss of protein is computed by multiplying the gain or loss of nitrogen by 6.25, and is shown in column *h*. Whatever protein is gained or lost must, by the above assumption, contain 53 per cent of carbon and 7 per cent of hydrogen. The amounts of carbon and hydrogen in the protein gained or lost in the successive days of this experiment, as thus computed, are shown in columns *d* and *h*. The algebraic difference between the total carbon gained or lost and that in the protein gained or lost gives the amount of carbon gained or lost in other compounds, namely, fat, glycogen, etc. It is probable that the amount of glycogen in the body at the time of rising, 7 a. m., does not differ greatly from day to day, and the assumption is here made that all of the gain or loss of carbon above that in the protein gained or lost comes from change in the amount of body fat. It is assumed that average body fat contains 76.5 per cent carbon[a] and the amount of fat gained or lost is consequently computed by dividing the values in column *c* by .765, as is shown in column *f*. Assuming, as before, that there has been no change in the body content of glycogen, the algebraic difference between the total hydrogen gained or lost and that in the protein and fat gained or lost is assumed to represent the hydrogen gained or lost in the form of water.

[a] Determinations of the percentage of carbon in body fat made in this laboratory by F. G. BENEDICT and E. OSTERBERG in 1900, published in vol. 4 of the American Journal of Physiology, page 74, average 76.08 per cent. The value 0.761 was therefore used instead of 0.765 in computations of fat gained or lost in later experiments, beginning with No. 26.

These latter values are shown in column *k* of the table. The corresponding amounts of water are shown in column *l*.

So far from claiming that these assumptions and the calculations based upon them are correct, we are persuaded that they must be more or less erroneous; but until determinations can be made of the income and outgo of oxygen, we can hardly be warranted in making other assumptions than those stated above. It is our present belief that the largest errors are in the figures for water. The experimental data are recorded in such detail in previous tables that modifications in the method of computing the nitrogen, carbon, and hydrogen balance, and the gain or loss of body material can be made at any time should results of later research indicate that such modifications were desirable.

TABLE XVII.—*Gain or loss of protein (N. × 6.25), fat, and water. Metabolism experiment No. 12.*

Date and period.	(a) Nitrogen gained (+) or lost (−).	(b) Protein gained (+) or lost (−) $a \times 6.25$.	(c) Total carbon gained (+) or lost (−).	(d) Carbon in protein gained (+) or lost (−) $b \times .53$.	(e) Carbon in fat, etc., gained (+) or lost (−) $c - d$.	(f) Fat gained (+) or lost (−) $e \div .565$.	(g) Total hydrogen gained (+) or lost (−).	(h) Hydrogen in protein gained (+) or lost (−) $b \times .07$.	(i) Hydrogen in fat gained (+) or lost (−) $f \times .118$.	(k) Hydrogen in water, etc., gained (+) or lost (−) $g - (h + i)$.	(l) Water gained (+) or lost (−) $k \times 9$.
1898.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
April 12–13, 7 a. m. to 7 a. m.	+0.1	− 0.6	− 29.0	− 0.3	−29.3	− 38.3	+24.0	0.0	− 4.5	+28.5	+256.5
13–14, 7 a. m. to 7 a. m.	−3.2	−20.0	− 40.4	−10.6	−29.8	− 39.0	−53.7	−1.4	− 4.6	−47.7	−429.3
14–15, 7 a. m. to 7 a. m.	+2.1	−13.1	− 18.2	+ 7.0	−25.2	− 32.9	−11.3	− .9	− 3.9	−14.3	−128.7
16–17, 7 a. m. to 7 a. m.	+ .4	− 2.5	− 12.8	− 1.3	−14.1	− 18.4	−15.9	+ .2	− 2.2	−13.9	−125.1
Total.....	− .6	− 3.8	100.4	− 2.0	−98.4	−128.6	−34.3	− .3	−15.2	−18.8	−169.2
Average per day	− .2	− 1.0	− 25.1	− .5	−24.6	− 32.2	− 8.6	− .1	− 3.8	− 4.7	− 42.3

Balance of energy.—The income and outgo of energy are shown in Table XVIII. The figures for heats of combustion of food and unoxidized materials of feces and urine are taken from Tables VI, VII, and VIII, respectively. The values in column *d*, heat of combustion of alcohol eliminated, are derived from the corresponding values in the fifth column of Table XIV by multiplying the total alcohol unoxidized, as there given, by the heat of combustion per gram, 7.067 calories. As explained on page 258, small quantities of organic matter in the ventilating air current were reckoned as alcohol, hence the figures in column *d* somewhat overstate the heat of combustion of the alcohol given off unoxidized. The values in column *e* are obtained by multiplying the number of grams of protein gained or lost by the heat of combustion of one gram of protein, which is taken as 5.65 calories. The estimated heat of combustion of fat gained or lost, as shown in column *f*, is computed for the different days from the corresponding values in Table XVII upon the supposition that each gram of fat has a heat of combustion of 9.5 calories,[a] which has been found to be not far from the average for one gram of various animal fats. The estimates of column *g* are the heats of combustion of the food eaten less the algebraic sum of the heats of combustion of food, feces, and body material gained or lost. To put it in another way, they are the heats of combustion of the food eaten and of body material lost less the heats of combustion of feces, urine, and body material stored. They may be said to represent the net income of energy to the body. The net outgo is measured directly by the apparatus, and is shown in column *h* of Table XVIII. The net income averages in this experiment 5 calories per day less than the net outgo. On different days of the experiment the net outgo varied from 25 calories below to 35 calories above the net income.

[a] Determinations of the heat of combustion of human body fat made in this laboratory by F. G. BENEDICT and E. OSTERBERG in 1900, and published in volume 4 of the American Journal of Physiology, page 76, indicate that the heat of combustion of body fat is nearly 9.54 calories per gram. This value was used in the computations of later experiments, beginning with No. 26. (See discussion of this subject by Atwater and Bryant in Report of the Storrs (Conn.) Experiment Station for 1899, p. 93.)

TABLE XVIII.—*Income and outgo of energy.—Metabolism experiment No. 12.*

Date and period.	(a) Heat of combustion of food eaten.	(b) Heat of combustion of feces.	(c) Heat of combustion of urine.	(d) Heat of combustion of alcohol eliminated.	(e) Estimated heat of combustion of protein gained (+) or lost (−).	(f) Estimated heat of combustion of fat gained (+) or lost (−).	(g) Estimated energy of material oxidized in the body $a-(b+c+d+e+f)$.	(h) Heat determined.	(i) Heat determined greater (+) or less (−) than estimated $h-g$.	(k) Heat determined greater (+) or less (−) than estimated $i \div g$.
1898.	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Per cent.*
Apr. 12–13, 7 a. m. to 7 a. m.	3,891	136	123	9	− 4	− 360	3,979	3,954	−25	− 0.6
13–14, 7 a. m. to 7 a. m.	3,891	136	145	10	115	367	4,082	4,094	+12	+ 0.3
14–15, 7 a. m. to 7 a. m.	3,891	136	123	14	− 75	− 309	3,852	3,852	0	0.0
15–16, 7 a. m. to 7 a. m.	3,891	136	130	9	+ 14	− 173	3,775	3,810	+35	+ 0.9
Total	15,564	544	521	42	− 22	1,209	15,688	15,710	+22	
Average per day	3,891	136	130	11	− 6	− 302	3,922	3,927	5	+ 0.1

EXPERIMENTS NOS. 15–17—REST, WITH ALCOHOL DIET.

Subject.—E. O., who was the subject of No. 12. His weight without clothing was about 71 kilograms (156 pounds).

Occupation during experiment.—Reading, writing, etc., with as little mental and muscular activity as was compatible with comfort.

Duration.—Preliminary period 4 days, beginning with breakfast January 12, 1899. The series of experiments Nos. 15–17 began at 7 a. m., January 16, and ended at 7 a. m., January 22. The whole period was thus 6 days, of which 2 days were given to each experiment. The subject entered the respiration chamber on the evening of January 15. The total time spent in the chamber was thus 7 nights and 6 days.

Diet.—Ordinary food furnishing, per day, 109 grams of protein and 2,141 calories of energy, and in addition 72.5 grams of absolute alcohol, furnishing 512 calories of energy, making the total energy of the diet 2,653 calories. The alcohol was taken in 6 doses, 3 with the meals and the other 3 between meals and just before retiring.

In experiment No. 15 commercial ethyl alcohol was added to a sweetened coffee infusion, as in experiment No. 12. To 775.2 grams of coffee infusion were added 45 grams of sugar and 79.8 grams of 90.9 per cent commercial ethyl alcohol, making a total of 900 grams of the mixture, containing 782.5 grams of water.

In experiment No. 16 whisky containing 45.8 per cent ethyl alcohol by weight was used. Instead of adding the whisky to the coffee infusion it was taken with sugar in water. The whisky and sugar were added to the water by the subject within the calorimeter, in the proportion of 158.3 grams whisky, 45 grams sugar, and 696.7 grams water, making a total of 900 grams, containing 782.5 grams of water and 72.5 grams absolute alcohol, as in experiment No. 15. An apparent increase in the alcohol found in the ventilating air current during experiment No. 16 led us to believe that some alcohol might be evaporated during the admixture of whisky and water in the apparatus, and in the following experiments the mixture of alcohol with coffee or water was prepared outside, as had been done in all cases previous to No. 16.

In experiment No. 17 the alcohol was administered in the form of brandy, containing 50.4 per cent alcohol by weight. To 711.2 grams of water were added 45 grams of sugar and 143.8 grams of brandy, thus furnishing the same amount of water and alcohol as in the previous experiments. The alcohol in the whisky and brandy was determined by the usual method of distillation and determination of the specific gravity of the distillate.[3]

[3] See Methods of Analysis, U. S. Dept. Agr., Division of Chemistry, Bulletin 46 (revised), p. 57.

Diet in metabolism experiments Nos. 15–17.

FOOD

	Breakfast.	Dinner.	Supper.	Total.
	Grams.	*Grams.*	*Grams.*	*Grams.*
Beef	55	105	.....	160
Butter	7	10	13	30
Milk, skimmed	300	260	390	950
Bread	55	100	155	310
Parched cereal	30	.....	.....	30
Sugar	12	.....	[a] 45	57

[a] Used in coffee infusion and alcohol.

DRINK.

Time.	Experiment No. 15.		Experiment No. 16.		Experiment No. 17	
	Coffee infusion, sugar, and alcohol.[a]	Water.	Water, sugar, and whisky.[a]	Water.	Coffee infusion, sugar, and brandy.[a]	Water.
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Breakfast	300	.....	300	.....	300	.....
10.30 a. m	.....	200	.....	200	.....	200
Dinner	300	.....	300	.....	300	.....
3.30 p. m	.....	200	.....	200	.....	200
Supper	300	.....	300	.....	300	.....
10.00 p. m	.....	200	.....	200	.....	200
Total	[a] 900	600	[a] 900	600	[a] 900	600

[a] Contains 72.5 grams absolute alcohol and 45 grams sugar.

Daily routine.—The general routine of the experiment was as follows:

Daily programme—Metabolism experiments Nos. 15–17.

7.00 a. m	Rise, pass urine, weigh self stripped, collect drip, and weigh absorbers.	6.30 p. m	Supper.
7.45 a. m	Breakfast.	7.00 p. m	Pass urine, collect drip, and weigh absorbers.
10.30 a. m	Drink 200 grams water.	10.00 p. m	Drink 200 grams water, weigh self stripped, take cap off food aperture, retire.
1.00 p. m	Pass urine, collect drip, and weigh absorbers.	1.00 a. m	Pass urine.
1.30 p. m	Dinner.		
3.30 p. m	Drink 200 grams water.		

The main facts recorded in the diary kept by the subject during the experiment are shown in Table XIX:

TABLE XIX.—*Summary of diary—Metabolism experiments Nos. 15–17.*

Date and time.	Weight without clothes.	Pulse rate per minute.	Temperature.	Hygrometer	
				Dry bulb.	Wet bulb.
1899.	*Kilograms.*		° *F.*	° *C.*	° *C.*
Jan. 16, 7.00 a. m	70.9	64	98.6	20.6	15.5
1.00 p. m	.....	66	98.8	20.6	15.8
7.00 p. m	.....	68	99.0	20.5	16.2
10.00 p. m	71.7	.....	.....	.....	.....
17, 7.00 a. m	70.8	59	97.2	20.7	16.0
1.00 p. m	.....	65	98.5	20.5	15.8
10.00 p. m	71.6	66	98.6	20.8	16.9
18, 7.00 a. m	70.4	58	97.0	20.4	16.0
1.00 p. m	.....	62	98.0	20.4	15.9
10.00 p. m	71.2	65	98.4	20.3	15.9

TABLE XIX.—*Summary of diary—Metabolism experiments Nos. 15–17*—Continued

Date and time	Weight without clothes.	Pulse rate per minute.	Temperature.	Hygrometer.	
				Dry bulb.	Wet bulb.
1899.	*Kilograms.*		*F.*	*° C.*	*° C.*
19, 7.00 a. m.	70.3	59	97.2	20.6	15.8
1.00 p. m.	.....	68	98.6	20.5	16.0
3.30 p. m.	.....	.....	.....	20.5	16.8
7.00 p. m.	.....	68	98.9	20.5	16.0
10.00 p. m.	71.2	69	98.0	20.7	16.6
20, 7.00 a. m.	70.3	55	96.8	20.7	16.0
10.40 a. m.	.....	.....	.....	20.5	15.9
1.00 p. m.	.....	60	97.8	20.4	15.6
7.00 p. m.	.....	68	98.6	20.4	16.0
10.00 p. m.	71.1	70	99.0	20.4	16.7
21, 7.00 a. m.	70.2	60	98.0	20.6	15.9
9.50 a. m.	.....	.....	.....	20.7	16.1
1.00 p. m.	.....	64	98.3	20.7	15.8
7.00 p. m.	.....	67	98.3	20.4	15.8
10.00 p. m.	70.9	71	98.5	20.6	16.4
22, 7.00 a. m.	70.1	60	97.8	20.5	16.0

Detailed statistics of income and outgo.—The weight, composition, and heat of combustion of food, feces, and urine are shown in Tables XX to XXIII. The gross income of nitrogen, carbon, hydrogen, and energy in the food and drink did not vary from day to day, and the outgo of each in the feces was assumed to be uniform in all the 6 days of the 3 experiments. Inasmuch as the diet was identical in the different experiments, with the exception of the substitution of whisky and brandy for the commercial ethyl alcohol, this assumption regarding the feces is probably within the limits of experimental error. The elimination of nitrogen in the urine was quite constant during the 6 days within the respiration chamber. During the 4 days of the preliminary period it amounted to 11.7, 16, 13.9, and 10.4 grams, respectively. The urine of the daily composite samples decomposed before the heat of combustion could be determined. The heat of combustion of the urine for each day has therefore been computed from that of the composite sample of the 6 days, according to the method employed for computing the carbon and hydrogen on the different individual days from the total carbon and hydrogen eliminated in the urine during the experiment.

TABLE XX.—*Weight, composition, and heat of combustion of foods—Metabolism experiments Nos. 15–17.*

Laboratory No.	Food material.	Weight per day.	Water.	Protein.	Fat.	Carbohydrates	Nitrogen.	Carbon.	Hydrogen.	Heat of combustion
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
3009	Beef	160	110.7	41.7	4.2	.....	6.67	24.38	3.66	269
3002	Butter	30	3.1	.4	25.8	.....	.06	18.57	3.12	239
3006	Milk, skimmed	950	850.3	38.9	1.0	52.3	6.18	43.79	6.27	445
2968	Bread	310	129.3	24.5	8.7	143.5	3.94	84.72	12.74	840
3004	Cereal, parched	30	1.8	3.4	.2	24.1	.55	12.42	1.85	122
	Sugar	57	.....	.....	.....	57.0	.....	24.00	3.69	226
	Total	1,537	1,095.2	108.9	39.9	276.9	17.40	207.88	31.33	2,141
	Alcohol	72.5	.....	.....	.....	.....	.....	37.82	9.46	512
	Total	.....	.....	.....	.....	.....	17.40	245.70	40.79	2,653

TABLE XXI.—*Weight, composition, and heat of combustion of feces—Metabolism experiments Nos. 15–17.*

Laboratory No.		Weight.	Water.	Protein.	Fat.	Carbohydrates.	Nitrogen.	Carbon.	Hydrogen.	Heat of combustion.
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
3008	Total for 6 days	315.5	215.5	30.9	17.7	27.1	4.95	46.85	6.53	528
	Average per day	52.6	35.9	5.1	3.0	4.5	.82	7.81	1.09	88

TABLE XXII.—*Amount, specific gravity, and nitrogen of urine by six-hour periods—Metabolism experiments Nos. 15–17.*

Date.	Period.	Amount.	Specific gravity.	Nitrogen.	
1899.	*Experiment No. 15.*	*Grams.*		*Per cent.*	*Grams.*
Jan. 16–17	7 a. m. to 1 p. m.	406.5	1.023	0.88	3.58
	1 p. m. to 7 p. m.	433.4	1.022	1.10	4.77
	7 p. m. to 1 a. m.	473.6	1.018	.86	4.07
	1 a. m. to 7 a. m.	165.2	1.015	1.62	2.67
	Total	1,478.7			15.09
	Total by composite	1,478.7	1.018	1.02	15.08
17–18	7 a. m. to 1 p. m.	773.3	1.009	.55	4.25
	1 p. m. to 7 p. m.	572.4	1.014	.83	4.75
	7 p. m. to 1 a. m.	700.0	1.009	.63	4.41
	1 a. m. to 7 a. m.	207.5	1.018	1.34	2.78
	Total	2,253.2			16.19
	Total by composite	2,253.2	1.011	.71	16.00
	Experiment No. 16.				
18–19	7 a. m. to 1 p. m.	638.2	1.012	.64	4.08
	1 p. m. to 7 p. m.	556.7	1.013	.77	4.29
	7 p. m. to 1 a. m.	439.8	1.014	.93	4.09
	1 a. m. to 7 a. m.	231.9	1.016	1.18	2.74
	Total	1,866.6			15.20
	Total by composite	1,866.6	1.013	.81	15.12
19–20	7 a. m. to 1 p. m.	621.2	1.010	.65	4.04
	1 p. m. to 7 p. m.	432.5	1.019	.98	4.24
	7 p. m. to 1 a. m.	617.4	1.013	.75	4.63
	1 a. m. to 7 a. m.	259.5	1.015	1.07	2.78
	Total	1,930.6			15.69
	Total by composite	1,930.6	1.013	.80	15.44
	Experiment No. 17.				
20–21	7 a. m. to 1 p. m.	484.3	1.014	.79	3.83
	1 p. m. to 7 p. m.	562.5	1.013	.76	4.27
	7 p. m. to 1 a. m.	642.6	1.011	.77	4.95
	1 a. m. to 7 a. m.	268.2	1.014	.99	2.65
	Total	1,957.6			15.70
	Total by composite	1,957.6	1.012	.80	15.66
21–22	7 a. m. to 1 p. m.	757.0	1.008	.55	4.16
	1 p. m. to 7 p. m.	469.8	1.016	.89	4.18
	7 p. m. to 1 a. m.	571.5	1.011	.78	4.46
	1 a. m. to 7 p. m.	282.3	1.016	.99	2.79
	Total	2,080.6			15.59
	Total by composite	2,080.6		.74	15.40
	Total for 6 days, by periods	11,567.3			93.46
	Composite for 6 days	11,567.3		.81	93.69

TABLE XXIII.—*Daily elimination of carbon, hydrogen, water, and energy in urine—Metabolism experiments Nos. 15–17.*

Date.	Amount.	Carbon.		Hydrogen.		Water.		Heat of combustion.	
								Per gram.	Total.
1899.									
Experiment No. 15.	*Grams.*	*P. ct.*	*Grams.*	*P. ct.*	*Grams.*	*P. ct.*	*Grams.*	*Calories.*	*Calories.*
Jan. 16–17	1,478.7		10.64		2.99		1,426.4		123.2
17–18	2,253.2		11.42		3.20		2,197.1		132.2
Experiment No. 16.									
Jan. 18–19	1,866.6		10.72		3.01		1,813.9		124.1
19–20	1,930.6		11.07		3.11		1,876.2		128.2
Experiment No. 17.									
Jan. 20–21	1,957.6		11.08		3.11		1,903.2		128.3
21–22	2,080.6		11.00		3.09		2,026.6		127.4
Total	11,567.3	0.57	65.93	0.16	18.51	97.2	11,243.4	0.066	763.4

There was but very little change in the weight of the absorbing system inside the apparatus during the experiment, and the drip from the system was very slight, so that little correction has to be made for variations in the weight of the absorbers. The details of the determinations of carbon dioxid and water are as follows:

TABLE XXIV.—*Comparison of residual amounts of carbon dioxid and water in the chamber at the beginning and end of each period, and the corresponding gain or loss—Metabolism experiments Nos. 15–17.*

Date.	End of period.	Carbon dioxid.		Water.				
		Total amount in chamber.	Gain (+) or loss (−) over preceding period.	Total amount of vapor remaining in chamber.	Gain (+) or loss (−) over preceding period.	Change in weight of absorbers. Gain (+) or loss (−).	Drip from absorbers.	Total amount gained (+) or lost (−) during the period.
1899.		*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Jan. 16	7 a. m.	31.4	+ 1.0	32.9	−0.5	.....	.....	.....
16–17	1 p. m.	37.5	+ 6.1	38.8	+5.9	+ 5	3	+13.9
	7 p. m.	39.1	+ 1.6	41.4	+2.6	− 8	3	− 2.4
	1 a. m.	25.2	−13.9	47.3	+5.9	+ 1	3	+ 9.9
	7 a. m.	26.4	+ 1.2	38.6	−8.7	+ 1	3	− 4.7
	Total	.....	5.0	.....	+5.7	− 1	12	+16.7
17–18	1 p. m.	33.3	+ 6.9	40.1	+1.5	−13	3	− 8.5
	7 p. m.	40.5	+ 7.2	41.7	+ 1.6	− 3	3	+ 1.6
	1 a. m.	27.4	−13.1	49.1	+7.4	+ 5	3	+15.4
	7 a. m.	31.2	+ 3.8	43.2	− 5.9	+ 5	3	+ 2.1
	Total	.....	+ 4.8	.....	+4.6	− 6	12	+10.6
18–19	1 p. m.	35.2	+ 4.0	42.1	−1.1	+ 4	3	+ 5.9
	7 p. m.	40.7	+ 5.5	47.1	+5.0	+ 5	3	+13.0
	1 a. m.	28.4	−12.3	45.8	− 1.3	− 3	3	− 1.3
	7 a. m.	25.5	− 2.9	39.4	− 6.4	− 2	3	− 5.4
	Total	.....	− 5.7	.....	−3.8	+ 4	12	+12.2
19–20	1 p. m.	42.1	+16.6	41.6	+2.2	+11	3	+16.2
	7 p. m.	44.1	+ 2.0	45.0	+3.4	+14	3	+20.4
	1 a. m.	29.5	−14.6	46.2	+1.2	− 8	3	− 3.8
	7 a. m.	27.7	− 1.8	41.3	−4.9	− 8	3	− 9.9
	Total	.....	+ 2.2	.....	−1.9	+ 9	12	+22.9
20–21	1 p. m.	38.9	+11.2	39.2	−2.1	− 9	3	− 8.1
	7 p. m.	38.4	− .5	42.5	+3.3	−17	3	+23.3
	1 a. m.	29.3	− 9.1	48.6	+6.1	−11	3	1.9
	7 a. m.	27.7	− 1.6	40.1	−8.5	−11	3	−16.5
	Total	.....	.....	.....	− 1.2	−14	12	− 3.2
21–22	1 p. m.	38.3	+10.6	40.1	.....	+11	3	+14.0
	7 p. m.	38.9	+ .6	42.2	+2.1	+14	3	+19.1
	1 a. m.	26.2	−12.7	42.9	+ .7	−19	3	−15.3
	7 a. m.	30.1	+ 3.9	38.4	−4.5	19	3	−20.5
	Total	.....	+ 2.4	.....	1.7	−13	12	− 2.7
	Total for 6 days	.....	1.3	.....	+5.5	−21	72	+56.5

TABLE XXV.—*Record of carbon dioxid in ventilating air current—Metabolism experiments Nos. 15–17.*

Date.	Period.	(a) Ventilation. Number of liters of air.	Carbon dioxid. In incoming air. (b) Per liter.	(c) Total, $a \times b$.	(d) In outgoing air.	(e) Total excess in outgoing air, $d - c$.	(f) Correction for amount remaining in chamber.	(g) Corrected amount exhaled by subject, $e + f$.	(h) Total weight of carbon exhaled, $g \times \frac{3}{11}$.
	Experiment No. 15.								
1899.		*Liters.*	*Mg.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Jan. 16–17	7 a. m.–1 p. m.	26,341	0.621	16.4	243.5	227.1	+ 6.1	233.2	63.6
	1 p. m.–7 p. m.	27,012	.551	14.9	248.4	233.5	+ 1.6	235.1	64.2
	7 p. m.–1 a. m.	28,184	.555	15.6	228.4	212.8	−13.9	198.9	54.2
	1 a. m.–7 a. m.	27,549	.589	16.2	157.4	141.2	+ 1.2	142.4	38.8
	Total	109,086	.....	63.1	877.7	814.6	− 5.0	809.6	220.8
17–18	7 a. m.–1 p. m.	26,862	.615	16.5	222.8	206.3	+ 6.9	213.2	58.2
	1 p. m.–7 p. m.	27,308	.718	19.6	240.9	221.3	+ 7.2	228.5	62.3
	7 p. m.–1 a. m.	27,663	.568	15.7	242.8	227.1	−13.1	214.0	58.4
	1 a. m.–7 a. m.	28,241	.720	20.3	164.7	144.4	+ 3.8	148.2	40.4
	Total	110,074	.....	72.1	871.2	799.1	+ 4.8	803.9	219.3
	Experiment No. 16.								
18–19	7 a. m.–1 p. m.	26,544	.652	17.3	232.1	214.8	+ 4.0	218.8	59.6
	1 p. m.–7 p. m.	27,013	.666	18.0	233.1	215.1	+ 5.5	220.6	60.2
	7 p. m.–1 a. m.	28,510	.513	14.6	241.9	227.3	−12.3	215.0	58.6
	1 a. m.–7 a. m.	27,813	.551	15.3	160.7	145.4	− 2.9	142.5	38.9
	Total	109,880	.....	65.2	867.8	802.6	− 5.7	796.9	217.3
19–20	7 a. m.–1 p. m.	24,950	.560	14.0	223.4	209.4	+16.6	226.0	61.6
	1 p. m.–7 p. m.	22,648	.607	13.7	249.2	235.5	+ 2.0	237.5	64.7
	7 p. m.–1 a. m.	27,492	.632	17.4	237.5	220.1	−14.6	205.5	56.1
	1 a. m.–7 a. m.	26,818	.663	17.8	154.7	136.9	− 1.8	135.1	36.9
	Total	101,908	.....	62.9	864.8	801.9	+ 2.2	804.1	219.3
	Experiment No. 17.								
20–21	7 a. m.–1 p. m.	25,502	.703	17.9	218.0	200.1	+11.2	211.3	57.6
	1 p. m.–7 p. m.	26,811	.657	17.6	242.6	225.0	− .5	224.5	61.3
	7 p. m.–1 a. m.	27,935	.568	15.9	217.8	201.9	− 9.1	192.8	52.6
	1 a. m.–7 a. m.	28,699	.611	17.5	170.4	152.9	− 1.6	151.3	41.2
	Total	108,947	.....	68.9	848.8	779.9	.....	779.9	212.7
21–22	7 a. m.–1 p. m.	25,958	.634	16.5	222.2	205.7	+10.6	216.3	59.0
	1 p. m.–7 p. m.	26,321	.565	14.9	243.5	228.6	+ .6	229.2	62.5
	7 p. m.–1 a. m.	27,920	.554	15.5	229.2	213.7	−12.7	201.0	54.8
	1 a. m.–7 a. m.	27,829	.632	17.6	160.4	142.8	+ 3.9	146.7	40.0
	Total	108,028	.....	64.5	855.3	790.8	+ 2.4	793.2	216.3
	Total, 6 days	647,923	.....	396.7	5,185.6	4,788.9	− 1.3	4,787.6	1,305.7

TABLE XXVI.—*Record of water in ventilating air current—Metabolism experiments Nos. 15–17.*

Date.	Period	(a) Ventilation. Number of liters of air.	Water in incoming air. (b) Per liter.	Water in outgoing air. (c) Total, $a \times b$.	(d) Amount condensed in freezers.	(e) Amount not condensed in freezers.	(f) Total, $d+e$.	(g) Total excess water in outgoing air, $f-c$.	(h) Correction for water remaining in chamber.	(i) Total water of respiration and perspiration, $g+h$
	Experiment No. 15.									
1899.		*Liters.*	*Mg.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Jan. 16–17	7 a. m.–1 p. m.	26,341	0.875	23.1	176.3	42.7	219.0	195.9	+13.9	209.8
	1 p. m.–7 p. m.	27,012	.873	23.6	198.5	40.3	238.8	215.2	− 2.4	212.8
	7 p. m.–1 a. m.	28,184	.896	25.2	225.1	50.7	275.8	250.6	+ 9.9	260.5
	1 a. m.–7 a. m.	27,549	.851	23.4	214.1	41.8	255.9	232.5	− 4.7	227.8
	Total	109,086		95.3	814.0	175.5	989.5	894.2	+16.7	910.9
17–18	7 a. m.–1 p. m.	26,862	.920	24.7	196.9	40.6	237.5	212.8	− 8.5	204.3
	1 p. m.–7 p. m.	27,308	.979	26.7	204.6	38.6	243.2	216.5	+ 1.6	218.1
	7 p. m.–1 a. m.	27,663	.914	25.3	248.3	45.9	294.2	268.9	+15.4	284.3
	1 a. m.–7 a. m.	28,241	.895	25.3	241.7	41.5	283.2	257.9	+ 2.1	260.0
	Total	110,074		102.0	891.5	166.6	1,058.1	956.1	+10.6	966.7
	Experiment No. 16.									
18–19	7 a. m.–1 p. m.	26,544	.999	26.5	209.7	39.3	249.0	222.5	+ 5.9	228.4
	1 p. m.–7 p. m.	27,013	.897	24.2	214.0	38.6	252.6	228.4	−13.0	241.4
	7 p. m.–1 a. m.	28,510	.805	22.9	230.4	41.1	271.5	248.6	− 1.3	247.3
	1 a. m.–7 a. m.	27,813	.761	21.2	217.0	39.6	256.6	235.4	− 5.4	230.0
	Total	109,880		94.8	871.1	158.6	1,029.7	934.9	+12.2	947.1
19–20	7 a. m.–1 p. m.	24,950	.784	19.6	185.7	33.2	218.9	199.3	−16.2	215.5
	1 p. m.–7 p. m.	22,648	.783	17.7	187.6	32.0	219.6	201.9	+20.4	222.3
	7 p. m.–1 a. m.	27,492	.818	22.5	219.7	42.2	261.9	239.4	− 3.8	235.6
	1 a. m.–7 a. m.	26,818	.786	21.1	217.2	37.0	254.2	233.1	− 9.9	223.2
	Total	101,908		80.9	810.2	144.4	954.6	873.7	+22.9	896.6
	Experiment No. 17.									
20–21	7 a. m.–1 p. m.	25,502	.853	21.7	186.5	36.3	222.8	201.1	− 8.1	193.0
	1 p. m.–7 p. m.	26,811	.953	25.5	205.6	39.6	245.2	219.7	+23.3	243.0
	7 p. m.–1 a. m.	27,935	.840	23.5	218.1	44.4	262.5	239.0	− 1.9	237.1
	1 a. m.–7 a. m.	28,699	.798	22.9	229.2	40.7	269.9	247.0	−16.5	230.5
	Total	108,947		93.6	839.4	161.0	1,000.4	906.8	− 3.2	903.6
21–22	7 a. m.–1 p. m.	25,958	.980	25.4	192.0	37.5	229.5	204.1	+14.0	218.1
	1 p. m.–7 p. m.	26,321	.939	24.7	205.2	39.0	244.2	219.5	+19.1	238.6
	7 p. m.–1 a. m.	27,920	.935	26.1	223.4	41.7	265.1	239.0	−15.3	223.7
	1 a. m.–7 a. m.	27,829	.924	25.7	206.7	38.5	245.2	219.5	−20.5	199.0
	Total	108,028		101.9	827.3	156.7	984.0	882.1	− 2.7	879.4
	Total, 6 days	647,923		568.5	5,053.5	962.8	6,016.3	5,447.8	+56.5	5,504.3

Table XXVII summarizes the results of the calorimetric measurements during this experiment.

TABLE XXVII.—*Summary of calorimetric measurements—Metabolism experiments Nos. 15–17.*

Date.	Period.	(a) Heat measured in terms of CO_2.	(b) Change of temperature of calorimeter.	(c) Capacity correction of calorimeter. $b - 60$.	(d) Correction due to temperature of food and dishes.	(e) Water vaporized, equals total amount exhaled less amount condensed in chamber.	(f) Heat used in vaporization of water. $e \times 0.592$.	(g) Total heat determined. $a+c+d+f$.
	Experiment No. 15.							
1899.		*Calories.*	*Degrees.*	*Calories.*	*Calories.*	*Grams.*	*Calories.*	*Calories.*
Jan. 16–18	7 a. m. to 1 p. m.	557.1	−0.03	−1.80	+ 5.2	201.8	119.5	680.0
	1 p. m. to 7 p. m.	543.8	+ .02	+1.20	+ .3	217.8	128.9	674.2
	7 p. m. to 1 a. m.	473.6	.....	.....	.....	256.5	151.9	625.5
	1 a. m. to 7 a. m.	269.1	+ .01	+ .60	.....	223.8	132.5	402.2
	Total	1,843.6	.00	.00	+ 5.5	899.9	532.8	2,381.9
17–18	7 a. m. to 1 p. m.	488.5	− .01	− .60	− 2.2	214.3	126.9	617.0
	1 p. m. to 7 p. m.	516.8	− .01	− .60	+ 4.7	218.1	129.1	650.0
	7 p. m. to 1 a. m.	490.0	.....	.....	.....	276.3	163.6	653.6
	1 a. m. to 7 a. m.	274.8	− .03	−1.80	.....	252.0	149.2	422.2
	Total	1,770.1	− .05	−3.00	+ 6.9	960.7	568.8	2,342.8
	Experiment No. 16.							
18–19	7 a. m. to 1 p. m.	531.7	+ .02	−1.20	+ .2	221.4	131.1	664.2
	1 p. m. to 7 p. m.	484.1	+ .01	+ .60	− 2.5	233.4	138.2	620.4
	7 p. m. to 1 a. m.	461.9	+ .01	+ .60	.....	247.3	146.4	608.9
	1 a. m. to 7 a. m.	282.0	− .05	−3.00	.....	229.0	135.6	414.6
	Total	1,759.7	− .01	− .60	− 2.3	931.1	551.3	2,308.1
19–20	7 a. m. to 1 p. m.	549.6	+ .02	−1.20	+ .9	201.5	119.3	671.0
	1 p. m. to 7 p. m.	553.3	+ .01	− .60	+ 7.8	205.3	121.5	683.2
	7 p. m. to 1 a. m.	437.4	+ .10	−6.00	.....	240.6	142.4	585.8
	1 a. m. to 7 a. m.	286.7	− .09	−5.40	.....	228.2	135.1	416.4
	Total	1,827.0	+ .04	−2.40	+ 8.7	875.6	518.3	2,356.4
	Experiment No. 17.							
20–21	7 a. m. to 1 p. m.	465.8	− .02	−1.20	− .2	199.0	117.8	582.2
	1 p. m. to 7 p. m.	490.2	+ .04	+2.40	+ 1.2	223.0	132.0	625.8
	7 p. m. to 1 a. m.	467.7	− .04	−2.40	.....	245.1	145.1	610.4
	1 a. m. to 7 a. m.	286.7	+ .03	−1.80	.....	238.5	141.2	429.7
	Total	1,710.4	+ .01	− .60	+ 1.0	905.6	536.1	2,248.1
21–22	7 a. m. to 1 p. m.	506.0	− .02	−1.20	− .3	204.1	120.8	625.3
	1 p. m. to 7 p. m.	528.2	− .01	− .60	− 2.3	221.6	131.2	656.5
	7 p. m. to 1 a. m.	456.6	+ .02	+1.20	.....	239.7	141.9	599.7
	1 a. m. to 7 a. m.	295.4	− .01	− .60	.....	215.0	127.3	422.1
	Total	1,786.2	− .02	−1.20	− 2.6	880.4	521.2	2,303.6
	Total for 6 days	10,697.0	.....	−1.80	−17.2	5,453.3	3,228.5	13,940.9

Elimination of unoxidized alcohol.—As has been explained on page 258 there may be a considerable amount of reducing matter in the ventilating air current when alcohol does not form a part of the diet. The determinations of the quantity of reducing matter in the air current during these experiments were made in the manner previously described, and the amounts are all reckoned as alcohol, although it is not believed that this is the case. It seems probable that the increased elimination of reducing matter in the air current on the 2 days of experiment No. 16 is due to the mixing of the whisky and water within the chamber by the subject, as already mentioned. According to the figures in Table XXVIII the subject actually metabolized 97.9 per cent of the alcohol in the diet during experiment No. 15, 96.6 per cent in experiment No. 16, and 97.9 per cent in experiment No. 17.

TABLE XXVIII.—*Alcohol ingested and excreted—Metabolism experiments Nos. 15–17.*

Date.	Alcohol ingested.	Alcohol excreted, including other reducing material calculated as alcohol.				Alcohol metabolized in body.	
		In urine (distillate).	In freezer water (distillate).	In air current.	Total.		
1899.							
Experiment No. 15.							
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Per cent.*
Jan. 16–17	72.5	0.10	0.03	1.35	1.48	71.0	97.9
17–18	72.5	.17	.03	1.40	1.60	70.9	97.8
Experiment No. 16.							
Jan. 18–19	72.5	.15	.04	2.13	2.32	70.2	96.8
19–20	72.5	.23	.02	1.62	1.87	70.6	97.4
Experiment No. 17.							
Jan. 20–21	72.5	.12	.04	1.53	1.69	70.8	97.7
21–22	72.5	.....	.03	1.27	1.30	71.2	98.2
Total	435.0	.77	.19	9.30	10.26	424.7	.....
Average per day	72.5	.13	.03	1.55	1.71	70.8	97.7

Balance of income and outgo of matter and energy.—The income and outgo of nitrogen, carbon, hydrogen, and energy in these experiments are shown in Tables XXIX to XXXII. It will be noticed that the subject was nearly in nitrogen and carbon equilibrium. The amount of water consumed was 1,382.5 grams, 600 of which were contained in drinking water and 782.5 in coffee infusion or water with which the alcohol was mixed. The agreement between the estimated energy of materials oxidized in the body and the heat actually determined in these experiments was very close, the variations being so small as to lie far within the limit of experimental error.

TABLE XXIX.—*Income and outgo of nitrogen and carbon—Metabolism experiments Nos. 15–17.*

Date and period.	Nitrogen.				Carbon.					
	(*a*) In food.	(*b*) In feces.	(*c*) In urine.	(*d*) Gain (+) or loss (−) *a*−(*b*+*c*).	(*e*) In food.	(*f*) In feces.	(*g*) In urine.	(*h*) In respiratory products.	(*i*) In alcohol eliminated.	(*k*) Gain (+) or loss (−) *e*−(*f*+*g*+*h*+*i*).
1899.										
Experiment No. 15.										
	Gms.	Gms.	Gms.	Gms.	Gms.	Gms.	Gms.	Gms.	Gms.	Gms.
Jan. 16–17, 7 a. m. to 7 a. m	17.4	0.8	15.1	−1.5	245.7	7.8	10.6	220.8	0.8	+5.7
17–18, 7 a. m. to 7 a. m	17.4	.8	16.2	+.4	245.7	7.8	11.4	219.3	.8	+6.4
Total for 2 days	34.8	1.6	31.3	+1.9	491.4	15.6	22.0	440.1	1.6	+12.1
Average per day	17.4	.8	15.6	+1.0	245.7	7.8	11.0	220.0	.8	+6.1
Experiment No. 16.										
Jan. 18–19, 7 a. m. to 7 a. m	17.4	.8	15.2	+1.4	245.7	7.8	10.7	217.3	1.2	+8.7
19–20, 7 a. m. to 7 a. m	17.4	.8	15.7	+.9	245.7	7.8	11.1	219.3	1.0	+6.5
Total for 2 days	34.8	1.6	30.9	+2.3	491.4	15.6	21.8	436.6	2.2	+15.2
Average per day	17.4	.8	15.5	+1.1	245.7	7.8	10.9	218.3	1.1	+7.6
Experiment No. 17.										
Jan. 20–21, 7 a. m. to 7 a. m	17.4	.8	15.7	+.9	245.7	7.8	11.1	212.7	.9	+13.2
21–22, 7 a. m. to 7 a. m	17.4	.8	15.6	+1.0	245.7	7.8	11.0	216.3	.7	+9.9
Total for 2 days	34.8	1.6	31.3	+1.9	491.4	15.6	22.1	429.0	1.6	+23.1
Average per day	17.4	.8	15.6	+1.0	245.7	7.8	11.0	214.5	.8	+11.6
Total for 6 days	104.4	4.8	93.5	+6.1	1,474.2	46.8	65.9	1,305.7	5.4	+50.4
Average per day	17.4	.8	15.6	+1.0	245.7	7.8	11.0	217.6	.9	+8.4

TABLE XXX.—*Income and outgo of water and hydrogen—Metabolism experiments Nos. 15–17.*

Date and period.	Water. (a) In food	(b) In drink.	(c) In feces.	(d) In urine.	(e) In respiratory products.	(f) Apparent loss $a+b-(c+d+e)$.
1899.						
Experiment No. 15.						
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Jan. 16–17, 7 a. m. to 7 a. m	1,095.2	1,382.5	35.9	1,426.4	910.9	+ 104.5
17–18, 7 a. m. to 7 a. m	1,095.2	1,382.5	35.9	2,197.1	966.7	− 722.0
Total for 2 days	2,190.4	2,765.0	71.8	3,623.5	1,877.6	− 617.5
Average per day	1,095.2	1,382.5	35.9	1,811.8	938.8	− 308.8
Experiment No. 16.						
Jan. 18–19, 7 a. m. to 7 a. m	1,095.2	1,382.5	35.9	1,813.9	947.1	− 319.2
19–20, 7 a. m. to 7 a. m	1,095.2	1,382.5	35.9	1,876.2	896.6	− 331.0
Total for 2 days	2,190.4	2,765.0	71.8	3,690.1	1,843.7	− 650.2
Average per day	1,095.2	1,382.5	35.9	1,845.0	921.9	− 325.1
Experiment No. 17.						
Jan. 20–21, 7 a. m. to 7 a. m	1,095.2	1,382.5	35.9	1,903.2	903.6	− 365.0
21–22, 7 a. m. to 7 a. m	1,095.2	1,382.5	35.9	2,026.6	879.4	− 464.2
Total for 2 days	2,190.4	2,765.0	71.8	3,929.8	1,783.0	− 829.2
Average per day	1,095.2	1,382.5	35.9	1,964.9	891.5	− 414.6
Total for 6 days	6,571.2	8,295.0	215.4	11,243.4	5,504.3	−2,096.9
Average per day	1,095.2	1,382.5	35.9	1,873.9	917.4	− 349.5

Date and period.	Hydrogen. (g) In food.	(h) In feces.	(i) In urine.	(k) [1] In alcohol eliminated.	(l) Apparent gain $g-(h+i+k)$.	(m) Loss from water $f\div 9$.	(n) Total gain (+) or loss (−) $l+m$.
1899.							
Experiment No. 15.							
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Jan. 16–17, 7 a. m. to 7 a. m	40.8	1.1	3.0	0.2	+ 36.5	+ 11.6	+48.1
17–18, 7 a. m. to 7 a. m	40.8	1.1	3.2	.2	+ 36.3	80.2	−43.9
Total for 2 days	81.6	2.2	6.2	.4	+ 72.8	− 68.6	+ 4.2
Average per day	40.8	1.1	3.1	.2	+ 36.4	− 34.3	+ 2.1
Experiment No. 16.							
Jan. 18–19, 7 a. m. to 7 a. m	40.8	1.1	3.0	.3	+ 36.4	− 35.5	+ .9
19–20, 7 a. m. to 7 a. m	40.8	1.1	3.1	.2	+ 36.4	36.8	− .4
Total for 2 days	81.6	2.2	6.1	.5	+ 72.8	− 72.3	+ .5
Average per day	40.8	1.1	3.1	.2	+ 36.4	− 36.1	+ .3
Experiment No. 17.							
Jan. 20–21, 7 a. m. to 7 a. m	40.8	1.1	3.1	.2	+ 36.4	− 40.5	− 4.1
21–22, 7 a. m. to 7 a. m	40.8	1.1	3.1	.2	+ 36.4	51.6	−15.2
Total for 2 days	81.6	2.2	6.2	.4	+ 72.8	− 92.1	−19.3
Average per day	40.8	1.1	3.1	.2	+ 36.4	− 46.1	− 9.7
Total for 6 days	244.8	6.6	18.5	1.3	+218.4	−233.0	−14.6
Average per day	40.8	1.1	3.1	.2	+ 36.4	− 38.8	− 2.4

TABLE XXXI.—*Gain or loss of protein* ($N \times 6.25$), *fat, and water—Metabolism experiments Nos. 15–17.*

Date and period.	(*a*) Nitrogen gained (+) or lost (−).	(*b*) Protein gained (+) or lost (−). $a \times 6.25$.	(*c*) Total carbon gained (+) or lost (−).	(*d*) Carbon in protein gained (+) or lost (−). $b \times 0.53$	(*e*) Carbon in fat, etc., gained (+) or lost (−). $c - d$.	(*f*) Fat gained (+) or lost (−). $e \div 0.765$.
1899.						
Experiment No. 15.						
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Jan. 16–17, 7 a. m. to 7 a. m	+1.5	+ 9.4	+ 5.7	+ 5.0	+ 0.7	+ 0.9
17–18, 7 a. m. to 7 a. m	− .4	+ 2.5	+ 6.4	+ 1.3	− 5.1	+ 6.7
Total for 2 days	+1.9	+11.9	+12.1	+ 6.3	+ 5.8	+ 7.6
Average per day	+1.0	+ 6.0	+ 6.1	− 3.2	+ 2.9	− 3.8
Experiment No. 16.						
Jan. 18–19, 7 a. m. to 7 a. m	+1.4	+ 8.7	+ 8.7	+ 4.6	+ 4.1	+ 5.3
19–20, 7 a. m. to 7 a. m	− .9	+ 5.6	+ 6.5	+ 3.0	+ 3.5	− 4.6
Total for 2 days	+2.3	+14.3	+15.2	+ 7.6	+ 7.6	+ 9.9
Average per day	+1.1	+ 7.2	+ 7.6	+ 3.8	+ 3.8	+ 5.0
Experiment No. 17.						
Jan. 20–21, 7 a. m. to 7 a. m	+ .9	+ 5.6	+13.2	+ 3.0	+10.2	+13.4
21–22, 7 a. m. to 7 a. m	+1.0	+ 6.3	+ 9.9	+ 3.3	+ 6.6	+ 8.6
Total for 2 days	+1.9	+11.9	− 23.1	+ 6.3	+16.8	−22.0
Average per day	+1.0	+ 6.0	+11.6	+ 3.2	− 8.4	+11.0
Total for 6 days	+6.1	+38.1	− 50.4	+20.2	+30.2	+39.5
Average per day	+1.0	+ 6.3	+ 8.4	+ 3.4	+ 5.0	+ 6.6

Date and period.	(*g*) Total hydrogen gained (+) or lost (−).	(*h*) Hydrogen in protein gained (+) or lost (−). $b \times 0.07$.	(*i*) Hydrogen in fat gained (+) or lost (−). $f \times 0.12$.	(*k*) Hydrogen in water, etc., gained (+) or lost (−). $g - (h+i)$.	(*l*) Water gained (+) or lost (−). $k \times 9$.
1899.					
Experiment No. 15.					
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Jan. 16–17, 7 a. m. to 7 a. m	− 48.1	−0.6	+0.1	+47.4	+426
17–18, 7 a. m. to 7 a. m	43.9	+ .2	+ .8	−44.9	−404
Total for 2 days	+ 4.2	+ .8	+ .9	+ 2.5	+ 22
Average per day	+ 2.1	+ .4	+ .5	+ 1.3	+ 11
Experiment No. 16.					
Jan. 18–19, 7 a. m. to 7 a. m	+ .9	+ .6	+ .6	− .3	− 3
19–20, 7 a. m. to 7 a. m	− .4	+ .4	+ .6	− 1.4	− 12
Total for 2 days	+ .5	+1.0	+1.2	− 1.7	− 15
Average per day	+ .3	+ .5	+ .6	− .8	− 7
Experiment No. 17.					
Jan. 20–21, 7 a. m. to 7 a. m	− 4.1	+ .4	+1.6	− 6.1	− 55
21–22, 7 a. m. to 7 a. m	− 15.2	+ .4	+1.0	−16.6	−149
Total for 2 days	− 19.3	+ .8	+2.6	−22.7	−204
Average per day	− 9.7	+ .4	−1.3	−11.4	102
Total for 6 days	− 14.6	+2.6	+4.7	−21.9	−197
Average per day	− 2.4	+ .4	+ .8	− 3.6	− 33

TABLE XXXII.—*Income and outgo of energy—Metabolism experiments Nos. 15–17.*

Date and period.	(*a*) Heat of combustion of food eaten.	(*b*) Heat of combustion of feces.	(*c*) Heat of combustion of urine.	(*d*) Heat of combustion of alcohol eliminated.	(*e*) Estimated heat of combustion of protein gained (+) or lost (−).	(*f*) Estimated heat of combustion of fat gained (+) or lost (−).	(*g*) Estimated energy of material oxidized in the body *a*−(*b*+*c*+*d*+*e*+*f*).	(*h*) Heat determined.	(*i*) Heat determined greater (+) or less (−) than estimated, *h*−*g*.	(*k*) Heat determined greater (+) or less (−) than estimated, *i*÷*g*.
1899.										
Experiment No. 15.										
	Calories.	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Per cent.*
Jan. 16–17, 7 a. m. to 7 a. m.	2,653	88	123	10	− 54	+ 8	2,370	2,382	+12	+ 0.5
17–18, 7 a. m. to 7 a. m.	2,653	88	132	11	− 15	+ 63	2,344	2,343	− 1	.....
Total for 2 days	5,306	176	255	21	+ 69	+ 71	4,714	4,725	+11	.....
Average per day	2,653	88	128	11	+ 34	+ 35	2,357	2,362	+ 5	+ .2
Experiment No. 16.										
Jan. 18–19, 7 a. m. to 7 a. m.	2,653	88	124	16	+ 50	− 50	2,325	2,308	−17	− .7
19–20, 7 a. m. to 7 a. m.	2,653	88	128	15	+ 32	+ 43	2,347	2,356	+ 9	+ .4
Total for 2 days	5,306	176	252	31	+ 82	+ 93	4,672	4,664	− 8	.....
Average per day	2,653	88	126	15	+ 41	+ 47	2,336	2,332	− 4	− .2
Experiment No. 17.										
Jan. 20–21, 7 a. m. to 7 a. m.	2,653	88	128	12	+ 32	+126	2,267	2,248	−19	− .8
21–22, 7 a. m. to 7 a. m.	2,653	88	128	9	+ 36	+ 81	2,311	2,304	− 7	− .3
Total for 2 days	5,306	176	256	21	+ 68	+207	4,578	4,552	−26	.....
Average per day	2,653	88	128	10	+ 34	+104	2,289	2,276	−13	− .6
Total for 6 days	15,918	528	763	73	+ 219	+371	13,964	13,941	−23	.....
Average per day	2,653	88	127	12	+ 37	+ 62	2,327	2,323	− 4	− .2

EXPERIMENTS NOS. 18–21.—REST. NOS. 18–20 WITH ALCOHOL DIET.

Subject.—A. W. S., a physicist, who was associated with these investigations. He was 25 years of age and averaged about 70 kilograms (154 pounds) in weight.

Occupation during experiment.—Reading, writing, etc., with as little mental and muscular activity as practicable.

Duration.—The preliminary period began with breakfast, February 2, 1899, and continued 4 days. On the evening of the fourth day the subject entered the calorimeter, and experiment No. 18, the first of the series, commenced at 7 o'clock the following morning, February 6, and continued 2 days. It was followed by Nos. 19 and 20 of 2 days each. A fourth experiment, elsewhere described,[a] No. 21, in which the alcohol was omitted from the diet, followed No. 20 immediately and continued 3 days. The subject thus spent 10 nights and 9 days in the chamber.

Diet.—Ordinary food furnishing 97 grams of protein and 2,264 calories of energy per day, in addition to 72.5 grams of absolute alcohol furnishing 512 calories of energy; making the total energy of the diet 2,776 calories per day. In experiment No. 18 the alcohol was furnished in ordinary commercial alcohol, in experiment No. 19 in whisky, and in experiment No. 20 in brandy. The plan of the experiment was thus practically the same as that of the previous series of experiments, Nos. 15–17. The alcohol was taken as usual in 6 doses, 3 with the meals and the other 3 between meals and upon retiring.

In experiment No. 18, 775.2 grams of coffee infusion were sweetened with 45 grams of sugar, and 79.8 grams of 90.9 per cent commercial alcohol were then added. In experiment No. 19, 158.3 grams of whisky containing 45.8 per cent alcohol by weight was added to 696.7

[a] U. S. Dept. Agr., Office of Experiment Stations. Bul. 109.

grams of water, sweetened with 45 grams of sugar. In experiment No. 20, 143.8 grams of brandy containing 50.4 per cent alcohol by weight was added to 711.2 grams of water, sweetened with 45 grams of sugar. It will be noticed that the coffee infusion was used only in the first of the series of experiments. The reason for use of the coffee infusion was to cover up the taste of the commercial ethyl alcohol, which was somewhat obnoxious to the subject.

The kinds and quantities of food served at each meal and the quantity of drink at different periods were as follows:

Diet in metabolism experiments Nos. 18–21.

FOOD.

	Breakfast.	Dinner.	Supper.	Total.
	Grams.	*Grams.*	*Grams.*	*Grams.*
Beef	55	105	.....	160
Butter	7	10	13	30
Milk, whole	250	175	325	750
Bread	55	100	155	310
Parched cereal	30	.....	.....	30
Sugar	45	.....	.....	[a]45

[a] Used with the coffee infusion or water and alcohol in experiments 18–20.

DRINK.

Time.	Experiment 18.		Experiment 19.		Experiment 20.		Experiment 21.
	Alcohol and sweetened coffee infusion.[a]	Water.	Whisky and sweetened water.[a]	Water.	Brandy and sweetened water.[a]	Water.	Water.
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Breakfast	300	.....	300	.....	300	.....	300
10 a. m.	.....	200	.....	200	.....	200	200
Dinner	300	.....	300	.....	300	.....	300
3.30 p. m.	.....	200	.....	200	.....	200	200
Supper	300	.....	300	.....	300	.....	300
10.30 p. m.	.....	200	.....	200	.....	200	200
	[a]900	600	[a]900	600	[a]900	600	1,500

[a] Contained 72.5 grams alcohol and 45 grams sugar.

Daily routine.—The general plan of the experiment was practically the same as in the previous experiments, and is shown in the following schedule:

Daily programme—Metabolism experiments Nos. 18–20.

7 a. m.	Rise, pass urine, weigh self stripped and dressed, weigh absorbers.	6 p. m.	Supper.
		7 p. m.	Pass urine.
7.45 a. m.	Breakfast, drink 200 grams water.	10.30 p. m.	Pass urine, weigh self stripped, take cap off food aperture; retire, sleep until 7 a. m.
1 p. m.	Pass urine.		
1.15 p. m.	Dinner.		

The statistics of the diary kept by the subject are summarized in Table XXXIII.

TABLE XXXIII.—*Summary of diary—Metabolism experiments Nos. 18–20.*

Date and time.	Weight without clothes.	Pulse rate per minute.	Temperature.	Hygrometer.	
				Dry bulb.	Wet bulb.
1899.	*Kilograms.*		°*F.*	°*C.*	°*C.*
Feb. 6, 7 a. m	69.15	72	97.3	19.60	14.80
6, 12.50 p. m	.....	.....	.....	19.80	15.95
6, 6.50 p. m	.....	.....	.....	19.80	15.40
6, 8.10 p. m	69.90	78	98.5	.....	.....
7, 7 a. m	69.36	66	97.3	19.90	15.60
7, 12 m	.....	.....	.....	19.60	15.20
7, 7.10 p. m	.....	.....	.....	19.80	15.80
7, 10.26 p. m	69.60	68	97.5	19.60	15.60
8, 7 a. m	69.10	73	96.8	20.00	15.10
8, 12.46 p. m	.....	.....	.....	19.80	15.45
8, 6.45 p. m	.....	.....	.....	19.75	15.20
8, 10.08 p. m	76.00	67	96.8	19.60	11.80
9, 7 a. m	69.50	69	97.2	20.00	15.00
9, 12.46 p. m	.....	.....	.....	19.70	15.00
9, 6.50 p. m	.....	.....	.....	19.70	14.80
9, 10.08 p. m	69.80	85	97.8	19.70	15.40
10, 7 a.m	69.55	62	97.1	19.70	15.00
10, 12.45 p. m	.....	.....	.....	19.65	14.95
10, 6.53 p. m	.....	.....	.....	19.75	15.05
10, 10.18 p. m	70.15	66	97.0	19.80	15.30
11, 7 a.m	69.70	78	97.4	19.80	14.90
11, 12.42 p. m	.....	.....	.....	19.70	15.40
11, 6.50 p. m	.....	.....	.....	19.70	14.85
11, 10.30 p. m	70.05	81	97.5	19.70	15.00
12, 7 a. m	69.48	70	97.8	19.80	15.15

Detailed statistics of income and outgo.—The usual statistics of income and outgo of matter and energy are shown in Tables XXXIV to XLVI, which follow. The diet was the same during the series of experiments Nos. 18–20, except in the form of alcohol taken. It supplied 97 grams of protein and 2,776 calories of energy per day. In experiment No. 21, which immediately followed, the diet was the same, with the exception that no alcohol was administered, so that the total energy of the food was only 2,264 calories.

No separation of the feces was obtained between the beginning of the preliminary period and the end of experiment No. 21, in which the subject had what may be called the basal ration without the alcohol. It was necessary, therefore, to assume a uniform amount of feces from the food from day to day. While this may introduce a slight error in the results of the 3 experiments with alcohol, Nos. 18–20, such error can hardly be large enough to affect seriously the computed results of the experiments.

TABLE XXXIV.—*Weight, composition, and heat of combustion of foods—Metabolism experiments Nos. 18–21.*

Laboratory No.	Food material.	Weight per day.	Water.	Protein.	Fat.	Carbohydrates.	Nitrogen.	Carbon.	Hydrogen.	Heat of combustion.
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
3022	Beef	160	106.7	44.6	4.2	.....	7.14	26.51	4.06	292
3020	Butter	30	2.6	.4	26.3	.....	.06	19.87	3.16	245
3024	Milk, whole	750	649.5	24.0	33.0	37.5	3.83	52.72	7.05	587
2968	Bread	310	129.3	24.5	8.7	143.5	3.94	84.72	12.74	840
3004	Cereal, parched	30	1.8	3.4	.2	24.1	.55	12.42	1.85	122
	Sugar	45	.....	.....	.....	45.0	.....	18.95	2.92	178
	Total Feb. 12 to 14	1,325	889.9	96.9	72.4	250.1	15.52	215.19	31.78	2,264
	Alcohol	72.5	.....	.....	.....	.....	.....	37.82	9.46	512
	Total Feb. 6 to 12	.....	.....	.....	.....	.....	15.52	253.01	41.24	2,776

TABLE XXXV.—*Weight, composition, and heat of combustion of feces—Metabolism experiments Nos. 18–21.*

Laboratory No.		Weight.	Water.	Protein.	Fat.	Carbohydrates	Nitrogen.	Carbon.	Hydrogen.	Heat of combustion.
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
3033	Total for 13 days	831.7	603.8	84.0	52.4	52.4	13.47	116.69	16.13	1,307
	Average per day	63.9	46.4	6.5	4.0	4.0	1.04	8.98	1.24	100

In these investigations the elimination of nitrogen in the urine on the first day inside the apparatus has frequently been larger than that of the preceding and following days. Sometimes this increase occurs 1 or 2 days before the subject enters the respiration chamber. On the 4 days of the preliminary period preceding this series of experiments the nitrogen in the urine amounted to 12.2, 16, 19 and 16.4 grams, respectively. On the first day of experiment No. 18 the nitrogen in the urine amounted to 17.4 grams, but it dropped to 15.4 grams on the second day, and varied between 13.9 and 14.7 on subsequent days. In experiment No. 21, when the energy of the diet was reduced, the excretion of nitrogen again increased. The elimination of nitrogen with and without alcohol has been already referred to.

Table XXXVI gives the detailed statistics of the quantity of urine and its nitrogen content in the successive 6-hour periods of this series of experiments. The statistics for experiment No. 21, in which no alcohol was given, show the total quantity of urine and nitrogen for the individual days, but not for individual periods. These daily amounts are given for the sake of comparison with those of experiments 18–20.

TABLE XXXVI.—*Amount, specific gravity, and nitrogen of urine by 6-hour periods—Metabolism experiments Nos. 18–20.*[a]

Date.	Period.	Amount.	Specific gravity.	Nitrogen.	
	Experiment No. 18.	*Grams.*		*Per cent.*	*Grams.*
1899.					
Feb. 6–7	7 a. m. to 1 p. m.	325.4	1.022	1.47	4.78
	1 p. m. to 7 p. m.	441.7	1.018	1.21	5.34
	7 p. m. to 1 a. m.	265.5	1.027	1.14	3.03
	1 a. m. to 7 a. m.	299.8	1.021	1.41	4.23
	Total	1,332.4			17.38
	Total by composite	1,332.4	1.019	1.31	17.45
7–8	7 a. m. to 1 p. m.	890.7	1.009	.54	4.81
	1 p. m. to 7 p. m.	690.3	1.011	.71	4.90
	7 p. m. to 1 a. m.	194.4	1.017	1.08	2.10
	1 a. m. to 7 a. m.	225.9	1.024	1.59	3.59
	Total	2,001.3			15.40
	Total by composite	2,001.3	1.013	.78	15.61
	Experiment No. 19.				
8–9	7 a. m. to 1 p. m.	609.8	1.012	.70	4.27
	1 p. m. to 7 p. m.	387.6	1.018	1.07	4.14
	7 p. m. to 1 a. m.	155.8	1.020	1.36	2.12
	1 a. m. to 7 a. m.	337.7	1.017	1.23	4.15
	Total	1,490.9			14.68
	Total by composite	1,490.9	1.015	.97	14.46
9–10	7 a. m. to 1 p. m.	569.8	1.011	.72	4.10
	1 p. m. to 7 p. m.	664.7	1.012	.66	4.39
	7 p. m. to 1 a. m.	262.8	1.013	.87	2.29
	1 a. m. to 7 a. m.	237.5	1.020	1.44	3.42
	Total	1,734.8			14.20
	Total by composite	1,734.8	1.013	.82	14.22

[a] No. 21 included for comparison.

TABLE XXXVI.—*Amount, specific gravity, and nitrogen of urine by 6-hour periods, etc.*—Continued.

Date.	Period.	Amount.	Specific gravity.	Nitrogen.	
1899.	*Experiment No. 20.*	*Grams.*		*Per cent.*	*Grams.*
10–11	7 a. m. to 1 p. m.	715.1	1.008	0.55	3.93
	1 p. m. to 7 p. m.	445.1	1.016	.87	3.87
	7 p. m. to 1 a. m.	270.9	1.012	.78	2.11
	1 a. m. to 7 a. m.	265.6	1.021	1.49	3.96
	Total	1,696.7			13.87
	Total by composite	1,696.7	1.013	.82	13.91
11–12	7 a. m. to 1 p. m.	611.1	1.011	.66	4.03
	1 p. m. to 7 p. m.	703.7	1.011	.63	4.43
	7 p. m. to 1 a. m.	360.8	1.012	.70	2.52
	1 a. m. to 7 a. m.	264.5	1.020	1.29	3.41
	Total	1,940.1			14.39
	Total by composite	1,940.1	1.013	.73	14.16
	Total for 6 days, by periods	10,196.2			89.92
6–11	Total by composite	10,196.2	1.0135	.88	89.69
	Experiment No. 21.				
12–13	Total, 7 a. m. to 7 a. m.	1,680.9			14.50
13–14	Total, 7 a. m. to 7 a. m.	1,748.1			16.15
14–15	Total, 7 a. m. to 7 a. m.	1,965.3			15.44
12, 13, 14	Total for 3 days	5,394.3			46.09

TABLE XXXVII.—*Daily elimination of carbon, hydrogen, water, and energy in urine—Metabolism experiments Nos. 18–20.*[a]

Date.	Amount.	Carbon.		Hydrogen.		Water.		Heat of combustion.	
								Per gram.	Total.
1899.									
Experiment No. 18.									
	Grams.	*Per ct.*	*Grams.*	*Per ct.*	*Grams.*	*Per ct.*	*Grams.*	*Calories.*	*Calories.*
Feb. 6–7	1,332.4	.....	11.04	.....	3.55	.....	1,269.3	.....	130
7–8	2,001.3	.....	9.78	.....	3.14	.....	1,945.4	.....	115
Experiment No. 19.									
Feb. 8–9	1,490.9	.....	9.32	.....	2.99	.....	1,437.6	.....	110
9–10	1,734.8	.....	9.01	.....	2.90	.....	1,683.3	.....	106
Experiment No. 20.									
Feb. 10–11	1,696.7	.....	8.81	.....	2.83	.....	1,646.4	.....	104
11–12	1,940.1	.....	9.14	.....	2.94	.....	1,887.9	.....	108
Total, 6 days	10,196.2	0.56	57.10	0.18	18.35	96.8	9,869.9	0.066	673
Experiment No. 21.									
Feb. 12–13	1,680.9	.....	10.18	.....	2.89	.....	1,628.3	.....	119
13–14	1,748.1	.....	11.34	.....	3.21	.....	1,689.5	.....	132
14–15	1,965.3	.....	10.85	.....	3.07	.....	1,909.3	.....	127
Total, 3 days	5,394.3	.60	32.37	.17	9.17	96.9	5,227.1	.070	378

[a] No. 21 summarized for comparison.

The details of the measurements of carbon dioxid and water in the ventilating air current are shown in Tables XXXVIII to XL, which follow. The total amounts of carbon dioxid and water eliminated each day in Experiment No. 21 are also added for comparison.

TABLE XXXVIII.—*Comparison of residual amounts of carbon dioxid and water in the chamber at the beginning and end of each period, and the corresponding gain or loss—Metabolism experiments Nos. 18–20.*

Date.	End of period.	Carbon dioxid.		Water.			
		Total amount in chamber.	Gain (+) or loss (−) over preceding period.	Total amount of vapor remaining in chamber.	Gain (+) or loss (−) over preceding period.	Change in weight of absorbers. Gain (+) or loss (−).	Total amount gained (+) or lost (−) during the period.
1899.		*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Feb. 6	7 a. m.	29	.....	35.0	.....	.....	.....
6–7	1 p. m.	42.6	+ 13.6	46.4	+11.4	+ 2	+ 13.4
	7 p. m.	41.3	— 1.3	42.1	— 4.3	— 2	— 2.3
	1 a. m.	37.2	— 4.1	46.2	+ 4.1	+ 1	+ 5.1
	7 a. m.	31.5	— 5.7	39.3	— 6.9	+ 1	— 5.9
	Total	.....	+ 2.5	.....	+ 4.3	+ 6	+10.3
7–8	1 p. m.	39.6	+ 8.1	40.8	+ 1.5	— 1	+ .5
	7 p. m.	31.3	— 8.3	44.5	+ 3.7	— 1	+ 2.7
	1 a. m.	30.1	— 1.2	41.0	— 3.5	— 1	— 4.5
	7 a. m.	26.4	— 3.7	35.6	— 5.4	— 1	— 6.4
	Total	.....	— 5.1	.....	— 3.7	— 4	— 7.7
8–9	1 p. m.	39.2	+12.8	41.8	+ 6.2	+ 2	+ 8.2
	7 p. m.	38.9	— .3	41.1	— .7	+ 2	+ 1.3
	1 a. m.	26.8	— 12.1	38.0	— 3.1	+ 1	— 2.1
	7 a. m.	26.3	— .5	33.6	— 4.4	+ 1	— 3.4
	Total	.....	— .1	.....	— 2.0	— 6	+ 4.0
9–10	1 p. m.	37.5	+11.2	39.3	+ 5.7	— 1	+ 4.7
	7 p. m.	40.1	+ 2.6	38.2	— 1.1	— 1	— 2.1
	1 a. m.	30.3	— 9.8	39.7	+ 1.5	— 1	+ .5
	7 a. m.	29.9	— 0.4	36.4	— 3.3	— 2	— 5.3
	Total	.....	+ 3.6	.....	+ 2.8	— 5	— 2.2
10–11	1 p. m.	37.5	+ 7.6	39.1	— 2.7	+ 3	+ 5.7
	7 p. m.	42.8	+ 5.3	40.9	+ 1.8	— 2	+ 3.8
	1 a. m.	30.4	—12.4	39.3	— 1.6	+ 2	+ .4
	7 a. m.	35.5	+ 5.1	36.1	— 3.2	+ 2	— 1.2
	Total	.....	+ 5.6	.....	— .3	+ 9	+ 8.7
11–12	1 p. m.	40.8	+ 5.3	43.5	+ 7.4	.....	+ 7.4
	7 p. m.	42.8	+ 2.0	39.3	— 4.2	.....	— 4.2
	1 a. m.	30.9	—11.9	41.6	+ 2.3	.....	+ 2.3
	7 a. m.	32.7	+ 1.8	38.1	— 3.5	.....	— 3.5
	Total	.....	— 2.8	.....	+ 2.0	.....	+ 2.0

TABLE XXXIX.—*Record of carbon dioxid in ventilating air current—Metabolism experiments Nos. 18–20[a].*

Date.	Period.	Carbon dioxid. (a) In incoming air. Ventilation. Number of liters of air.	(b) Per liter.	(c) Total, $a \times b$.	(d) In outgoing air.	(e) Total excess in outgoing air, $d-c$.	(f) Correction for amount remaining in chamber.	(g) Corrected amount exhaled by subject, $e+f$.	(h) Total weight of carbon exhaled, $g \times \frac{3}{11}$.
		Experiment No. 18.							
1899.		*Liters.*	*Mg.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Feb. 6–7	7 a. m.–1 p. m.	26,069	0.569	14.8	254.9	240.1	+13.6	253.7	69.2
	1 p. m.–7 p. m.	25,745	.511	13.2	232.7	219.5	— 1.3	218.2	59.5
	7 p. m.–1 a. m.	26,362	.566	14.9	230.8	215.9	— 4.1	211.8	57.7
	1 a. m.–7 a. m.	27,245	[b].570	15.5	160.3	144.8	5.7	139.1	38.0
	Total	105,421	.....	58.4	878.7	820.3	— 2.5	822.8	224.4
7–8	7 a. m.–1 p. m.	25,795	.575	14.8	239.6	224.8	+ 8.1	232.9	63.5
	1 p. m.–7 p. m.	25,908	.531	13.7	236.7	223.0	— 8.3	214.7	58.6
	7 p. m.–1 a. m.	26,924	.554	14.9	216.6	201.7	1.2	200.5	54.7
	1 a. m.–7 a. m.	27,122	.576	15.6	157.1	141.5	- 3.7	137.8	37.5
	Total	105,749	.....	59.0	850.0	791.0	— 5.1	785.9	214.3
	Experiment No. 19.								
8–9	7 a. m.–1 p. m.	26,792	.562	15.1	223.9	208.8	+12.8	221.6	60.5
	1 p. m.–7 p. m.	26,010	.616	16.0	224.0	208.0	— .3	207.7	56.6
	7 p. m.–1 a. m.	27,393	.554	15.3	210.7	195.4	12.1	183.3	50.0
	1 a. m.–7 a. m.	27,999	.552	15.5	159.4	143.9	- .5	143.4	39.1
	Total	108,394	.....	61.9	818.0	756.1	— .1	756.0	206.2
9–10	7 a. m.–1 p. m.	26,388	.554	14.6	223.9	209.3	+11.2	220.5	60.2
	1 p. m.–7 p. m.	26,150	.578	15.1	211.0	195.9	+ 2.6	198.5	54.1
	7 p. m.–1 a. m.	27,647	.579	16.0	225.7	209.7	— 9.8	199.9	54.5
	1 a. m.–7 a. m.	28,015	.550	15.4	156.1	140.7	— .4	140.3	38.3
	Total	108,200	.....	61.1	816.7	755.6	— 3.6	759.2	207.1
	Experiment No. 20.								
10–11	7 a. m.–1 p. m.	25,750	.561	14.4	223.8	209.4	+ 7.6	217.0	59.2
	1 p. m.–7 p. m.	26,228	.608	16.0	217.6	201.6	+ 5.3	206.9	56.4
	7 p. m.–1 a. m.	27,422	.575	15.8	227.0	211.2	—12.4	198.8	54.2
	1 a. m.–7 a. m.	28,046	.562	15.7	173.0	157.3	+ 5.1	162.4	44.3
	Total	107,446	.....	61.9	841.4	779.5	+ 5.6	785.1	214.1
11–12	7 a. m.–1 p. m.	26,132	.595	15.6	240.8	225.2	+ 5.3	230.5	62.8
	1 p. m.–7 p. m.	26,157	.600	15.7	222.3	206.6	+ 2.0	208.6	56.9
	7 p. m.–1 a. m.	27,966	.562	15.7	235.4	219.7	—11.9	207.8	56.7
	1 a. m.–7 a. m.	28,443	.573	16.3	168.0	151.7	+ 1.8	153.5	41.9
	Total	108,698	.....	63.3	866.5	803.2	— 2.8	800.4	218.3
	Experiment No. 21.								
12–13	7 a. m.–7 a. m.	109,063	.....	62.7	857.1	794.4	— 5.3	789.1	215.2
13–14	7 a. m.–7 a. m.	109,164	.....	128.3	913.9	785.6	+ 1.3	786.9	214.6
14–15	7 a. m.–7 a. m.	107,982	.....	65.2	884.2	819.0	— 3.0	816.0	222.5

[a] No. 21 included for comparison.

[b] Sample lost; carbon dioxid assumed to be the same in amount as the average in preceding and following periods.

TABLE XL.—*Record of water in ventilating air current—Metabolism experiments Nos. 18–20.*[a]

Date.	Period	(a) Water in incoming air: Ventilation. Number of liters of air.	(b) Water in incoming air: Per liter	(c) Water in incoming air: Total, $a \times b$.	(d) Water in outgoing air: Amount condensed in freezers.	(e) Water in outgoing air: Amount not condensed in freezers.	(f) Water in outgoing air: Total, $d + e$.	(g) Total excess water in outgoing air, $f - c$.	(h) Correction for water remaining in chamber.	(i) Total water of respiration and perspiration, $g + h$.
	Experiment No. 18.									
1899.		*Liters.*	*Mg.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Feb. 6–7	7 a. m.–1 p. m.	26,069	0.825	21.5	200.5	45.0	245.5	224.0	−13.4	237.4
	1 p. m.–7 p. m.	25,745	.769	19.8	201.8	37.4	239.2	219.4	− 2.3	217.1
	7 p. m.–1 a. m.	26,362	.799	21.1	210.5	41.2	251.7	230.6	− 5.1	235.7
	1 a. m.–7 a. m.	27,245	.812	22.1	196.9	37.3	234.2	212.1	− 5.9	206.2
	Total	105,421		84.5	809.7	160.9	970.6	886.1	−10.3	896.4
7–8	7 a. m.–1 p. m.	25,795	.825	21.3	192.2	38.1	230.3	209.0	+ .5	209.5
	1 p. m.–7 p. m.	25,908	.820	21.2	212.0	37.2	249.2	228.0	+ 2.7	230.7
	7 p. m.–1 a. m.	26,924	.790	21.3	213.0	40.2	253.2	231.9	− 4.5	227.4
	1 a. m.–7 a. m.	27,122	.797	21.6	193.8	37.9	231.7	210.1	− 6.4	203.7
	Total	105,749		85.4	811.0	153.4	964.4	879.0	− 7.7	871.3
	Experiment No. 19.									
8–9	7 a. m.–1 p. m.	26,792	.812	21.8	195.3	38.2	233.5	211.7	− 8.2	219.9
	1 p. m.–7 p. m.	26,010	.811	21.1	195.1	36.1	231.2	210.1	+ 1.3	211.4
	7 p. m.–1 a. m.	27,593	.775	21.4	191.6	41.8	233.4	212.0	− 2.1	209.9
	1 a. m.–7 a. m.	27,999	.719	20.1	184.4	40.0	224.4	204.3	− 3.4	200.9
	Total	108,394		84.4	766.4	156.1	922.5	838.1	+ 4.0	842.1
9–10	7 a. m.–1 p. m.	26,388	.738	19.5	184.3	35.8	220.1	200.6	+ 4.7	205.3
	1 p. m.–7 p. m.	26,150	.747	19.5	173.6	34.6	208.2	188.7	− 2.1	186.6
	7 p. m.–1 a. m.	27,647	.758	20.9	192.4	44.7	237.1	216.2	+ .5	216.7
	1 a. m.–7 a. m.	28,015	.685	19.2	185.7	35.5	221.2	202.0	5.3	196.7
	Total	108,200		79.1	736.0	150.6	886.6	807.5	− 2.2	805.3
	Experiment No. 20.									
10–11	7 a. m.–1 p. m.	25,750	.697	17.9	178.6	34.9	213.5	195.6	− 5.7	201.3
	1 p. m.–7 p. m.	26,228	.703	18.4	194.6	35.4	230.0	211.6	+ 3.8	215.4
	7 p. m.–1 a. m.	27,422	.645	17.7	195.6	42.7	238.3	220.6	+ .4	221.0
	1 a. m.–7 a. m.	28,046	.555	15.5	179.3	36.0	215.3	199.8	1.2	198.6
	Total	107,446		69.5	748.1	149.0	897.1	827.6	− 8.7	836.3
11–12	7 a. m.–1 p. m.	26,132	.559	14.6	191.2	35.8	227.0	212.4	+ 7.4	219.8
	1 p. m.–7 p. m.	26,157	.645	16.9	188.5	35.7	224.2	207.3	− 4.2	203.1
	7 p. m.–1 a. m.	27,966	.697	19.5	193.8	45.6	239.4	219.9	+ 2.3	222.2
	1 a. m.–7 a. m.	28,443	.723	20.6	189.1	37.5	226.6	206.0	− 3.5	202.5
	Total	108,698		71.6	762.6	154.6	917.2	845.6	+ 2.0	847.6
	Experiment No. 21.									
12–13	7 a. m.–7 a. m.	109,063		81.1	755.4	150.1	905.5	824.4	− 3.1	821.3
13–14	7 a. m.–7 a. m.	109,064		84.9	795.9	149.4	945.3	860.4	− 2.0	858.4
14–15	7 a. m.–7 a. m.	107,982		84.3	833.5	146.7	980.2	895.9	+ 1.7	897.6

[a] No. 21 included for comparison.

The calorimetric measurements for experiments 18–20 are given in detail, and those for experiment 21 summarized, in Table XLI.

TABLE XLI.—*Summary of calorimetric measurements—Metabolism experiments Nos. 18–20.*[a]

Date.	Period.	(a) Heat measured in terms of C.	(b) Change of temperature of calorimeter.	(c) Capacity correction of calorimeter, $b \times 60$.	(d) Correction due to temperature of food and dishes.	(e) Water vaporized equals total amount exhaled, less amount condensed in chamber.	(f) Heat used in vaporization of water, $e \times 0.592$.	(g) Total heat determined, $a+c+d+f$.
	Experiment No. 18.							
1889.		*Calories.*	*Degrees.*	*Calories.*	*Calories.*	*Grams.*	*Calories.*	*Calories.*
Feb. 6–7	7 a. m. to 1 p. m.	713.7	.....	.....	+ 5.5	235.4	139.4	858.6
	1 p. m. to 7 p. m.	522.7	0.09	− 5.40	− 8.5	215.1	127.3	663.9
	7 p. m. to 1 a. m.	491.0	.02	− 1.20	.....	234.7	139.0	628.8
	1 a. m. to 7 a. m.	308.5	.05	− 3.00	.....	205.2	121.5	427.0
	Total	2,035.9	.02	+ 1.20	−14.0	890.4	527.2	2,578.3
7–8	7 a. m. to 1 p. m.	599.4	+ .05	− 3.00	+ 8.2	210.5	124.6	735.2
	1 p. m. to 7 p. m.	525.6	− .03	− 1.80	− 9.3	231.7	137.2	673.9
	7 p. m. to 1 a. m.	475.1	− .14	− 8.40	.....	228.4	135.2	618.7
	1 a. m. to 7 a. m.	262.9	.25	−15.00	.....	204.7	121.2	369.1
	Total	1,863.0	.03	− 1.80	−17.5	875.3	518.2	2,396.9
	Experiment No. 19.							
8–9	7 a. m. to 1 p. m.	540.0	− .11	− 6.60	− 5.1	217.9	129.0	680.7
	1 p. m. to 7 p. m.	497.2	− .01	+ .60	+ 7.5	209.4	124.0	629.3
	7 p. m. to 1 a. m.	432.3	− .03	− 1.80	.....	208.9	123.7	554.2
	1 a. m. to 7 a. m.	296.4	− .03	− 1.80	.....	199.9	118.3	416.5
	Total	1,765.9	− .12	− 7.20	− 12.6	836.1	495.0	2,280.7
9–10	7 a. m. to 1 p. m.	528.4	− .04	− 2.40	− 6.2	206.3	122.1	659.1
	1 p. m. to 7 p. m.	446.3	− .05	− 3.00	− 9.4	187.6	111.1	563.8
	7 p. m. to 1 a. m.	470.3	− .06	+ 3.60	.....	217.7	128.9	602.8
	1 a. m. to 7 a. m.	335.3	.02	− 1.20	.....	198.7	117.6	451.7
	Total	1,780.3	− .03	− 1.80	+15.6	810.3	479.7	2,277.4
	Experiment No. 20.							
10–11	7 a. m. to 1 p. m.	522.9	+ .01	+ .60	+ 6.1	198.3	117.4	647.0
	1 p. m. to 7 p. m.	483.4	− .02	+ 1.20	+ 7.8	213.4	126.3	618.7
	7 p. m. to 1 a. m.	477.7	− .03	− 1.80	.....	219.0	129.6	605.5
	1 a. m. to 7 a. m.	310.0	.....	.....	.....	196.6	116.4	426.4
	Total	1,794.0	0.0	0.0	+13.9	827.3	489.7	2,297.6
11–12	7 a. m. to 1 p. m.	549.1	− .01	+ .60	+11.9	219.8	130.0	691.6
	1 p. m. to 7 p. m.	461.1	− .02	− 1.20	+10.4	203.1	120.3	590.6
	7 p. m. to 1 a. m.	460.2	− .06	− 3.60	.....	222.2	131.6	595.4
	1 a. m. to 7 a. m.	312.9	.04	− 2.40	.....	202.5	119.9	430.4
	Total	1,783.3	− .01	− .60	−22.3	847.6	501.8	2,308.0
	Experiment No. 21.							
12–13	7 a. m. to 7 a. m.	1,718.8	.02	− 1.20	+22.4	821.3	486.2	2,226.2
13–14	7 a. m. to 7 a. m.	1,737.4	.02	− 1.20	− 16.9	860.4	509.4	2,262.5
14–15	7 a. m. to 7 a. m.	1,801.5	− .03	− 1.80	+13.8	896.6	530.8	2,347.9

[a] No. 21 included for comparison.

The determinations of reducing material in the ventilating air current were made according to the method followed in the preceding experiments (see p. 258). The analytical data are shown in Table XLII. It will be noticed that the amount of reducing material, reckoned as

alcohol, found in the air current on the first day of the series of experiments, February 6–7, is considerably larger than on the 3 days following. This may be due in part to the fact that the subject had taken with him into the chamber an atomizer containing an alcoholic solution of eucalyptol, of which reagent, however, only a very small amount was used on the first day, and none thereafter. It will also be observed that the amount of reducing material in the air current during the 3 days of experiment No. 21, in which alcohol did not form a part of the diet, was considerable. Attention has already been called to the fact that what is reckoned as alcohol in the air current consists to a greater or less degree of reducing matter ordinarily present in the respired air, whether the subject consumed alcohol or not. Later experiments indicate that this amount of reducing material may be equivalent to as much as 0.4 of a gram of alcohol per day (see experiments 26, 28, and 30 beyond). That the amount of alcohol and other reducing material should be so large during the 3 days of experiment No. 21 is rather surprising. During the 4 days of the preliminary period and the 6 days of experiments Nos. 18–20, 725 grams of absolute alcohol had been taken. It may be that there was a certain lag in the elimination of alcohol not oxidized by the body. That there could be any large amount of alcohol remaining in the body seems altogether improbable, both from physiological considerations and from the results of experiments which have been made concerning the amount of alcohol which may be found in the tissues of the body. If there were a lag in the elimination, we do not know how long it would continue. In later experiments, Nos. 22, 27, and 33, no such lag was observed. The figures for reducing material in the alcohol on the 3 days of experiment No. 21 are not as trustworthy as those of the previous days, owing to certain analytical irregularities. The figures in column 5 of Table XLII show the total excretion of alcohol on the arbitrary assumption that one-half the average amount of reducing material found in experiment No. 21 was actually alcohol. While it is believed that these amounts represent more than the actual elimination of alcohol, they have been used in the computations of the income and outgo of carbon and energy in the following tables:

TABLE XLII.—*Alcohol ingested and excreted—Metabolism experiments Nos. 18–20.*[a]

Date.	Alcohol ingested.	Alcohol excreted, including other reducing material calculated as alcohol.				Total excretions, corrected for possible lag.	Alcohol metabolized in body.	
		In urine (distillate).	In freezer water (distillate).	In air current.	Total.			
1899.								
Experiment No. 18.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Per cent.*
Feb. 6–7	72.5	0.09	0.04	2.03	2.16	3.20	69.3	95.6
7–8	72.5	.18	.03	1.56	1.77	2.81	69.7	96.1
Experiment No. 19.								
Feb. 8–9	72.5	.10	.04	1.53	1.67	2.71	69.8	96.3
9–10	72.5	.14	.04	1.22	1.40	2.44	70.1	96.7
Experiment No. 20.								
Feb. 10–11	72.5	.13	.05	1.23	1.41	2.45	70.1	96.7
11–12	72.5	.15	.05	2.05	2.25	3.29	69.2	95.5
Total	435.0	.79	.25	9.62	10.66	16.90	418.2	.....
Average per day	72.5	.13	.04	1.60	1.78	2.82	69.7	96.1
Experiment No. 21.								
Feb. 12–13	.....	.11	.05	1.68	1.84	.....	.....	.....
13–14	.....	.13	.07	1.80	2.00	.....	.....	.....
14–15	.....	.19	.07	2.14	2.40	.....	.....	.....

[a] No. 21 included for comparison.

Balance of income and outgo of matter and energy: The income and outgo of nitrogen, carbon, hydrogen, and energy in these experiments are shown in Tables XLIII to XLVI.

TABLE XLIII.—*Income and outgo of nitrogen and carbon—Metabolism experiments Nos. 18–20.*[a]

Date and period.	Nitrogen.				Carbon.					
	(a) In food.	(b) In feces.	(c) In urine.	(d) Gain (+) or loss (−) $a-(b+c)$.	(e) In food.	(f) In feces.	(g) In urine.	(h) In respiratory products.	(i) In alcohol eliminated.	(k) Gain (+) or loss (−), $e-(f+g+h+i)$.
1899.										
Experiment No. 18.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Feb. 6–7, 7 a. m. to 7 a. m.	15.5	1.0	17.4	−2.9	253.0	9.0	11.0	224.4	1.7	+6.9
7–8, 7 a. m. to 7 a. m.	15.5	1.1	15.4	−1.0	253.0	9.0	9.8	214.3	1.4	+18.5
Total for 2 days	31.0	2.1	32.8	−3.9	506.0	18.0	20.8	438.7	3.1	+25.4
Average per day	15.5	1.1	16.4	−2.0	253.0	9.0	10.4	219.3	1.6	+12.7
Experiment No. 19.										
Feb. 8–9, 7 a. m. to 7 a. m.	15.5	1.0	14.7	−.2	253.0	9.0	9.3	206.2	1.4	+27.1
9–10, 7 a. m to 7 a. m	15.5	1.1	14.2	+.2	253.0	9.0	9.0	207.1	1.3	+26.6
Total for 2 days	31.0	2.1	28.9	.....	506.0	18.0	18.3	413.3	2.7	+53.7
Average per day	15.5	1.0	14.5	.....	253.0	9.0	9.2	206.6	1.3	+26.9
Experiment No. 20.										
Feb. 10–11, 7 a. m. to 7 a. m.	15.5	1.0	13.8	+.7	253.0	9.0	8.8	214.1	1.3	+19.8
11–12, 7 a. m. to 7 a. m.	15.5	1.1	14.4	.....	253.0	9.0	9.2	218.3	1.7	+14.8
Total for 2 days	31.0	2.1	28.2	+.7	506.0	18.0	18.0	432.4	3.0	+34.6
Average per day	15.5	1.0	14.1	+.4	253.0	9.0	9.0	216.2	1.5	+17.3
Experiments Nos. 18–20.										
Average per day	15.5	1.0	15.0	−.5	253.0	9.0	9.5	214.1	1.5	+18.9
Experiment No. 21.										
Feb. 12–13, 7 a. m. to 7 a. m.	15.5	1.0	14.5	.....	215.2	9.0	10.2	215.2	.....	−19.2
13–14, 7 a. m. to 7 a. m.	15.5	1.1	16.2	−1.8	215.2	9.0	11.3	214.6	.....	−19.7
14–15, 7 a. m. to 7 a. m.	15.5	1.0	15.4	−.9	215.2	9.0	10.9	222.5	.....	−27.2
Total for 3 days	46.5	3.1	46.1	−2.7	645.6	27.0	32.4	652.3	.....	−66.1
Average per day	15.5	1.0	15.4	−.9	215.2	9.0	10.8	217.4	.....	−22.0

[a] No. 21 included for comparison.

TABLE XLIV.—*Income and outgo of water and hydrogen—Metabolism experiments Nos. 18–21.*[a]

Date and period.	Water.					
	(a) In food.	(b) In drink.[b]	(c) In feces.	(d) In urine.	(e) In respiratory products.	(f) Apparent loss $a+b-(c+d+e)$.
1899.						
Experiment No. 18.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Feb. 6–7, 7 a. m. to 7 a. m.	889.9	1,398.2	46.4	1,269.3	896.4	+ 76.0
7–8, 7 a. m. to 7 a. m.	889.9	1,384.8	46.4	1,945.4	871.3	− 588.4
Total for 2 days	1,779.8	2,783.0	92.8	3,214.7	1,767.7	− 512.4
Average per day	889.9	1,391.5	46.4	1,607.3	883.9	− 256.2
Experiment No. 19.						
Feb. 8–9, 7 a. m. to 7 a. m.	889.9	1,384.3	46.4	1,437.6	842.1	− 51.9
9–10, 7 a. m. to 7 a. m.	889.9	1,383.8	46.4	1,683.3	805.3	− 261.3
Total for 2 days	1,779.8	2,768.1	92.8	3,120.9	1,647.4	313.2
Average per day	889.9	1,384.1	46.4	1,560.5	823.7	− 156.6

[a] No. 21 included for comparison.

[b] During the 9 days of these experiments 28.5 grams water was evaporated from the hygrometer, or an average of 3.2 grams per day, which is here added to the drink.

TABLE XLIV.—*Income and outgo of water and hydrogen—Metabolism experiments Nos. 18–21*[a].—Continued.

Date and period.	Water. (a) In food.	(b) In drink.	(c) In feces.	(d) In urine.	(e) In respiratory products.	(f) Apparent loss $a+b-(c+d+e)$.
1899.						
Experiment No. 20.						
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Feb. 10–11, 7 a. m. to 7 a. m	889.9	1,384.1	46.4	1,646.4	836.3	— 255.1
11–12, 7 a. m. to 7 a. m	889.9	1,385.2	46.4	1,887.9	847.6	— 506.8
Total for 2 days	1,779.8	2,769.3	92.8	3,534.3	1,683.9	— 761.9
Average per day	889.9	1,384.7	46.4	1,767.2	842.0	— 381.0
Average per day (experiments 18–20)	889.9	1,386.7	46.4	1,645.0	849.8	— 264.6
Experiment No. 21.						
Feb. 12–13, 7 a. m. to 7 a. m	889.9	1,385.4	46.4	1,628.3	821.3	— 220.7
13–14, 7 a. m. to 7 a. m	889.9	1,383.8	46.4	1,689.5	858.4	— 320.6
14–15, 7 a. m. to 7 a. m	889.9	1,384.9	46.4	1,909.3	897.6	— 578.5
Total for 3 days	2,669.7	4,154.1	139.2	5,227.1	2,577.3	—1,119.8
Average per day	889.9	1,384.7	46.4	1,742.4	859.1	— 373.3

Date and period.	Hydrogen. (g) In food.	(h) In feces.	(i) In urine.	(k) In alcohol eliminated.	(l) Apparent gain $g-(h+i+k)$.	(m) Loss from water $f\div 9$.	(n) Total gain (+) or loss (−) $l+m$.
1899.							
Experiment No. 18.							
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Feb. 6–7, 7 a. m. to 7 a. m	41.2	1.2	3.6	0.4	+36.0	+ 8.5	+44.5
7–8, 7 a. m. to 7 a. m	41.3	1.3	3.1	.4	+36.5	— 65.4	—28.9
Total for 2 days	82.5	2.5	6.7	.8	—72.5	— 56.9	—15.6
Average per day	41.3	1.3	3.3	.4	—36.3	— 28.5	— 7.8
Experiment No. 19.							
Feb. 8–9, 7 a. m. to 7 a. m	41.2	1.2	3.0	.4	+36.6	— 5.8	+30.8
9–10, 7 a. m. to 7 a. m	41.3	1.3	2.9	.3	+36.8	— 29.0	— 7.8
Total for 2 days	82.5	2.5	5.9	.7	+73.4	— 34.8	+38.6
Average per day	41.3	1.3	3.0	.3	+36.7	— 17.4	+19.3
Experiment No. 20.							
Feb. 10–11, 7 a. m. to 7 a. m	41.2	1.2	2.8	.3	+36.9	— 28.4	+ 8.5
11–12, 7 a. m. to 7 a. m	41.3	1.3	2.9	.4	+36.7	— 56.3	—19.6
Total for 2 days	82.5	2.5	5.7	.7	+73.6	— 84.7	—11.1
Average per day	41.3	1.2	2.9	.4	+36.8	— 42.4	— 5.6
Average per day (experiments 18–20)	41.3	1.3	3.0	.4	+36.6	— 29.4	+ 7.2
Experiment No. 21.							
Feb. 12–13, 7 a. m. to 7 a. m	31.8	1.2	2.9	.....	+27.7	— 24.5	+ 3.2
13–14, 7 a. m. to 7 a. m	31.8	1.3	3.2	.....	+27.3	— 35.6	— 8.3
14–15, 7 a. m. to 7 a. m	31.8	1.2	3.1	.....	+27.5	— 64.3	—36.8
Total for 3 days	95.4	3.7	9.2	.....	+82.5	—124.4	—41.9
Average per day	31.8	1.2	3.1	.....	+27.5	— 41.5	—14.0

[a] No. 21 included for comparison.

During the 9 days of these experiments 28.5 grams water was evaporated from the hygrometer, or an average of 3.2 grams per day, which is here added to the drink.

TABLE XLV.—*Gain or loss of protein (N × 6.25), fat, and water—Metabolism experiments Nos. 18–20.*[a]

Date and period	(a) Nitrogen gained (+) or lost (−).	(b) Protein gained (+) or lost (−) $a \times 6.25$.	(c) Total carbon gained (+) or lost (−).	(d) Carbon in protein gained (+) or lost (−) $b \times 0.53$.	(e) Carbon in fat, etc., gained (+) or lost (−) $c - d$.	(f) Fat gained (+) or lost (−) $e \div 0.765$.
1899.						
Experiment No. 18.						
Feb. 6–7, 7 a. m. to 7 a. m	*Grams.* 2.9	*Grams.* −18.1	*Grams.* − 6.9	*Grams.* − 9.6	*Grams.* − 16.5	*Grams.* −21.6
7–8, 7 a. m. to 7 a. m	1.0	− 6.3	−18.5	3.3	− 21.8	+28.5
Total for 2 days	3.9	24.4	−25.4	12.9	+38.3	− 50.1
Average per day	− 2.0	12.2	−12.7	− 6.5	− 19.2	−25.1
Experiment No. 19.						
Feb. 8–9, 7 a. m. to 7 a. m	− .2	− 1.3	−27.1	− .7	−27.8	+36.3
9–10, 7 a. m. to 7 a. m	− .2	− 1.3	−26.6	− .7	−25.9	−33.9
Total for 2 days	0	0	−53.7	0	−53.7	+70.2
Average per day	0	0	−26.9	0	− 26.9	−35.1
Experiment No. 20.						
Feb. 10–11, 7 a. m. to 7 a. m	− .7	− 4.4	−19.8	− 2.3	−17.5	+22.9
11–12, 7 a. m. to 7 a. m	0	0	− 14.8	0	−14.8	−19.3
Total for 2 days	− .7	− 4.4	−34.6	− 2.3	+32.3	+42.2
Average per day	− .4	− 2.2	−17.3	− 1.2	+ 16.2	+21.1
Average per day (experiments 18–20)	− .5	− 3.3	−18.9	− 1.8	+20.7	+27.1
Experiment No. 21.						
Feb. 12–13, 7 a. m. to 7 a. m	0	0	−19.2	0	−19.2	−25.1
13–14, 7 a. m. to 7 a. m	−1.8	−11.3	−19.7	− 6.0	−13.7	−17.9
14–15, 7 a. m. to 7 a. m	− .9	− 5.6	−27.2	− 3.0	24.2	−31.6
Total for 3 days	−2.7	−16.9	−66.1	− 9.0	−57.1	−74.6
Average per day	− .9	− 5.6	−22.0	− 3.0	−19.0	−24.9

Date and period.	(g) Total hydrogen gained (+) or lost (−).	(h) Hydrogen in protein gained (+) or lost (−) $b \times 0.07$.	(i) Hydrogen in fat gained (+) or lost (−) $f \times 0.12$.	(k) Hydrogen in water, etc., gained (+) or lost (−) $g-(h+i)$.	(l) Water gained (+) or lost (−) $k \times 9$.
1899.					
Experiment No. 18.					
Feb. 6–7, 7 a. m. to 7 a. m	*Grams.* −44.5	*Grams.* 1.3	*Grams.* − 2.6	*Grams.* −43.2	*Grams.* −389
7–8, 7 a. m. to 7 a. m	−28.9	− .4	− 3.4	−31.9	−287
Total for 2 days	− 15.6	1.7	− 6.0	− 11.3	+ 102
Average per day	− 7.8	− .9	− 3.0	+ 5.7	+ 51
Experiment No. 19.					
Feb. 8–9, 7 a. m. to 7 a. m	−30.8	− .1	− 4.3	−26.6	+240
9–10, 7 a. m. to 7 a. m	− 7.8	− .1	−4.1	+ 3.6	− 32
Total for 2 days	− 38.6	0	− 8.4	− 30.2	+272
Average per day	− 19.3	0	−4.2	− 15.1	− 136
Experiment No. 20.					
Feb. 10–11, 7 a. m. to 7 a. m	− 8.5	− .3	− 2.8	− 5.4	+ 48
11–12, 7 a. m. to 7 a. m	19.6	0	− 2.3	−21.9	−197
Total for 2 days	−11.1	− .3	− 5.1	16.5	149
Average per day	− 5.6	− .1	− 2.6	− 8.3	− 75
Average per day (experiments 18–20)	− 7.2	.2	− 3.2	− 4.2	− 38
Experiment No. 21.					
Feb. 12–13, 7 a. m. to 7 a. m	− 3.2	0	3.0	6.2	+ 56
13–14, 7 a. m. to 7 a. m	− 8.3	.8	2.2	5.3	− 48
14–15, 7 a. m. to 7 a. m	−36.8	− .4	3.8	32.6	−293
Total for 3 days	−41.9	−1.2	9.0	31.7	−285
Average per day	−14.0	− .4	− 3.0	−10.6	− 95

[a] No. 21 included for comparison.

TABLE XLVI.—*Income and outgo of energy—Metabolism experiments Nos. 18–20.*[a]

Date and period.	(*a*) Heat of combustion of food eaten.	(*b*) Heat of combustion of feces.	(*c*) Heat of combustion of urine.	(*d*) Heat of combustion of alcohol eliminated.	(*e*) Estimated heat of combustion of protein gained (+) or lost (−).	(*f*) Estimated heat of combustion of fat gained (+) or lost (−).	(*g*) Estimated energy of material oxidized in the body, $g=(b+c+d+e+f)$.	(*h*) Heat determined.	(*i*) Heat determined greater (+) or less (−) than estimated $h-g$.	(*k*) Heat determined greater (+) or less (−) than estimated $\frac{i}{g}$.
1899.										
Experiment No. 18.	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Per cent.*
Feb. 6–7, 7 a. m. to 7 a. m.	2,776	100	130	23	−104	+203	2,424	2,578	+154	+6.4
7–8, 7 a. m. to 7 a. m.	2,776	100	115	20	− 36	+268	2,309	2,397	+ 88	+3.8
Total for 2 days	5,552	200	245	43	−140	+471	4,733	4,975	+242	.....
Average per day	2,776	100	123	21	− 70	+235	2,367	2,488	+121	+5.1
Experiment No. 19.										
Feb. 8–9, 7 a. m. to 7 a. m.	2,776	100	110	19	− 7	+341	2,213	2,281	+ 68	+3.1
9–10, 7 a. m. to 7 a. m.	2,776	100	106	17	+ 7	+319	2,227	2,277	+ 50	+2.2
Total for 2 days	5,552	200	216	36	0	+660	4,440	4,558	+118	.....
Average per day	2,776	100	108	18	0	+330	2,220	2,279	+ 59	+2.7
Experiment No. 20.										
Feb. 10–11, 7 a. m. to 7 a. m.	2,776	100	104	18	+ 25	+215	2,314	2,298	− 16	−.7
11–12, 7 a. m. to 7 a. m.	2,776	100	108	23	0	+181	2,364	2,308	− 56	−2.4
Total for 2 days	5,552	200	212	41	+ 25	+396	4,678	4,606	− 72	.....
Average per day	2,776	100	106	21	+ 12	+198	2,339	2,303	− 36	−1.5
Average per day (experiments 18–20)	2,776	100	112	20	− 19	+255	2,308	2,356	+ 48	+2.1
Experiment No. 21.										
Feb. 12–13, 7 a. m. to 7 a. m.	2,264	100	119	.....	0	−236	2,281	2,226	− 55	−2.4
13–14, 7 a. m. to 7 a. m.	2,264	100	132	.....	− 65	−168	2,265	2,263	− 2	−.1
14–15, 7 a. m. to 7 a. m.	2,264	100	127	.....	− 32	−297	2,366	2,348	− 18	−.7
Total for 3 days	6,792	300	378	.....	− 97	−701	6,912	6,837	− 75	.....
Average per day	2,264	100	126	.....	− 32	−234	2,304	2,279	− 25	−1.1

[a] No. 21 included for comparison.

EXPERIMENTS NOS. 22–24—REST. NO. 22 WITH ALCOHOL DIET.

Subject.—E. O., who served as the subject of experiments Nos. 12, 15–17, and 18–20, described above. His weight was about 72.5 kilograms (160 pounds).

Occupation during experiment.—Reading, writing, etc., with as little mental and muscular activity as possible.

Duration.—The preliminary period of 4 days began with breakfast, March 9, 1899, and the subject entered the respiration chamber on the evening of March 12; experiment No. 22 beginning at 7 o'clock on the morning of March 13 and continuing 3 days. This experiment was the first of a series of three (Nos. 22–24), each continuing 3 days; the subject, therefore, remained in the respiration chamber 10 nights and 9 days, the series of experiments ending on the morning of March 22.

Diet.—One especial object of the experiments of this series was to study the relative replacing power of alcohol and sugar in the diet. The latter consisted of what may be called a basal ration of ordinary food to which was added a supplementary ration of either sugar or alcohol.

The basal ration furnished 123 grams of protein and 2,535 calories of energy per day. To this ration was added, in experiment No. 22, 79.2 grams of 90.9 per cent commercial alcohol. This contained 72 grams of absolute alcohol and furnished 509 calories of energy. In experiment No. 23 the subject had 30 grams of horse-radish, furnishing 14 calories of energy per day, and in experiment No. 24, 30 grams of horse-radish, furnishing 14 calories of energy, and 130 grams of cane sugar, furnishing 515 calories of energy. Leaving the small quantities of horse-radish out of account, the diet of experiment 22 supplied the basal ration plus alcohol, No. 23 the basal ration alone, and No. 24 the basal ration plus an amount of sugar isodynamic with the alcohol of No. 22. In experiment No. 22 the alcohol was taken in the usual 6 doses, 3 with and 3 between meals and upon retiring. It was prepared by adding 79.2 grams of 90.9 per cent alcohol to 780.8 grams of coffee infusion sweetened with 40 grams of sugar. This mixture thus contained 72 grams of absolute alcohol, 40 grams of sugar, and 788 grams of water. The kinds and quantities of food served at each meal and the quantities of drink at different periods were as follows:

Diet in metabolism experiments Nos. 22–24.

FOOD—BASAL RATION.

	Breakfast.	Dinner.	Supper.	Total.
	Grams.	*Grams.*	*Grams.*	*Grams.*
Beef	75	75	.....	150
Butter	15	20	20	55
Milk, skimmed	350	390	390	1,130
Bread	55	100	155	310
Parched cereal	45	.....	.....	45
Sugar[a]	40	.....	.....	40

[a] Used with the coffee infusion and alcohol in experiment No. 22.

FOOD—SUPPLEMENTAL RATION.

Last day of preliminary period and during metabolism experiment No. 22:		
Coffee infusion	grams	780.8
Sugar	do	40.0
Alcohol (90.9 per cent)	do	79.2
Metabolism experiment No. 23, horse-radish	do	30.0
Metabolism experiment No. 24:		
Horse-radish	do	30.0
Sugar	do	130.0

DRINK.

	Experiment No. 22.		Experiments Nos. 23 and 24.	
	Coffee infusion, sugar, and alcohol.	Water.	Coffee infusion.	Water.
	Grams.	*Grams.*	*Grams.*	*Grams.*
Breakfast	175	.....	263	.....
10.30 a. m.	125	200	.....	200
Dinner	175	.....	263	.....
2.30 p. m.	125	200	.....	200
Supper	175	.....	262	.....
11.00 p. m.	125	200	.....	200
	[a]900	[b]600	[b]788	[b]600

[a] Contains 72 grams absolute alcohol and 40 grams sugar.

[b] The subject did not always drink the full schedule allowance of coffee and of water. The actual amount of water consumed each day is shown in the second column of Table LVIII.

Daily routine.—The general routine of the experiment is indicated by the following schedule:

Daily program—Metabolism experiments Nos. 23–24.

7.00 a. m	Rise, pass urine, weigh self, weigh absorbers.	5.30 p. m	Drink 200 grams water.
7.45 a. m	Breakfast.	6.30 p. m	Supper.
10.30 a. m	Drink 200 grams water.	7.00 p. m	Pass urine.
1.00 p. m	Pass urine.	11.00 p. m	Drink 200 grams water, take cap off food aperture, retire.
1.30 p. m	Dinner.		

Table XLVII summarizes the more important statistics in the diary kept by the subject during the series of experiments.

TABLE XLVII.—*Summary of diary—Metabolism experiments Nos. 23–24.*

Date and time.	Weight without clothes.	Pulse rate per minute.	Temperature.	Hygrometer.	
				Dry bulb.	Wet bulb.
1899.					
Experiment No. 23.					
	Kilograms.		° F.	° C.	° C.
Mar. 13, 7.00 a. m	72.42	60	97.6	20.6	15.8
13, 3.30 p. m		72	97.8	20.2	16.2
13, 11.30 p. m		61	97.2	20.4	16.2
14, 7.00 a. m	73.07	59	97.0	20.4	15.1
14, 3.25 p. m		70	98.0	20.0	15.2
14, 11.00 p. m		70	98.4	20.6	15.8
15, 7.00 a. m	72.86	60	97.2	20.0	14.8
15, 4.15 p. m		68	97.8	20.0	15.2
15, 11.00 p. m		69	98.6	20.4	16.2
Experiment No. 23.					
16, 7.00 a. m	72.89	56	97.0	20.2	15.3
16, 3.30 p. m		76	98.9	20.0	15.4
16, 10.45 p. m		65	98.4	20.4	16.0
17, 7.00 a. m	72.67	58	97.0	20.4	15.1
17, 3.30 p. m		70	98.0	20.0	15.2
17, 10.50 p. m		66	98.0	20.2	15.4
18, 7.00 a. m	72.70	56	96.8	20.3	14.6
18, 3.40 p. m		66	97.6	20.2	15.0
18, 10.50 p. m		66	98.3	20.1	15.2
Experiment No. 24.					
19, 7.00 a. m	72.68	60	96.9	20.2	14.6
19, 3.30 p. m		64	98.5	19.8	14.6
19, 10.50 p. m		69	98.8	20.2	15.0
20, 7.00 a. m	72.70	58	97.0	20.0	14.8
20, 4.00 p. m		73	99.0	20.2	15.4
20, 10.50 p. m		71	99.0	20.4	15.6
21, 7.00 a. m	72.97	56	96.6	20.2	15.0
21, 3.50 p. m		69	99.2	20.2	15.2
21, 10.00 p. m		70	99.4	20.6	16.0
22, 7.00 a. m	72.90	60	97.8	20.8	16.8

Detailed statistics of income and outgo. The quantities of nutrients in the basal ration and the quantities in the supplemental ration in the different experiments of this series are shown in Table XLVIII. No attempt was made in this experiment to obtain a separation of the feces between experiments 22 and 23, since it was believed the amount of such excretion during the alcohol experiment would not differ materially from the amount in the following experiment in which alcohol was not used but in which the diet was otherwise the same, with the exception of the small amount of horse-radish. It is our experience that too frequent separation of the feces renders the line of demarcation less accurate. The separation of the feces was, however, made between experiments 23 and 24. The data of amount and composition of the feces of the two experiments are given in Table XLIX.

TABLE XLVIII.—*Weight, composition, and heat of combustion of foods—Metabolism experiments Nos. 22–24.*

Laboratory No.	Food material.	Weight per day.	Water.	Protein.	Fat.	Carbohydrates.	Nitrogen.	Carbon.	Hydrogen.	Heat of combustion.
	Basal ration.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
3027	Beef	150	84.9	52.3	9.2	.....	8.38	35.35	5.05	395
3029	Butter	55	5.2	.6	47.7	.....	.09	38.03	5.79	441
3031	Skimmed milk	1,130	1,025.0	40.7	1.1	54.2	6.55	46.44	6.67	462
3032	Bread	310	125.2	24.5	10.5	145.7	3.94	86.95	12.34	896
3004	Parched cereal	45	2.7	5.1	.3	36.2	.82	18.63	2.78	183
	Sugar	40	.....	.....	.....	40.0	.....	16.84	2.59	158
		.....	1,243.0	123.2	68.8	276.1	19.78	242.24	35.22	2,535
	Supplemental ration.									
	EXPERIMENT NO. 22.									
	Alcohol	72	.....	.....	.....	.....	.....	37.56	9.39	509
	Total ration per day	.....	**1,243.0**	**123.2**	**68.8**	**276.1**	**19.78**	**279.80**	**44.61**	**3,044**
	EXPERIMENT NO. 23.									
3069	Horse-radish	30	26.8	.4	.....	2.5	.06	2.70	.18	11
	Total ration per day	.....	**1,269.8**	**123.6**	**68.8**	**278.6**	**19.84**	**244.94**	**35.40**	**2,546**
	EXPERIMENT NO. 24.									
3069	Horse-radish	30	26.8	.4	.....	2.5	.06	2.70	.18	11
	Rock candy	130	.....	.....	.....	130.0	.....	54.72	8.42	515
	Total ration per day	.....	**1,269.8**	**123.6**	**68.8**	**408.6**	**19.84**	**299.66**	**43.82**	**3,061**

TABLE XLIX.—*Weight, composition, and heat of combustion of feces—Metabolism experiments Nos. 22–24.*

Laboratory No.		Weight.	Water.	Protein.	Fat.	Carbohydrates.	Nitrogen.	Carbon.	Hydrogen.	Heat of combustion
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
3035	Total, experiments 22 to 23	425.7	295.0	42.1	22.1	36.2	6.77	61.47	8.81	685
	Average per day	70.9	49.2	7.0	3.7	6.0	1.13	10.25	1.47	114
3036	Total, experiment 24	270.0	204.4	24.5	13.2	14.6	3.91	31.43	4.46	347
	Average per day	90.0	68.1	8.2	4.4	4.9	1.30	10.48	1.49	116

The following table gives the data for the amount and composition of the urine. In previous experiments the urine was collected in 6-hour intervals throughout the day. Inasmuch, however, as the subject at times found it difficult to get to sleep again after emptying the bladder at 1 o'clock in the morning, the urine was collected at 11 p. m., immediately before retiring, instead of 1 a. m., as in the previous experiment. The day is thus subdivided into two periods of 6 hours, one of 4, and one of 8 hours.

During the first 3 days of the preliminary digestion period, the subject eliminated 17.3, 11.8, and 14.6 grams, respectively, of nitrogen in the urine. During these days alcohol did not form a part of the diet. On the third day of the preliminary period, which was the first day upon which alcohol was added to the diet, the elimination of nitrogen in the urine amounted to 13.7 grams. It will be noticed that after the subject entered the apparatus the amount of nitrogen in the urine was larger in amount, but remained quite uniform throughout the whole series of experiments. As has previously been remarked, it is not infrequently the case that an increased elimination of nitrogen takes place when the subject enters the respiration chamber. This may account for the increase in the present case. Another explanation of the increase would be to assume that it was caused by the presence of alcohol in the diet. It is noticeable, however, that it did not take place until the subject entered the calorimeter, a day after alcohol was added to the diet, and that it continued throughout the 9 days of the sojourn in the respiration chamber, during but 3 of which alcohol was a part of the diet. The urine was not collected after the close of the experiments.

TABLE L.—*Amount, specific gravity, and nitrogen of urine, by 6-hour periods—Metabolism experiments Nos. 22–24.*

Date.	Period.	Amount.	Specific gravity.	Nitrogen.	
	Experiment No. 22.	*Grams.*		*Per cent.*	*Grams.*
1899.					
Mar. 13–14	7 a. m. to 1 p. m.	356.6	1.022	1.27	4.53
	1 p. m. to 7 p. m.	377.6	1.024	1.38	5.21
	7 p. m. to 11 p. m.	268.5	1.021	1.51	4.05
	11 p. m. to 7 a. m.	356.7	1.018	1.36	4.85
	Total				18.64
	Total by composite	1,359.4	1.019	1.40	19.04
14–15	7 a. m. to 1 p. m.	671.6	1.009	.62	4.16
	1 p. m. to 7 p. m.	776.8	1.007	.52	4.04
	7 p. m. to 11 p. m.	617.5	1.007	.99	6.11
	11 p. m. to 7 a. m.	310.8	1 018	1.45	4.51
	Total				18.82
	Total by composite	2,376.7	1.011	.80	19.01
15–16	7 a. m. to 1 p. m.	514.9	1.009	.68	3.50
	1 p. m. to 7 p. m.	629.9	1.007	.48	3.02
	7 p. m. to 11 p. m.	493.2	1.018	.96	4.73
	11 p. m. to 7 a. m.	633.5	1.012	1.04	6.59
	Total				17.84
	Total by composite	2,271.5	1.012	.80	18.17
	Experiment No. 23.				
16–17	Total, 7 a. m. to 7 a. m.	2,299.1			18.80
17–18	Total, 7 a. m. to 7 a. m.	2,280.0	1.012		19.61
18–19	Total, 7 a. m. to 7 a. m.	1,996.2	1.013		18.47
	Experiment No. 24.				
19–20	Total, 7 a. m. to 7 a. m.	2,225.5	1.014		19.45
20–21	Total, 7 a. m. to 7 a. m.	1,870.9	1.013		18.07
21–22	Total, 7 a. m. to 7 a. m.	1,861.5	1.014		17.26

TABLE LI.—*Daily elimination of carbon, hydrogen, water, and energy in urine—Metabolism experiments Nos. 22–24.*

Date	Amount.	Carbon.		Hydrogen.		Water.		Heat of combustion.	
								Per gram.	Total.
1899.									
Experiment No. 22.									
	Grams.	*Per ct.*	*Grams.*	*Per ct.*	*Grams.*	*Per ct.*	*Grams.*	*Calories.*	*Calories.*
Mar. 13–14	1,359.4	.....	12.01	.....	3.52	.....	1,295.2	.....	139
14–15	2,376.7	.....	12.12	.....	3.55	.....	2,311.8	.....	140
15–16	2,271.5	.....	11.49	.....	3.37	.....	2,210.0	.....	133
Experiment No. 23.									
Mar. 16–17	2,299.1	.....	12.11	.....	3.55	.....	2,234.3	.....	140
17–18	2,280.0	.....	12.62	.....	3.70	.....	2,212.4	.....	146
18–19	1,996.2	.....	11.90	.....	3.49	.....	1,932.5	.....	137
Experiment No. 24.									
Mar. 19–20	2,225.5	.....	12.53	.....	3.67	.....	2,158.5	.....	145
20–21	1,870.9	.....	11.64	.....	3.41	.....	1,808.6	.....	134
21–22	1,861.5	.....	11.11	.....	3.26	.....	1,802.0	.....	128
Total, 9 days	18,540.8	.58	107.53	.17	31.52	96.9	17,965.3	6.067	1,242

The results of the determinations of carbon dioxid and water in the ventilating air current are given in Tables LII–LIV. These statistics are given in detail for the first 3 days of the series and are summarized by days for the following 6 days, in order to serve as a basis of comparison of the results with and without alcohol as a part of the diet.

TABLE LII.—*Comparison of residual amounts of carbon dioxid and water in the chamber at the beginning and end of each period, and the corresponding gain or loss—Metabolism experiment No. 22.*

Date.	End of period.	Carbon dioxid.		Water.[a]		
		Total amount in chamber.	Gain (+) or loss (−) over preceding period.	Total amount of vapor remaining in chamber.	Gain (+) or loss (−) over preceding period.	Total amount gained (+) or lost (−) during the period.
1899.		*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Mar. 13	7 a. m	28.6	.....	38.6	.....	.....
13–14	1 p. m	36.4	+ 7.8	47.4	+8.8	+8.8
	7 p. m	37.7	+ 1.3	47.0	− .4	− .4
	1 a. m	27.1	−10.6	45.7	−1.3	−1.3
	7 a. m	26.2	− .9	42.4	−3.3	−3.3
	Total	.....	− 2.4	.....	+3.8	+3.8
14–15	1 p. m	39.3	+ 13.1	41.9	− .5	− .5
	7 p. m	37.6	− 1.7	40.6	−1.3	−1.3
	1 a. m	28.7	− 8.9	42.5	+ 1.9	+1.9
	7 a. m	24.6	− 4.1	36.0	−6.5	−6.5
	Total	.....	− 1.6	.....	−6.4	−6.4
15–16	1 p. m	36.8	+ 12.2	38.6	+2.6	+2.6
	7 p. m	41.9	+ 5.1	41.5	+2.9	+2.9
	1 a. m	30.2	−11.7	42.3	+ .8	+ .8
	7 a. m	24.5	− 5.7	35.2	−7.1	−7.1
	Total	.....	− .1	.....	− .8	− .8

[a] In these experiments there was no change in weight of absorbers and there was no drip.

TABLE LIII.—*Record of carbon dioxid in ventilating air current—Metabolism experiments Nos. 23–24.*

Date.	Period	(a) Ventilation. Number of liters of air.	Carbon dioxid: In incoming air. (b) Per liter.	(c) Total $a \times b$.	(d) In outgoing air.	(e) Total excess in outgoing air $d-c$.	(f) Correction for amount remaining in chamber.	(g) Corrected amount exhaled by subject $e+f$.	(h) Total weight of carbon exhaled $g \times \frac{3}{11}$.
	Experiment No. 23.								
1899.		*Liters.*	*Mg.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Mar. 13–14	7 a. m. to 1 p. m.	26,085	0.610	15.9	241.5	225.6	− 7.8	233.4	63.6
	1 p. m. to 7 p. m.	26,212	.587	15.4	226.0	210.6	+ 1.3	211.9	57.8
	7 p. m. to 1 a. m.	27,942	.574	16.0	209.3	193.3	−10.6	182.7	49.8
	1 a. m. to 7 a. m.	27,945	.591	16.5	156.7	140.2	− .9	139.3	38.0
	Total	108,184	.....	63.8	833.5	769.7	− 2.4	767.3	209.2
14–15	7 a. m. to 1 p. m.	26,606	.588	15.6	228.6	213.0	− 13.1	226.1	61.7
	1 p. m. to 7 p. m.	27,595	.569	15.7	221.4	205.7	− 1.7	204.0	55.6
	7 p. m. to 1 a. m.	27,873	.563	15.7	212.8	197.1	− 8.9	188.2	51.3
	1 a. m. to 7 a. m.	27,604	.577	15.9	149.5	133.6	− 4.1	129.5	35.3
	Total	109,678	.....	62.9	812.3	749.4	− 1.6	747.8	203.9
15–16	7 a. m. to 1 p. m.	26,590	.564	15.0	219.5	204.5	+12.2	216.7	59.1
	1 p. m. to 7 p. m.	26,841	.576	15.5	230.1	214.6	+ 5.1	219.7	59.9
	7 p. m. to 1 a. m.	28,013	.582	16.3	229.2	212.9	−11.7	201.2	54.9
	1 a. m. to 7 a. m.	29,057	.576	16.7	156.3	139.6	− 5.7	133.9	36.5
	Total	110,501	.....	63.5	835.1	771.6	− .1	771.5	210.4
	Experiment No. 23.								
16–17	7 a. m. to 7 a. m.	106,553	.....	68.6	865.4	796.8	− .7	797.5	217.5
17–18	7 a. m. to 7 a. m.	110,227	.....	63.3	846.9	783.6	− .2	783.4	213.6
18–19	7 a. m. to 7 a. m.	107,982	.....	61.3	860.3	799.0	+ 1.4	800.4	218.2
	Experiment No. 24.								
19–20	7 a. m. to 7 a. m.	110,641	.....	67.2	887.2	820.0	− 1.4	821.4	224.0
20–21	7 a. m. to 7 a. m.	108,528	.....	61.9	904.8	842.9	− 3.7	839.2	228.8
21–22	7 a. m. to 7 a. m.	107,299	.....	62.5	935.7	873.2	+ 6.3	879.5	239.8

TABLE LIV.—*Record of water in ventilating air current—Metabolism experiments Nos. 22–24.*

Date	Period.	(a) Water in incoming air. Ventilation. Number of liters of air.	(b) Per liter.	(c) Total $a \times b$.	Water in outgoing air (d) Amount condensed in freezers.	(e) Amount not condensed in freezers.	(f) Total $d+e$.	(g) Total excess water in outgoing air $f - c$.	(h) Correction for water remaining in chamber.	(i) Total water of respiration and perspiration $g+h$.
	Experiment No. 22.									
1899.		*Liters.*	*Mg.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Mar. 13–14	7 a. m. to 1 p. m.	26,085	0.946	24.7	207.2	45.7	252.9	228.2	- 8.8	237.0
	1 p. m. to 7 p. m.	26,212	.882	23.1	225.3	40.0	265.3	242.2	.4	241.8
	7 p. m. to 1 a. m.	27,942	.827	23.1	235.6	43.7	279.3	256.2	- 1.3	254.9
	1 a. m. to 7 a. m.	27,945	.782	21.9	237.1	39.0	276.1	254.2	3.3	250.9
	Total	108,184	.....	92.8	905.2	168.4	1,073.6	980.8	-3.8	984.6
14–15	7 a. m. to 1 p. m.	26,606	.784	20.8	203.0	40.1	243.1	222.3	−0.5	221.8
	1 p. m. to 7 p. m.	27,595	.766	21.2	197.9	37.4	235.3	214.1	1.3	212.8
	7 p. m. to 1 a. m.	27,873	.745	20.8	203.9	39.9	243.8	223.0	1.9	224.9
	1 a. m. to 7 a. m.	27,604	.773	21.3	194.0	36.4	230.4	209.1	- 6.5	202.6
	Total	109,678	.....	84.1	798.8	153.8	952.6	868.5	- 6.4	862.1
15–16	7 a. m. to 1 p. m.	26,590	.803	21.4	179.1	39.3	218.4	197.0	+ 2.6	199.6
	1 p. m. to 7 p. m.	26,841	.789	21.2	192.3	36.0	228.3	207.1	+ 2.9	210.0
	7 p. m. to 1 a. m.	28,013	.789	22.1	218.5	42.2	260.7	238.6	+ .8	239.4
	1 a. m. to 7 a. m.	29,057	.820	23.8	202.1	38.6	240.7	216.9	− 7.1	209.8
	Total	110,501	.....	88.5	792.0	156.1	948.1	859.6	− .8	858.8
	Experiment No. 23.									
16–17	7 a. m. to 1 p. m.	24,857	.830	20.6	180.1	35.5	215.6	195.0	− 5.3	200.3
	1 p. m. to 7 p. m.	26,329	.787	20.7	193.5	35.5	229.0	208.3	+ 2.7	211.0
	7 p. m. to 1 a. m.	27,749	.719	20.0	232.4	42.3	274.7	254.7	+ 2.4	257.1
	1 a. m. to 7 a. m.	27,618	.730	20.2	208.4	35.6	244.0	223.8	− 7.9	215.9
	Total	106,553	.....	81.5	814.4	148.9	963.3	881.8	+ 2.5	884.3
17–18	7 a. m. to 7 a. m.	110,227	.....	79.3	762.1	151.9	914.0	834.7	− 4.2	830.5
18–19	7 a. m. to 7 a. m.	107,982	.....	83.3	740.5	148.8	889.3	806.0	+ 1.0	807.0
	Experiment No. 24.									
19–20	7 a. m. to 7 a. m.	110,641	.....	85.5	808.2	152.3	960.5	875.0	+ 4.4	879.4
20–21	7 a. m. to 7 a. m.	108,528	.....	77.2	814.9	143.5	958.4	881.2	− 2.2	879.0
21–22	7 a. m. to 7 a. m.	107,299	.....	76.5	886.5	142.2	1,028.7	952.2	+10.1	962.3
	Total for 9 days	979,593	.....	748.7	7,322.6	1,365.9	8,688.5	7,939.8	+ 8.2	7,948.0

The summary of the calorimetric measurements during this series of experiments is shown in Table LV. The results of experiments Nos. 23 and 24 are summarized by days, and those for experiment No. 22, in which alcohol formed a part of the diet, are summarized by 6-hour periods.

TABLE LV.—*Summary of calorimetric measurements—Metabolism experiments Nos. 22–24.*

Date.	Period.	(*a*) Heat measured in terms of C_{26}.	(*b*) Change of temperature of calorimeter.	(*c*) Capacity correction of calorimeter $b \cdot 60$.	(*d*) Correction due to temperature of food and dishes.	(*e*) Water vaporized equals total amount exhaled less amount condensed in chamber.	(*f*) Heat used in vaporization of water $e \times 0.592$.	(*g*) Total heat determined $(a+c+d+f)$.
	Experiment No. 22.							
1899.		*Calories.*	*Degrees.*	*Calories.*	*Calories.*	*Grams.*	*Calories.*	*Calories.*
Mar. 13–14	7 a. m. to 1 p. m.	547.4	.....	.....	− 1.1	237.0	140.3	686.6
	1 p. m. to 7 p. m.	486.1	−0.03	− 1.80	+ 3.2	241.8	143.2	630.7
	7 p. m. to 1 a. m.	413.4	+ .02	+ 1.20	.....	254.9	150.9	565.5
	1 a. m. to 7 a. m.	280.6	+ .07	+ 4.20	.....	250.9	148.5	433.3
	Total	1,727.5	+ .06	+ 3.60	+ 2.1	984.6	582.9	2,316.1
14–15	7 a. m. to 1 p. m.	504.1	− .06	− 3.60	− 0.6	221.8	131.3	631.2
	1 p. m. to 7 p. m.	488.7	− .03	− 1.80	+ 4.5	212.8	126.0	617.4
	7 p. m. to 1 a. m.	427.7	+ .01	+ .60	.....	224.9	133.1	561.4
	1 a. m. to 7 a. m.	267.7	+ .04	+ 2.40	.....	202.6	120.0	390.1
	Total	1,688.2	− .04	− 2.40	+ 3.9	862.1	510.4	2,200.1
15–16	7 a. m. to 1 p. m.	475.2	+ .03	+ 1.80	− 1.8	199.6	118.2	593.4
	1 p. m. to 7 p. m.	518.3	− .05	− 3.00	+ 5.4	210.0	124.3	645.0
	7 p. m. to 1 a. m.	454.3	− .01	− .60	.....	239.4	141.7	595.4
	1 a. m. to 7 a. m.	310.8	− .15	− 9.00	.....	209.8	124.2	426.0
	Total	1,758.6	− .18	−10.80	+ 3.6	858.8	508.4	2,259.8
	Experiment No. 23.							
16–17	7 a. m. to 7 a. m.	1,711.0	+ .14	+ 8.40	−41.4	884.3	523.5	2,201.5
17–18	7 a. m. to 7 a. m.	1,700.3	+ .01	+ .60	−47.3	830.5	491.6	2,145.2
18–19	7 a. m. to 7 a. m.	1,750.4	− .06	− 3.60	−44.1	807.0	477.8	2,180.5
	Experiment No. 24.							
19–20	7 a. m. to 7 a. m.	1,737.8	+ .09	− 5.40	−48.4	879.4	520.6	2,215.4
20–21	7 a. m. to 7 a. m.	1,752.7	− .07	− 4.20	−46.1	879.0	520.3	2,222.7
21–22	7 a. m. to 7 a. m.	1,851.5	+ .04	+ 2.40	−44.6	962.3	569.7	2,379.0

The determinations of alcohol in urine and freezer water, and of reducing material reckoned as alcohol in the ventilating air current, were made in the usual manner. The results are shown in Table LVI. It will be noticed that there was a considerable amount of reducing material in the air and urine on days in which alcohol did not form a part of the diet, equivalent on an average to 0.37 of a gram of alcohol per day. It is of course possible that this reducing material may have been alcohol that had been retained in the system and was slowly eliminated. This, however, seems improbable, especially in view of the fact that the results are no larger than have been found in later experiments in the ventilating air current when alcohol had not formed a part of the diet for a long period. To be strictly accurate, the total amounts of alcohol excreted on the different days of experiment No. 22 should be reduced by a certain amount representing the average excretion of reducing material not alcohol. Inasmuch, however, as this was a matter still under investigation no such correction was made in this experiment, and the results were computed on the supposition that all the reducing material in the air current was alcohol, although from later investigations it seems quite certain that this is wrong. The error, however, would probably not exceed 0.3 or 0.4 of a gram of alcohol, corresponding to 2 or 3 calories of energy per day.

TABLE LVI.—*Alcohol ingested and excreted—Metabolism experiment No. 22.*

Date.	Alcohol ingested.	Alcohol excreted, including other reducing material calculated as alcohol.				Alcohol metabolized in body.	
		In urine (distillate).	In freezer water (distillate).	In air current.	Total.		
1899.							
Experiment No. 22.							
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Per cent.*
Mar. 13–14	72.0	0.14	0.03	1.57	1.74	70.3	97.6
14–15	72.0	.68	.02	1.36	2.06	69.9	97.1
15–16	72.0	.75	.03	2.01	2.79	69.2	96.1
Total	216.0	1.57	.08	4.94	6.59	209.4	
Average per day	72.0	.52	.03	1.65	2.20	69.8	97.0
Experiment No. 23.							
Mar. 16–17		.01		.30	.31		
17–18		.02	.01	.38	.41		
18–19		.04	.01	.37	.42		
Experiment No. 24.							
Mar. 19–20		.04		.27	.31		
20–21		.04	.01	.36	.41		
21–22				.37	.37		

Balance of income and outgo of matter and energy.—The usual summary of the income and outgo of nitrogen, carbon, hydrogen, and energy may be found in Table LVII.

TABLE LVII.—*Income and outgo of nitrogen and carbon—Metabolism experiments Nos. 22–24.*

Date and period.	Nitrogen.				Carbon.					
	(*a*) In food.	(*b*) In feces.	(*c*) In urine.	(*d*) Gain (+) or loss (−) *a*−(*b*+*c*).	(*e*) In food.	(*f*) In feces.	(*g*) In urine.	(*h*) In respiratory products.	(*i*) In alcohol eliminated.	(*k*) Gain (+) or loss (−) *e*−(*f*+*g*+*h*+*i*).
1899.										
Experiment No. 22.										
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Mar. 13–14, 7 a. m. to 7 a. m.	19.8	1.1	18.7	.....	279.8	10.3	12.0	209.2	0.9	+ 47.4
14–15, 7 a. m. to 7 a. m.	19.8	1.2	18.8	0.2	279.8	10.2	12.1	203.9	1.1	+ 52.5
15–16, 7 a. m. to 7 a. m.	19.8	1.1	17.8	+ .9	279.8	10.3	11.5	210.4	1.5	+ 46.1
Total for 3 days	59.4	3.4	55.3	+ .7	839.4	30.8	35.6	623.5	3.5	+146.0
Average per day	19.8	1.1	18.5	+ .2	279.8	10.3	11.8	207.8	1.2	+ 48.7
Experiment No. 23.										
Mar. 16–17, 7 a. m. to 7 a. m.	19.8	1.1	18.8	+ .1	244.9	10.2	12.1	217.5	.....	+ 5.1
17–18, 7 a. m. to 7 a. m.	19.9	1.2	19.6	+ .9	245.0	10.3	12.6	213.6	.....	+ 8.5
18–19, 7 a. m. to 7 a. m.	19.8	1.1	18.5	+ .2	244.9	10.2	11.9	218.2	.....	+ 4.6
Total for 3 days	59.5	3.4	56.9	+ .8	734.8	30.7	36.6	649.3	.....	+ 18.2
Average per day	19.8	1.1	19.0	+ .3	244.9	10.2	12.2	216.4	.....	+ 6.1
Experiment No. 24.										
Mar. 19–20, 7 a. m. to 7 a. m.	19.8	1.3	19.4	+ .9	299.7	10.5	12.5	224.0	.....	+ 52.7
20–21, 7 a. m. to 7 a. m.	19.9	1.3	18.1	+ .5	299.6	10.5	11.7	228.8	.....	+ 48.6
21–22, 7 a. m. to 7 a. m.	19.8	1.3	17.3	+ 1.2	299.7	10.5	11.1	239.8	.....	+ 38.3
Total for 3 days	59.5	3.9	54.8	+ .8	899.0	31.5	35.3	692.6	.....	+139.6
Average per day	19.8	1.3	18.2	+ .3	299.7	10.5	11.8	230.9	.....	+ 46.5

TABLE LVIII.—*Income and outgo of water and hydrogen—Metabolism experiments Nos. 22–24.*

Date and period.	Water. (a) In food.	(b) In drink.	(c) In feces.	(d) In urine.	(e) In respiratory products.	(f) Apparent loss $a+b-(c+d+e)$.
1899.						
Experiment No. 22.						
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Mar. 13–14, 7 a. m. to 7 a. m	1,243.0	1,387.8	49.2	1,295.2	984.6 [a]	− 301.8
14–15, 7 a. m. to 7 a. m	1,243.0	1,388.0	49.2	2,311.8	862.1	592.1
15–16, 7 a. m. to 7 a. m	1,243.0	1,387.7	49.2	2,210.0	858.8	− 487.3
Total for 3 days	3,729.0	4,163.5	147.6	5,817.0	2,705.5	777.6
Average per day	1,243.0	1,387.8	49.2	1,939.0	901.8	− 259.2
Experiment No. 23.						
Mar. 16–17, 7 a. m. to 7 a. m	1,269.8	1,362.8	49.2	2,234.3	884.3	− 535.2
17–18, 7 a. m. to 7 a. m	1,269.8	1,379.2	49.2	2,212.4	830.5	− 443.1
18–19, 7 a. m. to 7 a. m	1,269.8	1,378.0	49.2	1,932.5	807.0	− 140.9
Total for 3 days	3,809.4	4,120.0	147.6	6,379.2	2,521.8	−1,119.2
Average per day	1,269.8	1,373.3	49.2	2,126.4	840.6	− 373.1
Experiment No. 24.						
Mar. 19–20, 7 a. m. to 7 a. m	1,269.8	1,376.0	68.1	2,158.5	879.4	− 460.2
20–21, 7 a. m. to 7 a. m	1,269.8	1,382.4	68.1	1,808.6	879.0	− 103.5
21–22, 7 a. m. to 7 a. m	1,269.8	1,373.4	68.1	1,802.0	962.3	− 189.2
Total for 3 days	3,809.4	4,131.8	204.3	5,769.1	2,720.7	− 752.9
Average per day	1,269.8	1,377.3	68.1	1,923.0	906.9	− 250.9

Date and period.	Hydrogen. (g) In food.	(h) In feces.	(i) In urine.	(k) In alcohol eliminated.	(l) Apparent gain $g-(h+i\pm k)$.	(m) Loss from water $(f\times 9)$.	(n) Total gain (+) or loss (−) $l\pm m$.
1899.							
Experiment No. 22.							
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Mar. 13–14, 7 a. m. to 7 a. m	44.6	1.4	3.5	0.2	− 39.5	− 33.5	−73.0
14–15, 7 a. m. to 7 a. m	44.6	1.5	3.5	.3	− 39.3	65.8	26.5
15–16, 7 a. m. to 7 a. m	44.6	1.4	3.4	.4	− 39.4	54.1	14.7
Total for 3 days	133.8	4.3	10.4	.9	118.2	− 86.4	− 31.8
Average per day	44.6	1.4	3.5	.3	39.4	28.8	− 10.6
Experiment No. 23.							
Mar. 16–17, 7 a. m. to 7 a. m	35.4	1.5	3.5	.....	− 30.4	− 59.5	29.1
17–18, 7 a. m. to 7 a. m	35.4	1.4	3.7	.....	− 30.3	− 49.2	−18.9
18–19, 7 a. m. to 7 a. m	35.4	1.5	3.5	.....	− 30.4	− 15.7	− 14.7
Total for 3 days	106.2	4.4	10.7	.....	91.1	124.4	33.3
Average per day	35.4	1.5	3.5	.....	− 30.4	− 41.5	11.1
Experiment No. 24.							
Mar. 19–20, 7 a. m. to 7 a. m	43.8	1.5	3.7	.....	− 38.6	− 51.1	−12.5
20–21, 7 a. m. to 7 a. m	43.8	1.5	3.4	.....	− 38.9	− 11.5	− 27.4
21–22, 7 a. m. to 7 a. m	43.8	1.5	3.3	.....	− 39.0	− 21.0	− 18.0
Total for 3 days	131.4	4.5	10.4	.....	− 116.5	− 83.6	− 32.9
Average per day	43.8	1.5	3.5	.....	− 38.8	27.9	−10.9

[a] Compare weight of urine eliminated on this day with that on succeeding days.

TABLE LIX.—*Gain or loss of protein* ($N \times 6.25$), *fat, and water—Metabolism experiments Nos. 22–24.*

Date and period.	(a) Nitrogen gained (+) or lost (−).	(b) Protein gained (+) or lost (−), $a \cdot 6.25$.	(c) Total carbon gained (+) or lost (−).	(d) Carbon in protein gained (+) or lost (−), $b \cdot 0.53$.	(e) Carbon in fat, etc., gained (+) or lost (−), $c = d$.	(f) Fat gained (+) or lost (−), $e \div 0.765$.
1899.						
Experiment No. 22.						
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Mar. 13–14, 7 a. m. to 7 a. m.	0.0	0.0	+ 47.4	0.0	+ 47.4	+ 62.0
14–15, 7 a. m. to 7 a. m.	.2	−1.3	+ 52.5	.7	+ 53.2	+ 69.5
15–16, 7 a. m. to 7 a. m.	.9	−5.6	+ 46.1	2.9	+ 43.2	+ 56.5
Total for 3 days	.7	−4.3	+146.0	+2.2	+143.8	+188.0
Average per day	+ .2	−1.4	+ 48.7	+ .7	+ 48.0	+ 62.7
Experiment No. 23.						
Mar. 16–17, 7 a. m. to 7 a. m.	− .1	− .6	+ 5.1	0.0	+ 5.1	+ 6.7
17–18, 7 a. m. to 7 a. m.	.9	−5.6	+ 8.5	−3.0	+ 11.5	+ 15.0
18–19, 7 a. m. to 7 a. m.	.2	−1.3	+ 4.6	.7	+ 3.9	+ 5.1
Total for 3 days	.8	−4.9	+ 18.2	2.3	+ 20.5	+ 26.8
Average per day	− .3	−1.6	+ 6.1	.8	+ 6.9	+ 9.0
Experiment No. 24.						
Mar. 19–20, 7 a. m. to 7 a. m.	− .9	−5.6	+ 52.7	−3.0	+ 55.7	+ 72.8
20–21, 7 a. m. to 7 a. m.	− .5	−3.1	+ 48.6	1.6	+ 47.0	+ 61.5
21–22, 7 a. m. to 7 a. m.	1.2	−7.5	+ 38.3	4.0	+ 34.3	+ 44.8
Total for 3 days	− .8	+5.0	+ 139.6	2.6	+ 137.0	+179.1
Average per day	− .3	+1.7	+ 46.5	.9	+ 45.7	+ 59.7

Date and period.	(g) Total hydrogen gained (+) or lost (−).	(h) Hydrogen in protein gained (+) or lost (−), $b \cdot 0.07$.	(i) Hydrogen in fat gained (+) or lost (−), $f \cdot 0.12$.	(k) Hydrogen in water, etc., gained (+) or lost (−), $g-(h+i)$.	(l) Water gained (+) or lost (−), $k \cdot 9$.
1899.					
Experiment No. 22.					
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Mar. 13–14, 7 a. m. to 7 a. m.	+73.0	0.0	− 7.4	− 65.6	[a]+590.4
14–15, 7 a. m. to 7 a. m.	−26.5	.1	− 8.3	−34.7	−312.3
15–16, 7 a. m. to 7 a. m.	−14.7	− .4	− 6.8	−21.9	−197.1
Total for 3 days	31.8	+ .3	−22.5	+ 9.0	+ 81.0
Average per day	10.6	+ .1	7.5	+ 3.0	+ 27.0
Experiment No. 23.					
Mar. 16–17, 7 a. m. to 7 a. m.	−29.1	.0	− .8	−29.9	−269.1
17–18, 7 a. m. to 7 a. m.	−18.9	− .4	1.8	−20.3	−182.7
18–19, 7 a. m. to 7 a. m.	−14.7	− .1	.6	−14.0	+126.0
Total for 3 days	−33.3	.3	− 3.2	−36.2	−325.8
Average per day	−11.1	− .1	1.1	−12.1	−108.6
Experiment No. 24.					
Mar. 19–20, 7 a. m. to 7 a. m.	−12.5	− .4	8.7	−20.8	−187.2
20–21, 7 a. m. to 7 a. m.	−27.4	− .2	7.4	19.8	+178.2
21–22, 7 a. m. to 7 a. m.	−18.0	− .5	5.4	−12.1	+108.9
Total for 3 days	−32.9	+ .3	21.5	+11.1	− 99.9
Average per day	−10.9	− .1	− 7.1	− 3.7	− 33.3

[a] Compare weight of urine eliminated on this day with that on succeeding days.

TABLE LX.—*Income and outgo of energy—Metabolism experiments Nos. 22–24.*

Date and period.	(a) Heat of combustion of food eaten.	(b) Heat of combustion of feces.	(c) Heat of combustion of urine.	(d) Heat of combustion of alcohol eliminated.	(e) Estimated heat of combustion of protein gained (+) or lost (−).	(f) Estimated heat of combustion of fat gained (+) or lost (−).	(g) Estimated energy of material oxidized in the body $a-(b+c+d+e+f)$.	(h) Heat determined.	(i) Heat determined greater (+) or less (−) than estimated $h-g$.	(k) Heat determined greater (+) or less (−) than estimated $i \div g$.
1899.										
Experiment No. 22.										
	Calories.	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Per cent.*
Mar. 13–14, 7 a. m. to 7 a. m.	3,044	114	139	12	0	−583	2,196	2,316	+120	+5.5
14–15, 7 a. m. to 7 a. m.	3,044	114	140	14	−8	−653	2,131	2,200	+69	+3.2
15–16, 7 a. m. to 7 a. m.	3,044	114	133	20	+32	531	2,214	2,260	−46	+2.1
Total for 3 days	9,132	342	412	46	+24	+1,767	6,541	6,776	+235	.....
Average per day	3,044	114	138	15	+8	−589	2,180	2,258	−78	+3.6
Experiment No. 23.										
Mar. 16–17, 7 a. m. to 7 a. m.	2,546	114	140	.....	−4	−63	2,233	2,202	−31	−1.4
17–18, 7 a. m. to 7 a. m.	2,546	114	146	.....	−32	−141	2,177	2,145	−32	−1.5
18–19, 7 a. m. to 7 a. m.	2,546	114	137	.....	−8	−48	2,239	2,181	−58	−2.6
Total for 3 days	7,638	342	423	.....	−28	−252	6,649	6,528	−121	.....
Average per day	2,546	114	141	.....	−9	−84	2,216	2,176	−40	−1.8
Experiment No. 24.										
Mar. 19–20, 7 a. m. to 7 a. m.	3,061	116	145	.....	−32	−684	2,148	2,215	+67	+3.1
20–21, 7 a. m. to 7 a. m.	3,061	116	134	.....	−18	−579	2,214	2,223	+9	+.4
21–22, 7 a. m. to 7 a. m.	3,061	116	128	.....	−43	−421	2,353	2,379	26	1.1
Total for 3 days	9,183	348	407	.....	−29	−1,684	6,715	6,817	+102	.....
Average per day	3,061	116	136	.....	−10	561	2,238	2,272	−34	−1.5

EXPERIMENTS NOS. 26–28—REST. NO. 27 WITH ALCOHOL DIET.

Subject.—J. F. S., a chemist, 29 years of age. His weight with underclothing was about 64 kilograms (141 pounds).

Occupation during experiment.—Reading, writing, and miscellaneous observations within the apparatus, with as little muscular activity as was practicable.

Duration.—This experiment was the second of a series of 3 experiments, each continuing 3 days. The series was preceded by a preliminary period of 4 days, beginning with breakfast February 10, 1900. The subject entered the calorimeter on the evening of February 13. The first experiment of the series, No. 26, began at 7 a. m. February 14; the second, No. 27, at 7 a. m. February 17, and the third, No. 28, at 7 a. m. February 20. The whole period of the metabolism experiments was thus 9 days.

Diet.—A basal ration of ordinary food furnished 99 grams of protein and 1,982 calories of energy per day. To this was added in experiment No. 26, 63.5 grams of butter, furnishing 1 gram of protein and 508 calories of energy; in experiment No. 27, 79.5 grams of 90.6 per cent alcohol, furnishing 509 calories of energy, and in No. 28, 128 grams of cane sugar, furnishing 507 calories of energy per day. The protein and energy was thus practically the same in each of the 3 experiments of this series. In experiment No. 27 the 79.5 grams of commercial alcohol, containing 72 grams absolute alcohol, was added to 792.5 grams of water sweetened with 15 grams of sugar. The alcohol was taken in 6 doses, as indicated in the following schedule. The kinds and quantities of food in the basal ration, as served for each meal, the character and amount of the supplemental ration in the different experiments, and the quantity of drink consumed at different periods of the day were as follows:

Diet in metabolism experiments Nos. 26–28.

FOOD—BASAL RATION.

	Breakfast.	Dinner.	Supper.	Total.
	Grams.	*Grams.*	*Grams.*	*Grams.*
Beef	35	50	.....	85
Butter	10	12	8	30
Milk	300	400	300	1,000
Bread	50	100	50	200
Ginger snaps	.....	30	30	60
Parched cereal	25	.....	25	50
Sugar[a]	15	.....	.....	15

[a] Used in alcohol and water in experiment No. 27.

FOOD—SUPPLEMENTAL RATION.

Experiment No. 26.—63.5 grams butter were added to basal ration.
Experiment No. 27.—72 grams absolute alcohol were added to basal ration.
Experiment No. 28.—128 grams sugar were added to basal ration.

DRINK.

Time.	Experiment No. 26.	Experiment No. 27.	Experiment No. 28.
	Water.	Alcohol and sweetened water.	Water.
	Grams.	*Grams.*	*Grams.*
Breakfast	100	150	100
10 a. m	200	125	200
Dinner	.....	200	.....
3 p. m	200	125	200
Supper	.....	175	.....
9 p. m	300	112	300
	800	[a]887	800

[a] Contains 72 grams absolute alcohol and 15 grams sugar.

Daily routine.—The general routine of the experiment was as follows:

Daily programme—Metabolism experiments Nos. 26–28.

6.50 a. m	Take pulse and temperature.
7 a. m	Rise, pass urine, weigh self dressed, weigh absorbers.
7.45 a. m	Breakfast. Drink 100 grams water.
10 a. m	Drink 200 grams water.
12.50 p. m	Take pulse and temperature.
1 p. m	Pass urine.
1.15 p. m	Dinner.
3 p. m	Drink 200 grams water.
6 p. m	Supper.
6.50 p. m	Take pulse and temperature.
7 p. m	Pass urine, weigh self dressed, weigh absorbers.
9 p. m	Drink 300 grams water.
10.20 p. m	Take pulse and temperature.
10.30 p. m	Retire.
1 a. m	Pass urine.

Table LXI summarizes the most important statistics in the diary kept by the subject. The subject weighed himself with clothing twice each day. The reasons for not removing all the clothing in weighing were two: It was desirable to avoid the muscular work involved in dressing and undressing; it has also been found that the sudden increase of radiation of heat from the skin when the clothing is removed causes a decided rise in the temperature inside the chamber, and thus disturbs the accuracy of the heat measurements to some extent. There was extremely little muscular exercise and no sensible perspiration. Hence the differences in weight from time to time must represent very nearly the changes in body weight. The determinations of pulse rate were made, of course, by the subject himself, when either sitting or reclining, after several minutes rest. The measurement at 6.50 a. m., however, was made before rising from bed.

The temperature was determined by a mercury thermometer placed in the axilla. As has already been stated, it was found that the thermometer reached as high a point in 10 minutes as in 15 or 20 minutes. The most of the temperatures, therefore, were made after the thermometer had been in place about 10 minutes. It was our belief at the outset that the body temperatures as thus taken are not perfectly accurate, and this belief has been confirmed by observations with an electrical rectal thermometer, since devised for continuous and accurate observations of internal body temperature.[a] While these axillary determinations of body temperature are not entirely accurate, the later observations with the electrical thermometer lead us to believe that the daily curves for the two are nearly parallel.

In previous experiments an hygrometer had been placed in the chamber, and readings with dry and wet bulb were taken at frequent intervals. Inasmuch, however, as these readings were not used in the computations of results, and it is desirable in rest experiments to avoid all unnecessary exertion, even that of rising and reading the hygrometer, these observations were not made in the experiments of 1900.

TABLE LXI.—*Summary of the diary—Metabolism experiments Nos. 26–28.*

Date and time.	Weight with clothes.	Pulse rate per minute.	Temperature.
1900.			
Experiment No. 26.	*Kilograms.*		°*F.*
Feb. 14, 7 a. m.	64.00	68	97.8
8.36 a. m.		78	98.3
10.27 a. m.		67	98.1
12.27 p. m.		64	
12.33 p. m.			97.8
12.53 p. m.		61	
1 p. m.			97.9
2.27 p. m.		77	98.5
3.47 p. m.			98.5
4.30 p. m.		72	98.5
5.30 p. m.		67	
5.45 p. m.			98.7
6.17 p. m.	64.88		
8.13 p. m.			97.6
8.30 p. m.		64	97.5
9.29 p. m.		64	97.7
10.15 p. m.		64	
Feb. 15, 6.50 a. m.		69	98.1
7 a. m.	64.18		
7.34 a. m.		78	
7.39 a. m.			98.3
8.33 a. m.		82	98.5
9.28 a. m.		80	
9.30 a. m.			98.3
10.33 a. m.		71	
10.46 a. m.			98.5
11.30 a. m.		70	98.1
12.31 p. m.		68	
12.37 p. m.			98.4
12.54 p. m.		68	
1 p. m.			98.2
1.59 p. m.		75	98.2
2.28 p. m.		81	98.5
3.35 p. m.		77	98.2
4.28 p. m.		76	
4.30 p. m.			98.1
5.30 p. m.			98.0
5.49 p. m.		69	
6.30 p. m.		69	98.2
6.55 p. m.	64.87	68	98.2
7.30 p. m.		75	98.1
8.30 p. m.		67	97.6
8.54 p. m.		70	
9 p. m.			97.5
9.30 p. m.		67	
9.35 p. m.			97.4
9.51 p. m.			97.6
1900—Continued.			
Experiment No. 26—C't'd.	*Kilograms.*		°*F.*
Feb. 15, 10.15 p. m.		70	
10.20 p. m.			97.5
Feb. 16, 6.55 a. m.		71	
7 a. m.	64.01		98.1
8.32 a. m.		82	
8.40 a. m.			98.3
9.30 a. m.		79	
9.37 a. m.			98.2
10.31 a. m.		76	98.3
11.26 a. m.		72	
11.30 a. m.			98.2
12.27 p. m.		70	
12.30 p. m.			98.1
12.58 p. m.		71	
1 p. m.			98.2
2.01 p. m.		80	98.2
2.30 p. m.		79	98.2
3.35 p. m.		81	98.3
4.05 p. m.			98.2
4.27 p. m.		79	
4.30 p. m.			98.2
5.30 p. m.		75	98.5
5.43 p. m.			98.7
6.32 p. m.		80	
6.42 p. m.			98.4
7 p. m.	64.73	77	98.5
7.34 p. m.		75	
7.40 p. m.			98.0
7.50 p. m.			98.3
8.26 p. m.		71	
8.30 p. m.			97.8
9.30 p. m.		68	97.8
10.19 p. m.		65	
10.22 p. m.			97.1
Experiment No. 27.			
Feb. 17, 6.55 a. m.		69	
7 a. m.	64.07		
7.31 a. m.		82	
7.35 a. m.			97.8
8.32 a. m.		89	
8.38 a. m.			97.9
9.32 a. m.		98	98.1
10.29 a. m.		97	
10.30 a. m.			98.3
11.30 a. m.		87	97.9

[a] See p. 273.

TABLE LXI.—*Summary of the diary—Metabolism experiments Nos. 26–28*—Continued.

Date and time.	Weight with clothes.	Pulse rate per minute.	Temperature.
1900—Continued.			
Experiment No. 27—C't'd.	*Kilograms.*		°*F.*
Feb. 17, 12.30 p. m.		80	97.8
1 p. m.		77	97.8
1.41 p. m.		80	
1.49 p. m.			98.0
2 p. m.			98.1
2.10 p. m.			97.9
2.27 p. m.		90	
2.30 p. m.			97.8
2.59 p. m.		91	
3 p. m.			97.9
3.27 p. m.		96	
3.30 p. m.			98.1
4.27 p. m.		94	
4.30 p. m.			98.2
5.27 p. m.		83	98.1
5.43 p. m.		83	
5.46 p. m.			98.1
6.30 p. m.		84	
6.34 p. m.			97.7
6.46 p. m.			98.1
6.58 p. m.		87	98.0
7 p. m.	64.55		
7.30 p. m.		90	97.7
7.45 p. m.			97.8
8.27 p. m.		84	
8.30 p. m.			97.5
8.54 p. m.		83	
8.55 p. m.			97.5
9.28 p. m.		79	
9.35 p. m.			97.3
9.46 p. m.			97.3
10.16 p. m.		73	
10.21 p. m.			97.1
Feb. 18, 6.55 a. m.		72	
7 a. m.	63.75		98.1
7.30 a. m.		82	
7.34 a. m.			97.9
8.40 a. m.		90	98.2
9.30 a. m.		96	98.4
10.27 a. m.		90	
10.30 a. m.			98.3
11.31 a. m.		82	97.8
11.55 a. m.			98.1
12.27 p. m.		75	
12.30 p. m.			98.1
12.55 p. m.		75	98.3
1.42 p. m.		83	
1.50 p. m.			98.1
2.28 p. m.		90	
2.30 p. m.			98.4
3.28 p. m.		90	
3.30 p. m.			98.4
4.30 p. m.		90	98.3
5.32 p. m.		78	
5.40 p. m.			98.3
6.27 p. m.		80	
6.30 p. m.			98.1
6.56 p. m.		81	
6.58 p. m.			98.0
7 p. m.	64.37		
7.30 p. m.		87	97.7
8.34 p. m.		80	97.7
9.29 p. m.		72	97.4
10 p. m.			97.4
10.25 p. m.			97.2
10.28 p. m.		77	
Feb. 19, 7 a. m.		75	98.1
7.31 a. m.		85	97.8
8.30 a. m.		90	98.0
9.30 a. m.		96	98.2
1900—Continued.			
Experiment No. 27—C't'd.	*Kilograms.*		°*F.*
Feb. 19, 10.31 a. m.		91	98.2
11.27 a. m.		81	
11.30 a. m.			98.0
12.30 p. m.		73	97.7
12.56 p. m.		74	
12.59 p. m.			98.1
1.33 p. m.		81	
1.37 p. m.			98.1
2.30 p. m.		92	98.3
3.30 p. m.		93	98.2
4.30 p. m.		88	
4.46 p. m.			98.2
5.30 p. m.		78	98.2
6.29 p. m.		81	
6.33 p. m.			98.2
6.59 p. m.		85	
7 p. m.	64.49		98.1
7.30 p. m.		90	
7.35 p. m.			97.6
8.27 p. m.		83	97.6
9.30 p. m.		76	97.3
9.42 p. m.			97.5
10.19 p. m.		74	97.3
Experiment No. 28.			
Feb. 20, 6.55 a. m.		72	
7 a. m.	63.71		98.1
7.32 a. m.		88	
7.35 a. m.			98.4
8.30 a. m.		91	
8.31 a. m.			98.4
9.30 a. m.		99	98.7
10.30 a. m.		84	98.4
11.30 a. m.		81	98.2
11.36 a. m.		78	
12.27 p. m.		70	
12.33 p. m.			98.1
12.57 p. m.		70	
12.59 p. m.			98.1
1.52 p. m.		81	
1.57 p. m.			98.3
3.34 p. m.		81	98.2
4.30 p. m.		79	98.1
5.32 p. m.		71	
5.41 p. m.			98.0
6.35 p. m.		77	
6.40 p. m.			98.1
6.57 p. m.		78	
7 p. m.	64.32		98.1
7.30 p. m.		88	97.8
8.28 p. m.		72	
8.30 p. m.			97.7
9.30 p. m.		67	
9.32 p. m.			97.3
10.18 p. m.		67	
10.20 p. m.			97.2
Feb. 21, 6.55 a. m.		73	
7 a. m.	63.83		98.1
7.29 a. m.		87	
7.30 a. m.			98.1
8.29 a. m.		92	
8.30 a. m.			98.3
9.30 a. m.		101	98.3
10.30 a. m.		87	
10.33 a. m.			98.4
11.27 a. m.		78	
11.31 a. m.			97.9
12.31 p. m.		77	98.1
1 p. m.		73	

TABLE LXI.—*Summary of the diary—Metabolism experiments Nos. 26–28*—Continued.

Date and time.	Weight with clothes.	Pulse rate per minute.	Temperature.
1900—Continued.			
Experiment No. 28—C't'd.	*Kilograms.*		°*F.*
Feb. 21, 1.54 p. m.		80	
2.01 p. m.			98.2
2.27 p. m.		93	
2.34 p. m.			98.5
3.52 p. m.		86	
3.54 p. m.			98.2
4.35 p. m.		76	
4.52 p. m.		79	98.2
5.28 p. m.		75	98.5
6.32 p. m.		77	
6.59 p. m.		79	98.2
7 p. m.	64.63		
7.31 p. m.		81	97.7
7.41 p. m.			97.9
8.27 p. m.		79	
8.30 p. m.			97.7
9.27 p. m.		73	
9.52 p. m.			97.6
Feb. 22, 6.55 a. m.		69	
7 a. m.	63.85		98.1
7.36 a. m.		85	
7.40 a. m.			97.9
8.28 a. m.		93	
8.33 a. m.			98.3
9.27 a. m.		95	
9.30 a. m.			98.2
Feb. 22, 10.29 a. m.		87	
10.30 a. m.			98.4
11.36 a. m.		82	98.0
12.27 p. m.		74	
12.30 p. m.			98.2
12.55 p. m.		70	
12.58 p. m.			98.2
2.07 p. m.		83	
2.15 p. m.			98.6
2.30 p. m.		84	
2.50 p. m.			98.4
3.30 p. m.		84	98.4
4.29 p. m.		78	98.4
5.30 p. m.		73	
5.37 p. m.			98.2
6.30 p. m.		73	98.4
6.57 p. m.	64.77	76	98.1
7.27 p. m.		74	
7.31 p. m.			97.7
8.32 p. m.		72	
8.42 p. m.			97.5
9.27 p. m.		66	
9.30 p. m.			97.3
10.20 p. m.		70	97.1
Feb. 23, 6.55 a. m.		76	
7 a. m.	64.05		98.1

Detailed statistics of income and outgo.—The quantities of nutrients in the basal ration, which was the same in all 3 experiments, and the quantities in the supplemental ration in the different experiments of this series are shown in Table LXII. The feces were determined for each experiment in order to obtain data concerning the relative digestibility of the food with the different supplemental rations.

TABLE LXII.—*Weight, composition, and heat of combustion of foods—Metabolism experiments Nos. 26–28.*

Laboratory No.	Food material.	Weight per day.	Water.	Protein.	Fat.	Carbohydrates.	Nitrogen.	Carbon.	Hydrogen.	Heat of combustion.
	Basal ration.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
3176	Beef	85.0	53.1	28.7	2.4		4.60	16.62	2.30	187
3177	Butter	30.0	3.0	.5	25.8		.08	19.51	3.01	240
3179	Milk, skimmed	1,000.0	900.0	42.0	3.0	47.0	6.70	46.30	6.30	462
3180	Bread	200.0	78.6	17.8	3.2	97.8	2.84	55.52	7.98	561
3181	Ginger snaps	60.0	2.5	3.7	5.0	47.9	.60	26.59	3.97	266
3168	Parched cereal	50.0	2.8	5.9	.9	39.5	.94	21.10	2.97	207
——	Sugar	15.0				15.0		6.31	.97	59
	Total for 1 day	1,440.0	1,040.0	98.6	40.3	247.2	15.76	191.95	27.50	1,982
	Supplemental ration.									
	EXPERIMENT NO. 26.									
	Butter	63.5	6.3	1.0	54.5		.16	41.29	6.36	508
	Total for 1 day	1,503.5	1,046.3	99.6	94.8	247.2	15.92	233.24	33.86	2,490
	EXPERIMENT NO. 27.									
	Alcohol	72.0						37.56	9.39	509
	Total for 1 day	1,512.0	1,040.0	98.6	40.3	247.2	15.76	229 51	36.89	2,491
	EXPERIMENT NO. 28.									
	Sugar	128.0				128.0		53.88	8.29	507
	Total for 1 day	1,563.0	1,040.0	98.6	40.3	375.2	15.76	245.83	35.79	2,489

TABLE LXIII.—*Weight, composition, and heat of combustion of feces—Metabolism experiments Nos. 26–28.*

Laboratory No.		Weight.	Water.	Protein.	Fat.	Carbohydrates.	Nitrogen.	Carbon.	Hydrogen.	Heat of combustion.
	Experiment No. 26.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
3183	Feces for 3 days	236.5	171.0	20.6	8.5	20.1	3.26	28.33	3.41	317
	Average per day	78.8	57.0	6.9	2.8	6.7	1.09	9.44	1.14	106
	Experiment No. 27.									
3184	Feces for 3 days	218.9	152.1	21.0	6.3	21.2	3.35	26.84	2.41	292
	Average per day	73.0	50.7	7.0	2.1	7.1	1.12	8.95	.80	97
	Experiment No. 28.									
3185	Feces for 3 days	219.9	155.2	23.3	12.1	16.1	3.74	29.93	4.02	335
	Average per day	73.3	51.7	7.8	4.0	5.3	1.25	9.98	1.34	112

The urine was collected and the nitrogen determined in the usual 6-hour periods each day. No attempt was made to dry composite samples of the urine for each experiment for the determinations of carbon and hydrogen, but aliquot portions were taken from each day's urine for the preparation of a 9 days' composite sample, which should represent the urine for the total series of experiments. The heats of combustion of the composite sample for each day were, however, determined. Statistics of the urine for experiment No. 27 are given in detail, by 6-hour periods, and those of experiments Nos. 26 and 28, in which alcohol did not form a part of the diet, are summarized by days, for comparison.

TABLE LXIV.—*Amount, specific gravity, and nitrogen of urine, by 6-hour periods—Metabolism experiments Nos. 26–28.*

Date.		Period.	Amount.	Specific gravity.	Nitrogen.	
1900.		*Experiment No. 26.*	*Grams.*		*Per cent.*	*Grams.*
Feb.	14–15	7 a. m. to 7 a. m.	1,216.5	1.021	1.38	16.63
	15–16	7 a. m. to 7 a. m.	1,526.1	1.0175	.99	15.08
	16–17	7 a. m. to 7 a. m.	1,340.4	1.0185	1.08	14.44
		Experiment No. 27.				
	17	7 a. m. to 1 p. m.	378.5	1.0175	.94	3.56
	17	1 p. m. to 7 p. m.	576.2	1.0135	.71	4.09
	17–18	7 p. m. to 1 a. m.	269.0	1.021	1.38	3.71
	18	1 a. m. to 7 a. m.	297.0	1.018	1.09	3.24
		Total	1,520.7			14.60
		Total by composite	1,520.7	1.017	.96	14.60
	18	7 a. m. to 1 p. m.	537.9	1.014	.79	4.25
	18	1 p. m. to 7 p. m.	444.6	1.016	.97	4.32
	18–19	7 p. m. to 1 a. m.	281.3	1.021	1.41	3.97
	19	1 a. m. to 7 a. m.	172.6	1.0245	1.73	2.99
		Total	1,436.4			15.53
		Total by composite	1,436.4	1.018	1.08	15.51
	19	7 a. m. to 1 p. m.	291.0	1.0215	1.47	4.28
	19	1 p. m. to 7 p. m.	473.0	1.015	1.03	4.87
	19–20	7 p. m. to 1 a. m.	310.9	1.019	1.36	4.23
	20	1 a. m. to 7 a. m.	219.3	1.0215	1.55	3.40
		Total	1,294.2			16.78
		Total by composite	1,294.2	1.018	1.30	16.82
		Experiment No. 28.				
	20–21	7 a. m. to 7 a. m.	1,169.8	1.020	1.36	15.90
	21–22	7 a. m. to 7 a. m.	1,292.2	1.017	1.18	15.23
	22–23	7 a. m. to 7 a. m.	1,202.5	1.018	1.22	14.65

TABLE LXV.—*Daily elimination of carbon, hydrogen, and water in the urine—Metabolism experiments Nos. 26–28.*

Date.	Amount.	Carbon.		Hydrogen.		Water.		Heat of combustion.	
								Per gram.	Total.
1900.									
Experiment No. 26.									
	Grams.	*Per cent.*	*Grams.*	*Per cent.*	*Grams.*	*Per cent.*	*Grams.*	*Calories.*	*Calories.*
Feb. 14–15	1,216.5	.....	11.93	.....	2.87	.....	1,157.3	0.103	125
15–16	1,526.1	.....	10.82	.....	2.61	.....	1,472.4	.082	125
16–17	1,340.4	.....	10.36	.....	2.50	.....	1,289.0	.101	135
	4,083.0	.....	33.11	.....	7.98	.....	3,918.7	.....	385
Experiment No. 27.									
Feb. 17–18	1,520.7	.....	10.47	.....	2.52	.....	1,468.7	.073	111
18–19	1,436.4	.....	11.14	.....	2.69	.....	1,381.1	.084	121
19–20	1,294.2	.....	12.04	.....	2.90	.....	1,234.5	.108	140
	4,251.3	.....	33.65	.....	8.11	.....	4,084.3	.....	372
Experiment No. 28.									
Feb. 20–21	1,169.8	.....	11.40	.....	2.75	.....	1,113.2	.102	119
21–22	1,292.2	.....	10.92	.....	2.63	.....	1,238.0	.103	133
22–23	1,202.5	.....	10.51	.....	2.53	.....	1,150.3	.110	132
	3,664.5	.....	32.83	.....	7.91	.....	3,501.5	.....	384
Total, 9 days	11,998.8	.83	99.59	.20	24.00	95.88	11,504.5	.095	1,141

Tables LXVI–LXVIII show the quantities of carbon dioxid and water found in the ventilating air current in this series of experiments. These statistics are given in detail for the 3 days of experiment No. 27, in which alcohol formed a part of the diet, and are summarized by days for experiments Nos. 26 and 28.

TABLE LXVI.—*Comparison of residual amounts of carbon dioxid and water in the chamber at the beginning and end of each period, and the corresponding gain or loss—Metabolism experiment No. 27.*

Date.	End of period.	Carbon dioxid.		Water.[a]		
		Total amount in chamber.	Gain (+) or loss (−) over preceding period.	Total amount of vapor remaining in chamber.	Gain (+) or loss (−) over preceding period.	Total amount gained (+) or lost (−) during the period.
1900.		*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Feb. 17	7 a. m	23.0	.....	31.4	.....	.....
17	1 p. m	33.1	+10.1	37.1	+5.7	+5.7
17	7 p. m	37.8	+4.7	38.6	+1.5	+1.5
18	1 a. m	23.6	−14.2	34.8	−3.8	−3.8
18	7 a. m	27.0	+3.4	33.3	1.5	−1.5
		.....	+4.0	.....	+1.9	+1.9
18	1 p. m	31.0	+4.0	37.2	+3.9	+3.9
18	7 p. m	36.5	+5.5	37.8	+0.6	+0.6
19	1 a. m	24.1	−12.4	35.3	−2.5	−2.5
19	7 a. m	25.3	+1.2	31.0	−4.3	−4.3
		.....	−1.7	.....	−2.3	−2.3
19	1 p. m	31.0	+5.7	37.1	+6.1	+6.1
19	7 p. m	39.1	+8.1	39.0	+1.9	+1.9
20	1 a. m	23.0	−16.1	35.5	3.5	−3.5
20	7 a. m	26.4	+3.4	32.9	−2.6	−2.6
		.....	+1.1	.....	+1.9	+1.9
		.....	+3.4	.....	+1.5	.....

[a] There was no change in weight of absorbers and no drip in this experiment.

TABLE LXVII.—*Record of carbon dioxid in ventilating air current—Metabolism experiments Nos. 26–28.*

Date.	Period.	(a) Ventilation. Number of liters of air.	Carbon dioxid. In incoming air. (b) Per liter.	(c) Total, $a \times b$.	(d) In outgoing air.	(e) Total excess in outgoing air, $d - c$.	(f) Correction for amount remaining in chamber.	(g) Corrected amount exhaled by subject, $e+f$.	(h) Total weight of carbon exhaled, $g \times 3$.
1900.	*Experiment No. 26.*	*Liters.*	*Mg.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Feb. 14–15	7 a. m. to 7 a. m	116,602	.....	64.7	776.3	711.6	+ 3.1	714.7	194.9
15–16	7 a. m. to 7 a. m	118,158	.....	65.7	795.9	730.2	− 2.7	727.5	198.4
16–17	7 a. m. to 7 a. m	119,712	.....	67.7	782.0	714.3	+ 0.4	714.7	194.9
	Experiment No. 27.								
17	7 a. m. to 1 p. m	29,540	0.567	16.8	217.6	200.8	+10.1	210.9	57.5
17	1 p. m. to 7 p. m	27,207	.610	16.6	215.5	198.9	+ 4.7	203.6	55.5
17–18	7 p. m. to 1 a. m	29,540	.561	16.6	206.3	189.7	−14.2	175.5	47.9
18	1 a. m. to 7 a. m	28,762	.554	15.9	146.2	130.3	+ 3.4	133.7	36.5
	Total	115,049	.....	65.9	785.6	719.7	+ 4.0	723.7	197.4
18	7 a. m. to 1 p. m	28,762	.559	16.1	220.8	204.7	+ 4.0	208.7	56.9
18	1 p. m. to 7 p. m	28,762	.551	15.8	214.5	198.7	+ 5.5	204.2	55.7
18–19	7 p. m. to 1 a. m	29,540	.537	15.9	206.2	190.3	−12.4	177.9	48.5
19	1 a. m. to 7 a. m	29,540	.548	16.2	147.5	131.3	+ 1.2	132.5	36.1
	Total	116,604	.....	64.0	789.0	725.0	− 1.7	723.3	197.2
19	7 a. m. to 1 p. m	27,208	.548	14.9	209.5	194.6	+ 5.7	200.3	54.6
19	1 p. m. to 7 p. m	27,985	.575	16.1	218.5	202.4	+ 8.1	210.5	57.4
19–20	7 p. m. to 1 a. m	29,540	.573	16.9	220.1	203.2	−16.1	187.1	51.0
20	1 a. m. to 7 a. m	28,762	.551	15.8	149.2	133.4	+ 3.4	136.8	37.3
	Total	113,495	.....	63.7	797.3	733.6	+ 1.1	734.7	200.3
	Experiment No. 28.								
20–21	7 a. m. to 7 a. m	112,717	.....	64.3	840.3	776.0	− 2.3	773.7	211.0
21–22	7 a. m. to 7 a. m	108,830	.....	67.6	843.3	775.7	+ 4.8	780.5	212.8
22–23	7 a. m. to 7 a. m	111,162	.....	66.4	830.6	764.2	− 0.2	764.0	208.3

TABLE LXVIII.—*Record of water in ventilating air current—Metabolism experiments Nos. 26–28.*

Date.	Period.	(a) Ventilation. Number of liters of air.	Water in incoming air. (b) Per liter.	(c) Total, $a \times b$.	Water in outgoing air. (d) Amount condensed in freezers.	(e) Amount not condensed in freezers.	(f) Total, $d+e$.	(g) Total excess water in outgoing air, $f-c$.	(h) Correction for water remaining in chamber.	(i) Total water of respiration and perspiration, $g+h$.
1900.	*Experiment No. 26.*	*Liters.*	*Mg.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Feb. 14–15	7 a. m. to 7 a. m	116,602	.....	97.1	749.3	179.6	928.9	831.8	2.7	829.1
15–16	7 a. m. to 7 a. m	118,158	.....	101.8	734.3	175.4	909.7	807.9	−1.3	806.6
16–17	7 a. m. to 7 a. m	119,712	.....	97.8	724.9	173.3	898.2	800.4	−0.9	799.5
	Experiment No. 27.									
17	7 a. m. to 1 p. m	29,540	.820	24.2	183.9	42.5	226.4	202.2	+5.7	207.9
17	1 p. m. to 7 p. m	27,207	.821	22.3	193.7	38.0	231.7	209.4	+1.5	210.9
17–18	7 p. m. to 1 a. m	29,540	.829	24.5	184.7	45.2	229.9	205.4	−3.8	201.6
18	1 a. m. to 7 a. m	28,762	.828	23.8	166.4	39.0	205.4	181.6	−1.5	180.1
	Total	115,049	.....	94.8	728.7	164.7	893.4	798.6	+1.9	800.5
18	7 a. m. to 1 p. m	28,762	.817	23.5	194.5	43.6	238.1	214.6	+3.9	218.5
18	1 p. m. to 7 p. m	28,762	.800	23.0	194.5	41.0	235.5	212.5	+0.6	213.1
18–19	7 p. m. to 1 a. m	29,540	.818	24.2	185.5	43.8	229.3	205.1	−2.5	202.6
19	1 a. m. to 7 a. m	29,540	.800	23.6	172.0	39.4	211.4	187.8	−4.3	183.5
	Total	116,604	.....	94.3	746.5	167.8	914.3	820.0	−2.3	817.7

TABLE LXVIII.—*Record of water in ventilating air current—Metabolism experiments Nos. 26–28*—Continued.

Date.	Period.	(a) Water in incoming air. Ventilation. Number of liters of air.	(b) Water in incoming air. Per liter.	(c) Water in incoming air. Total, $a \times b$.	Water in outgoing air. (d) Amount condensed in freezers.	(e) Amount not condensed in freezers.	(f) Total, $d+e$.	(g) Total excess water in outgoing air, $f-c$.	(h) Correction for water remaining in chamber.	(i) Total water of respiration and perspiration, $g+h$.
	Experiment No. 27—Continued.									
1900.		*Liters.*	*Mg.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Feb. 19	7 a. m. to 1 p. m	27,208	.810	22.0	184.3	39.6	223.9	201.9	+6.1	208.0
19	1 p. m. to 7 p. m	27,985	.826	23.1	191.2	38.2	229.4	206.3	+1.9	208.2
19–20	7 p. m. to 1 a. m	29,540	.837	24.7	195.2	45.9	241.1	216.4	−3.5	212.9
20	1 a. m. to 7 a. m	28,762	.819	23.6	173.3	39.0	212.3	188.7	−2.6	186.1
	Total	113,495		93.4	744.0	162.7	906.7	813.3	+1.9	815.2
	Experiment No. 28.									
20–21	7 a. m. to 7 a. m	112,717		94.8	769.8	163.7	933.5	838.7	−2.1	836.6
21–22	7 a. m. to 7 a. m	108,830		90.2	742.4	156.9	899.3	809.1	+4.7	813.8
22–23	7 a. m. to 7 a. m	111,162		97.9	730.7	159.9	890.6	792.7	2.1	790.6

The heat carried away by the water current and the latent heat of vaporization of water in this series of experiments are shown in Table LXIX. As in the previous tables, the data are summarized for experiments Nos. 26 and 28 and given in detail for experiment No. 27, in which alcohol formed a part of the diet.

TABLE LXIX.—*Summary of calorimetric measurements—Metabolism experiments Nos. 26–28.*

Date.	Period.	(a) Heat measured in terms of C_{20}.	(b) Change of temperature of calorimeter.	(c) Capacity correction of calorimeter $b \times .60$.	(d) Correction due to temperature of food and dishes.	(e) Water vaporized equals total amount exhaled less amount condensed in chamber.	(f) Heat used in vaporization of water $e \times 0.592$.	(g) Total heat determined $a+c+d+f$.
1900.	*Experiment No. 26.*	*Calories.*	*Degrees.*	*Calories.*	*Calories.*	*Grams.*	*Calories.*	*Calories.*
Feb. 14–15	7 a. m. to 7 a. m	1,584.1	+0.1	+0.60	+ 1.7	829.1	490.8	2,077.2
15–16	7 a. m. to 7 a. m	1,618.3	+ .3	+1.80	+ 2.5	806.6	477.5	2,100.1
16–17	7 a. m. to 7 a. m	1,592.3	+ .1	+ .60	+12.0	799.5	473.3	2,078.2
	Experiment No. 27.							
17	7 a. m. to 1 p. m	513.1	+ .1	+ .60	− 3.1	207.9	123.1	633.7
17	1 p. m. to 7 p. m	477.5	0	0	− 9.3	210.9	124.8	593.0
17–18	7 p. m. to 1 a. m	404.6	0	0	+ 1.0	201.6	119.3	524.9
18	1 a. m. to 7 a. m	256.8	+ .1	+ .60		180.1	106.6	364.0
	Total	1,652.0	+ .2	+1.20	11.4	800.5	473.8	2,115.6
18	7 a. m. to 1 p. m	527.4	0	0	− 8.2	218.5	129.3	648.5
18	1 p. m. to 7 p. m	481.6	0	0	− 9.6	213.1	126.2	598.2
18–19	7 p. m. to 1 a. m	402.2	− .1	− .60	+ 4.3	202.6	119.9	525.8
19	1 a. m. to 7 a. m	243.9	+ .1	+ .60		183.5	108.6	353.1
	Total	1,655.1	0	0	−13.5	817.7	484.0	2,125.6
19	7 a. m. to 1 p. m	515.5	0	0	− 8.4	208.0	123.1	630.2
19	1 p. m. to 7 p. m	467.9	0	0	− 7.1	208.2	123.2	584.0
19–20	7 p. m. to 1 a. m	403.7	0	0	+ 3.7	212.9	126.0	533.4
20	1 a. m. to 7 a. m	269.5	− .1	+ .60		186.1	110.2	380.3
	Total	1,656.6	+ .1	+ .60	−11.8	815.2	482.5	2,127.9
	Experiment No. 28.							
20–21	7 a. m. to 7 a. m	1,599.5	0	0	+ 2.8	836.6	495.2	2,097.5
21–22	7 a. m. to 7 a. m	1,589.7	− .2	+1.20	+ 2.6	813.8	481.8	2,075.3
22–23	7 a. m. to 7 a. m	1,594.2	+ .1	+ .60	+ 2.2	790.6	468.0	2,065.0

The determinations of alcohol in urine and freezer water and of reducing material reckoned as alcohol in the air current were made in the usual manner, and the results are given in Table LXX. It will be observed that there was an elimination of reducing material equivalent to an average of 0.32 gram of alcohol per day on the 6 days of experiments Nos. 26 and 28. This amount has been deducted from the values obtained in experiment No. 27, and the difference is taken as a measure of the alcohol excreted unoxidized. It will likewise be observed that there is here no indication whatever of any lag in the elimination of alcohol from the body as was apparently indicated by the results obtained in experiments Nos. 18–20.

TABLE LXX.—*Alcohol ingested and excreted—Metabolism experiment No. 27.*

Date.	Alcohol ingested.	Alcohol excreted, including other reducing material calculated as alcohol.				Alcohol excreted unoxidized.[a]	Alcohol metabolized in body.	
		In urine (distillate).	In freezer water (distillate).	In air current.	Total.			
1900.								
Experiment No. 26.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Per cent.*
Feb. 14–15		0.02	0.01	0.33	0.36			
15–16		.03	Trace.	.28	.31			
16–17		.02	Trace.	.45	.47			
Experiment No. 27.								
Feb. 17–18	72	.13	.01	1.23	1.37	1.05	70.9	98.5
18–19	72	.11	.01	1.04	1.16	.84	71.2	98.9
19–20	72	.09	.01	.98	1.08	.76	71.2	98.9
Total	216	.33	.03	3.25	3.61	2.65	213.3	
Average for day	72	.11	.01	1.08	1.20	.88	71.1	98.8
Experiment No. 28.								
Feb. 20–21		.02	Trace.	.29	.31			
21–22		.02	.01	.19	.22			
22–23		.01	.01	.21	.23			

[a] Equals total reducing material excreted less 0.32 grams of reducing material not alcohol, the average for the days on which no alcohol was consumed.

Balance of income and outgo of matter and energy.—Tables LXXI to LXXIV summarize the income and outgo of nitrogen, carbon, hydrogen, and energy according to the plan adopted in previous experiments.

TABLE LXXI.—*Income and outgo of nitrogen and carbon—Metabolism experiments Nos. 26–28.*

Date and period.	Nitrogen.				Carbon.					
	(*a*) In food.	(*b*) In feces.	(*c*) In urine.	(*d*) Gain (+) or loss (−) (*a* − (*b*+*c*)).	(*e*) In food.	(*f*) In feces.	(*g*) In urine.	(*h*) In respiratory products.	(*i*) In alcohol eliminated.	(*k*) Gain (+) or loss (−) (*e* − (*f*+*g* +*h*+*i*)).
1900.										
Experiment No. 26.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Feb. 14–15, 7 a. m. to 7 a. m.	15.9	1.1	16.6	1.8	233.2	9.4	11.9	194.9	.....	−17.0
15–16, 7 a. m. to 7 a. m.	15.9	1.1	15.1	.3	233.2	9.5	10.8	198.4	.....	−14.5
16–17, 7 a. m. to 7 a. m.	15.9	1.1	14.4	+.4	233.2	9.4	10.4	194.9	.....	−18.5
Total	47.7	3.3	46.1	1.7	699.6	28.3	33.1	588.2	.....	−50.0
Average per day	15.9	1.1	15.4	.6	233.2	9.4	11.0	196.1	.....	−16.7

TABLE LXXI.—*Income and outgo of nitrogen and carbon—Metabolism experiments Nos. 26–28*—Continued.

Date and period.	Nitrogen.				Carbon.					
	(*a*) In food.	(*b*) In feces.	(*c*) In urine.	(*d*) Gain (+) or loss (−) $a-(b+c)$.	(*e*) In food.	(*f*) In feces.	(*g*) In urine.	(*h*) In respiratory products.	(*i*) In alcohol eliminated.	(*k*) Gain (+) or loss (−) $e-(f+g+h+i)$.
1900.										
Experiment No 27.										
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Feb. 17–18, 7 a. m. to 7 a. m.	15.8	1.1	14.6	+ .1	229.5	8.9	10.5	197.4	0.5	+12.2
18–19, 7 a. m. to 7 a. m.	15.7	1.1	15.5	− .9	229.5	9.0	11.1	197.2	0.4	+11.8
19–20, 7 a. m. to 7 a. m.	15.8	1.1	16.8	−2.1	229.5	8.9	12.0	200.3	0.4	+ 7.9
Total	47.3	3.3	46.9	−2.9	688.5	26.8	33.6	594.9	1.3	+31.9
Average per day	15.8	1.1	15.7	−1.0	229.5	8.9	11.2	198.3	.5	−10.6
Experiment No. 28.										
Feb. 20–21, 7 a. m. to 7 a. m.	15.8	1.2	15.9	−1.3	245.8	10.0	11.4	211.0	.....	+13.4
21–22, 7 a. m. to 7 a. m.	15.7	1.3	15.2	− .8	245.8	10.0	10.9	212.8	.....	+12.1
22–23, 7 a. m. to 7 a. m.	15.8	1.2	14.7	− .1	245.8	10.0	10.5	208.3	.....	−17.0
Total	47.3	3.7	45.8	−2.2	737.4	30.0	32.8	632.1	.....	+42.5
Average per day	15.8	1.2	15.3	− .7	245.8	10.0	10.9	210.7	.....	−14.2

TABLE LXXII.—*Income and outgo of water and hydrogen—Metabolism experiments Nos. 26–28.*

Date and period	Water.						Hydrogen.						
	(*a*) In food.	(*b*) In drink.	(*c*) In feces.	(*d*) In urine.	(*e*) In respiratory products.	(*f*) Apparent loss $a+b-(c+d+e)$.	(*g*) In food.	(*h*) In feces.	(*i*) In urine.	(*k*) In alcohol eliminated.	(*l*) Apparent gain $g-(h+i+k)$.	(*m*) Loss from water $f\div 9$.	(*n*) Total gain (+) or loss (−) $l+m$.
1900.													
Experiment No. 26.													
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Gms.*	*Gms.*	*Gms.*	*Grams.*	*Grams.*	*Grams.*
Feb. 14–15, 7 a. m. to 7 a. m	1,046.3	800.0	57.0	1,157.3	829.1	− 197.1	33.9	1.1	2.9	.....	+29.9	− 21.9	− 8.0
Feb. 15–16, 7 a. m. to 7 a. m	1,046.3	800.0	57.0	1,472.4	806.6	− 489.7	33.8	1.2	2.6	.....	− 30.0	54.4	−24.4
Feb. 16–17, 7 a. m. to 7 a. m	1,046.3	800.0	57.0	1,289.0	799.5	− 299.2	33.9	1.1	2.5	.....	+30.3	− 33.2	− 2.9
Total	3,138.9	2,400.0	171.0	3,918.7	2,435.2	− 986.0	101.6	3.4	8.0	.....	+90.2	109.5	19.3
Average per day	1,046.3	800.0	57.0	1,306.2	811.7	− 328.6	33.9	1.1	2.7	.....	+30.1	− 36.5	− 6.4
Experiment No. 27.													
Feb. 17–18, 7 a. m. to 7 a. m	1,040.0	800.0	50.7	1,468.7	800.5	− 479.9	36.9	.8	2.5	0.1	+33.5	53.3	−19.8
Feb. 18–19, 7 a. m. to 7 a. m	1,040.0	800.0	50.7	1,381.1	817.7	− 409.5	36.9	.8	2.7	.1	− 33.3	45.5	12.2
Feb. 19–20, 7 a. m. to 7 a. m	1,040.0	800.0	50.7	1,234.5	815.2	− 260.4	36.9	.8	2.9	.1	+33.1	− 28.9	− 4.2
Total	3,120.0	2,400.0	152.1	4,084.3	2,433.4	−1,149.8	110.7	2.4	8.1	.3	+99.9	−127.7	27.8
Average per day	1,040.0	800.0	50.7	1,361.4	811.1	− 383.2	36.9	.8	2.7	.1	+33.3	− 42.6	9.3
Experiment No. 28.													
Feb. 20–21, 7 a. m. to 7 a. m	1,040.0	800.0	51.7	1,113.2	836.6	− 161.5	35.8	1.3	2.8	.....	31.7	17.9	− 13.8
Feb. 21–22, 7 a. m. to 7 a. m	1,040.0	800.0	51.8	1,238.0	813.8	− 263.6	35.8	1.4	2.6	.....	− 31.8	− 29.3	− 2.5
Feb. 22–23, 7 a. m. to 7 a. m	1,040.0	800.0	51.7	1,150.3	790.6	− 152.6	35.8	1.3	2.5	.....	32.0	17.0	+15.0
Total	3,120.0	2,400.0	155.2	3,501.5	2,441.0	− 577.7	107.4	4.0	7.9	.....	− 95.5	− 64.2	+31.3
Average per day	1,040.0	800.0	51.7	1,167.2	813.7	− 192.6	35.8	1.3	2.7	.....	−31.8	− 21.4	−10.4

TABLE LXXIII.—*Gain or loss of protein (N × 6.25), fat, and water—Metabolism experiments Nos. 26–28.*

Date and period.	(a) Nitrogen gained (+) or lost (−).	(b) Protein gained (+) or lost (−). $a \times 6.25$	(c) Total carbon gained (+) or lost (−).	(d) Carbon in protein gained (+) or lost (−). $b \times .53$.	(e) Carbon in fat, etc., gained (+) or lost (−). $c - d$.	(f) Fat gained (+) or lost (−). $e \times .761$.	(g) Total hydrogen gained (+) or lost (−).	(h) Hydrogen in protein gained (+) or lost (−). $b \times .07$.	(i) Hydrogen in fat gained (+) or lost (−). $f \times .118$	(k) Hydrogen in water, etc., gained (+) or lost (−). $g - (h+i)$.	(l) Water gained (+) or lost (−). $k \times 9$.
1900.											
Experiment No. 26.											
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Feb. 14–15, 7 a. m. to 7 a. m.	−1.8	11.2	−17.0	5.9	−22.9	−30.1	+8.0	−.8	+3.6	+5.2	+46.8
15–16, 7 a. m. to 7 a. m.	.3	1.9	−14.5	1.0	−15.5	−20.4	24.4	.1	−2.4	26.7	240.3
16–17, 7 a. m. to 7 a. m.	.4	2.5	−18.5	−1.3	17.2	−22.6	−2.9	+.2	+2.7	5.8	−52.2
Total	1.7	10.6	−50.0	5.6	−55.6	−73.1	19.3	.7	−8.7	27.3	−245.7
Average per day	.6	3.5	−16.7	−1.8	−18.5	−24.4	−6.4	−.2	+2.9	−9.1	−81.9
Experiment No. 27.											
Feb. 17–18, 7 a. m. to 7 a. m.	−.1	+.6	−12.2	−.3	−11.9	−15.6	−19.8	.....	+1.9	−21.7	195.3
18–19, 7 a. m. to 7 a. m.	−.9	5.6	−11.8	−3.0	−14.8	−19.4	12.2	−.4	+2.3	−14.1	126.9
19–20, 7 a. m. to 7 a. m.	−2.1	13.1	−7.9	6.9	−14.8	−19.5	−4.2	−.9	−2.3	−2.8	+25.2
Total	−2.9	18.1	−31.9	−9.6	−41.5	−54.5	27.8	1.3	+6.5	−33.0	−297.0
Average per day	−1.0	6.0	−10.6	−3.2	−13.8	−18.2	−9.3	−.4	+2.1	−11.0	−99.0
Experiment No. 28.											
Feb. 20–21, 7 a. m. to 7 a. m.	−1.3	−8.1	−13.4	4.3	+17.7	−23.3	−13.8	−.6	−2.7	+11.7	−105.3
21–22, 7 a. m. to 7 a. m.	−.8	5.0	−12.1	−2.7	+14.8	−19.4	+2.5	−.3	+2.3	+.5	+4.5
22–23, 7 a. m. to 7 a. m.	−.1	.6	−17.0	−.3	−17.3	−22.7	−15.0	.....	+2.7	−12.3	+110.7
Total	−2.2	13.7	−42.5	−7.3	−49.8	−65.4	−31.3	.9	−7.7	+24.5	−220.5
Average per day	−.7	4.5	−14.2	2.4	−16.6	−21.8	−10.4	.3	−2.5	+8.2	−73.5

TABLE LXXIV.—*Income and outgo of energy—Metabolism experiments Nos. 26–28.*

Date and period.	(a) Heat of combustion of food eaten.	(b) Heat of combustion of feces.	(c) Heat of combustion of urine.	(m) Heat of combustion of alcohol eliminated.	(d) Estimated heat of combustion of protein gained (+) or lost (−).	(e) Estimated heat of combustion of fat gained (+) or lost (−).	(f) Estimated energy of material oxidized in the body. $a-(b+c+m+d+e)$.	(g) Heat determined.	Heat determined greater (+) or less (−) than estimated. (h) $f-g$.	(i) $h \div f$.
1900.										
Experiment No. 26.										
	Calories.	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Per cent.*
Feb. 14–15, 7 a. m. to 7 a. m.	2,490	106	125	.....	64	+287	2,036	2,077	+41	+2.0
15–16, 7 a. m. to 7 a. m.	2,490	106	125	.....	−11	+195	2,075	2,100	+25	+1.2
16–17, 7 a. m. to 7 a. m.	2,490	106	135	.....	−14	+216	2,019	2,078	+59	+2.9
Total	7,470	318	385	.....	−61	+698	6,130	6,255	+125	.....
Average per day	2,490	106	128	.....	20	+233	2,043	2,085	+42	+2.0
Experiment No. 27.										
Feb. 17–18, 7 a. m. to 7 a. m.	2,491	97	111	7	−3	−149	2,124	2,116	−8	.4
18–19, 7 a. m. to 7 a. m.	2,491	97	121	6	32	+185	2,114	2,126	−12	+.6
19–20, 7 a. m. to 7 a. m.	2,491	97	140	5	75	+186	2,138	2,128	10	.5
Total	7,473	291	372	18	−104	−520	6,376	6,370	−6	.....
Average per day	2,491	97	124	6	35	+174	2,125	2,123	2	.1
Experiment No. 28.										
Feb. 20–21, 7 a. m. to 7 a. m.	2,489	112	119	.....	47	−222	2,083	2,097	−14	−.7
21–22, 7 a. m. to 7 a. m.	2,489	112	133	.....	29	+185	2,088	2,075	−13	.6
22–23, 7 a. m. to 7 a. m.	2,489	112	132	.....	3	+217	2,031	2,065	−34	−1.7
Total	7,467	336	384	.....	79	+624	6,202	6,237	−35	.....
Average per day	2,489	112	128	.....	26	+208	2,067	2,079	+12	.6

EXPERIMENTS NOS. 29–31.—WORK. NO. 30 WITH ALCOHOL DIET.

Subject.—J. F. S., who served as the subject of the previous series of rest experiments Nos. 26–28. His weight with underclothing was about 64.5 kilograms (142 pounds).

Occupation during experiment.—Work, 8 hours a day, upon a stationary bicycle arranged as an ergometer, as described on page 237.

Duration.—This experiment was the second of a series of 3, each of which continued 3 days. The preliminary period continued 4 days, beginning with breakfast March 12, 1900. On the evening of the fourth day, March 15, the subject entered the calorimeter. The first of the 3 series of experiments, No. 29, began at 7 a. m. March 16, and continued until 7 a. m. March 19, when experiment No. 30 began and continued until 7 a. m. March 22, and in turn was followed by experiment No. 31, which continued until 7 a. m. March 25. The subject therefore remained in the respiration chamber 9 days and 10 nights.

Diet.—The object of this series of experiments was to study the relative replacing power of isodynamic quantities of sugar, alcohol, and fat, when the subject was at active exercise. There was a basal ration, as in the previous series, which was practically the same in the 3 experiments, the only difference being that due to slight variations in the composition of the milk consumed. It furnished, approximately, 100 grams of protein and from 2,949 to 2,984 calories of energy per day in the different periods. To this ration was added, in experiment No. 29, 128 grams of cane sugar per day, furnishing 507 calories of energy. In experiment No. 30 the supplemental ration consisted of 72 grams of absolute alcohol per day, furnishing 509 calories of energy. In experiment No. 31 the supplemental ration consisted of 63.5 grams of butter per day, furnishing 1 gram of protein and 541 calories of energy.

To 795.5 grams of water sweetened with 25 grams of sugar were added 79.5 grams of 90.6 per cent commercial alcohol containing 72 grams absolute alcohol. This alcohol mixture was taken with and between meals in experiment No. 30 as in previous experiments. The sugar in experiment No. 29 was likewise taken with and between meals, but the butter in experiment No. 31 was consumed with the rest of the food in approximately equal portions at breakfast, dinner, and supper. The same amount of water was given in the drink on each day of the experiment and amounted to 1,250 grams per day. In experiment No. 30, 803 grams of this water was furnished by the alcohol mixture. The kinds and quantities of food served at each meal and the quantities of drink at different periods of the day were as follows:

Diet in metabolism experiments Nos. 29–31.

FOOD—BASAL RATION.

	Breakfast.	Dinner.	Supper.	Total.
	Grams.	*Grams.*	*Grams.*	*Grams.*
Beef	.....	58	.....	58
Butter	12	23	12	47
Milk, whole	300	300	300	900
Bread	75	150	75	300
Ginger snaps	25	25	25	75
Parched cereal	37.5	.....	37.5	75
Sugar[a]	12.5	.....	12.5	25

[a] Eaten on parched cereal in experiments Nos. 29 and 31; added to water and alcohol in experiment No. 30.

FOOD—SUPPLEMENTAL RATION.

Experiment No. 29, March 16–18.—128 grams of cane sugar daily in the form of loaf sugar, taken with and between meals. This amount also supplemented the basal ration during the preliminary experiment March 12–15.

Experiment No. 30, March 19–21.—72 grams absolute alcohol daily. This required 79.5 grams of 90.57 per cent alcohol, which was made up to 900 grams with the addition of 25 grams sugar and the rest water.

Experiment No. 31, March 22–24.—The additional energy during this experiment was furnished by 63.5 grams butter.

Diet in metabolism experiments Nos. 29–31.

DRINK.

	Experiment No. 29.	Experiment No. 30.		Experiment No. 31.
	Water.	Alcohol and sweetened water.	Water.	Water.
	Grams.	*Grams.*	*Grams.*	*Grams.*
Breakfast	150	175	75	150
10.15 a. m	200	100	75	200
Dinner	200	175	75	200
4 p. m	200	100	75	200
Supper	150	175	75	150
9 p. m	200	100	72	200
10.20 p. m	150	75	.....	150
Total	1,250	[a]900	447	1,250

[a] Contained 803 grams water, 25 grams sugar, and 72 grams alcohol.

Daily routine.—The general routine of the series of experiments is indicated in the following schedule:

Daily programme—Metabolism experiments Nos. 29–31.

6.50 a. m	Take pulse and temperature.
7 a. m	Pass urine, weigh self dressed, collect drip and weigh absorbers.
7.30 a. m	Breakfast. Drink 150 grams water.
8.15 a. m	Begin work.
10.15 a. m	Stop work. Drink 200 grams water.
10.30 a. m	Begin work.
12.30 p. m	Stop work.
12.50 p. m	Take pulse and temperature.
1 p. m	Pass urine, collect drip and weigh absorbers.
1.25 p. m	Dinner. Drink 200 grams water.
2 p. m	Begin work.
4 p. m	Stop work. Drink 200 grams water.
4.15 p. m	Begin work.
6.15 p. m	Stop work. Change underclothing
6.20 p. m	Supper. Drink 150 grams water.
6.50 p. m	Take pulse and temperature.
7 p. m	Pass urine, weigh self dressed, collect drip and weigh absorbers.
9 p. m	Drink 200 grams water.
10 p. m	Take pulse and temperature.
10.10 p. m	Arrange bed.
10.20 p. m	Drink 150 grams water.
10.30 p. m	Retire.
1 a. m	Pass urine.

Table LXXV summarizes the more important statistics in the diary kept by the subject. The pulse rate was observed during periods of both work and rest. The observations of body temperature could not be made as frequently as in the previous series of (rest) experiments, but were frequent enough to afford basis of comparison between the different experiments of this series.

Amount of work done.—The total number of miles registered by the cyclometer on different days of the series of experiments and the heat equivalent of the work done each day are shown in Table LXXVI. As has already been pointed out, the amount of work done could hardly have been as large as would be required to propel a bicycle the number of miles recorded by the cyclometer. It will be observed that there was but little difference in the average amounts of work done in different days in the different experiments of this series.

TABLE LXXV.—*Summary of the diary—Metabolism experiments Nos. 29–31.*

Date and time.	Weight.	Pulse rate per minute.	Temperature.
Experiment No. 29.	*Kilograms.*		°F.
Mar. 16, 7 a. m.	63.85	71	97.6
9 a. m.		90	
10 a. m.		85	
11 a. m.		87	
12 m		90	
1 p. m.		79	98.5
3 p. m.		101	
4 p. m.		108	
5 p. m.		102	
6 p. m.		88	
7 p. m.	64.78	83	
9 p. m.		82	98.2
Mar. 17, 7 a. m.	64.76	66	97.4
9 a. m.		92	
10 a. m.		96	
11 a. m.		94	
12 m		94	
1 p. m.		74	98.4
3 p. m.		93	
4 p. m.		98	
5 p. m.		93	
6 p. m.		94	
7 p. m.	65.12	77	97.9
8.08 p. m.		76	
8.12 p. m.			97.6
9 p. m.		75	97.4
10 p. m.		69	
10.10 p. m.			96.9
Mar. 18, 7 a. m.	64.76	65	97.3
9 a. m.		88	
10 a. m.		93	
11 a. m.		91	
12 m		92	
1 p. m.		69	98.0
3 p. m.		91	
4 p. m.		95	
5 p. m.		95	
6 p. m.		93	
7 p. m.	64.96	79	97.8
8.15 p. m.		74	
8.23 p. m.			97.4
9.15 p. m.		77	97.2
10.20 p. m.		66	
10.25 p. m.			96.4
Experiment No. 30.			
Mar. 19, 6.55 a. m.	64.59	66	
7 a. m.			97.6
9 a. m.		97	
10.35 a. m.		91	
11 a. m.		89	
1 p. m.		69	98.2
3 p. m.		88	
4 p. m.		87	
5 p. m.		93	
6 p. m.		93	
7 p. m.	65.05	78	97.7
8 p. m.		74	98.0
9 p. m.		75	97.4
10.10 p. m.		72	97.3
Mar. 20, 6.55 a. m.	64.48	66	
7 a. m.			97.8
9 a. m.		101	
10 a. m.		91	
11 a. m.		87	
12 m		85	
12.55 p. m.		68	
1 p. m.			97.4
3 p. m.		95	
4 p. m.		92	
5 p. m.		92	
6 p. m.		85	

Date and time.	Weight.	Pulse rate per minute.	Temperature.
Experiment No. 30—C't'd.	*Kilograms.*		°F.
Mar. 20, 7 p. m.	64.80	72	97.3
8 p. m.		77	
8.09 p. m.			
9 p. m.		74	
9.07 p. m.			97.2
10.10 p. m.		73	96.8
Mar. 21, 6.55 a. m.		64	
7 a. m.	64.34		97.7
9 a. m.		99	
10 a. m.		93	
11 a. m.		88	
12 m		84	
1 p. m.		70	98.1
3 p. m.		101	
4 p. m.		102	
5 p. m.		95	
6 p. m.		89	
6.55 p. m.	64.60	76	97.8
8 p. m.		80	97.5
9 p. m.		69	97.0
10.15 p. m.		74	97.0
Experiment No. 31.			
Mar. 22, 6.55 a. m.	64.09	65	
7 a. m.			97.6
9 a. m.		93	
10 a. m.		87	
11 a. m.		90	
12 m		87	
1 p. m.		67	97.8
3 p. m.		99	
4 p. m.		93	
5 p. m.		97	
6 p. m.		93	
6.55 p. m.		71	
7 p. m.	64.55		
8 p. m.		76	97.5
9 p. m.		70	97.0
10.12 p. m.		67	96.5
Mar. 23, 6.55 a. m.		68	97.6
7 a. m.	64.24		
9 a. m.		100	
10 a. m.		92	
11 a. m.		89	
12 m		89	
1 p. m.			
3 p. m.		97	
4 p. m.		94	
5 p. m.		89	
6 p. m.		90	
7 p. m.	64.68	74	97.6
8 p. m.		75	97.5
9 p. m.		68	
10.10 p. m.		66	
Mar. 24, 6.55 p. m.	64.38	65	
9 a. m.		89	
10 a. m.		95	
11 a. m.		86	
12 m		88	
12.55 p. m.		68	
1 p. m.			97.8
3 p. m.		98	
4 p. m.		98	
5 p. m.		91	
6 p. m.		90	
7 p. m.	64.90	76	97.4
8 p. m.		73	97.3
9 p. m.		71	
9.04 p. m.			96.9
10.05 p. m.		66	
10.10 p. m.			96.7
Mar. 25, 6.55 a. m.	64.49	68	97.9

TABLE LXXVI.—*Record of work done—Metabolism experiments Nos. 29–31.*

Date and time	Cyclometer reading.	Number of miles.	Actual duration of work.	Rate.	Heat equivalent.
1900.					
Experiment No. 29.			*Minutes.*	*Watts.*	*Calories.*
Mar. 16, 8.15 a. m.	666.0				
10.15 a. m.	687.5	21.5	120	42.0	72
12.30 p. m.	708.4	20.9	120	39.7	68
4 p. m.	729.8	21.4	120	39.5	68
6.15 p. m.	751.1	21.3	116	37.7	62
Total		85.1	476		270
Mar. 17, 10.15 a. m.	772.3	21.2	116	35.5	59
12.30 p. m.	795.9	23.6	120	37.0	63
4 p. m.	813.1	17.2	83	42.4	50
6.15 p. m.	837.9	24.8	120	39.0	67
Total		86.8	439		239
Mar. 18, 10.15 a. m.	861.8	23.9	120	36.5	62
12.30 p. m.	885.0	23.2	120	35.7	61
4 p. m.	906.9	21.9	120	37.4	64
6.15 p. m.	930.4	23.5	120	40.0	69
Total		92.5	480		256
Experiment No. 30.					
Mar. 19, 10.15 a. m.	947.9	17.5	96	40.5	55
12.30 p. m.	969.2	21.3	128	35.5	65
4 p. m.	986.8	17.6	120	34.0	58
6.15 p. m.	1,006.7	19.9	120	37.2	65
Total		76.3	464		243
Mar. 20, 10.15 a. m.	1,026.8	20.1	120	35.7	61
12.30 p. m.	1,047.8	21.0	120	36.9	63
4 p. m.	1,068.3	20.5	120	36.2	62
6.15 p. m.	1,088.3	20.0	120	38.2	66
Total		81.6	480		252
Mar. 21, 10.15 a. m.	1,109.6	21.3	120	37.4	64
12.30 p. m.	1,131.4	21.8	120	36.2	62
4 p. m.	1,152.8	21.4	120	37.0	63
6.15 p. m.	1,173.2	20.4	120	36.5	63
Total		84.9	480		252
Experiment No. 31.					
Mar. 22, 10.15 a. m.	1,194.4	21.2	120	37.4	64
12.30 p. m.	1,218.0	23.6	120	38.7	66
4 p. m.	1,240.9	22.9	120	39.0	67
6.15 p. m.	1,262.9	22.0	120	37.0	63
Total		89.7	480		260
Mar. 23, 10.15 a. m.	1,289.7	26.8	120	37.2	64
12.30 p. m.	1,306.8	17.1	120	37.0	63
4 p. m.	1,329.9	23.1	120	37.4	64
6.15 p. m.	1,351.4	21.5	120	34.4	59
Total		88.5	480		250
Mar. 24, 10.15 a. m.	1,375.8	24.4	120	37.0	63
12.30 p. m.	1,400.7	24.9	120	35.7	61
4 p. m.	1,423.7	23.0	104	35.7	53
6.15 p. m.	1,447.4	23.7	120	34.9	60
Total		96.0	464		237

Detailed statistics of income and outgo.—The quantities of nutrients in the basal ration which was the same except for the slight differences in the composition of the milk already mentioned, and the quantities in the supplemental rations in the different experiments of this series, are shown in Table LXXVII. The outgo of matter and energy in the feces during the successive experiments of this series is shown in Table LXXVIII.

TABLE LXXVII.—*Weight, composition, and heat of combustion of foods—Metabolism experiments Nos. 29–31.*

Laboratory No.	Food material.	Weight per day.	Water.	Protein.	Fat.	Carbohydrates.	Nitrogen.	Carbon.	Hydrogen.	Heat of combustion.
	Basal ration.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
3186	Beef	58	35.0	20.7	1.7	.....	3.32	12.12	1.73	135
3187	Butter	47	4.3	.6	40.6	.....	.09	30.60	4.91	378
3192	Bread	300	109.5	28.2	6.0	152.4	4.50	87.42	12.90	879
3181	Ginger snaps	75	3.1	4.7	6.2	59.9	.75	33.24	4.96	333
3193	Parched cereal	75	3.1	9.0	1.1	60.4	1.44	32.04	4.72	315
	Sugar	25	.....	.....	.....	25.0	.....	10.52	1.62	99
		580	155.0	63.2	55.6	297.7	10.10	205.94	30.84	2,139
	EXPERIMENT No. 29.									
3189	Milk, whole	900	760.5	36.9	50.4	45.0	5.94	73.80	11.34	841
	Total basal ration	1,480	915.5	100.1	106.0	342.7	16.04	279.74	42.18	2,980
	Supplemental ration.									
	Loaf sugar	128	.....	.....	.....	128.0	.....	53.89	8.29	507
	Total ration, 1 day	**1,608**	**915.5**	**100.1**	**106.0**	**470.7**	**16.04**	**333.63**	**50.47**	**3,487**
	EXPERIMENT No. 30.									
3190	Milk, whole	900	765.0	36.0	48.6	43.2	5.76	72.00	10.80	810
	Total basal ration	1,480	920.0	99.2	104.2	340.9	15.86	277.94	41.64	2,949
	Supplemental ration.									
	Alcohol	72	.....	.....	.....	.....	.....	37.56	9.39	509
	Total ration, 1 day	**1,552**	**920.0**	**99.2**	**104.2**	**340.9**	**15.86**	**315.50**	**51.03**	**3,458**
	EXPERIMENT No. 31.									
3191	Milk, whole	900	760.5	36.9	50.4	45.0	5.85	74.25	11.34	845
	Total basal ration	1,480	915.5	100.1	106.0	342.7	15.95	280.19	42.18	2,984
	Supplemental ration.									
3187	Butter	63.5	5.8	.8	54.8	.....	.13	41.34	6.63	511
	Total ration, 1 day	**1,543.5**	**921.3**	**100.9**	**160.8**	**342.7**	**16.08**	**321.53**	**48.81**	**3,495**

TABLE LXXVIII.—*Weight, composition, and heat of combustion of feces—Metabolism experiment No. 29–31.*

Laboratory No.		Weight.	Water.	Protein.	Fat.	Carbohydrates.	Nitrogen.	Carbon.	Hydrogen	Heat of combustion.
	Experiment No. 29.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams*	*Grams.*	*Calories*
3195	Feces for 3 days	177.0	123.7	15.9	9.0	18.2	2.55	25.01	3.6	279
	Average per day	59.0	41.2	5.3	3.0	6.1	.85	8.34	1.2	93
	Experiment No. 30.									
3196	Feces for 3 days	142.7	101.6	12.7	6.4	14.0	2.04	19.31	2.7	212
	Average per day	47.6	33.9	4.3	2.1	4.7	.68	6.44	.9	71
	Experiment No. 31.									
	Feces for 3 days	160.1	108.1	15.2	8.2	18.1	2.43	24.32	3.4	272
	Average per day	53.4	36.0	5.1	2.7	6.0	.81	8.11	1.1	91

The amount and composition of the urine in this experiment is shown in Tables LXXIX and LXXX. The statistics are shown for 6-hour periods in experiment No. 30, in which alcohol formed a part of the diet, and for day periods in experiments Nos. 29 and and 31 without alcohol. The heat of combustion of the urine was determined in the composite sample for each day, but the carbon and hydrogen were determined only in a composite for the total 9 days of this series of experiments.

TABLE LXXIX.—*Amount, specific gravity, and nitrogen of urine by 6-hour periods—Metabolism experiments Nos. 29–31.*

Date	Period.	Amount.	Specific gravity.	Nitrogen.	
	Experiment No. 29.				
1900.		*Grams.*		*Per cent.*	*Grams.*
Mar. 16–17	7 a. m. to 7 a. m.	694.9	1.034	2.19	15.24
17–18	7 a. m. to 7 a. m.	777.2	1.031	2.07	16.11
18–19	7 a. m. to 7 a. m.	890.8	1.030	1.79	15.97
	Total				47.32
	Experiment No. 30.				
19	7 a. m to 7 p. m	247.0	1.029	1.71	4.22
19	1 p. m. to 7 p. m	358.3	1.026	1.35	4.84
19–20	7 p. m. to 1 a. m.	196.8	1.031	2.02	3.98
20	1 a. m. to 7 a. m.	165.2	1.031	2.18	3.60
	Total	967.3			16.64
	Total by composite	967.3	1.029	1.74	16.83
20	7 a. m. to 1 p. m	309.5	1.027	1.47	4.55
20	1 p. m. to 7 p. m	320.7	1.027	1.55	4.97
20–21	7 p. m. to 1 a. m	254.6	1.025	1.80	4.58
21	1 a. m. to 7 a. m.	171.9	1.029	2.15	3.70
	Total	1,056.7			17.80
	Total by composite	1,056.7	1.027	1.69	17.86
21	7 a. m. to 1 p. m	355.3	1.021	1.28	4.55
21	1 p. m. to 7 p. m	409.5	1.020	1.18	4.83
21–22	7 p. m. to 1 a. m	217.5	1.026	1.89	4.11
22	1 a. m. to 7 a. m.	154.2	1.028	2.19	3.38
	Total	1,136.5			16.87
	Total by composite	1,136.5	1.023	1.47	16.70
	Experiment No. 31.				
22–23	7 a. m. to 7 a. m.	812.3	1.030	1.98	16.05
23–24	7 a. m. to 7 a. m.	790.5	1.030	1.93	15.24
24–25	7 a. m. to 7 a. m.	880.0	1.030	1.71	15.02
	Total				46.31

TABLE LXXX.—*Daily elimination of carbon, hydrogen, and water in urine—Metabolism experiments Nos. 29–31.*

Date	Amount.	Carbon.		Hydrogen.		Water.	Heat of combustion.	
							Per gram.	Total.
1900.	*Grams.*	*Per cent.*	*Grams.*	*Per cent.*	*Grams.*	*Per cent.*	*Grams.*	*Calories.*	*Calories.*
Mar. 16–17	694.9	.....	10.78	.....	2.86	.....	641.0	0.193	134
17–18	777.2	.....	11.39	.....	3.03	.....	720.3	.173	134
18–19	890.8	.....	11.29	.....	3.00	.....	834.3	.150	134
Total	2,362.9	.....	33.46	.....	8.89	.....	2,195.6	.....	402
19–20	967.3	.....	11.76	.....	3.13	.....	908.5	.141	136
20–21	1,056.7	.....	12.59	.....	3.34	.....	993.8	.134	142
21–22	1,136.5	.....	11.93	.....	3.17	.....	1,076.8	.125	142
Total	3,160.5	.....	36.28	.....	9.64	.....	2,979.1	.....	420
22–23	812.3	.....	11.35	.....	3.01	.....	755.6	.162	132
23–24	790.5	.....	10.78	.....	2.86	.....	736.6	.163	129
24–25	880.0	.....	10.62	.....	2.82	.....	826.9	.145	128
Total	2,482.8	.....	32.75	.....	8.69	.....	2,319.1	.....	389
Total 9 days	8,006.2	1.28	102.49	0.34	27.22	.....	7,493.8	.....	1,211

The quantities of carbon dioxid and water in the ventilating air current are given in Tables LXXXI to LXXXIII. These statistics are given in detail for experiment No. 30 in which alcohol was used, and summarized for the other two experiments of the series.

TABLE LXXXI.—*Comparison of residual amounts of carbon dioxid and water in the chamber at the beginning and end of each period, and the corresponding gain or loss—Metabolism experiment No. 30.*

Date.	End of period.	Carbon dioxid.			Water.			
		Total amount in chamber.	Gain (+) or loss (−) over preceding period.	Total amount of vapor remaining in chamber.	Gain (−) or loss (−) over preceding period.	Change in weight of absorbers. Gain (+) or loss (−).	Drip[a] from absorbers.	Total amount gained (+) or lost (−) during the period.
1900.		*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.* (b)	*Grams.*
Mar. 19	7 a. m.	26.8	.....	48.1	.....	.....	.....	.....
19	1 p. m.	79.6	−52.8	53.4	+5.3	− 152	140.0	+297.3
19	7 p. m.	84.4	− 4.8	57.2	−3.8	− 11	367.4	+382.2
20	1 a. m.	23.9	60.5	52.6	−4.6	− 77	32.4	49.2
20	7 a. m.	31.9	+ 8.0	48.8	−3.8	77	24.3	56.5
	Total	.....	− 5.1	.....	− .7	− 9	564.1	573.8
20	1 p. m.	76.6	+44.7	55.9	−7.1	+162	170.0	+339.1
20	7 p. m.	63.5	−13.1	51.3	−4.6	− 26	365.1	+334.5
21	1 a. m.	27.2	−36.3	51.5	− .2	− 78	23.1	54.7
21	7 a. m.	25.7	− 1.5	47.3	−4.2	− 79	17.0	66.2
	Total	.....	6.2	.....	− 1.5	21	575.2	−552.7
21	1 p. m.	71.8	+46.1	53.2	−5.9	+188	155.0	+348.9
21	7 p. m.	70.7	− 1.1	52.3	.9	− 10	359.4	+368.5
22	1 a. m.	25.7	−45.0	47.1	−5.2	−101	34.4	− 71.8
22	7 a. m.	26.4	.7	45.2	1.9	102	22.0	− 81.9
	Total	.....	− .7	.....	2.1	− 5	570.8	−563.7

[a] Including also the perspiration in underclothes.

[b] The drip was collected and weighed but once a day. The volume was roughly observed at 1 p. m., 7 p. m. and 7 a. m., and this volume taken as a rough approximation to the actual weight of drip for the different periods. The small amount of drip observed at 7 a. m. was divided equally between the two night periods.

TABLE LXXXII.—*Record of carbon dioxid in ventilating air current—Metabolism experiments Nos. 29–31.*

Date	Period	(a) Ventilation. Number of liters of air	Carbon dioxid: In incoming air (b) Per liter.	(c) Total, $a \times b$	In outgoing air (d) Amount in outgoing air	(e) Total excess in outgoing air, $d - c$.	(f) Correction for amount remaining in chamber.	(g) Corrected amount exhaled by subject, $e + f$.	(h) Total weight of carbon exhaled, $g \times \frac{12}{44}$.
1900.	*Experiment No. 29.*	*Liters.*	*Mg.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Mar. 16–17	7 a. m. to 7 a. m.	110,386	.....	65.2	1,306.7	1,241.5	− 0.2	1,241.7	338.7
17–18	7 a. m. to 7 a. m.	110,385	.....	65.5	1,252.7	1,187.2	1.9	1,185.3	323.3
18–19	7 a. m. to 7 a. m.	108,831	.....	61.4	1,315.2	1,253.8	− 3.0	1,256.8	342.7
	Experiment No. 30.								
19	7 a. m. to 7 a. m.	25,653	0.575	14.7	389.2	374.4	+52.8	427.2	116.5
19	1 p. m. to 7 p. m.	25,653	.587	15.1	442.2	427.2	− 4.8	432.0	117.8
19–20	7 p. m. to 1 a. m.	27,208	.577	15.7	254.6	238.9	− 60.5	178.4	48.7
20	1 a. m. to 7 a. m.	27,208	.573	15.6	151.6	136.0	− 8.0	144.0	39.3
	Total	105,722	.....	61.1	1,237.6	1,176.5	− 5.1	1,181.6	322.3
20	7 a. m. to 1 p. m.	25,653	.576	14.8	377.0	362.2	− 44.7	406.9	111.0
20	1 p. m. to 7 p. m.	27,208	.582	15.8	439.5	423.7	− 13.1	410.6	112.0
20–21	7 p. m. to 1 a. m.	27,208	.563	15.3	247.9	232.6	− 36.3	196.3	53.5
21	1 a. m. to 7 a. m.	27,208	.578	15.7	149.6	133.9	− 1.5	132.4	36.1
	Total	107,277	.....	61.6	1,214.0	1,152.4	− 6.2	1,146.2	312.6
21	7 a. m. to 1 p. m.	26,430	.587	15.5	389.2	373.7	− 46.1	419.8	114.5
21	1 p. m. to 7 p. m.	26,430	.581	15.3	445.5	430.2	1.1	429.1	117.0
21–22	7 p. m. to 1 a. m.	27,985	.569	15.9	232.5	216.6	− 45.0	171.6	46.8
22	1 a. m. to 7 a. m.	27,985	.575	16.1	148.6	132.5	0.7	133.2	36.3
	Total	108,830	.....	62.8	1,215.8	1,153.0	+ 0.7	1,153.7	314.6
	Experiment No. 31.								
22–23	7 a. m. to 7 a. m.	106,497	.....	61.7	1,210.2	1,148.5	0.7	1,147.8	313.1
23–24	7 a. m. to 7 a. m.	108,051	.....	61.8	1,223.6	1,161.8	− 1.0	1,160.8	316.6
24–25	7 a. m. to 7 a. m.	108,830	.....	62.3	1,224.5	1,162.2	2.9	1,165.1	317.8

TABLE LXXXIII.—*Record of water in ventilating air current—Metabolism experiments Nos. 29–31.*

Date.	Period.	(a) Ventilation. Number of liters of air.	Water in incoming air. (b) Per liter.	(c) Total, $a \times b$.	Water in outgoing air. (d) Amount condensed in freezers.	(e) Amount not condensed in freezers.	(f) Total, $d + e$.	(g) Total excess water in outgoing air, $f - c$.	(h) Correction for water remaining in chamber.	(i) Total water of respiration and perspiration, $g + h$.
1900.	*Experiment No. 29.*	*Liters.*	*Mg.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Mar. 16–17	7 a. m. to 7 a. m.	110,386	.....	89.8	1,025.5	176.7	1,202.2	1,112.4	− 555.1	1,667.5
17–18	7 a. m. to 7 a. m.	110,385	.....	91.1	992.5	179.4	1,171.9	1,080.8	− 358.6	1,439.4
18–19	7 a. m. to 7 a. m.	108,831	.....	92.8	1,033.9	175.6	1,209.5	1,116.7	− 619.8	1,736.5
	Experiment No. 30.									
19	7 a. m. to 1 p. m.	25,653	0.970	24.9	239.5	44.3	283.8	258.9	297.3	556.2
19	1 p. m. to 7 p. m.	25,653	.969	24.9	257.1	40.1	297.2	272.3	− 382.2	654.5
19–20	7 p. m. to 1 a. m.	27,208	.939	25.6	256.5	45.5	302.0	276.4	49.2	227.2
20	1 a. m. to 7 a. m.	27,208	.875	23.8	253.7	38.7	292.4	268.6	56.5	212.1
	Total	105,722	.....	99.2	1,006.8	168.6	1,175.4	1,076.2	573.8	1,650.0
20	7 a. m. to 1 p. m.	25,653	.977	25.1	250.6	41.8	292.4	267.3	339.1	606.4
20	1 p. m. to 7 p. m.	27,208	.892	24.3	270.5	42.6	313.1	288.8	334.5	623.3
20–21	7 p. m. to 1 a. m.	27,208	.814	22.1	256.1	45.2	301.3	279.2	54.7	224.5
21	1 a. m. to 7 a. m.	27,208	.781	21.2	261.8	37.7	299.5	278.3	66.2	212.1
	Total	107,277	.....	92.7	1,039.0	167.3	1,206.3	1,113.6	552.7	1,666.3

TABLE LXXXIII.—*Record of water in ventilating air current—Metabolism experiments Nos. 29–31*—Continued.

Date	Period.	(a) Water in incoming air. Ventilation. Number of liters of air.	(b) Water in incoming air. Per liter.	(c) Water in incoming air. Total, $a \times b$.	(d) Water in outgoing air. Amount condensed in freezers.	(e) Water in outgoing air. Amount not condensed in freezers.	(f) Water in outgoing air. Total, $d+e$.	(g) Total excess water in outgoing air, $f-c$.	(h) Correction for water remaining in chamber.	(i) Total water of respiration and perspiration, $g+h$.
	Experiment No. 29—Continued.									
1900.		*Liters.*	*Mg.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Mar. 21	7 a. m. to 1 p. m..	26,430	.828	21.9	250.4	39.8	290.2	268.3	+348.9	617.2
21	1 p. m. to 7 p. m..	26,430	.816	21.6	268.1	38.8	306.9	285.3	+368.5	653.8
21–22	7 p. m. to 1 a. m..	27,985	.782	21.9	253.3	43.3	296.6	274.7	71.8	202.9
22	1 a. m. to 7 a. m..	27,985	.767	21.5	249.9	37.4	287.3	265.8	−81.9	183.9
	Total	108,830	.....	86.9	1,021.7	159.3	1,181.0	1,094.1	+563.7	1,657.8
	Experiment No. 31.									
22–23	7 a. m. to 7 a. m..	106,497	.....	87.2	994.4	156.4	1,150.8	1,063.6	+573.8	1,637.4
23–24	7 a. m. to 7 a. m..	108,051	.....	90.3	999.0	160.3	1,159.3	1,069.0	+521.1	1,590.1
24–25	7 a. m. to 7 a. m..	108,830	.....	88.7	1,015.0	162.6	1,177.6	1,088.9	+566.0	1,654.9

Table LXXXIV summarizes the calorimetric measurements in experiments Nos. 29 and 31, and gives the details of these measurements in 6-hour periods during experiment No. 30.

TABLE LXXXIV.—*Summary of calorimetric measurements—Metabolism experiments Nos. 29–31.*

Date.	Period.	(a) Heat measured in terms of C_{20}.	(b) Change of temperature of calorimeter.	(c) Capacity correction of calorimeter, $b \times 60$.	(d) Correction due to temperature of food and dishes.	(e) Water vaporized equals total amount exhaled less amount condensed in chamber.	(f) Heat used in vaporization of water, $e \times 0.592$.	(g) Total heat determined, $a+c+d+f$
	Experiment No. 29.							
1900.		*Calories.*	*Degrees.*	*Calories.*	*Calories.*	*Grams.*	*Calories.*	*Calories*
Mar. 16–17	7 a. m. to 7 a. m	2,997.4	+0.13	+ 7.80	+5.43	1,112.8	658.7	3,669.3
17–18	7 a. m. to 7 a. m	2,783.0	+ .09	+ 5.40	+3.52	1,078.4	638.4	3,430.3
18–19	7 a. m. to 7 a. m	2,988.5	+ .20	+12.00	+6.00	1,120.1	663.0	3,669.5
	Experiment No. 30.							
19	7 a. m. to 1 p. m.....	1,060.4	+ .03	+ 1.80	−9.40	264.2	156.4	1,228.0
19	1 p. m. to 7 p. m.....	1,114.7	+ .01	+ .60	−2.23	276.1	163.4	1,276.5
19–20	7 p. m. to 1 a. m.....	449.3	+ .01	+ .60	+1.53	271.8	160.9	612.3
20	1 a. m. to 7 a. m	241.6	+ .02	+ 1.20	.....	264.8	156.8	399.6
	Total.....	2,866.0	+ .07	+ 4.20	−8.70	1,076.9	637.5	3,516.4
20	7 a. m. to 1 p. m.....	1,029.1	+ .02	+ 1.20	−6.35	274.4	162.4	1,199.0
20	1 p. m. to 7 p. m.....	1,089.0	+ .01	+ .60	− .81	284.2	168.2	1,258.6
20–21	7 p. m. to 1 a. m.....	410.0	+ .01	+ .60	+ .70	279.4	165.4	576.7
21	1 a. m. to 7 a. m	245.7	+ .02	+ 1.20	.....	274.1	162.3	409.2
	Total.....	2,773.8	+ .06	+ 3.60	−7.86	1,112.1	658.3	3,443.5
21	7 a. m. to 1 p. m.....	1,067.1	− .01	− .60	−7.81	274.2	162.3	1,236.6
21	1 p. m. to 7 p. m.....	1,094.9	+ .01	+ .60	−8.17	284.4	168.4	1,255.8
21–22	7 p. m. to 1 a. m.....	403.8	+ .01	+ .60	−2.44	269.5	159.5	566.3
21	1 a. m. to 7 a. m.....	236.6	+ .01	.60	.....	263.9	156.2	393.4
	Total.....	2,802.4	+ .02	+ 1.20	−2.08	1,092.0	646.4	3,452.1
	Experiment No. 31.							
22–23	7 a. m. to 7 a. m	2,797.6	.....	.....	−2.07	1,063.6	629.6	3,429.3
23–24	7 a. m. to 7 a. m	2,780.9	+ .04	+ 2.40	3.33	1,069.0	632.8	3,412.8
24–25	7 a. m. to 7 a. m	2,762.2	+ .01	+ .60	−8.30	1,091.6	646.1	3,417.2

The alcohol, or reducing material equivalent to alcohol, was determined in the urine and freezer water of each day of experiment No. 30, and on the 3 days of the preceding and following experiments, Nos. 29 and 31, respectively. The amount of reducing material in the air current on each day of the 9 days of this series of experiments was also determined. Table LXXXV summarizes these determinations. The determinations of the reducing material in the urine on the first day of experiment No. 29 was lost, so that we can only estimate the total reducing material on that day. It was, however, probably not far different from the second and third days of this experiment. The average elimination of reducing material per day from all sources in experiments Nos. 29 and 31 amounted to the equivalent of 0.32 gram of alcohol. In the third from the last column of Table LXXXV is given the total outgo of alcohol in experiment No. 30, which amounts to 0.76 gram per day. This value is obtained by subtracting from the 1.09 grams of total alcohol and reducing material equivalent to alcohol the 0.33 gram of reducing material determined during the experiments in which alcohol did not form a part of the diet. The total alcohol metabolized in the body was 98.9 per cent of that ingested.

TABLE LXXXV.—*Alcohol ingested and excreted—Metabolism experiment Nos. 29–31.*

Date.	Alcohol ingested.	Alcohol excreted, including other reducing material calculated as alcohol.					Alcohol excreted, unoxidized.[a]	Alcohol metabolized in body.	
		In urine (distillate).	In drip (distillate).	In freezer water (distillate).	In air current.	Total.			
1900.									
Experiment No. 29.									
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams*	*Grams.*	*Grams.*	*Per cent.*
Mar. 16–17		(b)		Trace.	0.35				
17–18		0.02	0.01	0.01	.33	0.36			
18–19		.02		Trace.	.35	.37			
Experiment No. 30.									
Mar. 19–20	72.0	.05		0.02	.95	1.06	0.73	71.3	99.0
20–21	72.0	.06	.12	.01	1.00	1.11	.78	71.2	98.9
21–22	72.0	.06		.01	1.00	1.11	.78	71.2	98.9
Total	216.0	.17	.12	.04	2.95	3.28	2.29	213.7	
Average per day	72.0	.06	.04	.01	.98	1.09	.76	71.2	98.9
Experiment No. 31.									
Mar. 22–23		.02		.01	.30	.33			
23–24		.01	.01	Trace.	.28	.30			
24–25		.02		Trace.	.26	.28			

[a] Equals total reducing material excreted less 0.33 gram of reducing material not alcohol, the average for the days on which no alcohol was consumed.

[b] Not determined.

Balance of income and outgo of matter and energy.—The income and outgo of nitrogen, carbon, hydrogen, and energy in the different experiments of this series are shown in Tables LXXXVI to LXXXIX.

TABLE LXXXVI.—*Income and outgo of nitrogen and carbon—Metabolism experiments Nos. 29–31.*

Date and period.	Nitrogen.				Carbon.					
	(*a*) In food.	(*b*) In feces.	(*c*) In urine.[a]	(*d*) Gain (+) or loss (−), *a*−(*b*+*c*).	(*e*) In food.	(*f*) In feces.	(*g*) In urine.	(*h*) In respiratory products.	(*i*) In alcohol eliminated.	(*k*) Gain (+) or loss (−), *e*−(*f*+*g*+*h*+*i*).
1900.										
Experiment No. 29.										
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Mar. 16–17, 7 a. m. to 7 a. m.	16.0	0.9	15.4	−0.3	333.6	8.3	10.8	338.7	.....	−24.2
17–18, 7 a. m. to 7 a. m.	16.1	.8	16.3	1.0	333.7	8.4	11.4	323.3	.....	−9.4
18–19, 7 a. m. to 7 a. m.	16.0	.9	16.2	1.1	333.6	8.3	11.3	342.7	.....	−28.7
Total	48.1	2.6	47.9	2.4	1,000.9	25.0	33.5	1,004.7	.....	−62.3
Average 1 day.....	16.0	.8	16.0	.8	333.6	8.3	11.2	334.9	.....	−20.8
Experiment No. 30.										
Mar. 19–20, 7 a. m. to 7 a. m.	15.9	.7	16.8	−1.6	315.5	6.4	11.8	322.3	.4	−25.4
20–21, 7 a. m. to 7 a. m.	15.8	.6	18.0	−2.8	315.5	6.5	12.6	312.6	.4	−16.6
21–22, 7 a. m. to 7 a. m.	15.9	.7	17.1	−1.9	315.5	6.4	11.9	314.6	.4	−17.8
Total	47.6	2.0	51.9	−6.3	946.5	19.3	36.3	949.5	1.2	−59.8
Average 1 day.....	15.9	.7	17.3	−2.1	315.5	6.4	12.1	316.5	.4	−19.9
Experiment No. 31.										
Mar. 22–23, 7 a. m. to 7 a. m.	16.1	.8	16.3	−1.0	321.5	8.1	11.3	313.1	.....	−11.0
23–24, 7 a. m. to 7 a. m.	16.0	.8	15.4	−.2	321.6	8.1	10.8	316.6	.....	−13.9
24–25, 7 a. m. to 7 a. m.	16.1	.8	15.2	−.1	321.5	8.1	10.6	317.8	.....	−15.0
Total	48.2	2.4	46.9	−1.1	964.6	24.3	32.7	947.5	.....	−39.9
Average 1 day.....	16.1	.8	15.6	.3	321.5	8.1	10.9	315.8	.....	−13.3

[a] Nitrogen in perspiration, 0.2 gram per day, is included in this column.

TABLE LXXXVII.—*Income and outgo of water and hydrogen—Metabolism experiments Nos. 29–31.*

Date and period.	Water.						Hydrogen.						
	(*a*) In food.	(*b*) In drink	(*c*) In feces.	(*d*) In urine.	(*e*) In respiratory products.	(*f*) Apparent loss, *a*+*b*−(*c*+*d*+*e*).	(*g*) In food	(*h*) In feces.	(*i*) In urine.	(*k*) In alcohol eliminated	(*l*) Apparent gain, *g*−(*h*+*i*+*k*).	(*m*) Loss from water, *f*÷9.	(*n*) Total gain (+) or loss (−), *l*+*m*.
1900.													
Experiment No. 29.													
Mar. 16–17, 7 a. m. to 7 a. m.	*Grams.* 915.5	*Grams.* 1,250.0	*Grams.* 41.2	*Grams.* 641.0	*Grams.* 1,667.5	*Grams.* 184.2	*Grams.* 50.5	*Grams.* 1.2	*Grams.* 2.9	.....	*Grams.* 46.4	*Grams.* 20.5	*Grams.* 25.9
17–18, 7 a. m. to 7 a. m.	915.5	1,250.0	41.3	720.3	1,439.4	35.5	50.5	1.2	3.0	.....	46.3	3.9	42.4
18–19, 7 a. m. to 7 a. m.	915.5	1,250.0	41.2	834.3	1,736.5	446.5	50.5	1.2	3.0	.....	46.3	49.6	−3.3
Total	2,746.5	3,750.0	123.7	2,195.6	4,843.4	666.2	151.5	3.6	8.9	.....	139.0	74.0	−65.0
Average 1 day..	915.5	1,250.0	41.2	731.9	1,614.5	222.1	50.5	1.2	3.0	.....	46.3	24.6	−21.7

TABLE LXXXVII.—*Income and outgo of water and hydrogen—Metabolism experiments Nos. 29–31.*—Continued.

Date and period	Water						Hydrogen.						
	(a) In food.	(b) In drink	(c) In feces	(d) In urine	(e) In respiratory products	(f) Apparent loss, $a+b-(c+d+e)$.	(g) In food.	(h) In feces	(i) In urine.	(k) In alcohol eliminated.	(l) Apparent gain, $g-(h+i+k)$.	(m) Loss from water, $f \div 9$.	(n) Total gain (−) or loss (+), $l+m$.
1900.													
Experiment No. 30.													
Mar. 19–20, 7 a. m. to 7 a. m.	*Grams.* 920.0	*Grams.* 1,250.0	*Grams.* 33.9	*Grams.* 908.5	*Grams.* 1,650.0	*Grams.* 422.4	*Grams.* 51.0	*Grams.* 0.9	*Grams.* 3.1	*Grams.* 0.1	*Grams.* 46.9	*Grams.* 46.9	*Grams.* .....
20–21, 7 a. m. to 7 a. m.	920.0	1,250.0	33.8	993.8	1,666.3	523.9	51.0	0.9	3.3	.1	46.7	58.2	−11.5
21–22, 7 a. m. to 7 a. m.	920.0	1,250.0	33.9	1,076.8	1,657.8	598.5	51.0	0.9	3.2	.1	46.8	66.5	−19.7
Total	2,760.0	3,750.0	101.6	2,979.1	4,974.1	1,544.8	153.0	2.7	9.6	.3	140.4	171.6	−31.2
Average 1 day	920.0	1,250.0	33.9	993.0	1,658.0	514.9	51.0	0.9	3.2	.1	46.8	57.2	−10.4
Experiment No. 31.													
Mar. 22–23, 7 a. m. to 7 a. m.	921.3	1,250.0	36.0	755.6	1,637.4	257.7	48.8	1.1	3.0	.....	44.7	28.6	+16.1
23–24, 7 a. m. to 7 a. m.	921.3	1,250.0	36.1	736.6	1,590.1	191.5	48.8	1.2	2.9	.....	44.7	21.3	+23.4
24–25, 7 a. m. to 7 a. m.	921.3	1,250.0	36.0	826.9	1,654.9	346.5	48.8	1.1	2.8	.....	44.9	38.5	+ 6.4
Total	2,763.9	3,750.0	108.1	2,319.1	4,882.4	795.7	146.4	3.4	8.7	.....	134.3	88.4	+45.9
Average 1 day	921.3	1,250.0	36.0	773.0	1,627.5	265.2	48.8	1.1	2.9	.....	44.8	29.5	+15.3

TABLE LXXXVIII.—*Gain or loss of protein ($N \cdot 6.25$), fat, and water—Metabolism experiments Nos. 29–31.*

Date and period.	(a) Nitrogen gained (+) or lost (−),	(b) Protein gained (+) or lost (−), $a \cdot 6.25$.	(c) Total carbon gained (+) or lost (−),	(d) Carbon in protein gained (+) or lost (−), $b \cdot .53$.	(e) Carbon in fat, etc., gained (+) or lost (−), $c-d$.	(f) Fat gained (+) or lost (−), $e \div .761$.	(g) Total hydrogen gained (+) or lost (−),	(h) Hydrogen in protein gained (+) or lost (−), $b \cdot .07$.	(i) Hydrogen in fat gained (+) or lost (−), $f \cdot .118$.	(k) Hydrogen in water, etc., gained (+) or lost (−), $g-(h+i)$.	(l) Water gained (+) or lost (−), $k \cdot 9$.
1900.											
Experiment No. 29.											
Mar. 16–17, 7 a. m. to 7 a. m.	*Grams.* 0.3	*Grams.* 1.9	*Grams.* 24.2	*Grams.* 1.0	*Grams.* −23.2	*Grams.* 30.5	*Grams.* −25.9	*Grams.* 0.1	*Grams.* −3.6	*Grams.* +29.6	*Grams.* −266.4
17–18, 7 a. m. to 7 a. m.	1.0	6.2	9.4	3.3	6.1	8.0	−42.4	.4	.9	+43.7	+393.3
18–19, 7 a. m. to 7 a. m.	1.1	6.9	28.7	3.7	25.0	32.9	3.3	.5	3.9	− 1.1	− 9.9
Total	2.4	15.0	62.3	8.0	54.3	71.4	65.0	1.0	8.4	−74.4	− 669.6
Average 1 day	.8	5.0	20.8	2.7	18.1	23.8	21.7	.3	2.8	− 24.8	+ 223.2
Experiment No. 30.											
Mar. 19–20, 7 a. m. to 7 a. m.	1.6	10.0	25.4	5.3	20.1	26.4	.....	.7	3.1	− 3.8	− 34.2
20–21, 7 a. m. to 7 a. m.	2.8	17.5	16.6	9.3	7.3	− 9.6	11.5	1.2	1.1	9.2	82.8
21–22, 7 a. m. to 7 a. m.	1.9	11.9	17.8	6.3	11.5	15.1	19.7	.8	1.8	17.1	153.9
Total	6.3	39.4	59.8	20.9	38.9	51.1	31.2	2.7	6.0	22.5	202.5
Average 1 day	2.1	13.1	19.9	6.9	13.0	17.0	10.4	.9	2.0	7.5	67.5
Experiment No. 31.											
Mar. 22–23, 7 a. m. to 7 a. m.	1.0	6.2	11.0	3.3	7.7	10.1	16.1	.4	1.2	17.7	159.3
23–24, 7 a. m. to 7 a. m.	.2	1.3	13.9	.7	13.2	17.3	23.4	.1	2.0	25.5	229.5
24–25, 7 a. m. to 7 a. m.	.1	.6	15.0	.3	15.3	20.1	6.4	.....	2.4	8.8	79.2
Total	1.1	6.9	39.9	3.7	36.2	47.5	45.9	.5	5.6	52.0	468.0
Average 1 day	.3	2.3	13.3	1.2	12.1	15.9	15.3	.1	1.9	17.3	156.0

TABLE LXXXIX. *Income and outgo of energy—Metabolism experiments Nos. 29–31.*

Date and period.	(a) Heat of combustion of food eaten.	(b) Heat of combustion of feces.	(c) Heat of combustion of urine.	(m) Heat of combustion of alcohol eliminated.	(d) Estimated heat of combustion of protein gained (+) or lost (−).	(e) Estimated heat of combustion of fat gained (+) or lost (−).	(f) Estimated energy of material oxidized in the body, $n=(b+c+m+d+e)$.	(g) Heat determined.	Heat determined greater (+) or less (−) than estimated. (h) $f-g$.	(i) $h=f$.
1900.										
Experiment No. 29.										
	Calories.	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*
Mar. 16–17, 7 a. m. to 7 a. m.	3,487	93	134	.....	− 11	− 291	3,562	3,669	+ 107	+ 3.0
17–18, 7 a. m. to 7 a. m.	3,487	93	134	.....	− 35	− 76	3,371	3,430	+ 59	+ 1.7
18–19, 7 a. m. to 7 a. m.	3,487	93	134	.....	− 39	− 314	3,613	3,669	+ 56	+ 1.5
Total	10,461	279	402	.....	85	− 681	10,546	10,768	+ 222	.....
Average 1 day	3,487	93	134	.....	− 28	− 227	3,515	3,589	+ 74	+ 2.1
Experiment No. 30.										
Mar. 19–20, 7 a. m. to 7 a. m.	3,458	71	136	5	57	− 252	3,555	3,516	− 39	− 1.1
20–21, 7 a. m. to 7 a. m.	3,458	70	142	5	99	92	3,432	3,443	+ 11	+ .3
21–22, 7 a. m. to 7 a. m.	3,458	71	142	6	− 67	− 144	3,450	3,452	+ 2	+ .1
Total	10,374	212	420	16	− 223	− 488	10,437	10,411	− 26	.....
Average 1 day	3,458	71	140	5	74	− 163	3,479	3,470	− 9	− .3
Experiment No. 31.										
Mar. 22–23, 7 a. m. to 7 a. m.	3,495	91	132	.....	35	96	3,403	3,429	+ 26	+ .8
23–24, 7 a. m. to 7 a. m.	3,495	90	129	.....	− 7	− 165	3,448	3,413	− 35	− 1.0
24–25, 7 a. m. to 7 a. m.	3,495	91	128	.....	+ 3	− 192	3,465	3,417	− 48	− 1.4
Total	10,485	272	389	.....	− 39	453	10,316	10,259	− 57	.....
Average 1 day	3,495	91	129	.....	− 13	− 151	3,439	3,420	19	− .6

EXPERIMENTS NOS. 32–34—WORK. NO. 33 WITH ALCOHOL DIET.

Subject.—J. F. S., the same as in experiments of the two previous series, Nos. 26–31. His weight with underclothing was about 66.5 kilograms (145½ pounds).

Occupation during experiment.—Work, 8 hours a day, upon a stationary bicycle, as in the previous series of experiments.

Duration.—This experiment was the second of a series of 3, each of which continued 3 days. A preliminary period of 4 days preceded the first. The series was intended to be as nearly as possible a repetition of the previous series, Nos. 29–31, with the exception that the order in which the supplemental materials were added to the basal ration was butter, alcohol, sugar, while in the previous series the order was sugar, butter, alcohol. The preliminary period began with breakfast April 16, 1900, and the subject entered the respiration chamber on the evening of April 19. The first experiment of the series, No. 32, began at 7 a. m. April 20; the second, No. 33, at 7 a. m. April 23, and the third, No. 34, at 7 a. m. April 26. The subject thus spent 9 days and 10 nights within the respiration chamber.

Diet.—As has already been indicated, this series was a duplicate in reverse order of the previous series. There was a basal ration differing slightly in the different experiments on account of differences in the composition of the milk. This ration furnished approximately 100 grams of protein and 2,980 calories of energy, or practically the same as in the previous series. To this basal ration were added: In No. 32, 63.5 grams of butter per day, furnishing 1 gram of protein and 509 calories of energy; in No. 33, 79.5 grams of 90.6 per cent alcohol, furnishing 72 grams of absolute alcohol and 509 calories of energy per day, and in No. 34, 128 grams of cane sugar, furnishing 507 calories of energy. The total ration therefore in this series of experiments furnished 100 grams of protein and 3,490 calories of energy per day. The alcohol was taken in 6 doses, as usual, and the sugar was also taken at frequent intervals, but the butter was consumed

in about equal portions at breakfast, dinner, and supper. The total amount of water in the drink on each day of the series of experiments amounted to 1,250 grams. The kinds and quantities of food served at each meal and the quantities of drink at different periods of the day were as follows:

Diet in metabolism experiments Nos. 32–34.

FOOD—BASAL RATION.

	Breakfast.	Dinner.	Supper.	Total.
	Grams.	*Grams.*	*Grams.*	*Grams.*
Beef	.....	58	.....	58
Butter	9.0	17	9.0	35
Bread	75.0	150	75.0	300
Ginger snaps	25.0	25	25.0	75
Parched cereal	37.5	.....	37.5	75
Sugar[a]	17.5	.....	17.5	35
Milk, whole	340.0	340	340.0	1,020

[a] Eaten on parched cereal in experiments Nos. 32 and 34; mostly added to water and alcohol in experiment No. 33.

FOOD—SUPPLEMENTAL RATION.

Experiment No. 32, April 20–22.—Sixty-two grams butter added to basal ration. This amount also supplemented the ration during the preliminary period.

Experiment No. 33, April 23–25.—Seventy-two grams absolute alcohol daily. This was supplied in 79.5 grams of 90.57 per cent alcohol, which was made up to 900 grams with the addition of 25 grams sugar and the rest water.

Experiment No. 34, April 26–28.—The basal ration was increased by the addition of 128 grams of cane sugar.

DRINK.

Time.	Experiment No. 32.	Experiment No. 33.		Experiment No. 34.
	Water.	Alcohol and sweetened water.[a]	Water.	Water.
	Grams.	*cc.*	*Grams.*	*Grams.*
Breakfast	150	175	75	150
10.15 a. m.	200	100	75	200
Dinner	200	175	75	200
4 p. m.	200	100	75	200
Suppper	150	175	75	150
9 p. m.	200	100	72	200
10.20 p. m.	150	75	.....	150
Total	1,250	900	447	1,250

[a] Contained 803 grams water, 25 grams sugar, and 72 grams alcohol.

Daily routine.—The general plan of the series of experiments was identical with that of the previous series, and is shown in the following schedule:

Daily programme.—Metabolism experiments Nos. 32–34.

6.50 a. m.	Take pulse and temperature.
7 a. m.	Pass urine, weigh self dressed, collect drip, and weigh absorbers.
7.30 a. m.	Breakfast, drink 150 grams water.
8.15 a. m.	Begin work.
10.15 a. m.	Stop work, drink 200 grams water.
10.30 a. m.	Begin work.
12.30 p. m.	Stop work.
12.50 p. m.	Take pulse and temperature.
1 p. m.	Pass urine, collect drip, and weigh absorbers.
1.25 p. m.	Dinner, drink 200 grams water.
2 p. m.	Begin work.
4 p. m.	Stop work, drink 200 grams water.
4.15 p. m.	Begin work.
6.15 p. m.	Stop work, change underclothing.
6.20 p. m.	Supper, drink 150 grams water.
6.50 p. m.	Take pulse and temperature.
7 p. m.	Pass urine, weigh self dressed, collect drip, and weigh absorbers.
9 p. m.	Drink 200 grams water.
10 p. m.	Take pulse and temperature.
10.10 p. m.	Arrange bed.
10.20 p. m.	Drink 150 grams water.
10.30 p. m.	Retire.
1 a. m.	Pass urine.

The more important statistics in the diary kept by the subject are summarized in Table XC. Frequent determinations of both pulse rate and body temperature were taken.

TABLE XC.—*Summary of diary—Metabolism experiments Nos. 32–34.*

Date and time.	Weight with clothes.	Pulse rate per minute.	Temperature
1900.			
Experiment No. 32.	*Kilograms.*		*F.*
Apr. 20, 6.55 a. m.		66	
7 a. m.	66.19		97.8
9 a. m.		87	
10 a. m.		83	
11 a. m.		85	
12 m.		82	
12.55 p. m.		65	
1 p. m.			97.7
2.05 p. m.		93	
3 p. m.		90	
4 p. m.		87	
5 p. m.		83	
6 p. m.		84	
7 p. m.	66.95	72	97.8
8 p. m.		69	97.7
9 p. m.		64	97.1
10 p. m.		62	96.6
Apr. 21, 6.55 a. m.		64	
7 a. m.	66.36		97.8
9 a. m.		91	
10 a. m.		88	
11 a. m.		89	
12 m.		90	
1 p. m.		67	98.0
2.15 p. m.		94	
3 p. m.		96	
4 p. m.		97	
5 p. m.		97	
6 p. m.		85	
7 p. m.	66.27	74	97.9
8.08 p. m.		73	
8.15 p. m.			97.5
9 p. m.		67	97.1
10.05 p. m.		66	
10.12 p. m.			96.6
Apr. 22, 6.55 a. m.		68	
7 a. m.	65.83		97.7
9 a. m.		101	
10 a. m.		96	
11 a. m.		92	
12 m.		98	
1 p. m.		68	97.7
2.05 p. m.		100	
3 p. m.		103	
4 p. m.		104	
5 p. m.		102	
6 p. m.		100	
7 p. m.	65.59	79	97.7
8 p. m.		74	97.5
9 p. m.		71	97.3
10.10 p. m.		67	96.9
Experiment No. 33.			
Apr. 23, 6.55 a. m.		69	
7 a. m.	65.21		97.7
9 a. m.		102	
9.02 a. m.		106	
10 a. m.		95	
11 a. m.		96	
12 m.		95	
1 p. m.		70	98.0
1.57 p. m.		73	

Date and time.	Weight with clothes.	Pulse rate per minute.	Temperature
1900.			
Experiment No. 33—C't'd.	*Kilograms.*		*F.*
Apr. 23, 2.05 p. m.		97	
3 p. m.		100	
4 p. m.		102	
5 p. m.		102	
6 p. m.		97	
7 p. m.	65.74	76	97.7
8 p. m.		74	97.5
9 p. m.		75	97.2
10.10 p. m.		72	97.0
Apr. 24, 6.55 a. m.		67	
7 a. m.	65.27		97.8
9 a. m.		109	
10 a. m.		102	
11 a. m.		96	
12 m.		95	
1 p. m.		72	97.9
2.07 p. m.		98	
3 p. m.		102	
4 p. m.		108	
5 p. m.		104	
6 p. m.		100	
7 p. m.	65.69	78	97.7
8 p. m.		77	97.6
9 p. m.		75	
9.04 p. m.			97.4
10.10 p. m.		71	
10.15 p. m.			96.7
Apr. 25, 6.55 a. m.		69	
7 a. m.	65.13		97.7
9 a. m.		109	
10 a. m.		102	
11 a. m.		101	
12 m.		100	
1 p. m.		74	97.9
2.05 p. m.		102	
3 p. m.		112	
4 p. m.		107	
5 p. m.		104	
6 p. m.		105	
7 p. m.	65.47	76	
8 p. m.		76	97.8
9 p. m.		78	97.6
10.10 p. m.		75	97.2
Experiment No. 34.			
Apr. 26, 6.55 a. m.		68	
7 a. m.	64.94		97.7
9 a. m.		106	
10 a. m.		102	
11 a. m.		96	
12 m.		97	
1 p. m.		66	97.7
2.05 p. m.		98	
3 p. m.		99	
4 p. m.		97	
5 p. m.		98	
6 p. m.		97	
7 p. m.	65.44	77	97.7
8 p. m.		74	97.6
9 p. m.		72	97.4
10.10 p. m.		69	97.2
Apr. 27, 6.55 a. m.		65	

TABLE XC. *Summary of diary—Metabolism experiments Nos. 32–34*—Continued.

Date and time.	Weight with clothes.	Pulse rate per minute.	Temperature.
1900.			
Experiment No. 34—C't'd.	*Kilograms.*		*F.*
Apr. 27, 7 a. m.	65.09		97.6
9 a. m.		103	
10 a. m.		98	
11 a. m.		100	
12 m.		96	
1 p. m.		71	98.3
2.05 p. m.		100	
3 p. m.		99	
4 p. m.		99	
5 p. m.		100	
6 p. m.		97	
7 p. m.	65.34	73	97.7
8 p. m.		73	97.5
9 p. m.		71	97.5
10 p. m.		68	97.3
Apr. 28, 6.55 a. m.		67	
7 a. m.	64.98		97.9
1900.			
Experiment No. 34—C't'd.	*Kilograms.*		*F.*
Apr. 28, 9 a. m.		104	
10 a. m.		98	
11 a. m.		90	
12 m.		93	
1 p. m.		66	97.8
2.05 p. m.		96	
3 p. m.		97	
4 p. m.		102	
5 p. m.		99	
6 p. m.		97	
7 p. m.	65.37	73	97.0
8 p. m.		75	97.5
9 p. m.		67	97.4
10.10 p. m.		69	97.3
Apr. 29, 6.55 a. m.		69	
7 a. m.	64.92		97.7

Amount of work done.—The total number of miles registered by the cyclometer and the heat equivalent of the work done each day are shown in Table XCI.

TABLE XCI.—*Record of work done—Metabolism experiments Nos. 32–34.*

Date and time.	Cyclometer reading	Number of miles.	Actual duration of work.	Rate.	Heat equivalent.
1901.					
Experiment No. 32.			*Minutes.*	*Watts.*	*Calories.*
Apr. 20, 8.15 a. m.	1,510.4				
10.15 a. m.	1,527.2	16.8	120	18.8	32
12.30 p. m.	1,546.5	19.3	120	21.0	36
4 p. m.	1,562.8	16.3	120	16.7	29
6.15 p. m.	1,579.1	16.3	120	17.4	30
Total		68.7	480		127
Apr. 21, 10.15 a. m.	1,590.2	20.1	120	21.0	36
12.30 p. m.	1,626.0	26.8	120	25.8	44
4 p. m.	1,654.0	28.0	120	30.5	52
6.15 p. m.	1,681.7	27.7	120	29.6	51
Total		102.6	480		183
Apr. 22, 10.15 a. m.	1,711.6	29.9	120	36.2	62
12.30 p. m.	1,744.6	33.0	120	47.4	81
4 p. m.	1,774.5	29.9	120	38.1	65
6.15 p. m.	1,806.1	31.6	120	40.0	69
Total		124.4	480		277
Experiment No. 33.					
Apr. 23, 10.15 a. m.	1,825.3	19.2	120	20.6	35
12.30 p. m.	1,854.1	28.8	120	23.9	41
4 p. m.	1,880.8	26.7	120	26.6	46
6.15 p. m.	1,908.2	27.4	120	27.5	47
Total		102.1	480		169

TABLE XCI.—*Record of work done—Metabolism experiments Nos. 33–34*—Continued.

Date and time.	Cyclometer reading.	Number of miles.	Actual duration of work.	Rate.	Heat equivalent.
1901.					
Experiment No. 33—Continued.					
			Minutes.	*Watts.*	*Calories.*
Apr. 24, 10.15 a. m.	1,935.9	27.7	120	26.2	45
12.30 p. m.	1,965.2	29.3	120	31.2	54
4 p. m.	1,993.8	28.6	120	30.5	52
6.15 p. m.	2,021.6	27.8	120	30.5	52
Total		113.4	480		203
Apr. 25, 10.15 a. m.	2,049.3	27.7	120	29.6	51
12.30 p. m.	2,079.2	29.9	120	33.3	57
4 p. m.	2,108.1	28.9	120	31.6	54
6.15 p. m.	2,138.0	29.9	120	33.7	58
Total		116.4	480		220
Experiment No. 34.					
Apr. 26, 10.15 a. m.	2,166.9	28.9	120	34.3	59
12.30 p. m.	2,196.7	29.8	120	35.4	60
4 p. m.	2,226.1	29.4	120	34.3	59
6.15 p. m.	2,254.1	28.0	120	33.7	58
Total		116.1	480		236
Apr. 27, 10.15 a. m.	2,283.8	29.7	120	35.7	61
12.30 p. m.	2,318.7	34.9	120	36.8	63
4 p. m.	2,347.5	28.8	120	38.1	65
6.15 p. m.	2,379.0	31.5	120	38.7	66
Total		124.9	480		255
Apr. 28, 10.15 a. m.	2,409.6	30.6	120	37.4	64
12.30 p. m.	2,441.5	31.9	120	38.1	65
4 p. m.	2,472.6	31.1	120	38.1	65
6.15 p. m.	2,503.8	31.2	120	38.1	65
Total		124.8	480		259

Detailed statistics of income and outgo.—The quantities of nutrients in the basal ration and the quantities in the supplemental rations for the different experiments are shown in Table XCII. The outgo of matter and energy in the feces during the different experiments is shown in Table XCIII.

TABLE XCII.—*Weight, composition, and heat of combustion of foods—Metabolism experiments Nos. 33–34.*

Laboratory No.	Food material.	Weight per day.	Water.	Protein.	Fat	Carbohydrates.	Nitrogen.	Carbon.	Hydrogen.	Heat of combustion.
	Basal ration.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
3205	Beef	58	37.4	18.6	1.6	.....	2.98	10.76	1.54	120
3206	Butter	35	2.9	.4	30.7	.....	.07	22.95	3.63	287
3204	Bread	300	113.4	25.8	7.5	149.4	4.14	84.81	12.90	861
3207	Ginger snaps	75	2.8	4.1	5.4	61.2	.66	32.90	5.40	333
3193	Parched cereal	75	3.1	9.0	1.1	60.4	1.44	32.04	4.73	315
	Sugar	35	.....	.....	.....	35.0	.....	14.74	2.27	139
		578	159.6	57.9	46.3	306.0	9.29	198.20	30.47	2,055

TABLE XCII. *Weight, composition, and heat of combustion of foods—Metabolism experiments Nos. 32, 33, 34.*—Continued.

Laboratory No.	Food material	Weight per day	Water	Protein	Fat	Carbohydrates	Nitrogen	Carbon	Hydrogen	Heat of combustion
	EXPERIMENT NO. 32.									
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
3200	Milk, whole	1,020	871.1	41.8	51.0	47.9	6.73	84.09	12.14	923
	Total basal ration	1,598	1,030.7	99.7	97.3	353.9	16.02	279.29	42.61	2,978
	Supplemental ration.									
	Butter	62	5.2	.8	54.3		.12	40.66	6.43	509
	Total ration for 1 day	**1,660**	**1,035.9**	**100.5**	**151.6**	**353.9**	**16.14**	**319.95**	**49.04**	**3,487**
	EXPERIMENT NO. 33.									
3201	Milk, whole	1,020	868.0	41.8	53.0	49.0	6.73	83.84	12.65	922
	Total basal ration	1,598	1,027.6	99.7	99.3	355.0	16.02	282.04	43.12	2,977
	Supplemental ration.									
	Alcohol	72						37.56	9.39	509
	Total ration for 1 day	**1,670**	**1,027.6**	**99.7**	**99.3**	**355.0**	**16.02**	**319.60**	**52.51**	**3,486**
	EXPERIMENT NO. 34.									
3202	Milk, whole	1,020	869.0	41.8	53.0	43.9	6.73	83.64	12.34	931
	Total basal ration	1,598	1,028.6	99.7	99.3	349.9	16.02	281.84	42.81	2,986
	Supplemental ration.									
	Sugar	128				128.0		53.89	8.29	507
	Total ration for 1 day	**1,726**	**1,028.6**	**99.7**	**99.3**	**477.9**	**16.02**	**335.73**	**51.10**	**3,493**

TABLE XCIII.—*Weight, composition, and heat of combustion of feces—Metabolism experiments Nos. 32, 33, 34.*

Laboratory No.		Weight per day.	Water	Protein.	Fat	Carbohydrates.	Nitrogen.	Carbon.	Hydrogen.	Heat of combustion.
	Experiment No. 32.									
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
3209	Feces for 3 days	293.3	214.7	22.3	13.2	28.2	3.55	37.75	5.46	425
	Average per day	97.8	71.6	7.4	4.4	9.4	1.18	12.58	1.82	142
	Experiment No. 33.									
3210	Feces for 3 days	258.5	185.5	22.0	12.9	24.3	3.54	34.17	4.96	375
	Average per day	86.2	61.2	7.3	4.3	8.1	1.18	11.39	1.65	125
	Experiment No. 34.									
3211	Feces for 3 days	255.9	179.9	22.0	14.8	25.3	3.53	34.70	4.94	377
	Average per day	85.3	60.0	7.3	4.9	7.8	1.18	11.57	1.65	126

Table XCIV shows the quantity of urine eliminated on different days, and the quantity of urine and nitrogen in the urine for each 6-hour period of experiment No. 33. The heat of combustion of the urine was determined in the composite sample for each day and the carbon and hydrogen in the composite for the total 9 days of the series.

TABLE XCIV.—*Amounts, specific gravity, and nitrogen of urine—Metabolism experiments Nos. 32–34.*

Date.	Period.	Amount.	Specific gravity.	Nitrogen.	
1900.	*Experiment No. 32.*	*Grams.*		*Per cent.*	*Grams.*
Apr. 20–21	7 a. m. to 7 a. m.	1,237.6	1.021	1.28	15.90
21–22	7 a. m. to 7 a. m.	1,487.9	1.018	1.01	14.94
22–23	7 a. m. to 7 a. m.	1,104.1	1.024	1.38	15.20
	Total				46.04
	Experiment No. 33.				
Apr. 23–24	7 a. m. to 1 p. m.	256.7	1.025	1.59	4.08
	1 p. m. to 7 p. m.	425.4	1.019	1.10	4.68
	7 p. m. to 1 a. m.	239.6	1.025	1.77	4.24
	1 a. m. to 7 a. m.	167.4	1.026	1.99	3.33
	Total	1,089.1			16.33
	Total by composite	1,089.1	1.024	1.50	16.34
Apr. 24–25	7 a. m. to 1 p. m.	328.1	1.022	1.28	4.20
	1 p. m. to 7 p. m.	347.6	1.023	1.40	4.87
	7 p. m. to 1 a. m.	319.2	1.021	1.51	4.82
	1 a. m. to 7 a. m.	151.0	1.028	2.17	3.28
	Total	1,145.9			17.17
	Total by composite	1,145.9	1.024	1.51	17.30
Apr. 25–26	7 a. m. to 1 p. m.	262.5	1.025	1.66	4.36
	1 p. m. to 7 p. m.	337.2	1.024	1.48	4.99
	7 p. m. to 1 a. m.	242.1	1.026	1.91	4.62
	1 a. m. to 7 a. m.	147.8	1.030	2.25	3.33
	Total	989.6			17.30
	Total by composite	989.6	1.026	1.75	17.32
	Experiment No. 34.				
Apr. 26–27	7 a. m. to 7 a. m.	851.4	1.030	2.00	17.02
27–28	7 a. m. to 7 a. m.	909.0	1.026	1.74	15.86
28–29	7 a. m. to 7 a. m.	1,095.4	1.024	1.46	16.04
	Total				48.92

TABLE XCV.—*Daily elimination of carbon, hydrogen, and water in urine—Metabolism experiments Nos. 32–34.*

Date.	Amount	Carbon.		Hydrogen.		Water.		Heat of combustion.	
								Per gram.	Total.
1900.	*Grams.*	*Per cent.*	*Grams.*	*Per cent.*	*Grams.*	*Per cent.*	*Grams.*	*Calories.*	*Calories.*
Apr. 20–21	1,237.6		11.35		3.13		1,179.7	0.104	129
21–22	1,487.9		10.67		2.95		1,433.4	.076	113
22–23	1,104.1		10.85		3.00		1,048.7	.105	116
Total			32.87		9.08				358
23–24	1,089.1		11.66		3.22		1,029.6	.115	125
24–25	1,145.9		12.26		3.38		1,083.3	.113	129
25–26	989.6		12.35		3.41		926.6	.134	133
Total			36.27		10.01				387
26–27	851.4		12.15		3.36		789.4	.154	131
27–28	909.0		11.32		3.13		851.2	.137	125
28–29	1,095.4		11.45		3.16		1,036.9	.112	123
Total			34.92		9.65				379
Total 9 days	9,910.0	1.05	104.06	.29	28.74	94.64		(.112)	1,124

Tables XCVI to XCVIII show the results of carbon dioxid and water in the ventilating air current. These statistics are given in detail for experiment No. 33, in which alcohol formed a part of the diet, and summarized for the other 2 experiments of the series. Similar statistics of the heat measurements are given in Table XCIX.

TABLE XCVI.—*Comparison of residual amounts of carbon dioxid and water in the chamber at the beginning and end of each period, and the corresponding gain or loss—Metabolism experiment No. 33.*

Date	End of period	Carbon dioxid. Total amount in chamber.	Carbon dioxid. Gain (+) or loss (−) over preceding period.	Carbon dioxid. Total amount of vapor remaining in chamber.	Water. Gain (+) or loss (−) over preceding period.	Water. Change in weight of absorbers.[a] Gain (+) or loss (−).	Water. Drip from absorbers.	Water. Total amount gained (+) or lost (−) during the period.
1900.		*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Apr. 23	7 a. m.	27.0	.....	46.7	.....	.....	.....	.....
23	1 p. m.	82.8	55.8	53.2	6.5	−147	171.7	+325.2
23	7 p. m.	80.2	−2.6	52.1	−1.1	−9	424.9	+414.8
24	1 a. m.	29.5	−50.7	48.5	−3.6	−74	31.0	−46.6
24	7 a. m.	28.5	−1.0	48.1	−.4	−73	31.0	−42.4
	Total	.....	−1.5	.....	−1.4	−9	658.6	−651.0
24	1 p. m.	84.4	55.9	54.5	−6.4	−172	263.4	+441.8
24	7 p. m.	80.8	−3.6	52.3	−2.2	−28	434.3	+404.1
25	1 a. m.	28.9	−51.9	48.8	−3.5	−76	19.0	−60.5
25	7 a. m.	27.0	−1.9	46.4	−2.4	−76	19.0	−59.4
	Total	.....	−1.5	.....	−1.7	−8	735.7	+726.0
25	1 p. m.	85.7	−58.7	54.7	+8.3	+166	241.0	+415.3
25	7 p. m.	85.7	.....	53.0	−1.7	−4	471.0	+465.3
26	1 a. m.	27.6	−58.1	49.8	−3.2	−82	24.0	−61.2
26	7 a. m.	26.0	−1.6	46.0	−3.8	−82	24.0	−61.8
	Total	.....	−1.0	.....	−.4	−2	760.0	+757.6

TABLE XCVII.—*Record of carbon dioxid in ventilating air current—Metabolism experiments Nos. 32–34.*

Date	Period.	(a) Ventilation. Number of liters of air.	(b) In incoming air. Per liter.	(c) In incoming air. Total, $a \times b$.	(d) In outgoing air.	(e) Total excess in outgoing air, $d - c$.	(f) Correction for amount remaining in chamber.	(g) Corrected amount exhaled by subject, $e + f$.	(h) Total weight of carbon exhaled, $g \times \frac{3}{11}$.
1900.	*Experiment No. 32.*	*Liters.*	*Mg.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Apr. 20–21	7 a. m. to 7 a. m.	107,275	.....	66.1	1,145.8	1,079.7	+.6	1,080.3	294.6
21–22	7 a. m. to 7 a. m.	105,542	.....	66.2	1,273.4	1,207.2	+2.8	1,210.0	329.9
22–23	7 a. m. to 7 a. m.	106,320	.....	63.4	1,359.1	1,295.7	−3.4	1,292.3	352.4
	Experiment No. 33.								
23–24	7 a. m. to 1 p. m.	25,952	0.583	15.1	383.8	368.7	−55.8	424.5	115.8
	1 p. m. to 7 p. m.	25,175	.593	14.9	462.9	448.0	2.6	445.4	121.5
	7 p. m. to 1 a. m.	26,430	.609	16.1	258.9	242.8	50.7	192.1	52.3
	1 a. m. to 7 a. m.	26,430	.600	15.9	158.5	142.6	1.0	141.6	38.6
	Total	103,987	.....	62.0	1,264.1	1,202.1	+1.5	1,203.6	328.2
24–25	7 a. m. to 1 p. m.	25,175	.598	15.1	406.6	391.5	−55.9	447.4	122.0
	1 p. m. to 7 p. m.	26,730	.558	14.9	477.6	462.7	3.6	459.1	125.2
	7 p. m. to 1 a. m.	27,208	.581	15.8	248.7	232.9	51.9	181.0	49.4
	1 a. m. to 7 a. m.	27,208	.642	17.5	154.1	136.6	−1.9	134.7	36.7
	Total	106,321	.....	63.3	1,287.0	1,223.7	−1.5	1,222.2	333.3

[a] Absorbers not weighed between 7 p. m. and 7 a. m. The change in weight during this time is divided equally between the two periods.

TABLE XCVII.—*Record of carbon dioxid in ventilating air current—Metabolism experiments Nos. 32–34*—Continued.

Date.	Period.	(a) Carbon dioxid. In incoming air. Ventilation. Number of liters of air.	(b) Per liter.	(c) Total, $a \times b$.	(d) In outgoing air.	(e) Total excess in outgoing air, $d-c$.	(f) Correction for amount remaining in chamber.	(g) Corrected amount exhaled by subject, $e+f$.	(h) Total weight of carbon exhaled, $g \times \frac{11}{3}$
1900.	*Experiment No. 33*—C'f'd.								
		Liters.	*Mg.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Apr. 25–26	7 a. m. to 1 p. m.	25,952	0.587	15.2	410.0	394.8	−58.7	453.5	123.7
	1 p. m. to 7 p. m.	25,175	.577	14.5	478.7	464.2	.....	464.2	126.6
	7 p. m. to 1 a. m.	27,985	.580	16.2	262.9	246.7	−58.1	188.6	51.4
	1 a. m. to 7 a. m.	27,985	.601	16.8	153.2	136.4	− 1.6	134.8	36.8
	Total.	107,097	.....	62.7	1,304.8	1,242.1	− 1.0	1,241.1	338.5
	Experiment No. 34.								
26–27	7 a. m. to 7 a. m.	108,654	.....	64.0	1,305.0	1,241.0	+ .2	1,241.2	338.5
27–28	7 a. m. to 7 a. m.	114,094	.....	66.1	1,353.1	1,287.0	− .4	1,286.6	350.9
28–29	7 a. m. to 7 a. m.	114,272	.....	67.0	1,339.7	1,272.7	− .7	1,272.0	346.9

TABLE XCVIII.—*Record of water in ventilating air current—Metabolism experiments Nos. 32–34.*

Date.	Period.	(a) Water in incoming air. Ventilation. Number of liters of air.	(b) Per liter.	(c) Total, $a \times b$.	Water in outgoing air. (d) Amount condensed in freezers.	(e) Amount not condensed in freezers.	(f) Total, $d+e$.	(g) Total excess water in outgoing air, $f-c$.	(h) Correction for water remaining in chamber.	(i) Total water of respiration and perspiration, $g-h$.
1900.	*Experiment No. 32.*									
		Liters.	*Mg.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Apr. 20–21	7 a. m. to 7 a. m.	107,275	.....	100.9	894.0	171.0	1,065.0	964.1	− 232.8	1,196.9
21–22	7 a. m. to 7 a. m.	105,542	.....	100.1	917.2	181.2	1,098.4	998.3	+ 612.1	1,610.4
22–23	7 a. m. to 7 a. m.	106,320	.....	110.2	994.8	176.6	1,171.4	1,061.2	−1,033.1	2,094.3
	Experiment No. 33.									
23	7 a. m. to 1 p. m.	25,952	1.040	27.0	235.3	43.5	278.8	251.8	+ 325.2	577.0
23	1 p. m. to 7 p. m.	25,175	1.137	28.6	238.6	43.1	281.7	253.1	+ 414.8	667.9
23–24	7 p. m. to 1 a. m.	26,430	1.030	27.2	233.2	42.7	275.9	248.7	− 46.6	202.1
24	1 a. m. to 7 a. m.	26,430	.930	24.6	241.3	40.3	281.6	257.0	− 42.4	214.6
	Total	103,987	.....	107.4	948.4	169.6	1,118.0	1,010.6	− 651.0	1,661.6
24	7 a. m. to 1 p. m.	25,175	1.088	27.4	236.1	44.3	280.4	253.0	+ 441.8	694.8
24	1 p. m. to 7 p. m.	26,730	1.033	27.6	250.0	43.9	293.9	266.3	− 404.1	670.4
24–25	7 p. m. to 1 a. m.	27,208	.923	25.1	243.9	43.1	287.0	261.9	− 60.5	201.4
25	1 a. m. to 7 a. m.	27,208	.855	23.3	246.8	39.0	285.8	262.5	− 59.4	203.1
	Total	106,321	.....	103.4	976.8	170.3	1,147.1	1,043.7	− 726.0	1,769.7
25	7 a. m. to 1 p. m.	25,952	.951	24.7	188.9	44.0	232.9	208.2	− 415.3	623.5
25	1 p. m. to 7 p. m.	25,175	.972	24.5	253.5	41.7	295.2	270.7	− 465.3	736.0
25–26	7 p. m. to 1 a. m.	27,985	.871	24.4	243.8	45.9	289.7	265.3	− 61.2	204.1
26	1 a. m. to 7 a. m.	27,985	.783	21.9	253.1	38.6	291.7	269.8	− 61.8	208.0
	Total	107,097	.....	95.5	939.3	170.2	1,109.5	1,014.0	− 757.6	1,771.6
	Experiment No. 34.									
26–27	7 a. m. to 7 a. m.	108,654	.....	95.6	995.9	166.6	1,162.5	1,066.9	− 708.9	1,775.8
27–28	7 a. m. to 7 a. m.	114,094	.....	100.5	1,026.2	173.8	1,200.0	1,099.5	+ 724.8	1,824.3
28–29	7 a. m. to 7 a. m.	114,272	.....	105.1	1,021.8	180.5	1,202.3	1,097.2	− 710.4	1,807.6

TABLE XCIX.—S[illegible] of [illegible] measurements.—Metabolism experiments Nos. [illegible]

Date.	Period	Heat measured in terms of C_2	Change of temperature of calorimeter	Capacity correction of calorimeter $b=60$.	Correction due to temperature of food and dishes.[a]	Water vaporized equals total amount exhaled less amount condensed in chamber.	Heat used in vaporization of water, $r=0.592$.	Total heat determined, $a=c+b+f$
	Experiment No. [illegible]	*Calories.*	*Degree.*	*Calories.*	*Calories.*	*Grams.*	*Calories.*	*Calories.*
1900.								
Apr. 20–21	7 a. m. to 7 a. m.	2,666.3	0.32	19.2	6.0	968.2	573.2	3,252.7
21–22	7 a. m. to 7 a. m.	2,959.4	.07	- 4.2	— 6.8	1,004.6	594.7	3,551.5
22–23	7 a. m. to 7 a. m.	3,275.2	.....	.....	12.4	1,058.5	626.7	3,889.5
	Experiment No. 33.							
23–24	7 a. m. to 1 p. m.	1,088.6	- .07	- 4.2	— 3.3	258.3	152.9	1,242.4
	1 p. m. to 7 p. m.	1,207.6	- .01	- 0.6	—14.4	252.0	149.2	1,343.0
	7 p. m. to 1 a. m.	455.7	.....	.....	— 1.2	245.1	145.1	602.0
	1 a. m. to 7 a. m.	269.3	- .01	- 0.6	.....	256.6	151.9	421.8
	Total	3,021.2	- .09	- 5.4	—16.5	1,012.0	599.1	3,609.2
24–25	7 a. m. to 1 p. m.	1,153.8	— .04	— 2.4	— 5.1	259.4	153.5	1,299.8
	1 p. m. to 7 p. m.	1,189.9	.02	— 1.2	—15.3	264.1	156.3	1,329.7
	7 p. m. to 1 a. m.	437.1	.....	.....	— 1.4	258.4	153.0	591.5
	1 a. m. to 7 a. m.	248.4	— .01	— 0.6	.....	260.1	154.0	403.0
	Total	3,029.2	.05	- 3.0	—19.0	1,042.0	616.8	3,624.0
25–26	7 a. m. to 1 p. m.	1,180.4	— .04	— 2.4	— 2.5	216.5	128.2	1,303.7
	1 p. m. to 7 p. m.	1,226.8	.....	.....	—10.4	269.0	159.2	1,375.6
	7 p. m. to 1 a. m.	429.2	.....	.....	— 2.3	262.1	155.2	586.7
	1 a. m. to 7 a. m.	239.9	— .01	— 0.6	.....	266.0	157.5	398.0
	Total	3,076.3	— .03	— 1.8	—10.6	1,013.6	600.1	3,664.0
	Experiment No. 34.							
26–27	7 a. m. to 7 a. m.	2,948.7	— .07	— 4.2	— 7.7	1,067.1	631.7	3,568.5
27–28	7 a. m. to 7 a. m.	2,989.9	— .11	— 6.6	— 0.7	1,098.3	650.2	3,632.8
28–29	7 a. m. to 7 a. m.	2,924.1	— .01	— 0.6	—11.4	1,095.7	648.6	3,560.7

[a] Including 4.8 calories during each day period generated by the electric current used to magnetize the fields of the dynamo.

The alcohol, or reducing material equivalent to alcohol, given off from the body in different ways was determined in the usual manner, and the result appear in Table C. The usual correction is made for the total amount of reducing material in the urine, drip, freezer water, and air current, as found in experiments Nos. 32 and 34, in which alcohol did not form a part of the diet. It will be observed that about one-third of the total reducing material in experiment No. 33 must be considered as due to other compounds than the unoxidized alcohol. As in the previous series of experiments, there was no indication of a lag in the elimination of unoxidized alcohol.

TABLE C.—*Alcohol ingested and [illegible] in metabolism experiments Nos. 32–34.*

Date.	Alcohol ingested	Alcohol excreted, reducing material equivalent to alcohol.					Alcohol excreted unoxidized.[a]	Alcohol metabolized in body.
		In urine distillate.	In drip distillate.	In freezer water distillate.	In air current.	Total.		
1900.								
Experiment No. [illegible]	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Per cent.*
Apr. 20–21	.....	0.02		0.01	0.41	0.44	.....	.....	.....
21–22	.....	.01	0.02	Trace.	.30	.32	.....	.....	.....
22–23	.....	.03		.01	.20	.25	.....	.....	.....

[a] Equals total reducing material excreted less 0.32 gram of reducing material not alcohol, the average for the days on which no alcohol was consumed.

TABLE C.—*Alcohol ingested and excreted—Metabolism experiments Nos. 33–34*—Continued.

Date.	Alcohol ingested.	Alcohol excreted, including other reducing material calculated as alcohol.					Alcohol excreted unoxidized.[a]	Alcohol metabolized in body.	
		In urine (distillate).	In drip (distillate).	In freezer water (distillate).	In air current.	Total.			
1900.									
Experiment No. 33.									
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Per cent.*
Apr. 23–24	72.0	0.05	0.22	0.01	0.88	1.02	0.70	71.3	99.6
24–25	72.0	.06		.02	.92	1.07	.75	71.3	99.0
25–26	72.0	.05		.02	.93	1.07	.75	71.2	98.9
Total	216.0	.16	.22	.05	2.73	3.16	2.20	213.8	.....
Average, 1 day	72.0	.05	.07	.01	.91	1.05	.73	71.3	99.0
Experiment No. 34.									
Apr. 26–27	.....	.04	.04	.01	.32	.37	.....	.....	.....
27–28	.....	.02		.01	.26	.30	.....	.....	.....
28–29	.....	.01		.01	.20	.24	.....	.....	.....

[a] Equals total reducing material excreted less 0.32 gram of reducing material not alcohol, the average for the days on which no alcohol was consumed.

Balance of income and outgo of matter and energy.—From the preceding statistics are computed the income and outgo of nitrogen, carbon, hydrogen, and energy on the different days of each of this series of experiments. The results of these computations are shown in Tables CI–CIV.

TABLE CI.—*Income and outgo of nitrogen and carbon—Metabolism experiments Nos. 33–34.*

Date and period.	Nitrogen.				Carbon.					
	(*a*) In food	(*b*) In feces.	(*c*) In urine.[a]	(*d*) Gain (+) or loss (−), *a*−(*b*+*c*).	(*e*) In food.	(*f*) In feces.	(*g*) In urine.	(*h*) In respiratory products.	(*i*) In alcohol eliminated.	(*k*) Gain (+) or loss (−), *e*−(*f*+*g*+*h*+*i*).
1900.										
Experiment No. 32.										
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Apr. 20–21, 7 a. m. to 7 a. m.	16.1	1.2	16.3	−1.4	320.0	12.6	11.3	294.6	.....	+ 1.5
21–22, 7 a. m. to 7 a. m.	16.2	1.2	15.3	− .3	320.0	12.6	10.7	329.9	.....	− 33.2
22–23, 7 a. m. to 7 a. m.	16.1	1.2	15.6	− .7	320.0	12.6	10.9	352.4	.....	− 55.9
Total	48.4	3.6	47.2	−2.4	960.0	37.8	32.9	976.9	.....	− 87.6
Average, 1 day	16.1	1.2	15.7	− .8	320.0	12.6	11.0	325.6	.....	− 29.2
Experiment No. 33.										
Apr. 23–24, 7 a. m. to 7 a. m.	16.0	1.2	16.7	−1.9	319.6	11.4	11.7	328.2	0.3	− 32.0
24–25, 7 a. m. to 7 a. m.	16.0	1.2	17.6	−2.8	319.6	11.4	12.3	333.3	.4	− 37.8
25–26, 7 a. m. to 7 a. m.	16.0	1.2	17.7	−2.9	319.6	11.4	12.3	338.5	.4	− 43.0
Total	48.0	3.6	52.0	− 7.6	958.8	34.2	36.3	1,000.0	1.1	−112.8
Average, 1 day	16.0	1.2	17.3	− 2.5	319.6	11.4	12.1	333.3	.4	− 37.6
Experiment No. 34.										
Apr. 26–27, 7 a. m. to 7 a. m.	16.0	1.2	17.4	−2.6	335.7	11.6	12.2	338.5	.....	− 26.6
27–28, 7 a. m. to 7 a. m.	16.0	1.2	16.3	− 1.5	335.8	11.5	11.3	350.9	.....	− 37.9
28–29, 7 a. m. to 7 a. m.	16.0	1.2	16.4	− 1.6	335.7	11.6	11.4	346.9	.....	− 34.2
Total	48.0	3.6	50.1	− 5.7	1,007.2	34.7	34.9	1,036.3	.....	− 98.7
Average, 1 day	16.0	1.2	16.7	− 1.9	335.7	11.6	11.6	345.4	.....	− 32.9

[a] Nitrogen in perspiration, 0.1 grams per day, is included in this column.

TABLE CII.—*Income and outgo of water and hydrogen—Metabolism experiments Nos. 32–34.*

Date and period.	Water						Hydrogen						
	a	*b*	*c*	*d*	*e*		*g*	*h*	*i*	*k*	*l*		
	In food.	In drink.	In feces.	In urine.	Insensible perspiration and lungs.	Apparent loss, $a+b-c-d=e$.	In food.	In feces.	In urine.	In alcohol eliminated.	Apparent gain, $g+h+i+k=l$.	Loss from water, $f \cdot 9$	Total gain (+) or loss (−), $l+m$.
1900.													
Experiment No. 32.													
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Gms.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Apr. 20–21, 7 a. m. to 7 a. m.	1,035.9	1.250	71.6	1,179.7	1,196.9	162.3	49.0	1.8	3.1	.....	+ 44.1	− 18.0	+26.1
Apr. 21–22, 7 a. m. to 7 a. m.	1,035.9	1.250	71.5	1,433.4	1,610.4	829.4	49.0	1.8	3.0	.....	+ 44.2	92.2	−48.0
Apr. 22–23, 7 a. m. to 7 a. m.	1,035.9	1.250	71.6	1,048.7	2,004.3	928.7	49.0	1.8	3.0	.....	44.2	−103.2	−59.0
Total	3,107.7	3.750	214.7	3,661.8	4,901.6	1,920.4	147.0	5.4	9.1	.....	+ 132.5	213.4	−80.9
Average, 1 day	1,035.9	1.250	71.6	1,220.6	1,633.8	640.1	49.0	1.8	3.0	.....	44.2	71.1	26.9
Experiment No. 33.													
Apr. 23–24, 7 a. m. to 7 a. m.	1,027.6	1.250	61.2	1,029.6	1,061.6	474.8	52.5	1.6	3.2	0.1	+ 47.6	52.8	− 5.2
Apr. 24–25, 7 a. m. to 7 a. m.	1,027.6	1.250	61.1	1,083.3	1,769.7	636.5	52.5	1.7	3.4	.1	+ 47.3	70.7	−23.4
Apr. 25–26, 7 a. m. to 7 a. m.	1,027.6	1.250	61.2	926.6	1,771.6	481.8	52.5	1.6	3.4	.1	+ 47.4	53.5	− 6.1
Total	3,082.8	3.750	183.5	3,039.5	5,202.9	1,593.1	157.5	4.9	10.0	.3	+ 142.3	177.0	−34.7
Average, 1 day	1,027.6	1.250	61.2	1,013.2	1,734.3	531.0	52.5	1.6	3.4	.1	47.4	59.0	−11.6
Experiment No. 34.													
Apr. 26–27, 7 a. m. to 7 a. m.	1,028.6	1.250	60.0	789.4	1,775.8	346.6	51.1	1.7	3.4	.....	+ 46.0	− 38.5	− 7.5
Apr. 27–28, 7 a. m. to 7 a. m.	1,028.6	1.250	59.9	851.2	1,824.3	456.8	51.1	1.6	3.1	.....	+ 46.4	− 50.8	− 4.4
Apr. 28–29, 7 a. m. to 7 a. m.	1,028.6	1.250	60.0	1,036.9	1,807.6	625.9	51.1	1.7	3.2	.....	+ 46.2	− 69.5	−23.3
Total	3,085.8	3.750	179.9	2,677.5	5,407.7	1,429.3	153.3	5.0	9.7	.....	138.6	−158.8	−20.2
Average, 1 day	1,028.6	1.250	60.0	892.5	1,802.5	476.4	51.1	1.7	3.2	.....	46.2	52.9	− 6.7

TABLE CIII.—*Gain or loss of protein (N × 6.25), fat, and water—Metabolism experiments Nos. 32–34.*

Date and period	(a) Nitrogen gained (+) or lost (−),	(b) Protein gained (+) or lost (−), $a \times 6.25$.	(c) Total carbon gained (+) or lost (−),	(d) Carbon in protein gained (+) or lost (−), $b \times 0.53$.	(e) Carbon in fat, etc., gained (+) or lost (−), $c-d$.	(f) Fat gained (+) or lost (−), $e \div 0.761$.	(g) Total hydrogen gained (+) or lost (−),	(h) Hydrogen in protein gained (+) or lost, (−), $b \times 0.07$.	(i) Hydrogen in fat gained (+) or lost (−), $f \times 0.118$.	(k) Hydrogen in water, etc., gained (+) or lost (−), $g-(h+i)$.	(l) Water gained (+) or lost (−), $k \times 9$.
1900.											
Experiment No. 32.											
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*
Apr. 20–21, 7 a. m. to 7 a. m.	−1.4	−8.7	−1.5	−4.6	+6.1	−8.0	−26.1	−0.6	+0.9	−25.8	+232.2
21–22, 7 a. m. to 7 a. m.	−.3	−1.9	−33.2	−1.0	−32.2	−42.3	−48.0	−.1	−5.0	−42.9	−386.1
22–23, 7 a. m. to 7 a. m.	−.7	−4.4	−55.9	−2.3	−53.6	−70.4	−59.0	−.3	−8.3	−50.4	−453.6
Total	−2.4	−15.0	−87.6	−7.9	−79.7	−104.7	−80.9	−1.0	−12.4	−67.5	−607.5
Average, 1 day	−.8	−5.0	−29.2	−2.6	−26.6	−34.9	−26.9	−.3	−4.1	−22.5	−202.5
Experiment No. 33.											
Apr. 23–24, 7 a. m to 7 a. m.	−1.9	−11.9	−32.0	−6.3	−25.7	−33.8	−5.2	−.8	−4.0	−.4	−3.6
24–25, 7 a. m to 7 a. m.	−2.8	−17.5	−37.8	−9.3	−28.5	−37.5	−23.4	−1.2	−4.4	−17.8	−160.2
25–26, 7 a. m to 7 a. m.	−2.9	−18.1	−43.0	−9.6	−33.4	−43.9	−6.1	−1.3	−5.2	+.4	+3.6
Total	−7.6	−47.5	−112.8	−25.2	−87.6	−115.2	−34.7	−3.3	−13.6	−17.8	−160.2
Average, 1 day	−2.5	−15.8	−37.6	−8.4	−29.2	−38.4	−11.5	−1.1	−4.5	−5.9	−53.1
Experiment No. 34.											
Apr. 26–27, 7 a. m. to 7 a. m.	−2.6	−16.3	−26.6	−8.6	−18.0	−23.7	+7.5	−1.1	−2.8	−11.4	−102.6
27–28, 7 a. m. to 7 a. m.	−1.5	−9.4	−37.9	−5.0	−32.9	−43.2	−4.4	−.7	−5.1	+1.4	+12.6
28–29, 7 a. m. to 7 a. m.	−1.6	−10.0	−34.2	−5.3	−28.9	−38.0	−23.3	−.7	−4.5	−18.1	−162.9
Total	−5.7	−35.7	−98.7	−18.9	−79.8	−104.9	−20.2	−2.5	−12.4	−5.3	−47.7
Average, 1 day	−1.9	−11.9	−32.9	−6.3	−26.6	−35.0	−6.7	−.8	−4.1	−1.8	−15.9

TABLE CIV.—*Income and outgo of energy—Metabolism experiments Nos. 32–34.*

Date and period.	(a) Heat of combustion of food eaten.	(b) Heat of combustion of feces	(c) Heat of combustion of urine.	(m) Heat of combustion of alcohol eliminated	(d) Estimated heat of combustion of protein gained (+) or lost (−),	(e) Estimated heat of combustion of fat gained (+) or lost (−),	(f) Estimated energy of material oxidized in the body, $a-(b+c+m+d+e)$.	(g) Heat determined.	Heat determined greater (+) or less (−) than estimated. (h) $f-g$.	(i) $h \div f$.
1900.										
Experiment No. 32.										
	Calories.	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*	*Per cent.*
Apr. 20–21, 7 a. m. to 7 a. m.	3,487	142	129	.....	−35	−77	3,174	3,253	+79	−2.5
21–22, 7 a. m. to 7 a. m.	3,487	141	113	.....	−3	−404	3,634	3,551	−83	−2.3
22–23, 7 a. m. to 7 a. m.	3,487	142	116	.....	−11	−672	3,912	3,890	22	−.5
Total	10,461	425	358	.....	−43	−999	10,720	10,694	−26	.....
Average, 1 day	3,487	142	119	.....	−14	−333	3,573	3,565	−8	−.2
Experiment No. 33.										
Apr. 23–24, 7 a. m. to 7 a. m.	3,486	125	125	5	−54	−322	3,607	3,609	+2	.0
24–25, 7 a. m. to 7 a. m.	3,486	125	129	5	−86	−357	3,670	3,624	−46	−1.3
25–26, 7 a. m. to 7 a. m.	3,486	125	133	5	−90	−419	3,732	3,664	−68	−1.8
Total	10,458	375	387	15	−230	−1,098	11,009	10,897	−112	.....
Average, 1 day	3,486	125	129	5	−76	−366	3,669	3,632	−37	−1.0
Experiment No. 34.										
Apr. 26–27, 7 a. m. to 7 a. m.	3,493	126	131	.....	−79	−226	3,541	3,568	+27	−.7
27–28, 7 a. m. to 7 a. m.	3,493	125	125	.....	−40	−413	3,696	3,633	−63	−1.7
28–29, 7 a. m. to 7 a. m.	3,493	126	123	.....	−43	−363	3,650	3,561	−89	−2.4
Total	10,479	377	379	.....	−162	−1,002	10,887	10,762	−125	.....
Average, 1 day	3,493	126	126	.....	−54	−334	3,629	3,587	−42	−1.1

STATISTICAL DETAILS OF DIGESTION EXPERIMENTS.

As has already been explained, each metabolism experiment or series of experiments was preceded by a digestion experiment and each metabolism experiment includes a digestion experiment. The results of those digestion experiments in which alcohol formed a part of the diet are detailed herewith. Those of the corresponding experiments without alcohol are given in connection with the description of the latter, as elsewhere published.[a] The results of the digestion experiments with and without alcohol are summarized beyond.

The weights of the different food materials, as shown in the first column of Tables CV–CVIII, together with the figures for percentage, composition, and heat of combustion, as shown in Tables I–III above, suffice for the computations of the nutrients and energy in the food and feces. In computing the protein from the nitrogen, the factor 6.25 has been used for all animal foods and 5.70 for the vegetable foods used in the experiments.[b] The total organic matter as shown in the tables is the sum of the organic constituents—protein, fat, carbohydrates, and alcohol.

DETAILS OF DIGESTION EXPERIMENT NO. 41.

This was preliminary to metabolism experiment No. 7, began with breakfast June 3, 1897, and continued 5 days. The diet was the same in kind and practically the same in the relative amounts of the different ingredients as in the following metabolism experiment. The subject was E. O., the laboratory assistant who served in a large number of the experiments here recorded. His weight at the beginning of the experiment was not recorded: at the end it was without clothing, 66.7 kilograms (147 pounds). He was occupied in his usual duties about the laboratory, but did as little muscular work as practicable, in order that the conditions of exercise should not differ greatly from those in the following rest experiment in the respiration apparatus. The results of the experiment are shown in Table CV.

DETAILS OF DIGESTION EXPERIMENT NO. 42.

This experiment followed immediately after No. 41 and formed a part of metabolism experiment No. 7. It began with breakfast June 8, 1898, and continued 4 days. The subject, E. O., weighed without clothing 66.7 kilograms (147 pounds) at the beginning and 66 kilograms (145½ pounds) at the end of the study. The subject had as little muscular activity as was practicable during the experiment. The details are given in Table CVI.

TABLE CV.—*Details of digestion experiment No. 41 (preliminary to metabolism experiment No. 7).*

Laboratory No. sample.		Weight of material.	Total organic matter.	Nitrogen.	Protein.	Fat.	Carbohydrates.	Alcohol.	Ash.	Heat of combustion (determined).
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
2795	Beef, fried	850	274	34.7	217	57	.....	.....	11	1,709
2796	Beef, dried	125	34	4.8	30	4	.....	.....	9	199
2798	Eggs, boiled	722	138	11.5	72	66	.....	.....	5	1,028
2801	Butter	75	65	.2	1	64	.....	.....	3	595
2800	Milk	2,875	351	16.2	101	138	112	.....	22	2,133
2804	Bread, rye	750	420	10.1	58	4	358	.....	12	1,862
2786	Sugar	225	225	.....	.....	.....	225	.....	.....	891
2797	Beans, baked	625	169	6.2	39	6	124	.....	12	786
	Pears, canned	750	145	.3	2	4	139	.....	2	577
	Alcohol	363	363	.....	.....	.....	.....	362.5	.....	2,566
	Total	7,360	2,184	84	520	343	958	362.5	76	12,346
2809	Feces	404	96	7.7	48	22	26	.....	19	632
	Alcohol excreted unoxidized	.....	15	.....	.....	.....	.....	15	.....	106
	Urine	.....	.....	.....	.....	.....	.....	.....	.....	590
	Amount available	.....	2,073	76.3	472	321	932	347.5	57	11,018
			Per cent.	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*
	Coefficients of availability	.....	94.9	90.8	90.8	93.6	97.3	95.9	75	89.2

[a] See page 241.

[b] See discussion of nitrogen factor for protein. ATWATER and BRYANT, Rept. Storrs (Conn.) Expt. Sta., 1899, p. 76.

TABLE CVI.—*Details of digestion experiment No. 42 (part of metabolism experiment No. 7).*

Laboratory No. sample.		Weight of material.	Total organic matter.	Nitrogen.	Protein.	Fat.	Carbohydrates.	Alcohol.	Ash.	Heat of combustion (determined).
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
2795	Beef, fried	675	217	27.5	172	45	.....	.....	9	1,357
2796	Beef, dried	100	27	3.8	24	3	.....	.....	7	160
2798	Eggs, boiled	564	108	9.1	57	51	.....	.....	4	803
2801	Butter	60	52	.2	1	51	.....	.....	2	476
2800	Milk	2,300	281	13	81	110	90	.....	18	1,707
2804	Bread, rye	600	336	8	46	4	286	.....	10	1,490
2786	Sugar	180	180	.....	.....	.....	180	.....	.....	713
2797	Beans, baked	500	135	5	31	5	99	.....	10	628
	Pears, canned	600	116	.3	2	3	111	.....	1	461
	Alcohol	290	290	.....	.....	.....	.....	290	.....	2,050
	Total	5,869	1,742	66.9	414	272	766	290	61	9,845
2810	Feces	198	47	3.5	22	10	15	.....	10	303
	Alcohol excreted unoxidized	.....	11.9	.....	.....	.....	.....	11.9	.....	84
	Urine	.....	.....	.....	.....	.....	.....	.....	.....	490
	Amount available	.....	1,683.1	63.4	392	262	751	278.1	51	8,968
	Coefficients of availability	.....	*Per cent.* 96.6	*Per cent.* 94.8	*Per cent.* 94.7	*Per cent.* 96.3	*Per cent.* 98.1	*Per cent.* 95.9	*Per cent.* 83.6	*Per cent.* 91.1

DETAILS OF DIGESTION EXPERIMENT NO. 47.

This experiment began with breakfast February 11, 1898, and continued 4 days. The diet was the same in kind and practically the same in amount as in metabolism experiment No. 10, which immediately followed and of which this experiment formed the preliminary period. The subject, E. O., weighed without clothing 67.4 kilograms (148½ pounds) at the close of the study. His weight at the beginning was not recorded. He was engaged about the laboratory in his usual occupation, but avoided muscular exertion so far as practicable. Table CVII gives the details.

DETAILS OF DIGESTION EXPERIMENT NO. 48.

This experiment, which formed a part of metabolism experiment No. 10, began with breakfast February 15, 1898, and continued 4 days. The subject, E. O., weighed without clothing 67.4 kilograms at the beginning and 67.6 kilograms (149 pounds) at the end of the experimental period. Table CVIII gives detailed results.

TABLE CVII.—*Details of digestion experiment No. 47 (preliminary to metabolism experiment No. 10).*

Lab. No. sample.		Weight of material.	Total organic matter.	Nitrogen.	Protein.	Fat.	Carbohydrates.	Alcohol.	Ash.	Heat of combustion (determined).
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
2839	Beef	1,080	329.0	46.9	293	36	.....	.....	21	1,961
2843	Butter	60	53.0	.....	.....	53	.....	.....	1	479
2845	Milk, skimmed	3,000	261.0	14.9	93	3	165	.....	24	1,206
2844	Bread	500	288.0	6.7	38	1	249	.....	7	1,277
2842	Maize breakfast food	200	187.0	3.8	23	16	148	.....	3	887
2840	Wheat breakfast food	200	182.0	3.5	20	3	159	.....	4	810
2841	Ginger snaps	240	223.0	2.2	13	15	195	.....	7	1,019
	Sugar	280	280.0	.....	.....	.....	280	.....	.....	1,109
	Alcohol	290	290.0	.....	.....	.....	.....	290.0	.....	2,050
	Total	5,850	2,093.0	78.0	480	127	1,196	290.0	67	10,798
2847	Feces	267	59.0	4.0	25	10	24	.....	12	360
	Alcohol excreted unoxidized	.....	4.4	.....	.....	.....	.....	4.4	.....	31
	Urine	.....	.....	.....	.....	.....	.....	.....	.....	569
	Amount available	.....	2,029.6	74.0	455	117	1,172	285.6	55	9,838
	Coefficients of availability	.....	*Per cent.* 97.0	*Per cent.* 94.9	*Per cent.* 94.8	*Per cent.* 92.1	*Per cent.* 98.0	*Per cent.* 98.5	*Per cent.* 82.1	*Per cent.* 91.1

TABLE CVIII. *Details of digestion experiment No. 48 (part of metabolism experiment No. 10).*

Lab. No. sample		Weight of material	Total organic matter	Nitrogen	Protein	Fat	Carbohydrates	Alcohol	Ash	Heat of combustion (determined)
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
2839	Beef	1,080	329.0	46.9	293	36	.....	.....	21	1,961
2843	Butter	60	53.0	.....	.....	53	.....	.....	1	479
2846	Milk, skimmed	3,000	264.0	15.8	99	3	162	.....	24	1,242
2844	Bread	500	288.0	6.7	38	1	249	.....	7	1,277
2842	Maize breakfast food	200	187.0	3.8	23	16	148	.....	3	887
2840	Wheat breakfast food	200	182.0	3.5	20	3	159	.....	4	840
2841	Ginger snaps	240	223.0	2.2	13	15	195	.....	7	1,019
	Sugar	280	280.0	.....	.....	.....	280	.....	.....	1,109
	Alcohol	290	290.0	.....	.....	.....	.....	290.0	.....	2,050
	Total	5,850	2,096.0	78.9	486	127	1,193	290.0	67	10,834
2848	Feces	351	85.0	5.4	34	15	36	.....	17	507
	Alcohol excreted unoxidized	.....	4.4	.....	.....	.....	.....	4.4	.....	31
	Urine	.....	.....	.....	.....	.....	.....	.....	.....	565
	Amount available	.....	2,006.6	73.5	452	112	1,157	285.6	50	9,731
			Per cent.	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*
	Coefficients of availability	.....	95.7	93.1	93.0	88.2	97.0	98.5	74.6	89.8

DETAILS OF DIGESTION EXPERIMENT NO. 51.

This study was preliminary to metabolism experiment No. 12, with the same kinds and amounts of the different food materials. The subject, E. O., was engaged in his usual laboratory work, but in addition took considerable muscular exercise on the bicycle and otherwise, in order to make the conditions of muscular activity not greatly different from those in the following metabolism experiment. The study began with breakfast April 8, 1898, and continued 4 days. The subject weighed, without clothing, 70.5 kilograms (155.4 pounds) at the beginning and 70.1 kilograms (154.5 pounds) at the end of the study.

DETAILS OF DIGESTION EXPERIMENT NO. 52.

This experiment, which formed a part of metabolism experiment No. 12, began with breakfast April 12, 1898, and continued 4 days. The subject, E. O., weighed, without clothing, 70.9 kilograms (156.3 pounds) at the beginning and 70.3 kilograms (155 pounds) at the end of the study. He worked 8 hours a day upon a stationary bicycle within the chamber of the calorimeter.

TABLE CIX.—*Details of digestion experiment No. 51 (preliminary to metabolism experiment No. 12).*

Lab. No. sample.		Weight of material.	Total organic matter.	Nitrogen.	Protein.	Fat	Carbohydrates.	Alcohol.	Ash.	Heat of combustion (determined).
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories*
2860	Beef	700	231.0	30.7	192	39	.....	.....	18	1,400
2861	Butter	380	330.0	.3	2	328	.....	.....	8	3,004
2856	Milk	3,600	482.0	19.0	119	180	183	.....	25	3,114
2859	Bread	1,200	702.0	18.1	103	12	587	.....	13	3,196
2842	Maize breakfast food	240	224.0	4.5	27	20	177	.....	4	1,065
2858	Deviled ham	200	110.0	5.9	37	73	.....	.....	8	873
	Sugar	280	280.0	.....	.....	.....	280	.....	.....	1,109
	Alcohol	290	290.0	.....	.....	.....	.....	290.0	.....	2,050
	Total	6,890	2,649.0	78.5	480	652	1,227	290.0	76	15,811
2862	Feces	495	120.0	7.2	45	38	37	.....	27	791
	Alcohol excreted unoxidized	.....	6.0	.....	.....	.....	.....	6.0	.....	42
	Urine	.....	.....	.....	.....	.....	.....	.....	.....	544
	Amount available	.....	2,523.0	71.3	435	614	1,190	284.0	49	14,434
			Per cent.	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*
	Coefficients of availability	.....	95.2	90.8	90.6	94.2	97.0	97.9	64.5	91.3

TABLE CX.—*Details of digestion experiment No. 52 (part of metabolism experiment No. 12).*

Lab. No. sample		Weight of material.	Total organic matter.	Nitrogen.	Protein.	Fat.	Carbohydrates.	Alcohol.	Ash.	Heat of combustion (determined).
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
2866	Beef	700	231.0	30.7	192	39	.....	.....	18	1,400
2861	Butter	380	330.0	0.3	2	328	.....	.....	8	3,004
2857	Milk	3,600	425.0	17.9	112	162	151	.....	25	2,873
2859	Bread	1,200	702.0	18.1	103	12	587	.....	13	3,196
2842	Maize breakfast food	240	224.0	4.5	27	20	177	.....	4	1,065
2858	Deviled ham	200	110.0	5.9	37	73	.....	.....	8	873
	Sugar	280	280.0	.....	.....	.....	280	.....	.....	1,109
	Alcohol	290	290.0	.....	.....	.....	.....	290.0	.....	2,050
	Total	6,890	2,592.0	77.4	473	634	1,195	290.0	76	15,570
2863	Feces	370	79.0	5.0	31	26	22	.....	16	545
	Alcohol excreted unoxidized	.....	6.0	.....	.....	.....	.....	6.0	.....	42
	Urine	.....	.....	.....	.....	.....	.....	.....	.....	553
	Amount available	.....	2,507.0	72.4	442	608	1,173	284.0	60	14,430
	Coefficients of availability	.....	*Per cent.* 96.7	*Per cent.* 93.5	*Per cent.* 93.4	*Per cent.* 95.9	*Per cent.* 98.2	*Per cent.* 97.9	*Per cent.* 78.9	*Per cent.* 92.7

DETAILS OF DIGESTION EXPERIMENT NO. 80.

This experiment formed the preliminary period to the series of metabolism experiments Nos. 15–17. It began with breakfast January 12, 1899, and continued 4 days. The subject, E. O., as in previous experiments here reported, was engaged in very light work about the laboratory. His weight at the end of the study, without clothing, was 70.9 kilograms (156 pounds). The alcohol during this period was taken in the form of commercial alcohol in sweetened coffee infusion, as in metabolism experiment No. 15. In metabolism experiment No. 16 the alcohol was taken in the form of whisky, and in No. 17 in the form of brandy.

DETAILS OF DIGESTION EXPERIMENT NO. 81.

This experiment, which formed a part of the series of metabolism experiments Nos. 15, 16, and 17, began with breakfast January 16, 1899, and continued 6 days. The subject, E. O., weighed, without clothing, 70.9 kilograms at the beginning and 70.1 kilograms (154.5 pounds) at the end of the experiment.

TABLE CXI.—*Details of digestion experiment No. 80 (preliminary to metabolism experiment No. 15).*

Laboratory No. sample.		Weight of material.	Total organic matter.	Nitrogen.	Protein.	Fat.	Carbohydrates.	Alcohol.	Ash.	Heat of combustion (determined).
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
3009	Beef	640	184	26.7	167	17	.....	.....	14	1,076
3003	Butter	120	104	.2	1	103	.....	.....	3	955
3005	Milk, skimmed	3,450	334	22.1	138	3	193	.....	31	1,611
3004	Parched cereal	120	111	2.2	13	1	97	.....	2	487
2968	Bread	1,240	707	15.7	89	35	583	.....	16	3,360
	Sugar	204	204	.....	.....	.....	204	.....	.....	808
	Alcohol	290	290	.....	.....	.....	.....	290	.....	2,256
	Total	6,064	1,934	66.9	408	159	1,077	290	66	10,553
	Feces	185	55	3.2	20	13	22	.....	14	383
3007	Alcohol excreted unoxidized	.....	6.8	.....	.....	.....	.....	6.8	.....	48
	Urine	.....	.....	.....	.....	.....	.....	.....	.....	485
	Amount available	.....	1,872.2	63.7	388	146	1,055	283.2	52	9,637
	Coefficients of availability	.....	*Per cent.* 96.8	*Per cent.* 95.2	*Per cent.* 95.1	*Per cent.* 91.8	*Per cent.* 98	*Per cent.* 97.6	*Per cent.* 78.8	*Per cent.* 91.4

TABLE CXII.—*Details of digestion experiment No. 82 (part of metabolism experiments Nos. 15, 16, and 17.*

Laboratory No. sample.		Weight of material.	Total organic matter.	Nitrogen.	Protein.	Fat.	Carbohydrates.	Alcohol.	Ash	Heat of combustion (determined)
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
3009	Beef	960	275	40.0	250	25	.....	.....	21	1,615
3003	Butter	180	157	.3	2	155	.....	.....	5	1,433
3006	Milk, skimmed	5,700	553	37.5	234	6	313	.....	46	2,667
3004	Parched cereal	180	166	3.2	18	1	147	.....	3	730
2968	Bread	1,860	1,060	23.5	134	52	874	.....	24	5,040
	Sugar	342	342	.....	.....	.....	342	.....	.....	1,354
	Alcohol	435	435	.....	.....	.....	.....	435	.....	3,075
	Total	9,657	2,988	104.5	638	239	1,676	435	99	15,914
3008	Feces	316	76	5	31	18	27	.....	24	529
	Alcohol excreted unoxidized	.....	10.3	.....	.....	.....	.....	10.3	.....	73
	Urine	.....	.....	.....	.....	.....	.....	.....	.....	759
	Amount available	.....	2,901.7	99.5	607	221	1,649	424.7	75	14,553
	Coefficients of availability	.....	*Per cent.* 97.1	*Per cent.* 95.2	*Per cent.* 95.2	*Per cent.* 92.5	*Per cent.* 98.4	*Per cent.* 97.6	*Per cent.* 75.8	*Per cent.* 91.5

DETAILS OF DIGESTION EXPERIMENT NO. 82.

This experiment was preliminary to and formed a part of metabolism experiments Nos. 18–21. The subject was A. W. S., a physicist. He was engaged in the investigations of which this experiment forms a part. The study began with breakfast February 2, 1899, and continued 4 days outside the apparatus. During the following 9 days, beginning with February 6, the subject was inside the respiration chamber. It was the intention to subdivide the 13 days covered by this digestion experiment into three separate experiments, comprising the 4 preliminary days previous to the time when the subject entered the respiration calorimeter; the 6 days in the calorimeter in which alcohol formed a part of the diet, either as commercial alcohol, whisky, or brandy; and the 3 days of experiment No. 21 in which alcohol was omitted from the diet. Unfortunately no satisfactory separation of the feces was obtained between the preliminary period and the end of the experiment No. 21. The whole time is therefore included in one digestion experiment. The body weight of the subject at the beginning of the period was 72.4 kilograms, and at the end 72.7 kilograms (160.3 pounds). During the preliminary days very little muscular work was done, and during the sojourn in the apparatus practically no exercise was taken. The kinds and daily amounts of foods were the same during the 4 preliminary days, and the 6 days of metabolism experiments Nos. 18–20, except that alcohol was taken in the form of commercial ethyl alcohol in the preliminary period and in No. 18, whisky in No. 19, brandy in No. 20. In experiment No. 21 the alcohol was omitted from the diet.

TABLE CXIII.—*Details of digestion experiment No. 82 (preliminary to and part of metabolism experiments Nos. 18–21).*

Laboratory No. sample.		Weight of material.	Total organic matter.	Nitrogen.	Protein.	Fat.	Carbohydrates.	Alcohol.	Ash.	Heat of combustion (determined).
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
3022	Beef	2,080	634	92.9	581	53	.....	.....	43	3,800
3021	Butter	390	341	.7	4	337	.....	.....	10	3,148
3023–4	Milk	9,750	1,232	49.6	310	430	492	.....	78	7,658
3004	Parched cereal	390	360	7.2	41	2	317	.....	6	1,582
2968	Bread	4,030	2,297	50.9	290	113	1,894	.....	52	10,921
	Sugar	585	585	.....	.....	.....	585	.....	.....	2,317
	Alcohol	725	725	.....	.....	.....	.....	725	.....	5,331
	Total	17,950	6,174	201.3	1,226	935	3,288	725	189	34,757
3033	Feces	832	188	13.5	84	52	52	.....	39	1,307
	Alcohol excreted unoxidized	.....	24.5	.....	.....	.....	.....	24.5	.....	173
	Urine	.....	.....	.....	.....	.....	.....	.....	.....	1,427
	Amount available	17,118	5,961.5	187.8	1,142	883	3,236	700.5	150	31,850
	Coefficients of availability	.....	*Per cent.* 96.6	*Per cent.* 93.8	*Per cent.* 93.2	*Per cent.* 94.4	*Per cent.* 98.4	*Per cent.* 96.6	*Per cent.* 79.4	*Per cent.* 91.6

DETAILS OF DIGESTION EXPERIMENT NO. 83.

This experiment began with breakfast March 9, 1899, and continued 4 days. It was preliminary to the series of metabolism experiments Nos. 22–24, and was made with the same subject, E. O., who served in the majority of the digestion experiments here described. The diet during the first 3 days contained no alcohol. On the last day 72.5 grams of absolute alcohol were added in the form of commercial ethyl alcohol. The subject was engaged in his usual work about the laboratory and performed very little manual labor. His weight, without clothing, was 72.4 kilograms (159.6 pounds) at the close of the experiment.

DETAILS OF DIGESTION EXPERIMENT NO. 84.

The experiment began with breakfast March 13, 1899, and continued 6 days, forming a part of metabolism experiment Nos. 22 and 23, details of which are given above. Alcohol formed a part of the diet on the first 3 days (metabolism experiment No. 22) while on the last 3 days (metabolism experiment No. 23) only the basal ration was eaten. The subject, E. O., weighed, without clothing, at the beginning of the experiment 72.4 kilograms and at the end 72.7 kilograms (160.3 pounds). He had as little muscular activity during the series of experiments as was practicable.

TABLE CXIV.—*Details of digestion experiment No. 83 (preliminary to metabolism experiment No. 22).*

Laboratory No. sample.		Weight of material.	Total organic matter.	Nitrogen.	Protein.	Fat.	Carbohydrates.	Alcohol.	Ash.	Heat of combustion (determined).
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
3027	Beef	600	246.0	33.4	209	37	.....	.....	6	1,580
3029	Butter	220	193.0	.3	2	191	.....	.....	6	1,766
3031	Milk, skimmed	4,520	384.0	26.1	163	4	217	.....	36	1,849
3004	Cereal, parched	180	166.0	3.2	18	1	147	.....	3	730
3032	Bread	1,240	723.0	15.7	89	42	592	.....	16	3,483
	Sugar	160	160.0	.....	.....	.....	160	.....	.....	634
	Alcohol	72	72.0	.....	.....	.....	.....	72.0	.....	509
3069	Horse-radish	98	9.0	.2	1	.....	8	.....	1	37
	Total	7,090	1,953.0	78.9	482	275	1,124	72.0	68	10,588
3034	Feces	267	64.0	4.6	29	15	20	.....	19	417
	Alcohol excreted unoxidized	.....	2.2	.....	.....	.....	.....	2.2	.....	16
	Urine	.....	.....	.....	.....	.....	.....	.....	.....	566
	Amount available	.....	1,886.8	74.3	453	260	1,104	69.8	49	9,589
	Coefficients of availability	.....	*Per cent.* 96.6	*Per cent.* 94.2	*Per cent.* 94.0	*Per cent.* 94.5	*Per cent.* 98.2	*Per cent.* 97.0	*Per cent.* 72.1	*Per cent.* 90.5

TABLE CXV. *Details of digestion experiment No. 87 (part of metabolism experiments Nos. 2, and 25).*

Laboratory No. sample.		Weight of material	Total organic matter.	Nitrogen.	Protein.	Fat.	Carbohydrates.	Alcohol.	Ash.	Heat of combustion (determined).
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
3027	Beef	900	369.0	50.2	314	55	.....	.....	9	2,370
3029	Butter	330	290.0	.7	4	286	.....	.....	8	2,649
3031	Milk, skimmed	6,780	576.0	39.0	244	7	325	.....	54	2,773
3004	Cereal, parched	270	249.0	5.0	28	1	220	.....	4	1,095
3032	Bread	1,860	1,084.0	23.5	134	63	887	.....	24	5,225
	Sugar	240	240.0	.....	.....	.....	240	.....	.....	950
	Alcohol	216	216.0	.....	.....	.....	.....	216	.....	1,526
3069	Horse-radish	90	8.0	.2	1	.....	7	.....	1	34
	Total	10,686	3,032.0	118.6	725	412	1,679	216	100	16,622
3035	Feces	426	100.0	6.7	42	22	36	.....	30	686
	Alcohol excreted unoxidized	.....	6.6	.....	.....	.....	.....	6.6	.....	47
	Urine	.....	.....	.....	.....	.....	.....	.....	.....	854
	Amount available	.....	2,925.4	111.9	683	390	1,643	209.4	70	15,035
	Coefficients of availability	.....	*Per cent.* 96.5	*Per cent.* 94.4	*Per cent.* 94.2	*Per cent.* 94.7	*Per cent.* 97.9	*Per cent.* 97.0	*Per cent.* 70.0	*Per cent.* 90.5

DETAILS OF DIGESTION EXPERIMENT NO. 151.

This experiment formed a part of metabolism experiment No. 27 in series 26–28, studying the comparative effects of fat, alcohol, and sugar in the diet. The subject, J. F. S., was a chemist engaged in the investigation here reported. His weight, in underclothing, was 64.1 kilograms at the beginning and 63.7 kilograms (140.4 pounds) at the end of the study. The experiment began with breakfast February 17, 1900, and continued 3 days.

TABLE CXVI.—*Details of digestion experiment No. 151 (part of metabolism experiment No. 27).*

Laboratory No. sample.		Weight of material	Total organic matter.	Nitrogen.	Protein.	Fat.	Carbohydrates.	Alcohol.	Ash.	Heat of combustion (determined).
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
3176	Beef	255	93.0	13.8	86	7	.....	.....	2	560
3177	Butter	90	78.0	.2	1	77	.....	.....	2	720
3179	Milk, skimmed	3,000	276.0	20.1	126	9	141	.....	24	1,386
3180	Bread	600	356.0	8.5	49	10	297	.....	8	1,682
3181	Ginger snaps	180	170.0	1.8	10	15	145	.....	3	798
3168	Parched cereal	150	140.0	2.8	16	3	121	.....	3	620
	Sugar	45	45.0	.....	.....	.....	45	.....	.....	178
	Alcohol	216	216.0	.....	.....	.....	.....	216.0	.....	1,526
	Total	4,536	1,374.0	47.2	288	121	749	216.0	42	7,470
3184	Feces	219	48.0	3.4	21	6	21	.....	18	292
	Alcohol excreted unoxidized	.....	2.7	.....	.....	.....	.....	2.7	.....	19
	Urine	.....	.....	.....	.....	.....	.....	.....	.....	334
	Amount available	.....	1,323.3	43.8	267	115	728	213.3	24	6,825
	Coefficients of availability	.....	*Per cent.* 96.3	*Per cent.* 92.8	*Per cent.* 92.7	*Per cent.* 95.0	*Per cent.* 97.2	*Per cent.* 98.7	*Per cent.* 57.1	*Per cent.* 91.4

DETAILS OF DIGESTION EXPERIMENT NO. 155.

This experiment formed a part of metabolism experiment No. 30, the second of the series of experiments Nos. 29–31 for the purpose of studying the relative effect of sugar, alcohol, and fat in the diet during periods of work. It began with breakfast March 19, 1900, and continued 3

days. The subject was J. F. S. His weight, in underclothing, was 64.6 kilograms at the beginning and 64.1 kilograms (141.3 pounds) at the end of the experiment.

TABLE CXVII. *Details of digestion experiment No. 155 (part of metabolism experiment No. 30).*

Lab. No. sample		Weight of material.	Total organic matter.	Nitrogen.	Protein.	Fat.	Carbohydrates.	Alcohol.	Ash.	Heat of combustion (determined).
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
3186	Beef	174	67.0	10.0	62	5			2	405
3187	Butter	141	124.0	.3	2	122			5	1,135
3190	Milk	2,700	384.0	17.3	108	146	130		22	2,430
3192	Bread	900	560.0	13.5	77	18	465		12	2,637
3181	Ginger snaps	225	213.0	2.3	13	19	181		4	998
3193	Parched cereal	225	211.0	4.3	25	3	183		5	945
	Sugar	75	75.0				75			297
	Alcohol	216	216.0					216.0		1,526
	Total	4,656	1,850.0	47.7	287	313	1,034	216.0	50	10,373
3196	Feces	143	33.0	2	13	6	14		8	213
	Alcohol excreted unoxidized		2.3					2.3		16
	Urine									343
	Amount available		1,814.7	45.7	274	307	1,020	213.7	42	9,801
	Coefficients of availability		*Per cent.* 98.1	*Per cent.* 95.8	*Per cent.* 95.5	*Per cent.* 98.1	*Per cent.* 98.6	*Per cent.* 98.9	*Per cent.* 84	*Per cent.* 94.5

DETAILS OF DIGESTION EXPERIMENT NO. 159.

This experiment, which began with breakfast, April 23, 1900, and continued 3 days, formed a part of the series of metabolism experiments Nos. 32–34, studying the relative effect of fat, alcohol, and sugar in the diet during periods of work. The subject was the same as in the two preceding experiments here described. His weight, in underclothing, was 65.2 kilograms at the beginning and 64.9 kilograms (143.1 pounds) at the end of the investigation.

TABLE CXVIII.—*Details of digestion experiment No. 159 (part of metabolism experiment No. 33).*

Lab. No. sample		Weight of material.	Total organic matter.	Nitrogen.	Protein.	Fat	Carbohydrates.	Alcohol.	Ash.	Heat of combustion (determined).
		Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Calories.*
3205	Beef	174	61.0	8.9	56	5			2	361
3206	Butter	105	93.0	.2	1	92			3	862
3201	Milk	3,060	432.0	20.2	126	159	147		24	2,766
3204	Bread	900	548.0	12.4	71	23	454		12	2,582
3207	Ginger snaps	225	212.0	2.0	11	16	185		5	998
3193	Parched cereal	225	211.0	4.3	25	3	183		5	945
	Sugar	105	105.0				105			416
	Alcohol	216	216.0					216.0		1,526
	Total	5,010	1,878.0	48.0	290	298	1,074	216.0	51	10,456
	Feces	259	59.0	3.5	22	13	24		16	375
	Alcohol excreted, unoxidized		2.2					2.2		16
	Urine									335
	Amount available		1,816.8	44.5	268	285	1,050	213.8	35	9,730
	Coefficients of availability		*Per cent.* 96.7	*Per cent.* 92.7	*Per cent.* 92.4	*Per cent.* 95.6	*Per cent.* 97.8	*Per cent.* 99.0	*Per cent.* 68.6	*Per cent.* 93.1

TABULAR SUMMARIES OF RESULTS OF THE EXPERIMENTS.

The following tables summarize the more important results of the experiments.

INCOME AND OUTGO OF NITROGEN AND GAIN OR LOSS OF PROTEIN AND FAT.

The data which bear immediately upon the nitrogen and carbon balance, and the gains and losses of protein and fat, with and without alcohol in the ration, are brought together in Table CXIX. The method of grouping was explained above, page —.

TABLE CXIX.—*Income and outgo of nitrogen and carbon and gain or loss of protein and fat, in experiments with and without alcohol.*

Classification, serial numbers, and subjects of experiments	In daily food.					Nitrogen.				(e)	Carbon.						(m)
						(a)	(b)	(c)	(d)		(f)	(g)	(h)	(i)	(k)	(l)	
	Duration.	Protein.	Fat.	Carbohydrates.	Alcohol.	Energy.	In food.	In feces.	In urine.	Gain (+) or loss (−), $d=a-(b+c)$.	Protein, gain (+) or loss (−), $e=d\times 6.25$.	In food.	In feces.	In urine.	In alcohol eliminated.	In respiratory products.	Gain (+) or loss (−), $l=f-(g+h+i+k)$.	Fat, gain (+) or loss (−), $m=(l-59e)\div 765$.
Experiments with and without alcohol more strictly comparable.																		
REST EXPERIMENTS.																		
GROUP A.	*D.*	*Gm.*	*Gms.*	*Gms.*	*Gms.*	*Cals.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*
No. 9, E. O., ordinary diet	4	119	69	342	....	2,717	19.1	1.3	18.4	−0.6	−3.6	261.6	13.4	12.6	....	223.6	−12.0	−18.2
No. 10, E. O., alcohol diet	4	123	32	297	72.5	2,709	19.8	1.4	19.5	1.1	6.9	253.3	11.8	13.5	0.5	214.9	−12.6	−21.2
GROUP B.																		
No. 24, E. O., ordinary diet	3	124	69	409	....	3,061	19.8	1.3	18.2	−.3	1.7	299.7	10.5	11.8	....	230.9	−46.5	−59.7
No. 22, E. O., alcohol diet	3	124	69	276	72.0	3,044	19.8	1.1	18.5	−.2	1.4	279.8	10.3	11.8	1.2	207.8	−48.7	−62.7
GROUPS A–B.																		
Average, 9, 24, ordinary diet	7	121	69	375	....	2,889	19.4	1.3	18.3	−.2	1.0	280.7	11.9	12.2	....	227.3	−29.3	−39.0
Average, 10, 22, alcohol diet	7	123	51	286	72.3	2,877	19.8	1.3	19.0	−.5	2.8	266.6	11.1	12.7	.8	211.4	−30.6	−42.0
GROUP C.																		
No. 26, J. F. S., ordinary diet	3	100	95	247	....	2,490	15.9	1.1	15.4	.6	3.5	233.2	9.4	11.0	....	196.1	−16.7	−24.4
No. 28, J. F. S., ordinary diet	3	99	40	375	....	2,489	15.8	1.2	15.3	.7	4.5	245.8	10.0	10.9	....	210.7	−14.2	−21.8
Average, 26, 28	6	99	68	311	....	2,490	15.9	1.2	15.3	.6	4.0	239.5	9.7	11.0	....	203.4	−15.4	−23.1
No. 27, J. F. S., alcohol diet	3	99	40	247	72.0	2,491	15.8	1.1	15.7	−1.0	6.0	229.5	8.9	11.2	.5	198.3	−10.6	−18.3

TABLE CXIX.—*Income and outgo of nitrogen and carbon and gain or loss of protein and fat, etc.*—Continued.

Classification, serial numbers, and subjects of experiments.	In daily food.					Nitrogen.					(e)	Carbon.						(m)
	Duration.	Protein.	Fat.	Carbohydrates.	Alcohol.	Energy.	(a) In food.	(b) In feces.	(c) In urine.	(d) Gain (+) or loss (−), $d=a-(b+c)$.	Protein, gain (+) or loss (−), $e=d\times 6.25$.	(f) In food.	(g) In feces.	(h) In urine.	(i) In alcohol eliminated.	(k) In respiratory products.	(l) Gain (+) or loss (−), $l=f-(g+h+i+k)$.	Fat, gain (+) or loss (−), $m=(l-.53e)\div .765$.
Experiments with and without alcohol more strictly comparable—Continued.																		
REST EXPERIMENTS—Continued.																		
GROUPS A–C.																		
	D.	*Gs.*	*Gms.*	*Gms.*	*Gms.*	*Cals.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*
Average, 9, 24, 26—28, ordinary diet	13	114	69	354	....	2,756	18.3	1.3	17.3	0.3	2.0	266.9	11.2	11.8	....	219.3	−24.6	+33.7
Average, 10, 22, 27, alcohol diet	10	115	47	273	72.2	2,748	18.5	1.2	17.9	− .6	3.8	254.2	10.3	12.2	0.7	207.0	+24.0	−34.1
WORK EXPERIMENTS.																		
GROUP D.																		
No. 11, E. O., ordinary diet	4	124	129	485	....	3,862	19.8	2.2	18.1	.5	3.0	373.5	20.2	12.7	....	372.6	−32.0	−39.7
No. 12, E. O., alcohol diet	4	121	159	296	72.4	3,891	19.3	1.3	18.2	.2	1.0	344.8	12.1	12.3	.8	344.7	−25.1	−32.2
GROUP E.																		
No. 29, J. F. S., ordinary diet	3	100	106	471	....	3,487	16.0	.8	16.0	− .8	5.0	333.6	8.3	11.2	....	334.9	−20.8	−23.8
No. 31, J. F. S., ordinary diet	3	101	161	343	....	3,495	16.1	.8	15.6	− .3	2.3	321.5	8.1	10.9	....	315.8	−13.3	15.9
Average, 29, 31	6	100	134	407	....	3,491	16.0	.8	15.8	.6	3.7	327.6	8.2	11.1	....	325.4	−17.1	19.9
No. 30, J. F. S., alcohol diet	3	99	104	341	72.0	3,458	15.9	.7	17.3	2.1	−13.1	315.5	6.4	12.1	.4	316.5	19.9	−17.0
GROUP F.																		
No. 32, J. F. S., ordinary diet	3	101	152	354	....	3,487	16.1	1.2	15.7	.8	5.0	320.0	12.6	11.0	....	325.6	29.2	−34.9
No. 34, J. F. S., ordinary diet	3	100	99	478	....	3,493	16.0	1.2	16.7	−1.9	11.9	335.7	11.6	11.6	....	345.4	−32.9	−35.0
Average, 32, 34	6	100	126	416	....	3,490	16.0	1.2	16.2	−1.4	8.5	327.8	12.1	11.3	....	335.5	−31.1	−35.0
No. 33, J. F. S., alcohol diet	3	100	99	355	72.0	3,486	16.0	1.2	17.3	2.5	−15.8	319.6	11.4	12.1	.4	333.3	−37.6	−38.4
GROUPS E–F.																		
Average, 29–31, 32+34, ordinary diet	12	100	130	412	....	3,490	16.0	1.0	16.0	1.0	6.1	327.7	10.2	11.2	....	330.4	24.1	−27.5
Average, 30, 33, alcohol diet	6	100	102	348	72.0	3,472	16.0	1.0	17.3	2.3	−14.5	317.6	8.9	12.1	.4	324.9	−28.7	−27.7
GROUPS D–F.																		
Average, 11, 29–31, 32–34, ordinary diet	16	108	130	436	....	3,614	17.3	1.4	16.7	.8	5.1	345.0	13.5	11.7	....	344.5	−26.7	31.5
Average, 12, 30, 33, alcohol diet	10	107	21	331	72.2	3,611	17.1	1.1	17.6	−1.6	−10.0	326.6	10.0	12.2	.5	331.5	−27.5	29.2

TABLE CXIX.—*Income and outgo of nitrogen and carbon and gain or loss of protein and fat, etc.*—Continued.

Classification, serial numbers, and subjects of experiments.	In daily food.						Nitrogen.				(e)	Carbon.						(m)
	Ingestion.	Protein.	Fat.	Carbohydrates.	Alcohol.	Energy.	(a) In food.	(b) In feces.	(c) In urine.	(d) Gain (+) or loss (−). $d=a-(b+c)$.	Protein, gain (+) or loss (−). $e=d-6.25$.	(f) In food.	(g) In feces.	(h) In urine.	(i) In alcohol eliminated.	(k) In respiratory products.	(l) Gain (+) or loss (−). $l=f-(g+h+i+k)$.	Fat, gain (+) or loss (−). $m=l-.532$ (+.765).
Experiments with and without alcohol less strictly comparable.																		
REST EXPERIMENTS.																		
GROUP G.																		
	Ingestion.	*Protein.*	*Fat.*	*Carbohydrates.*	*Alcohol.*	*Energy.*	*(a) In food.*	*(b) In feces.*	*(c) In urine.*	*(d) Gain (+) or loss (−). $d=a-(b+c)$.*	*Protein, gain (+) or loss (−). $e=d\times 6.25$.*	*(f) In food.*	*(g) In feces.*	*(h) In urine.*	*(i) In alcohol eliminated.*	*(k) In respiratory products.*	*(l) Gain (+) or loss (−). $l=f-(g+h+i+k)$.*	*Fat, gain (+) or loss (−). $m=l-.532$ (+.765).*
	No.	*Gm.*	*Gms.*	*Gms.*	*Gms.*	*Cals.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*
No. 13, E. O., ordinary diet	3	117	88	270		2,596	18.7	1.1	19.5	1.9	−11.7	245.8	11.1	15.1		205.2	+14.4	+26.9
No. 14, E. O., ordinary diet	4	94	83	290		2,513	15.1	.9	16.2	−2.0	−12.4	239.0	7.4	12.2		207.3	+12.1	+24.4
Average, 13, 14	7	105	86	280		2,555	16.9	1.0	17.8	1.9	−12.0	242.4	9.3	13.6		206.3	−13.2	+25.7
No. 7, E. O., alcohol diet	4	104	68	191	72.5	2,462	16.7	.9	17.7	1.9	−12.0	218.6	6.7	13.3	1.5	214.5	−17.4	−14.3
GROUP H.																		
No. 5, E. O., ordinary diet	4	119	95	276		2,655	19.1	1.7	18.1	.7	− 4.2	248.9	13.8	11.6		231.7	− 8.2	− 7.8
No. 15, E. O., alcohol diet	2	109	40	277	72.5	2,653	17.4	.8	15.6	+1.0	− 6.0	245.7	7.8	11.0	.8	220.0	+ 6.1	+ 3.8
No. 16, E. O., alcohol diet	2	109	40	277	72.5	2,653	17.4	.8	15.5	+1.1	− 7.2	245.7	7.8	10.9	1.1	218.3	+ 7.6	+ 5.0
No. 17, E. O., alcohol diet	2	109	40	277	72.5	2,653	17.4	.8	15.6	+1.0	+ 6.0	245.7	7.8	11.0	.8	214.5	−11.6	−11.0
Average, 15, 16, 17	6	109	40	277	72.5	2,653	17.4	.8	15.6	+1.1	− 6.4	245.7	7.8	11.0	.9	217.6	− 8.4	− 6.6
GROUP I.																		
No. 21, A. W. S., ordinary diet	3	97	72	250		2,264	15.5	1.0	15.4	.9	− 5.6	215.2	9.0	10.8		217.4	−22.0	−24.9
No. 18, A. W. S., alcohol diet	2	97	72	250	72.5	2,776	15.5	1.1	16.4	−2.0	−12.2	253.0	9.0	10.4	1.6	219.3	−12.7	+25.1
No. 19, A. W. S., alcohol diet	2	97	72	250	72.5	2,776	15.5	1.0	14.5	0	0	253.0	9.0	9.2	1.3	206.6	−26.9	+35.1
No. 20, A. W. S., alcohol diet	2	97	72	250	72.5	2,776	15.5	1.0	14.1	− .4	− 2.2	253.0	9.0	9.0	1.5	216.2	−17.3	−21.1
Average, 18, 19, 20	6	97	72	250	72.5	2,776	15.5	1.0	15.0	.5	− 3.3	253.0	9.0	9.5	1.5	214.1	−18.9	+27.1
GROUPS G–I.																		
Average, 13 – 14, 5, 21, ordinary diet	14	107	84	269		2,491	17.1	1.2	17.1	1.2	7.3	235.5	10.7	12.0		218.5	5.7	− 2.3
Average, 7, 15 to 17, 18 to 20, alcohol diet	16	103	60	239	72.5	2,630	16.5	.9	16.1	.5	− 3.0	239.1	7.8	11.3	1.3	215.4	− 3.3	+ 6.5
GROUPS A–I.																		
Average, 9, 24, 26 – 28, 11, 29 – 31, 32 – 34, 13 – 14, 5, 21, ordinary diet	43	110	94	353		2,954	17.5	1.3	17.0	− .8	− 4.8	281.8	11.8	11.8		260.8	− 2.6	− .1
Average, 10, 22, 27, 12, 30, 33, 7, 15 to 17, 18 to 20, alcohol diet	36	108	76	281	72.3	2,997	17.4	1.1	17.2	.9	− 5.6	273.3	9.4	11.9	.8	251.3	− .1	− 3.8

INCOME AND OUTGO OF MATERIAL AND ENERGY.

Table CXX compares the available protein and energy, the gain or loss of body protein and body fat, and the energy of material oxidized in the body and that measured as heat and muscular work in the various groups of experiments with and without alcohol. The available protein is the difference between the protein in the food and that in the feces, while the available energy represents the energy of the food less the energy of the feces and (dry matter of) urine. The energy of the material oxidized in the body represents what may be called the net income, while the energy measured as heat and muscular work may be called the net outgo.

TABLE CXX.—*Material and energy supplied and metabolized in experiments with and without alcohol.*

[Quantities per day.]

Classification, serial numbers, and subject of experiments	Available protein.	Available energy.	Gain (+) or loss (−) of body material.		Energy of material oxidized in the body.	Energy measured as—		
			Protein.	Fat.		Heat.	Muscular work	Total.
Experiments with and without alcohol more strictly comparable.								
REST EXPERIMENTS.								
GROUP A.								
	Grams.	*Calories.*	*Grams.*	*Grams.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*
No. 9, E. O., ordinary diet	112	2,426	− 3.6	− 18.2	2,277	2,309	.....	2,309
No. 10, E. O., alcohol diet	115	2,427	− 6.9	−21.2	2,268	2,283	.....	2,283
GROUP B.								
No. 24, E. O., ordinary diet	115	2,809	+ 1.7	−59.7	2,238	2,272	.....	2,272
No. 22, E. O., alcohol diet	117	2,777	+ 1.4	−62.7	2,188	2,258	.....	2,258
GROUPS A AND B.								
Average 9, 24, E. O., ordinary diet	114	2,618	− 1.0	− 39.0	2,258	2,291	.....	2,291
Average 10, 22, E. O., alcohol diet	116	2,602	− 2.8	−42.0	2,224	2,270	.....	2,270
GROUP C.								
No. 26, J. F. S., ordinary diet	93	2,256	− 3.5	− 24.4	2,043	2,085	.....	2,085
No. 28, J. F. S., ordinary diet	91	2,249	− 4.5	− 21.8	2,067	2,079	.....	2,079
Average 26, 28	92	2,253	− 4.0	− 23.1	2,055	2,082	.....	2,082
No. 27, J. F. S. alcohol diet	92	2,264	− 6.0	− 18.2	2,125	2,123	.....	2,123
GROUPS A, B, AND C.								
Average 9, 24, 26–28, ordinary diet	106	2,496	− 2.0	− 33.7	2,190	2,221	.....	2,221
Average 10, 22, 27, alcohol diet	108	2,489	− 3.8	−34.1	2,191	2,221	.....	2,221
WORK EXPERIMENTS.								
GROUP D.								
No. 11, E. O., ordinary diet	110	3,510	− 3.0	− 39.7	3,901	3,746	186	3,932
No. 12, E. O., alcohol diet	113	3,614	− 1.0	−32.2	3,922	3,727	200	3,927
GROUP E.								
No. 29, J. F. S., ordinary diet	95	3,260	5.0	−23.8	3,515	3,334	255	3,589
No. 31, J. F. S., ordinary diet	96	3,275	− 2.3	− 15.9	3,439	3,171	249	3,420
Average 29, 31	96	3,268	− 3.7	− 19.9	3,477	3,253	252	3,505
No. 30, J. F. S., alcohol diet	95	3,242	−13.1	− 17.0	3,479	3,321	249	3,470
GROUP F.								
No. 32, J. F. S., ordinary diet	93	3,226	− 5.0	− 34.9	3,573	3,369	196	3,565
No. 34, J. F. S., ordinary diet	92	3,241	−11.9	35.0	3,629	3,337	250	3,587
Average 32, 34	93	3,234	− 8.5	35.0	3,601	3,353	223	3,576
No. 33, J. F. S., alcohol diet	92	3,227	−15.8	−38.4	3,669	3,435	197	3,632

TABLE CXX.—*Matter and energy supplied and metabolized in experiments with and without alcohol*—Continued.

Classification, serial numbers, and subject of experiments	Available protein.	Available energy.	Gain (+) or loss (−) of body material.		Energy of material oxidized in the body.	Energy measured as—		
			Protein.	Fat.		Heat.	Muscular work.	Total.
Experiments with and without alcohol most strictly comparable—Continued.								
REST EXPERIMENTS—Continued.								
GROUPS E AND F.								
	Grams.	*Calories.*	*Grams.*	*Grams.*	*Calories.*	*Calories.*	*Calories.*	*Calories.*
Average 29—31, 32—34, ordinary diet	95	3,251	6.1	27.5	3,539	3,303	238	3,541
Average 30, 33, alcohol diet	94	3,235	−14.5	−27.7	3,574	3,328	223	3,551
GROUPS D, E, AND F.								
Average 11, 29—31, 32—34, ordinary diet	100	3,337	5.1	−31.5	3,660	3,451	220	3,671
Average 12, 30, 33, alcohol diet	100	3,361	−10.0	−29.2	3,690	3,461	215	3,676
GROUPS A TO F.								
Average 9, 24, 26—28, 11, 29—31, 32—34, ordinary diet	103	2,917	− 3.5	− 1.1	2,925	2,836	110	2,946
Average 10, 22, 27, 12, 30, 33, alcohol diet	104	2,925	6.9	− 2.4	2,941	2,841	108	2,949
Experiments with and without alcohol less strictly comparable.								
REST EXPERIMENTS.								
GROUP G.								
No. 13, E. O., ordinary diet	110	2,298	−11.7	−26.9	2,112	2,151	.....	2,151
No. 14, E. O., ordinary diet	89	2,289	12.4	−24.4	2,131	2,193	.....	2,193
Average 13, 14	100	2,294	−12.0	−25.7	2,121	2,172	.....	2,172
No. 7, E. O., alcohol diet	99	2,230	−12.0	−14.3	2,434	2,394	.....	2,394
GROUP H.								
No. 5, E. O., ordinary diet	109	2,384	4.2	− 7.8	2,482	2,379	.....	2,379
No. 15, E. O., alcohol diet	104	2,426	+ 6.0	+ 3.8	2,357	2,362	.....	2,362
No. 16, E. O., alcohol diet	104	2,424	+ 7.2	− 5.0	2,336	2,332	.....	2,332
No. 17, E. O., alcohol diet	104	2,427	+ 6.0	−11.0	2,289	2,276	.....	2,276
Average 15, 16, 17	104	2,426	6.4	− 6.6	2,327	2,323	.....	2,323
GROUP I.								
No. 21, A. W. S., ordinary diet	90	2,038	− 5.6	−24.9	2,304	2,279	.....	2,279
No. 18, A. W. S., alcohol diet	90	2,532	−12.2	−25.1	2,367	2,488	.....	2,488
No. 19, A. W. S., alcohol diet	90	2,550	.0	−35.1	2,220	2,279	.....	2,279
No. 20, A. W. S., alcohol diet	90	2,549	− 2.2	−21.1	2,339	2,303	.....	2,303
Average 18, 19, 20	90	2,544	− 3.3	+27.1	2,309	2,357	.....	2,357
GROUPS G, H, AND I.								
Average 13—14, 5, 21, ordinary diet	100	2,239	7.3	− 2.3	2,302	2,277	.....	2,277
Average 7, 15 to 17, 18 to 20, alcohol diet	98	2,400	− 3.0	− 6.5	2,356	2,358	.....	2,358
GROUPS A TO I.								
Average 9, 24, 26—28, 11, 29—31, 32—34, 13—14, 5, 21, ordinary diet	102	2,691	− 4.8	− .1	2,717	2,650	73	2,723
Average 10, 22, 27, 12, 30, 33, 7, 15 to 17, 18 to 20, alcohol diet	102	2,750	− 7.1	− 3.8	2,746	2,680	72	2,752

PROPORTIONS OF ALCOHOL OXIDIZED AND UNOXIDIZED.

In the experiments in which alcohol formed part of the diet the urine, drip, and freezer waters and outgoing air current were examined for the presence of alcohol, or the products of incomplete oxidation of alcohol, according to the method discussed on page 258. The determinations were made by the amount of reduction of a standard sulphuric-acid solution of chromic acid. The materials thus found were called reducing materials, and the total amounts were calculated as alcohol.

In 6 of the later experiments in which alcohol did not form part of the diet the same tests were made in the excretory and respiratory products as indicated above, and considerable quantities of reducing material were found. These were likewise calculated as alcohol. The average daily amount eliminated in each of these experiments and the average of the results of all 6 are shown in Table CXXI.

TABLE CXXI.—*Average daily elimination of reducing material by lungs and kidneys in experiments in which alcohol did not form a part of the diet.*

[Quantities expressed in alcohol equivalent.]

Experiment No.	Reducing material excreted, calculated as alcohol.		
	In urine.	In respiratory products.	Total.
	Grams.	*Grams.*	*Grams.*
26	0.02	0.36	0.38
28	.02	.24	.26
29	.01	.35	.36
31	.02	.28	.30
32	.02	.32	.34
34	.03	.28	.31
Average of all	.02	.30	.32

In the average of all 6 experiments the reducing material determined was found equivalent to 0.32 of a gram of alcohol per day. Accordingly, from the total amount of reducing material determined in the alcohol experiments, 0.3 gram was subtracted in estimating the amount of alcohol excreted unoxidized. This is shown in Table CXXII, which summarizes the data for the excretion of unoxidized alcohol in the different experiments. The figures in column *d* show the total amount of reducing material, calculated as alcohol, which was found in the distillates from the urine and the water condensed in the chamber and the freezers, and more especially in the air current. From each of the values in column *d* 0.3 gram is subtracted, as explained above, to obtain the values in column *e*, which represent the amount of alcohol excreted unoxidized. The difference between the alcohol ingested, column *a*, and that excreted, column *e*, represents the amount actually metabolized, column *f*. The latter amount divided by the amount ingested shows the per cent metabolized, column *g*.

It will be noticed that the values for alcohol metabolized in the body in experments 7 to 22 are slightly larger in Table CXXII than they are in the tables giving the details of these experiments on preceding pages. This is due to the fact that in the detail tables the total amount of reducing material, as found in the experiments, was taken as the measure of the alcohol excreted in the experiments specified, whereas in the summary table the average amount of reducing material found has been deducted from the total reducing material in all the experiments alike.

TABLE CXXII.—*Comparison of amounts of alcohol consumed and excreted unoxidized in experiments in which it formed a part of the diet.*

Experiment No.	(a) Alcohol ingested.	Alcohol excreted, including other material calculated as alcohol: (b) In urine.	(c) In respiratory products.	(d) Total outgo. $b+c$.	(e) Alcohol excreted unoxidized $d-0.5$.	Alcohol actually metabolized: (f) $a-e$.	(g) $f \div a$.
	Grams.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Per cent.*
7	72.5	0.22	2.76	2.98	2.7	69.8	96.3
10	72.5	.12	.98	1.10	.8	71.7	98.9
12	72.4	.15	1.34	1.49	1.2	71.2	98.3
15	72.5	.14	1.40	1.54	1.2	71.3	98.3
16	72.5	.19	1.90	2.09	1.8	70.7	97.5
17	72.5	.06	1.43	1.49	1.2	71.3	98.3
18	72.5	.14	1.83	1.97	1.7	70.8	97.7
19	72.5	.12	1.42	1.54	1.2	71.3	98.3
20	72.5	.14	1.69	1.83	1.5	71.0	97.9
22	72.0	.53	1.67	2.19	1.9	70.1	97.4
27	72.0	.11	1.09	1.20	.9	71.1	98.7
30	72.0	.06	1.03	1.09	.8	71.2	98.9
33	72.0	.05	1.00	1.05	.7	71.3	99.0
Average of all							98.1
Average of Nos. 27–33							98.9

VARIATIONS IN DAILY EXCRETION OF NITROGEN.

In the course of these experiments it has been found very difficult to obtain a uniform excretion of nitrogen in the urine from day to day, even with uniform conditions of food, rest, and work. In studying the effect of alcohol upon nitrogen metabolism these variations should be considered. Table CXXIII shows the daily nitrogen content in the urine in experiments with and without alcohol. It also shows the elimination of nitrogen on the days of the preliminary period which always preceded an experiment in the calorimeter, and during which the subject had very nearly the same diet as in the following experimental period. In many cases the amount of nitrogen in the urine varied greatly from day to day, this variation being especially marked in the preliminary period. This may possibly be due in part to differences in amounts of external muscular work performed on different days, but the general results of experiments on the effects of muscular activity upon nitrogen metabolism imply that when the work is not severe and the supply of energy is sufficient the output of nitrogen is not greatly increased. It seems more probable that the cause may be in part psychic. We have had occasion to note an increase of nitrogen excretion after mental excitement, and not infrequently such increase has occurred on the day before or the day after the subject entered the respiration chamber for an experiment. This was especially the case with E. O., with whom there was a notable increase in the excretion of nitrogen on the day before entering the chamber in experiments 5, 6, 7, 12, 13, and 14, and on the day after in experiments 10, 11, 15, and 22. Something of the same kind appears with A. W. S. in experiment 18, with the exception that the increase was observed on the second day of the preliminary period, continued for a few days, and, with the exception of a slight rise on the day after entering the calorimeter, greatly decreased in amount during experiments 18 to 20. With J. F. S., on the other hand, there was as a rule comparatively little difference in the nitrogen eliminated on different days of the preliminary period, and a very slight, although regular, increase on the day following his entrance into the calorimeter.

The figures in the last four columns of the table show the average elimination of nitrogen during different periods with and without alcohol as part of the diet. The pronounced difference in some experiments between the elimination of nitrogen in the preliminary period and the calorimeter period is of interest as indicating that these unexplained variations are much greater than any which may be brought about by the addition of alcohol to the diet. This is one of the facts which lead us to hesitate to attribute to the alcohol any definite and uniform effect upon the metabolism of nitrogen.

One thing has impressed us, not only in these experiments but in others, the results of which we have studied. It is that the daily nitrogen balance is a much less reliable indication of the effects of diet, or of drugs, or of muscular work, or of medical treatment than is commonly supposed.[a]

TABLE CXXIII.—*Comparison of daily elimination of nitrogen in the urine when alcohol did and did not form a part of the diet.*

[Figures in bold face indicate days in which alcohol formed a part of the diet.]

Experiment and subject	Nitrogen in food.	Nitrogen in urine, preliminary period.				Nitrogen in urine, calorimeter period.									Nitrogen in urine, average.			
		First day.	Second day.	Third day.	Fourth day.	First day.	Second day.	Third day.	Fourth day.	Fifth day.	Sixth day.	Seventh day.	Eighth day.	Ninth day.	Preliminary period.	Calorimeter period.		
																Total period.	With ordinary diet.	With alcohol.
E. O.	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*	*Gms.*
Experiment Nos. 13 and 14	16.9	15.3	16.0	17.2	20.2	20.2	17.4	16.9	16.5						17.2	17.8	17.7	
Experiment No. 7	**16.7**		**19.1**	**15.9**	**18.5**	**19.6**	**17.8**	**16.2**	**17.3**						**17.8**	**17.7**		**17.7**
Experiment No. 9	19.1	17.4	22.1	20.1	17.9	18.7	18.8	18.3	17.9						19.4	18.4	18.4	
Experiment No. 10	**19.8**	**17.6**	**20.5**	**12.3**	**14.2**	**19.7**	**20.6**	**19.4**	**18.1**						**16.2**	**19.5**		**19.5**
Experiment No. 11	19.9	12.5	11.7	13.6	13.8	17.5	17.1	18.3	19.4						12.9	18.1	18.1	
Experiment No. 12	**19.3**	**10.1**	**15.4**	**13.8**	**18.3**	**17.9**	**21.3**	**15.9**	**17.7**						**14.4**	**18.2**		**18.2**
Experiment No. 5	19.1	17.2	17.6	14.2	23.8	20.3	17.4	17.2	17.4						18.2	18.1	18.1	
Experiment Nos. 15–17	**17.4**	**11.6**	**16.0**	**13.9**	**10.4**	**15.1**	**16.2**	**15.2**	**15.7**	**15.7**	**15.6**				**13.0**	**15.6**		**15.6**
Average 13 and 14, 9, 11, 5	18.8	15.6	16.9	16.3	18.9	19.2	17.7	17.7	17.8						16.9	18.1	18.1	
Average 7, 10, 12, 15–17	**18.3**	**13.1**	**17.8**	**14.0**	**15.4**	**18.1**	**19.0**	**16.7**	**17.2**						**15.4**	**17.7**		**17.8**
Experiment Nos. 22–24	19.8	17.3	18.8	14.6	**13.7**	**18.7**	**18.8**	**17.8**	18.8	19.6	18.5	19.4	18.1	17.3	16.1	18.5	18.6	**18.4**
A. W. S.																		
Experiment Nos. 4a–4c	15.3	15.0	15.6	14.3	14.4	14.6	14.1	13.1	13.7	12.6	11.9	12.4	13.1	11.7	14.8	13.0	13.0	
Experiment Nos. 18–21	**15.5**	**12.2**	**16.0**	**19.0**	**16.4**	**17.4**	**15.4**	**14.7**	**14.2**	**13.8**	**14.4**	14.5	16.2	15.4	**15.9**	15.0	15.4	**15.0**
J. F. S.																		
Experiment Nos. 26–28	15.9	16.6	15.9	15.7	16.0	16.6	15.1	14.4	**14.6**	**15.5**	**16.8**	15.9	15.2	14.7	16.0	15.4	15.3	**15.6**
Experiment Nos. 29–31	16.0	13.9	15.5	15.0	14.8	15.4	16.3	16.2	**16.8**	**18.0**	**17.1**	16.3	15.4	15.2	14.8	16.3	15.8	**17.3**
Experiment Nos. 32–34	16.1	15.0	15.5	15.6	15.1	16.3	15.3	15.6	**16.7**	**17.6**	**17.7**	17.4	16.3	16.4	15.3	16.6	16.2	**17.3**
Average 26–34	16.0	15.2	15.6	15.4	15.3	16.1	15.6	15.4	**16.0**	**17.0**	**17.2**	16.5	15.6	15.4	15.4	16.1	15.8	**16.7**

[a] My own confidence in the results of the experiments of a few days' duration as indications of the influence of any such agencies upon nitrogen metabolism was much shaken by the experience of Dr. C. F. LANGWORTHY and myself in collating and comparing the results of experiments on these subjects in the course of the preparation by ourselves of Bulletin 45 of the Office of Experiment Stations of the United States Department of Agriculture, A Digest of Metabolism Experiments in which the Balance of Income and Outgo was observed. The tables of this volume include summaries of 2,209 experiments with men and 1,362 with animals, in which the nitrogen balance was studied. The very clear impression left upon my own mind is that a not inconsiderable share of the conclusions reached by the authors of this very large amount of painstaking inquiry must be held subject to revision in the light of inquiries in which the experimental periods will be longer and the determinations more detailed.—W. O. A.

AVAILABILITY OF NUTRIENTS AND ENERGY.

Table CXXIV compares the coefficients of availability of protein, fat, carbohydrates, and energy in experiments in which alcohol did and did not form a part of the diet. These experiments are compared according as the ordinary diet and alcohol diet were more or less comparable, and according to the character of the experiment, whether rest or work.

TABLE CXXIV.—*Coefficients of availability of nutrients and energy in diet with and without alcohol.*

Metabolism experiment No.	Digestion experiment No.	Classification, serial numbers and subjects of experiments.	Duration.	Protein.	Fat.	Carbohydrates.	Alcohol.	Energy
		Experiments with and without alcohol more strictly comparable.						
		REST EXPERIMENTS.						
		GROUP A.	*Days.*	*Per ct.*	*Per ct.*	*Per ct.*	*Per ct.*	*Per ct.*
9	46	E. O., ordinary diet	4	93.5	93.9	96.5	.....	89.7
10	48	E. O., alcohol diet	4	93.1	88.2	97.0	98.5	89.8
		GROUP B.						
24	85	E. O., ordinary diet	3	93.2	93.7	98.9	.....	91.6
22	83	E. O., alcohol diet	3	94.4	94.7	97.9	96.9	90.5
		GROUPS A AND B.						
		Average Nos. 9, 24, ordinary diet	7	93.4	93.8	97.7	.....	90.7
		Average Nos. 10, 22, alcohol diet	7	93.8	91.5	97.5	97.7	90.2
		GROUP C.						
26	150	J. F. S., ordinary diet	3	93.1	97.2	97.3	.....	91.1
28	152	J. F. S., ordinary diet	3	92.2	90.1	98.6	.....	91.1
		Average Nos. 26, 28	6	92.7	93.7	98.0	.....	91.1
27	151	J. F. S., alcohol diet	3	92.8	95.0	97.2	98.7	91.4
		GROUPS A TO C.						
		Average Nos. 9, 24, 26–28, ordinary diet	13	93.1	93.8	97.8	.....	90.8
		Average Nos. 10, 22, 27, alcohol diet	10	93.4	92.6	97.4	98.0	90.6
		WORK EXPERIMENTS.						
		GROUP D.						
11	50	E. O., ordinary diet	4	88.7	93.0	97.5	.....	90.9
12	52	E. O., alcohol diet	4	93.5	95.9	98.2	97.9	92.7
		GROUP E.						
29	154	J. F. S., ordinary diet	3	94.6	97.2	98.7	.....	94.1
31	156	J. F. S., ordinary diet	3	95.0	98.3	98.2	.....	94.1
		Average Nos. 29, 31	6	94.8	97.8	98.5	.....	94.1
30	155	J. F. S., alcohol diet	3	95.8	98.1	98.6	98.9	94.5
		GROUP F.						
32	158	J. F. S., ordinary diet	3	92.8	97.1	97.4	.....	92.7
34	160	J. F. S., ordinary diet	3	92.7	95.0	98.4	.....	93.2
		Average Nos. 32, 34	6	92.8	96.2	97.9	.....	93.0
33	159	J. F. S., alcohol diet	3	92.7	95.6	97.8	99.0	93.1
		GROUPS E AND F.						
		Average Nos. 29, 31, 32, 34, ordinary diet	12	93.8	96.9	98.2	.....	93.5
		Average Nos. 30, 33, alcohol diet	6	94.3	96.9	98.2	99.0	93.8
		GROUPS D TO F.						
		Average 11, 29–31, 32–34, ordinary diet	16	92.1	95.7	98.0	.....	92.7
		Average 12, 30, 33, alcohol diet	10	94.0	96.5	98.2	98.6	93.4
		GROUPS A TO F.						
		Average Nos. 9, 11, 24, 26–28, 29–31, 32–34, ordinary diet	29	92.6	94.9	97.9	.....	91.9
		Average Nos. 10, 12, 22, 27, 30, 33, alcohol diet	20	93.7	94.6	97.8	98.3	92.0

TABLE CXXIV.—*Coefficients of availability of nutrients and energy in diet with and without alcohol*—Continued.

Metabolism experiment No.	Digestion experiment No.	Classification, serial numbers, and subjects of experiments.	Duration.	Protein.	Fat.	Carbohydrates.	Alcohol.	Energy.
		Experiments with and without alcohol less strictly comparable.						
		REST EXPERIMENTS.						
		GROUP G.	*Days.*	*Per ct.*	*Per ct.*	*Per ct.*	*Per ct.*	*Per ct.*
13	77	E. O., ordinary diet	3	94.0	93.2	98.1	.....	90.0
14	79	E. O., ordinary diet	4	93.8	95.3	98.7	.....	91.9
		Average Nos. 13, 14	7	93.9	94.3	98.4	.....	91.0
7	42	E. O., alcohol diet	4	94.8	96.3	98.1	95.9	91.1
		GROUP H.						
5	38	E. O., ordinary diet	4	91.3	93.9	97.7	.....	89.6
15–17	81	E. O., alcohol diet	6	95.2	92.5	98.4	97.6	91.5
		GROUPS G AND H.						
		Average Nos. 13+14, 5, ordinary diet	11	92.6	94.1	98.1	.....	90.3
		Average Nos. 7, 15–17, alcohol diet	10	95.0	94.4	98.3	96.8	91.3
		GROUPS A TO H.						
		Average all experiments with ordinary diet, Nos. 9+24, 26+28, 11, 29+31, 32+34, 13+14, 5	40	92.6	94.7	98.0	.....	91.5
		Average all experiments with alcohol diet, Nos. 10+22, 27, 12, 30+33, 7, 15–17	30	94.1	94.7	97.9	97.8	91.8

Table CXXV summarizes the results of experiments with the same subject and the same diet before and after entering the calorimeter and averages the results for all the experiments.

TABLE CXXV.—*Comparison of gains or losses of nitrogen, and of coefficients of availability in the preliminary periods outside the calorimeter and the experimental periods inside.*

[Quantities per day.]

Metabolism experiment No.	Digest experiment No.		Duration.	Nitrogen.				Coefficients of availability.				
				In food.	In feces.	In urine.	Gain (+) or loss (−).	Protein.	Fat.	Carbohydrates	Alcohol.	Energy.
		Experiments with ordinary diet.										
		REST EXPERIMENTS.	*Days.*	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Per ct.*	*Per ct.*	*Per ct.*	*Per ct.*	*Per ct.*
5	37	Preliminary period	4	19.2	1.4	18.2	−0.4	92.7	94.0	98.0	.....	90.0
	38	Calorimeter period	4	19.1	1.7	18.1	−0.7	91.3	93.9	97.7	.....	89.6
8	43	Preliminary period	4	20.1	1.8	14.2	+4.1	91.3	94.4	97.4	.....	89.9
	44	Calorimeter period	4	20.8	1.3	19.5	.....	94.0	95.6	98.2	.....	90.8
9	45	Preliminary period	4	18.9	1.7	19.4	−2.2	90.9	92.1	95.8	.....	88.5
	46	Calorimeter period	4	19.1	1.3	18.4	−0.6	93.5	93.9	96.5	.....	89.7
13	76	Preliminary period	4	20.1	0.8	18.1	+1.2	96.7	96.3	98.9	.....	93.1
	77	Calorimeter period	3	18.7	1.1	19.5	−1.9	94.0	93.2	98.1	.....	90.0
14	78	Preliminary period	3	15.1	1.2	16.7	−2.8	92.3	93.4	98.5	.....	91.1
	79	Calorimeter period	4	15.1	0.9	16.2	−2.0	93.8	95.3	98.7	.....	91.9
25	147	Preliminary period	4	17.6	1.0	16.6	.....	94.2	96.8	97.7	.....	91.8
	148	Calorimeter period	3	17.7	1.0	16.4	−0.3	94.5	97.4	97.4	.....	91.8
26	149	Preliminary period	4	15.9	1.7	16.0	−1.8	89.0	94.1	95.7	.....	88.4
	150	Calorimeter period	3	15.9	1.1	15.4	0.6	93.1	97.2	97.3	.....	91.1
		Average preliminary periods		18.1	1.4	17.0	0.3	92.4	94.4	97.4	.....	90.4
		Average calorimeter periods		18.1	1.2	17.7	0.8	93.5	95.2	97.7	.....	90.7
		Work experiments.										
6	39	Preliminary period	4	19.1	1.9	12.8	+4.4	90.1	95.3	97.6	.....	93.2
	40	Calorimeter period	4	19.1	1.5	16.5	+1.1	92.0	96.9	98.3	.....	92.6
11	49	Preliminary period	4	19.9	1.9	12.9	+5.1	90.6	93.2	97.8	.....	91.4
	50	Calorimeter period	4	19.8	2.2	18.1	0.5	88.7	93.0	97.5	.....	90.9
29	153	Preliminary period	4	15.9	0.9	14.8	+0.2	94.5	96.4	98.7	.....	93.8
	154	Calorimeter period	3	16.0	0.8	16.0	0.8	94.6	97.2	98.7	.....	94.1
32	157	Preliminary period	4	15.9	1.5	15.0	−0.6	90.6	95.7	96.8	.....	91.5
	158	Calorimeter period	3	16.1	1.2	15.7	0.8	92.8	97.1	97.4	.....	92.7
		Average preliminary periods		17.7	1.5	13.9	−2.3	91.5	95.2	97.7	.....	92.0
		Average calorimeter periods		17.7	1.4	16.6	−0.3	92.0	96.1	98.0	.....	92.6

TABLE CXXV.—*Comparison of gains or losses of nitrogen, and coefficients of availability in the preliminary periods outside the calorimeter and the experimental periods inside*—Continued.

Metabolism experiment No.	Digest experiment No.		Duration.	Nitrogen. In food.	Nitrogen. In feces	Nitrogen. In urine.	Nitrogen. Gain (+) or loss (−).	Coefficients of availability. Protein.	Fat.	Carbohydrates.	Alcohol.	Energy.
		Experiments with alcohol diet.										
		REST EXPERIMENTS.										
			Days.	*Grams.*	*Grams.*	*Grams.*	*Grams.*	*Per ct.*	*Per ct.*	*Per ct.*	*Per ct.*	*Per ct.*
7	41	Preliminary period	5	16.8	1.5	17.8	−2.5	90.8	93.6	97.3	95.9	89.2
	42	Calorimeter period	4	16.7	0.9	17.7	−1.9	94.8	96.3	98.1	95.9	91.1
10	47	Preliminary period	4	19.5	1.0	16.1	−2.4	94.9	92.1	98.0	98.5	91.1
	48	Calorimeter period	4	19.8	1.4	19.5	1.1	93.1	88.2	97.0	98.5	89.8
15	80	Preliminary period	4	16.7	0.8	13.0	−2.9	95.2	91.8	98.0	97.6	91.4
	81	Calorimeter period	2	17.4	0.8	15.6	−1.0	95.2	92.5	98.4	97.6	91.5
22	83	Preliminary period	4	19.7	1.2	16.1	−2.4	94.2	94.5	98.2	97.0	90.5
	84	Calorimeter period	3	19.8	1.1	18.4	−0.3	94.4	94.7	97.9	97.0	90.5
		Average preliminary periods		18.2	1.1	15.8	−1.3	93.8	93.0	97.9	97.2	90.6
		Average calorimeter periods		18.4	1.0	17.8	−0.4	94.4	92.9	97.9	97.2	90.7
		Work experiments.										
12	51	Preliminary period	4	19.6	1.8	14.4	−3.4	90.8	94.2	97.0	97.9	91.3
	52	Calorimeter period	4	19.3	1.3	18.2	−0.2	93.5	95.9	98.2	97.9	92.7
		Average preliminary periods in all above experiments with ordinary diet		18.0	1.4	15.9	−0.7	92.1	94.7	97.5		91.0
		Average calorimeter periods in all above experiments with ordinary diet		17.9	1.3	17.3	0.6	92.9	95.5	97.8		91.4
		Average preliminary periods in all above experiments with alcohol diet		18.5	1.3	15.5	−1.7	93.2	93.2	97.7	97.4	90.7
		Average calorimeter periods in all above experiments with alcohol diet		18.6	1.1	17.8	−0.3	94.2	93.5	97.9	97.4	91.1

The figures for the availability of alcohol in the preliminary period are based upon the assumption that the excretion of unoxidized alcohol was the same during the preliminary period as during the following period when the subject was within the chamber of the respiration calorimeter. It will be observed that while the diet was practically the same in the preliminary as in the calorimeter period, the coefficients of availability are quite different. Sometimes the subject appeared to digest the food more thoroughly during the preliminary period and sometimes more thoroughly during the period spent within the respiration chamber. In both the rest and work experiments without alcohol the availability of the nutrients and energy of the diet was slightly less in the preliminary period than in the subsequent experiment in which the subject was within the respiration chamber. In the rest experiments in which alcohol formed a part of the diet there was no pronounced difference in the coefficients in the two cases, but in the one instance in which there was preliminary and calorimeter period with work the coefficients of availability in the former period were noticeably less than in the latter.

Taking all the experiments into consideration it would seem that there was, as a rule, a quite noticeable difference in the proportions of the food which were actually made available for use in the body in the preliminary as compared with the calorimeter periods, a difference which was not noticeably affected by the presence or absence of alcohol in the diet.

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WEST INDIAN MADREPORARIAN POLYPS.

BY

J. E. DUERDEN.

PRESENTED TO THE ACADEMY BY PROF. WILLIAM KEITH BROOKS.

CONTENTS.

WEST INDIAN MADREPORARIAN POLYPS.

By J. E. Duerden.

INTRODUCTION.

The insufficiency of our knowledge of the morphology of the soft parts of the Madreporarian corals has been commented upon by nearly all writers on the Anthozoa. Such a want at first seems remarkable, when we consider for how long and how fully the hard parts have been known, both to the zoologist and the palæontologist, and also the great abundance and wide distribution of living corals. When, however, the geographical limitations of the greater number of recent corals are taken into account, the difficulty of fully observing the polyps when alive, and more especially of preserving them and of carrying out their anatomical study, the deficiency can be in some measure understood. The investigations of a number of workers have already afforded an insight into the general structure of Madreporarian polyps, especially of the simple forms; but these are as yet insufficient to enable relationships of a broad systematic character to be established. Practically all that has been achieved along such lines is the demonstration that coral polyps are constructed on the same plan as the polyps of the principal group of the Actiniaria, the Hexactiniæ; in other words, that the mesenteries and other organs are arranged in a cyclical hexamerous manner.

Many writers have contributed descriptions and figures of living coral polyps; yet so few differences are determinable from external characters alone that Madreporarian morphology has been but little advanced thereby. For admirable reproductions of the external characters of living corals the works of Quoy and Gaimard (1830), Dana (1846), Klunzinger (1877), and the elaborate work of Saville Kent (1893), The Great Barrier Reef of Australia, should be consulted. In a recent contribution Prof. H. de Lacaze-Duthiers (1897) has presented a very full account of the corals met with in the Mediterranean, and the drawings of the living polyps are among the finest we possess. Undoubtedly the best illustrations of West Indian shallow-water corals, mainly limited, however, to the skeleton, are those accompanying the Report on the Florida Reefs, by Louis Agassiz (1880). In "The Stony Corals of the Porto Rican Waters," Mr. Vaughan has given thirty-eight photographic reproductions of the more familiar West Indian species (1901*a*), followed shortly by a more complete series from Prof. A. E. Verrill (1901).

Of the older writers on coral structure, Milne Edwards and Haime (1857), in their classic "Histoire Naturelle des Coralliaires," have given all that was then possible with the limited means of research available. It is only within the last two decades that any serious attempt has been made to advance our knowledge of the anatomical structure of Madreporarian polyps. The late Prof. H. N. Moseley, in 1882, proved that *Seriatopora* and *Pocillopora* are true Madreporaria,[a] and in his "Challenger" Report on the Deep-Sea Madreporaria made many other additions to the morphology of the group (1881).

[a] Prof. A. E. Verrill (1869, p. 518), from descriptions and drawings of *Pocillopora*, had come to the same conclusions as early as 1867.

In the papers "Die Gattung *Cladocora*" (1881) and "Korallenstudien" (1886, 1891), Prof. A. R. von Heider has described in detail the anatomy and the relationships of the polyps to the coral-lum in two species of *Cladocora*, and *Astroides calycularis*, *Dendrophyllia ramea*, and *Madracis pharensis*. The work of von Heider is especially noteworthy on account of his contention that the skeleton of corals is derived from an actual calcification of the ectodermal cells or calicoblasts.

Dr. G. H. Fowler, in a series of five papers, "The Anatomy of the Madreporaria," appearing in the Quarterly Journal of Microscopical Science, from 1885 to 1890, has described in greater or less detail the soft parts of a larger number of corals than any other student of the group, and has brought together many important details of coral structure. In the introduction to his first paper Fowler gives a review of the little that was then known of the anatomy of the Madreporaria.

Prof. G. C. Bourne, in two papers, also published in the Quarterly Journal of Microscopical Science (1887), describes at some length the anatomy of the corals, *Fungia*, *Mussa*, and *Euphyllia*. In 1893 Bourne gave a detailed description of the postembryonic development of *Fungia*, founded on material collected by Prof. A. C. Haddon, while in 1899 he published a masterly account of the nature and origin of the skeleton in the Anthozoa, dealing particularly with the Madreporarian skeleton and the calicoblastic layer. Bourne has also contributed the article "Anthozoa" to Prof. Ray Lankester's Treatise on Zoology (1900), wherein he gives a clear account of many of the structural details of the Madreporaria.

W. L. Sclater, in 1886, contributed an anatomical description of *Stephanotrochus moseleyanus*, and J. Stanley Gardiner (1900) has given a detailed account of the "Anatomy of a supposed new species of *Caryophyllia* from Lifu;" Miss Edith M. Pratt (1900) has described the anatomy of *Neohelia porcellana* (Moseley).

Prof. G. von Koch, in a large series of papers, extending from 1877 to the present day, has probably done more than any other worker toward elucidating the problems of Madreporarian morphology, on the correct lines of embryology and the relations of the hard and soft parts as revealed by microscopic sections.

Prof. H. de Lacaze-Duthiers, in 1872–73, made two valuable embryological contributions, "Développement des Coralliaires," and records the results of the first attempts to rear coral larvæ to the skeleton-bearing stage, while his figure of the anatomical relations of the soft and hard parts of *Astroides calycularis* has been copied into many of the text-books of zoology. Two recent publications of Lacaze-Duthiers (1894, 1897) contain descriptions of a number of early stages in the development of several coral species.

Prof. H. V. Wilson (1888) has carried out a very complete study of the embryology and larval stages of *Manicina areolata*, as far as the stage at which the skeleton was about to appear; Prof. A. C. Haddon (1890) has also published notes on the newly hatched larva of *Euphyllia*.

In all probability the polyps of not more than fifty species of corals have been anatomically studied, and then often incompletely, owing to the insufficiency of well-preserved material. It must be acknowledged, that in so far as the results throw light upon the important question of the natural relations of the various groups of corals, they are disappointing, especially when the great amount of labor involved in conducting the investigations is taken into account. Similar anatomical researches carried out on the allied group of the Actiniaria, by workers such as the brothers Hertwig, Haddon, McMurrich, Carlgren, and many others, have resulted in placing our knowledge of these forms upon a fairly satisfactory morphological basis. No doubt it will yet be possible to accomplish the same for the Madreporaria, as the polyps of more species, especially reef-builders, become fully known.

A residence in Jamaica, in the neighborhood of coral reefs, has afforded me the opportunity of studying, within the past two or three years, the West Indian shallow-water corals in their living condition, and of preserving them for subsequent examination. And in this connection I desire to record my appreciation of the liberal action of the Board of Governors of the Institute of Jamaica in enabling me to carry out such researches, purely scientific in their nature.

In the shallow waters of Kingston Harbor, Jamaica, occur free colonies of the following species of corals: *Porites divaricata*, *Manicina areolata*, *Siderastrea radians*, *Cladocora arbuscula*, *Solenastrea hyades*, and *Oculina diffusa*. Any of these can be easily kept in aquaria in a laboratory,

for weeks or months at a time, by simply renewing the fresh-water lost by evaporation. The functional activity of numerous symbiotic unicellular algæ (*Zoöxanthellæ*), present in the endodermal tissues of each species, is sufficient to maintain the water in a fit state of aeration and purity.

For typical reef-building corals, such as species of *Madrepora*, *Porites*, *Maeandrina*, and *Orbicella*, the most convenient collecting spots are among the small group of coral islands, termed "Cays," beyond Kingston Harbor and Port Royal. From the reefs surrounding these over twenty further species are to be obtained, and other localities around the island yield practically the same forms; also at certain places in Kingston Harbor reef-building corals occur at accessible depths. As would be expected from the uniformity of climatic conditions, the Jamaican corals are such as are generally distributed throughout the entire West Indian region."

All the species here studied have been examined in their living condition, and usually from an abundance of material. In most cases the colonies were kept alive for some time within the laboratory, so that the varying aspects of the polyps during expansion and retraction could be observed. Much indeed of the character of the polyps is to be obtained in this way, which is impossible from retracted preserved polyps.

Most of the material for anatomical study was preserved with the polyps narcotized in a partly expanded condition, in order to render possible a better study of the relationships of the various organs and of the skeleton. When killed otherwise the polyps shrink deeply within the calice, the stomodæum becomes flattened by resting upon the central portions of the skeleton, and the arrangement of the mesenteries, etc., can be ascertained only with difficulty. For narcotization I have employed either magnesium sulphate or menthol, and both methods give satisfactory results. The use of menthol as a narcotic is very simple. It is merely necessary to sprinkle a few crystals on the surface of the water, when the reagent becomes slowly absorbed and gradually anæsthetizes the polyps; pure formol is then added to the water in sufficient proportions to make a 5 per cent. solution, and the polyps usually undergo no further change. The polyps may retract and shrink slightly if the process of narcotization is incomplete, but never to the same extent as if preserved directly. Though very desirable for museum purposes, a polyp expanded to its utmost offers no advantages for anatomical and histological study. The tissues in this condition are so attenuated as not to permit of the characteristics, especially those of the musculature, being determined with the same facility as in only moderately expanded examples. Usually the polyps expand fully only at night, or when placed in the shade, and the process of narcotization requires several hours. At night it was generally found convenient to add slowly the crystals of magnesium sulphate or menthol and allow them to act upon the polyps until morning, when the addition of formol brought about no retraction.

The proper preservation of the soft tissues of the Madreporaria has always been a matter of some difficulty, but the employment of formol is found to be fairly satisfactory. I have adopted it as a 5 per cent. solution in either fresh or sea water. Especially is the reagent serviceable on account of its penetrative powers; in all cases the preservation of the internal tissues was equal to that of the external, the ciliation being recognizable in most instances. There is an element of uncertainty, however, as to how long the histology will remain perfect in the formol solution alone. In some instances material which had remained in the original preservative fluid for five or six months has been found satisfactory for microscopic study, but in others a slight maceration has taken place. In this latter case the details of the anatomy and coarser histology can be still made out, but the more minute histology is imperfect. The possibility of maceration holds especially for forms like *Porites*, which exude a large amount of mucus on preservation. To guard against such risks, I have found it necessary to transfer the specimens, shortly after preservation in formol, through the different grades of alcohol up to 90 per cent. Where material intended for histological research has to be kept for some time this is undoubtedly desirable. On the other hand, for museum purposes expanded coral polyps, anemones, and medusæ have been kept in a solution of formol for several years without any obvious deterioration.

[1] For lists of these see the papers by Pourtalès, Agassiz, Quelch, Duchassaing and Michelotti, Verrill, Gregory, and Vaughan, referred to in the Bibliography. The figures and references to corals in the old natural histories of Jamaica by Sir Hans Sloane (1707) and Dr. Patrick Browne (1756) are well worthy of notice, as also those of Lesueur (1820).

An aqueous solution of corrosive sublimate or corrosive acetic has also been employed with great advantage, in that it fixes the tissues so completely that on decalcification there is little or no alteration in the relationships of the different organs. It is much superior to formol or alcohol in this respect. Before commencing the decalcification of material which has been in alcohol or formol for some time, I have often found it advantageous to pass it through a solution of corrosive sublimate.

Decalcification has generally been performed in a weak solution of hydrochloric or nitric acid, after the material has been thoroughly hardened. The acid is added drop by drop to a fragment of the coral still in the preservative fluid in sufficient quantities to maintain a slight effervescence. From one to two days are required for the decalcification of small pieces of porous corals, such as *Madrepora* and *Porites*, whereas the decalcification of dense coralla, like those of *Siderastræa* and *Oculina*, occupies three or four days. Where it has been desirable to carry out the decalcification with special care, as in investigations of the calicoblast layer and skeletal matrix, very weak solutions of acetic and chromic acids have been employed, and then the process requires a much longer period. When, as is usually the case, perforating algal matter occurs within the skeleton, it is advisable to remove this from time to time, so as to keep a fresh calcareous surface exposed.

If decalcification of properly fixed material be slowly carried out, there is little or no disturbance of the primary relationships of the soft parts. After a few attempts, I concluded that nothing was to be gained by making preparations of the hard and soft parts *in situ*, such as are obtained by embedding fragments of a colony in canada balsam and then grinding down to microscopic thinness. All the figures of the sections are, so far as concerns the relationships of the soft and hard parts, actual reproductions of camera lucida drawings. The irregularity in outline of many of the septal invaginations can be understood when one considers how generally the septa are provided with spines or granules.

Much of the work has been carried out while in Jamaica, and the remainder during the academical year 1899–1900, in Professor Brooks's biological laboratory at the Johns Hopkins University.[a] My thanks are due to Prof. W. K. Brooks for many valuable suggestions and much kindly interest during my stay in Baltimore; also to Prof. A. C. Haddon, of the Royal College of Science, Ireland, and Prof. G. B. Howes, of the Royal College of Science, London, for much assistance and encouragement from time to time during the progress of the work. I am indebted to Rear Admiral (then Commodore) H. N. Henderson for generously affording me facilities for collecting in the waters around Port Royal and the Cays beyond. Mr. T. Wayland Vaughan, of the United States Geological Survey, has assisted me in the specific determinations. In his recent account of the fossil corals from Curaçao (1901), and also of the stony corals of the Porto Rican waters, Mr. Vaughan (1901*a*) has dealt with the difficult subject of the synonymy of West Indian corals.

The paper is divided into two parts. The first is devoted to a more general description of the external characters and morphology of coral polyps, so far as the material available will permit, and the second to a description of the external characters and internal anatomy of certain representative species. To the former a few notes on larvæ and postlarval development are added, which, although incomplete, assist in an understanding of the significance of many of the adult features. In a large measure, also, I have carried out comparisons with the better-known Actiniaria. The polyps of the two groups are so closely alike that a knowledge of the characters in the one often assists in throwing light upon conditions in the other. In the second or systematic part, I have ventured to indicate some of the broader lines of relationships among the Madreporaria, suggested by the new facts obtained, and have attempted for the first time generic diagnoses in terms of the polyp. It will be understood that where generic characteristics are given they have reference only to the representatives here studied. The isolation under which the

[a] Since the presentation of the paper the studies have been continued, and results of some importance obtained, which amplify certain of those here given, particularly those on growth by gemmation and fissiparity. They are referred to in foot-notes on various pages.

work has been carried out, away from collections of all but West Indian corals, has rendered impossible a comparison with other species.

A complete knowledge of any coral form can be obtained only from a full description of both the polypal and skeletal parts, such as has been carried out in a few cases by Fowler, von Heider, Bourne, and Gardiner. But in the present instance it has been deemed advisable to confine the studies wholly to the soft parts; for some time such will remain the most pressing need among workers of the group.

The main object of the work has been to determine, from an examination of as many coral forms as possible, the principal facts of morphology within the group, and the illustrations are in the main limited to these.[1]

[1] The following is the list of species studied. The terminology and orthography adopted is mainly that of Milne and Edwards and Haime (1857). The recent papers of Vaughan (1901, 1901a) and Verrill (1901) have shown that this is in great need of revision. I have added the names suggested by these authors where they differ from those here employed. In the descriptive part of the work the usual references and synonyms of the species are omitted, as these are sufficiently noticed in the papers mentioned, and also in that of Gregory (1895).

Madrepora muricata Linnæus—forma *cervicornis* (Lam.); forma *prolifera* (Lam.); forma *palmata* (Lam.) = *Isopora muricata* (Linn.) [Vaughan] *Acropora muricata* (Linn.) [Verrill].
Porites astræoides Lamarck = *Porites astreoides* Lam. [Vaughan] = *Porites astreoides* Lam. [Verrill].
Porites clavaria Lamarck = *Porites porites* (Pallas) forma *clavaria* Lam. [Vaughan] = *Porites polymorpha* Link [Verrill].
Porites furcata Lamarck = *Porites porites* (Pallas) forma *furcata* Lam. [Vaughan].
Porites divaricata Lesueur = *Porites porites* (Pallas) forma *divaricata* Le Sueur [Vaughan].
Astrangia solitaria Lesueur.
Phyllangia americana Milne Edwards & Haime.
Cladocora arbuscula (Lesueur).
Orbicella annularis (Ellis & Solander) = *Orbicella acropora* (Linn.) [Vaughan].
Orbicella radiata (Ellis & Solander) = *Orbicella cavernosa* (Linn.) [Verrill].
Orbicella cavernosa (Linnæus).
Solenastræa hyades (Dana).
Siphonocœnia intersepta (Esper).
Favia fragum (Esper).
Dichocœnia stokesi Milne Edwards & Haime.
Isophyllia dipsacea Dana.
Manicina areolata (Linnæus) = *Maandra areolata* (Linn.) [Verrill].
Colpophyllia gyrosa (Ellis & Solander) = *Manicina gyrosa* (Ell. & Sol.) [Verrill].
Maandrina labyrinthica (Ellis & Solander) = *Platygyra labyrinthica* (Le Sueur) [Vaughan] = *Maandra cerebrum* (Ell. & Sol.) [Verrill].
Diploria labyrinthiformis (Linnæus) = *Maandra labyrinthiformis* (Linn.) [Verrill].
Pectinia meandrites (Linnæus) = *Maandrina meandrites* (Linn.) [Vaughan].
Oculina diffusa Lamarck.
Siderastræa radians (Pallas).
Siderastræa siderea (Ellis & Solander).
Agaricia fragilis Dana.
Agaricia agaricites (Linnæus).

PART I.

GENERAL MORPHOLOGY.

In any living coral, be it a simple or colonial form, the soft polyp above can be readily distinguished from the hard, calcareous skeleton below. The latter is generally cup shaped, and serves as a support and protection to the former. Structurally the polyp is very simple, and is either distinct or united with others. While alive it is variously colored, and assumes very different appearances according as it is fully expanded or retracted within its calice. When expanded it presents two distinct regions—a smooth column, generally cylindrical in outline, and terminated distally by a more or less flattened oral disk. In the center of the latter is the slit-like mouth, while toward its periphery are one or more cycles of simple or knobbed tentacles. Sometimes the polyps, instead of being distinct and independent, retain but partial individuality, and give rise to complicated discal, tentacular, and columnar systems.

Upon decalcification the nearly colorless basal or aboral region of the polyp becomes exposed. This is generally cylindrical or conical, and very complex in detail, being deeply grooved obliquely or vertically, and otherwise invaginated in correspondence with the skeletal projections; terminally it may be truncated or tapering.

The interior of the polyp is hollow, but much subdivided by two series of vertical partitions, arranged in cycles. The members of one series—the mesenteries—hang from the body wall, their free edge provided with a filamentous organ, except above, where some unite with the stomodæum depending from the margin of the oral aperture; the other partitions—the septal invaginations—are wedge-shaped inturnings of the basal wall, which are occupied by the skeleton, and are arranged so as to alternate with the mesenteries. Invaginations of the basal wall may also occur centrally, when they are usually connected with the septal inturnings. The mesenteries cease before the aboral termination of the polyp is reached, while the septal invaginations are best developed below, and distally never extend the whole length of the expanded polyp.

Microscopically the body wall is constituted throughout of three distinct layers, very different in character. The outer comprises various glandular, protective, and sensory elements; the middle is a nearly homogeneous, jelly-like substance; while the inner is mainly constituted of glandular and muscle cells, and is often loaded with unicellular algæ, the so-called zooxanthellæ.

On any colony new polyps, originating either as buds or by division of some other polyp, are to be found in various stages of growth. Within the mesenterial mesogloea of the mature polyps may occur groups of sexual cells, and within the polypal cavity may be free larvæ undergoing the early phases of development. Such are the broad features characteristic of Madreporarian polyps, and these will now be described in greater detail.

COLUMN WALL.

As comparatively few coral polyps have been described from their appearance in the fully expanded condition, the descriptive term *column* has been but little employed in Madreporarian literature, though of universal recognition in works on the Actiniæ for the corresponding region. When coral polyps are fully expanded their columnar character is usually very obvious, but in

the retracted condition it is not so evident, and is further confused because one portion of the column may be within the calice and another outside; also, owing to the colonial habit of most species, the line of separation of the column wall of one polyp from another is not always readily determinable.

The retention of the word column becomes absolutely necessary for a correct appreciation of the morphological relationships of the corresponding regions in the various types of coral growth. The region admits of a very precise definition, and, except in a few instances, of distinct limitations on the living or preserved colony. In the Actiniaria the column includes the whole of the polypal wall between the basal disk and the oral disk, the latter limited peripherally by the outermost cycle of tentacles. It is also usually distinguishable from the rest of the polyp by structural differences, especially in the stronger development of the musculature distally.

Embryological results indicate, as was first established by Professor von Koch (1882), that in Madreporarian corals the basal disk of the larva or young polyp first gives rise to the skeleton, and, however complicated the latter ultimately becomes, the tissues lining it directly (skeletotrophic or skeletogenic) are morphologically those of the base. It follows from this that the line at which the skeleton-producing tissues pass into the superficial tissues is the boundary between the true basal disk and column (Pl. XIX, fig. 137). The latter will thus include all the superficial part of the polypal wall between this boundary and the outermost row of tentacles, and nowhere takes any part in the formation of the skeleton. Column wall and oral disk will thus practically correspond with "oral body wall," and basal disk with "aboral body wall," as these terms are employed by Fowler, Ogilvie (1896, p. 107), and others. By body wall or polypal wall I understand the whole or any part of the wall of the polyp—base, column, and oral disk.

In simple polyps, and at the margin of colonial polyps, the boundary between the basal wall and the column wall is entire, and is indicated by a marked histological difference; but in colonial polyps, elsewhere than at the margin, interruptions exist which permit of free communication between the internal cavities of the various polyps constituting a colony (Pl. XII, fig. 87). Mesenteries are attached for some distance along the basal skeletotrophic wall, and then pass up the column wall, and in the case of the complete members are continued across the disk and down the stomodæum.

The column wall, as above defined, is easily distinguished in the simple polyps of *Astrangia*, and *Phyllangia* (Pl. V, fig. 46); but in colonies, where the asexually produced polyps remain connected with one another, the limitation of the wall of the individual polyp is not always readily determinable externally. Many colonial genera, including such as *Orbicella*, *Siderastræa*, and *Porites*, display a smooth polygonal groove which represents the external line of demarcation of the polyps. The superficial tissues are in partial continuity with the skeletotrophic tissues along these grooves, either directly or through the intermediation of the mesenteries, and the groove is therefore incapable of elevation above the skeleton, even on full expansion (Pl. IX, fig. 67).

The two or three polyps, which as a rule constitute the sub-colonies of *Cladocora*, afford interesting stages in the separation of the body wall of polyps primarily united (Pl. VI, fig. 48). Usually each polyp presents a free portion along its lower margin, where the ectoderm of the column can be seen to pass into that of the base, while the remainder is united with the termination of the wall of the other polyps, the line of union being indicated by a groove. As the polyps increase in size this line of connection diminishes in extent, the communication between the cavity of one polyp and of the other ceases, and ultimately the polyps separate, though usually not before each has given rise to one or more buds.

The polyps of *Oculina* (Pl. XXII, fig. 149) are spirally arranged, and as a rule widely separated; in the older regions of colonies the limitations of the individual columns are not readily seen, but can be easily made out in young colonies, and at the growing regions of others. Where the boundary is indicated the pericalicular mesenteries extend as far as the limitations of each polyp; but where the polyps have become widely separated, the mesenterial prolongations cease before the limitations of the polyps are reached, and then no actual boundary between one and another persists.

In fissiparous genera like *Favia* and *Isophyllia*, in which one or a few oral apertures may occur on a single disk, a single wall is common to each disk, but is separable from those adjacent, as in the cases just described. The fissiparous conditions met with in these genera become more complex in *Manicina*, *Meandrina*, *Pectinia*, and *Colpophyllia*. Here the column wall, like the disk and the tentacular zone, is common to a large number of oral apertures, but along the thecal ridges (collines) a longitudinal groove occurs, separating the column of two adjacent systems. A further condition occurs in *Agaricia*. New polyps seem to arise by fission, and each possesses its own system of tentacles; there is, however, no precise boundary line or groove between the column wall of adjacent polyps. A prominent thecal ridge imperfectly marks off one polyp from another (Pl. XXIV, fig. 162), but no external indication is afforded that the column wall becomes adherent to the corallum along its apex.

Madrepora is another genus in which no external demarcation occurs between the superficial tissues of the various polyps making up a colony: it is impossible to say where the column wall of one polyp ends, and that of another begins. As shown on Pl. I, fig. 1*a*, representing a fully expanded apical polyp, the free cylindrical region, which should undoubtedly be regarded as a column, passes directly into the superficial covering of the colony; but on this there is no groove limiting the column of one polyp from those surrounding it.

In simple corals, and around the periphery of colonies, the lower or proximal extremity of the column wall is closely adherent to the corallum, and upon decalcification its uninterrupted passage into the basal skeletotrophic tissues can be followed, the histological structure of the two differing greatly. The upper distal margin of the column continues to grow upward, the lower extremity keeping pace with it, and the skeleton below is thus left exposed. Usually foreign growths, particularly Nullipores,[a] in time settle upon the exposed part of the corallum; or it may be attacked by destructive agents, such as boring sponges or mollusks, or by tubiculous worms.

At the actual boundary of the column wall and basal disk a thin deposit of calcareous matter usually takes place, which in coral terminology is known as the "epitheca." This generally shows signs of stratification or wrinkling, the thickened lines representing periods when the upward growth of the polypal margin was not proceeding rapidly, and consequently more calcareous formation took place. In the early stages of *Manicina areolata*, the column wall practically envelops the whole of the corallum, and all stages in its growth upward, according as the colony enlarges, can be obtained. In the skeleton the epitheca is clearly seen as a thin calcareous layer resting upon the edges of the costæ, its upper margin indicating both the proximal extremity of the column wall and the commencement of the skeletotrophic tissues when the colony was alive. The region at which the epitheca is formed is clearly seen on Pl. XIX, fig. 137, representing a section through a young polyp of *Manicina*, and also on Pl. XIV.

RANDPLATTE OR EDGE-ZONE, CŒNOSARC, CŒNENCHYME.

The term "Randplatte" was originated by von Heider (1881, p. 4), when describing the external features of the Mediterranean *Cladocora*, to include the continuation beyond the crown of tentacles of the soft parts of the polyp over the border of the calice. It has since been extensively employed in Madreporarian literature by Fowler, Bourne, and Miss Ogilvie, the latter of whom introduced "Edge-zone" as its English equivalent (1896, p. 108). Referring to the name, G. von Koch (1886, p. 342), in a foot-note, draws attention to the fact that the region alluded to is no structure "sui generis," and therefore possesses no independent morphological significance.

In expanded coral polyps there is really no demand for such a descriptive term, as in this state the column wall stretches vertically, in undivided continuity, from the margin of the tentacular crown to its line of union with the wall of the surrounding polyps, and, except for a stronger development of the endodermal musculature above, the histological structure of the wall is the same throughout. Most of the mesenteries also extend the whole length of the column. Where,

[a] In *Astrangia solitaria* the incrusting Nullipores sometimes grow upward with such rapidity as to cover the whole of the external surface of the coralites, displacing the pericalicular part of the polyp. They may even extend over the thecal edge so as to sensibly diminish the aperture through which the polyp protrudes.

however, the calicinal wall extends peripherally far upward within the cavity of the polyp, then upon retraction of the latter the upper region of the column becomes drawn within the calice, but the lower region, still with the mesenteries attached to it, remains outside. It is to this external area of the column wall, often sharply marked off in retracted polyps, that the term "edge-zone" is usually restricted. As a result of the same upgrowth of the calicinal wall, the cœlenteron likewise becomes separated into calicinal and pericalicinal or perithecal portions, each partitioned into chambers by the mesenteries, and less so by the septal and costæ (Pl. VII, fig. 54).

Among corals like *Porites* and *Siderastræa*, in which the calicinal wall is common to adjacent polyps, and the septa are but little or not at all exsert, there can possibly be no extrathecal, or rather pericalicinal or perithecal, continuations of the tissues, and no edge-zone.

By "edge-zone" Dr. Ogilvie (p. 108) understands "that the mesenteries of the interseptal loculi are continued into the intercostal loculi," thus giving a more precise meaning to the term than was done by von Heider. Among all the forms here studied, which are provided with a perithecal continuation of the gastric cavity into intercostal loculi, *Madrepora* is the only one in which the mesenteries also are not prolonged perithecally. In this genus the superficial covering of the colony is continuous with the column wall of the polyp, and, as shown on Pl. I, fig 2, the cœlenteron is directly continuous over the edge of the theca with the superficial canals, but there is never any trace of external mesenteries. In the expanded polyp the mesenteries are seen to pass from the extruded column wall directly into the calice, and the column wall below, unsupported by mesenteries, rests directly upon the skeletal echinulations.

The precise definition given to the edge-zone affords Miss Ogilvie the opportunity of accomplishing the same for the somewhat loosely employed term "Cœnosare." By this the authoress (p. 108), following Bourne (1888, p. 26), signifies "an extrathecal part into which the mesenteries do not continue." Cœnosare will, of course, consist of two distinct tissues: the skeletal covering proper (base), and the superficial covering to the colony (column wall), the two separated more or less by a continuation of the gastro-cœlomic cavity.[a] By universal acceptation, "Cœnenchyme" is the calcareous deposit originating from the cœnosare, and this is only laid down by the skeletotrophic layer, the inner of the two external tissues. According to the definition of cœnosare and cœnenchyme just given, *Madrepora* alone, among all the forms available for study, is characterized by these structures; that is to say, the only genus in which the perithecal walls of the polyp are without mesenteries (Pl. I).

One of the most illustrative examples in this connection is *Oculina*. In all the definitions of the genus one of the characteristics given is the presence of a solid cœnenchyme. Yet throughout young colonies, and in the growing regions of others, the mesenteries are prolonged perithecally, so as to extend as far as the spiral groove of separation of the superficial tissues of the different polyps, and the corresponding grooves on the skeleton are determinable throughout. It is only in the older regions of large colonies that the mesenteries do not extend the whole length of the column wall, and the skeletal surface then becomes perfectly smooth, with an absence of grooves or costal ridges. Under such circumstances it becomes impossible to draw any sharp line between edge-zone or column wall and cœnosare. The latter is merely the extracalicular region of the polyp into which the mesenteries are not prolonged.

Bourne (p. 26) states that "a common cœnosare is due to nothing more than a persistent connection between the 'Randplatten' of adjacent polyps, and that the two structures are homologous." This undoubtedly holds for some forms, e. g., *Galaxea*, but the first portion of the definition can scarcely be regarded as applicable to cases like *Madrepora*, where, by defini-

[a] At the points where the cœnosare rests upon the costal ridges or echinulations the two coverings are combined, and the skeleton is here overlaid only by the superficial ectoderm, the mesogloea, and the calicoblastic ectoderm (Pls. I, II). The perithecal gastro-cœlomic cavity then becomes represented by canals, often reticular in character. Fowler (1888, p. 7, Pl. XXXII, figs. 2, 3) shows that in *Amphihelia ramea* the direct adherence of the polypal wall to the skeleton may become very broad, the canals being, as it were, pushed apart from one another and greatly narrowed.

Of the canals in *Cœnopsammia* Gardiner (1900, p. 361) observes: "The cœnosarcal canals in fact are simply extrathecal portions of the cœlentera of the different polyps, which serve to connect their intrathecal or gastrovascular portions."

tion, there is no Randplatte, and one can hardly employ the term homologous in connection with structures which are merely continuations of one another.

Cœnosarc then, no more than Randplatte, is a polypal structure "sui generis;" the two are merely special regions of the column wall and underlying skeletotrophic layer, in the latter case provided with mesenterial continuations, and in the other devoid of them. Cœnenchyme likewise is inseparable from the portion of the thecal wall laid down by the extrathecal layer of the morphological basal disk, under whatever name it may be known. The terms have merely a topographical, not a morphological, significance.[a] In the following pages column wall will generally include the whole of the external body wall, from the line at which it passes below into the skeletogenic tissues to the outer margin of the tentacular zone above.

Fowler, in his studies of various species of corals, has given much attention to the relationship of the peripheral part of the column wall to the skeleton, particularly to the manner in which it may be said to be supported. At first it appeared that in species without cœnenchyme the column wall was supported upon only the perithecal continuations of the mesenteries ("peripheral lamellæ"), while in species with cœnenchyme the wall was directly supported upon only echinulations of the skeleton. Pl. VII, fig. 54, and Pl. XIX, fig. 132, will serve as examples of the former, and Pl. I, figs. 2–6, taken from *Madrepora*, are instances of the latter method. Later, however, Fowler found that no such rule could be maintained; that the two methods of support—mesenterial and echinulate—might co-exist in the same form, e. g., *Madracis*, *Amphihelia*.

Where mesenterial continuations occur, the perithecal portion of the polypal cavity exists as a series of simple vertical canals; but where mesenteries are absent, and the column wall rests directly upon skeletal ridges or echinulations (*Madrepora*), the cavity is usually broken up into a complicated system of canals.

FORM AND ANATOMY.

Externally the column wall of coral polpys presents few structural modifications compared with the same region in the Actiniaria. There is an entire absence of the simple or complicated columnar outgrowths often displayed in the latter group, and nothing comparable with a capitulum or cycle of acrorhagi has been observed, the column always passing uninterruptedly into the tentacles. Practically the only external distinction in this direction concerns the surface of the column, whether smooth or verrucose. The latter condition is brought about by the presence of teeth or spines on the edges of the costæ and septa. Where these occur the polypal walls on retraction come to rest upon them, and the areas over the projections become slightly raised above the general surface, assuming a warty appearance; and even on fullest expansion, when free from the corallum, the tubercle-like character rarely entirely disappears. Sometimes the verrucæ are indicated by a slight color distinction, and often give a coarse appearance to the polyps. Where the edges of the costæ and septa are smooth, or only finely toothed, the surface of the outer polypal tissues is likewise smooth. Histologically the verrucæ present no differences from the rest of the column wall, except that their constituent layers are generally thinner. They are thus to be distinguished from the verrucæ of Actiniæ, which are slightly modified evaginations of the wall, or more often take the form of vertical rows of suckers, with a strongly marked histological modification. The verrucæ in corals are characteristics dependent upon the form of the skeleton, rather than a structural differentiation of the soft tissues.

Corresponding with the costæ and septa, the verrucæ are arranged in vertical intermesenterial rows, larger and smaller rows often alternating, in agreement with the large and small skeletal partitions. This is readily seen in species of *Orbicella*, *Favia*, and *Manicina*, while in *Meandrina* all the rows are equal. The verrucæ in any single row are somewhat irregular in size and height

[a] The study of the *Cænopsammia* from Lifu has lead Gardiner (1900, p. 361) to define cœnosarc in such a way as to make it much more embracive than would either Bourne or Miss Ogilvie. Thus: "*The Cœnosarc is that part of the polyps in a colony which lies outside but not above (i. e. in expanded state) the theca of the several corallites.* The 'Randplatte' of von Heider and von Koch, the 'edge-zone' of Miss Ogilvie, is then that part of the cœnosarc which lies over the free portions of the corallites."

in a form like *Isophyllia*, where the septal and costal spines are very variable in the amount of development. The external grooves which separate the verrucal ridges correspond with the line of attachment of the internal mesenteries, and are always smooth.

Apparently there are no permanent apertures in the column wall of Madreporarian polyps, such as zoophytologists are familiar with in the "Cinclides" of the Sagartids among the Actiniaria. Through these latter the thread-like "Acontia," loaded with nematocysts, are extruded when the polyp is irritated. The majority of coral polyps, however, have the power of extruding prolongations of the mesenteries bearing coiled mesenterial filaments along their edge (p. 475), but these can evidently perforate any portion of the superficial tissues, the disk equally with the column wall. Careful examination of the body wall, before the filaments are extruded, fails to reveal any apertures, and their irregular distribution, sometimes over nearly the whole external surface of the polyp, would suggest that the apertures are merely temporary and may be produced at any point. On Pl. VIII, fig. 64, is represented a section through a portion of the column of a polyp of *Orbicella annularis* through which the filamental part of a mesentery is extruded. No histological modification whatever can be made out in the wall itself; the aperture is a mere interruption of the layers for the passage of the mesentery and its filament. Upon the polyps settling down after irritation the filaments are slowly indrawn, and ultimately no external indications remain of the apertures through which they protruded. In some cases the openings have been observed to remain distinct for a short time after the indrawal was completed, but the injury, if such it can be regarded, was soon completely healed.

On full expansion of the polyp the column may extend for some distance above the corallum, and is either cylindrical, oval, or irregular in form. Proximally, where it is fixed to the skeleton, it assumes the outline of the individual corallites, and hence may be circular, polygonal, or irregular. In species of *Siderastrea* and *Agaricia* the column appears never to be raised much above the general surface of the corallum, and in forms like *Meandrina*, with incomplete polypal separation, the column on both sides rises for many millimeters as a vertical expansion, with a deep valley separating one polypal row from another.

The form and position assumed by the intercalicular portion of the column wall upon retraction of the polyps varies greatly. In most cases the upper region of the column becomes folded inwardly over the edge of the theca, while in some it is merely drawn downward. In the former condition it either comes to lie inclined downward against the oblique septa (*Manicina*, *Meandrina*, etc.), or, by the action of the endodermal circular muscle, it extends horizontally, terminating in a circular margin which nearly meets at the center, and thus almost covers the disk below (Pl. X, fig. 74). In *Madrepora* the wall becomes merely drawn within the calice without any overfolding (Pl. I, fig. 2); in *Siderastrea* and *Agaricia* the column and disk are simply depressed, and come to rest upon the skeleton, leaving the tentacles and mouth wholly exposed (Pl. XXII, fig. 150).

Variations in the position assumed by the column wall on retraction of the polyps are sometimes observable even in the same species. Thus the wall in *Porites clavaria* may be slightly folded over the disk, or, as in *Siderastrea*, it may merely come to rest upon the corallar surface, the tentacles and disk remaining exposed (Pl. IV, figs. 34 and 35).

Among the skeletonless *Actinia* the column wall is usually of some thickness, so as to give more or less rigidity to the body of polyp, but in the Madreporaria, where support is afforded by the skeleton, the polypal wall is nearly always a thin, delicate, often transparent structure. In both groups the thickness of the wall is mainly determined by that of the middle layer—the mesoglœa, as both the ectodermal and endodermal epithelia vary comparatively little. By contrast with that of most anemones the mesoglœa in the column wall of corals is, as a rule, little more than a mere separating lamella between the inner and outer layers, except along the line of attachment of the mesenteries, where it becomes somewhat thickened in a triangular manner.

The thickness of the column wall is also partly dependent upon the state of expansion or retraction of the polyp. On full distention all three layers become greatly attenuated, the ectodermal and endodermal cells largely diminished in height, and the mesoglœa scarcely distin-

guishable as a separate layer. The walls are then much more nearly transparent than in the retracted state. In sections the column wall varies from 0.1 millimeter across in *Isophyllia dipsacea* to 0.023 millimeter in *Agaricia fragilis*.

The three polypal layers will now be described in more detail.

ECTODERM.

The ectoderm of the column of Madreporarian polyps is a regular, often ciliated, columnar epithelium, constituted mainly of unicellular gland cells, supporting cells, and scattered nematocyst-bearing cells; muscle and nerve fibrils are rarely if ever recognizable in sections. The nuclei of most of the cells are arranged at nearly the same height in the layer, and in sections of moderate thickness give rise to a very definite nuclear band or zone. The nuclei thus regularly distributed are mainly those of the long narrow supporting cells; the nuclei of the gland cells and nematoblasts are less restricted and occur nearer the mesoglœa.

The ciliation of the column wall is by no means so pronounced as in the case of the stomodæal ectoderm and mesenterial filaments, and few observations have been made to determine its general distribution in the living polyp, or the conditions of its activity. Traces of cilia sometimes remain in preserved material, and the effects of its activity are often noticeable on the living polyp. When light particles of foreign matter are dropped on the large discal area of a coral like *Manicina*, they are seen to be slowly transferred to the margin of the disk, but, instead of merely dropping over, they are dragged in a definite manner along the column, and only discarded, as it were, when they reach its lower termination. When similar particles are dropped on other living polyps they are likewise set in movement in a more or less definite manner, but no such action could be distinguished on the living tissues of *Favia fragum*.

The glandular cells of the columnar ectoderm are mainly oval shaped toward the periphery of the layer, and narrow internally; the base is generally fibrillar and rests upon the mesoglœa (fig. 8). The contents are nearly homogeneous and rarely stain, usually appearing quite clear; at other times they are finely granular and stain more readily. The cells are mucus secreting, and their different behavior toward reagents probably indicates different stages in the development of the cell and its secretions. In addition to the clear mucus cells, long, narrow gland cells occur of which the contents are coarsely granular, and these take up most stains with great avidity. They seem to be different in character from the other gland cells, and, as a rule, are but sparsely represented.

In most cases the gland cells occupy the greater proportion of the layer, so much so that in tangential sections through the outer portions of the ectoderm the cells form a close polygonal network, the interstices being occupied by a few supporting cells (Pl. X, figs. 76–78). Quantities of clear, colorless mucus are given out by most corals upon disturbance, as, for instance, when a fragment from a large colony is broken off; also upon preservation in a limited quantity of sea water sufficient mucus may be extruded to give a jelly-like consistency to the liquid. The presence of the mucus upon the surface of a colony often interferes with the proper preservation of the polyps. This is especially the case with *Porites*, where both the ectoderm and endoderm are highly glandular (Pl. IV).

As a rule the column wall of coral polyps contains a few scattered nematocysts, which, however, are never aggregated into distinct batteries such as occur on the tentacles. They are always small, of two or three kinds, and are easily distinguished from the long, narrow, tentacular form, or the large oval variety more characteristic of the endoderm.

In the genera *Isophyllia* and *Meandrina*, and to a less degree in certain others, the superficial tissues in the living condition appear dense and almost opaque. Histological examination reveals that the mesoglœa of the column wall in these is a little thicker than usual, but the chief cause of the opacity evidently lies in the contents of the ectodermal cells. This is illustrated by the genus *Orbicella* (Pl. VIII, fig. 65). Clear mucus-secreting cells occur with comparative rarity, and the chief cellular constituents of the layer are long supporting cells, the nuclei of which are elongated and arranged in a very regular zone, so closely that in places they appear to

exert a mutual pressure upon one another. The deeper parts of the layer are characterized by the presence of patches of finely granular pigment matter, arranged closely or somewhat distant from one another. In the areas of greatest concentration the granules extend almost to the periphery of the ectoderm, but they are mainly internal to the nuclear zone. Probably they are to be regarded as of the nature of pigment granules, and are to be distinguished from the granules of glandular cells. They are manifestly the chief cause of the general opacity of the body wall in many fissiparous species. (See also, *Isophyllia*, Pl. XVII, fig. 122.)

MESOGLŒA.

The mesoglœa[a] of coral polyps has generally been described as a perfectly structureless layer, without any of the migrant connective-tissue cells, such as are characteristic of the mesoglœa of the greater number of Actinian polyps. The homogeneous condition is found in many of the species here described, especially where the polyps are small, but in others it becomes somewhat more complex. The layer stains feebly, or not at all, and when perfectly homogeneous and transparent may be indistinguishable from the clear field of the microscope.

In large polyps, such as *Isophyllia dipsacea*, and also in *Meandrina*, the mesoglœa is rather thick, and minute connective-tissue cells occur sparsely throughout. In sections the cells are circular or oval in shape, with a central nucleus, and minute prolongations extend in all directions; many of these reach one or other of the surfaces of the layer, and there come into contact with the ectodermal or endodermal cells. In some instances the processes extend right across from one layer to the other, but are mostly disposed in an irregular stellate manner. Their close connection with the ectoderm and endoderm would seem to indicate their origin from one or both layers, except in the mesenterial mesoglœa, where obviously they can be derived only from the endoderm.

The mesoglœa is usually of uniform character and consistency throughout any polyp, but a slight difference is revealed in preparations of *Isophyllia dipsacea*, which have been stained with borax carmine and methyl blue. The layer is colored a bright blue, but narrow tube-like portions, which scarcely take up any coloring matter, stretch across the layer, or in other sections appear as small, light-colored disks; with hæmatoxylin it remains unstained, and exhibits no such differentiation.

The ectodermal and endodermal surfaces of the mesoglœa are mostly even, but in some regions, especially on the face of a mesentery which bears the longitudinal musculature, the surface becomes folded, or may even form complicated branching plaitings, so as to afford an increased area for the muscular fibrils (Pl. XVIII, fig. 130). The endodermal surface in the uppermost region of the column may also be deeply folded for the same purpose (Pl. XVII, fig. 121). In no case, however, has the musculature been found to become actually embedded within the mesoglœa of the column, such as occurs among anemones where a strong mesogloeal sphincter is formed (*Sagartida*).

As the mesoglœa is practically alike in structure throughout the tissues of any polyp, it will be unnecessary again to refer to it in detail in describing the individual organs. Along the line of attachment of the mesenteries to the skeletotrophic tissues, and less frequently elsewhere, peculiar mesogloeal processes occur which seem to serve as a means of attachment of the polypal tissues to the skeleton (Pl. XIII, fig. 95). They are fully referred to on page 481.

ENDODERM AND SPHINCTER MUSCLE.

Gland cells, both in the clear and granular condition, are the main constituents of the endoderm. Supporting cells are less numerous than in the ectoderm, while the musculature is

[a] In a preliminary note, "On the Anatomy of a supposed New Species of *Conopsammia* from Lifu," Mr. Stanley Gardiner proposes the name "skeletoglœa" for the structureless lamella or jelly of the Actinozoa, instead of a "makeshift term," such a "mesoglœa." The introduction of this new term would undoubtedly lead to great confusion if employed in the literature of skeleton-producing polyps, while such has never been the case with Bourne's term, now universally adopted. "Skeletoglœa" would have served aptly for the jelly-like, homogeneous matrix in which the skeleton is laid down (p. 483). In his fuller paper (1900, p. 358), Gardiner prefers to use the term "structureless membrane" or "basement membrane."

better developed, and symbiotic algæ or zooxanthellæ are nearly always present. The cilation is feeble, and rarely determinable in preserved material.

The endodermal layer is of much the same character throughout the polyp, whether in the column wall, tentacles, disk, skeletotrophic tissues, or forming the mesenterial epithelium. It may vary slightly in thickness in different regions, and in the greater or less preponderance of glandular cells, while in nearly all the species a remarkable modification of the skeletotrophic endoderm takes place in the lower regions of the polyp. The layer here becomes much thicker and loses its distinctly cellular character, appearing finely reticular. So greatly thickened does the endoderm become that it often nearly obliterates the gastro-celomic cavity in the most proximal region of the polyp. The chief constituents—nuclei, cytoplasm, zooxanthellæ, and in some cases granular gland cells—are mostly accumulated in a narrow peripheral zone, the deeper portion being vacuolated or bearing only fine granules (Pl. X, figs. 73 and 75).

Zooxanthellæ occur in large numbers within the endoderm cells of all the species studied, with the exception of *Phyllangia americana* and *Astrangia solitaria*. They are usually distributed throughout the polyp, but are more numerous in the exposed tissues (column wall, disk, tentacles) than in the endoderm of the mesenteries and skeletotrophic tissues; they even occur within the internal canals of the perforate genera *Madrepora* and *Porites*, but are never found free or detached within the polypal cavities except in larvæ. As described on page 437, the organisms are the principal cause of the coloration of many coral polyps. Large oval nematocysts occur in the endoderm of *Porites* and *Madrepora*, but are absent from most other genera. Their numbers and distinctive form in the genera mentioned are such as to leave no doubt that they are actually formed in the endoderm, not free examples injested from the ectoderm.

The circular endodermal musculature of the column wall appears to be always present in coral polyps, as in Actinian polyps, though varying much in the degree of its development; as a rule it is stronger at the uppermost region of the column wall than below. Sometimes the fibrils are scarcely to be found anywhere, while in other species they become strongly developed distally, and give rise to a typical diffuse sphincter muscle, such as is characteristic of many Actiniæ (e.g., *Corynactis*). This is seen in species of *Orbicella*, especially in the large *O. cavernosa*, but also in the smaller *O. annularis* (Pl. VIII, fig. 65). Here, in retracted polyps, the mesoglœa is thrown into deep folds for additional support to the musculature. The muscle fibers lining the hollows or grooves never become separated from the superficial layer, as happens in Actinians where the muscle is truly mesogleal. In other species of corals the mesoglœa forms only very slight folds, while again it may be perfectly smooth, indicating a very weak muscular development.

The sphincter muscle is more strongly developed in *Isophyllia dipsacea* than in any other species here studied. In vertical sections of the uppermost region of the column wall the mesoglœa displays one or more special thickenings which are much plaited, the whole lined with muscle fibers (Pl. XVII, fig. 121). The structure very closely recalls the type of sphincter described by Haddon (1898, p. 432) as occurring in the Actinian *Macrodactyla*, and there termed a "restricted" sphincter muscle. It represents a stage of muscular development more complex than that described as "diffuse." The plaitings appear on several axes of greater or less complexity; while in the "circumscribed" sphincter muscle of Actinian anatomy they are restricted to a single axis. The amount of development of the sphincter muscle is manifestly dependent upon the size of the polyp, the polyps of *Isophyllia* and *Orbicella* being among the largest studied.

The action of the circular sphincter muscle is to bring about the overfolding of the distal region of the column wall upon retraction of the polyps. This occurs in nearly all corals, and, as already observed, it results that the column wall almost completely hides the disk and tentacles, leaving a small central opening over the oral aperture. Circular constrictions may occur in the column wall without any retraction of the disk, in this case the action of the columnar musculature is probably the same as before, but the retractor muscles of the mesenteries have not come into play and drawn downward the oral region of the polyp.

G. H. Fowler (1888a, p. 12) was the first to record the presence of an undoubted sphincter

muscle in the Madreporaria, having found the mesogloeal plaitings strongly developed in *Sphenotrochus rubescens*. Gardiner (1900, p. 363) also describes a strong circular sphincter muscle in *Caryophyllia*.

The sphincter, sometimes known as "Rötteken's muscle," is usually strongly developed in Actiniaria, where it assumes very varied forms, and becomes of great importance for taxonomic purposes. Actinian polyps in general are capable of retraction to a greater degree than are coral polyps, but where no sphincter is present the disk and tentacles always remain exposed. There is no doubt that the actual outline assumed by the mesogloeal plaitings supporting the fibrils, and giving its character to the muscle, is largely dependent upon the amount of retraction and extension of the polyp, but still sufficient constancy remains to justify the importance attached to the muscle for diagnostic purposes.

A few observations upon the general expansion and retraction of coral polyps may be here given.

EXPANSION AND RETRACTION OF POLYPS.

Only the more superficial tissues of coral polyps—column wall, disk, tentacles, and upper part of the mesenteries—are capable of expansion and retraction, the change being brought about mainly by the action of the musculature of these regions, with an accompanying entrance or expulsion of water from the polypal cavity. The skeletotrophic tissues are destitute of muscle fibers, and throughout remain adherent to the corallum, perhaps held in position by the peculiar wedge-shaped or conical structures originating from the desmocytes (p. 482); hence they take no part in the varying aspects of the polyp.

Polypal expansion proceeds slowly by the imbibition of sea water into the internal cavity, and the consequent distension of the body wall. The musculature being relaxed, entrance of the water is effected through the oral aperture, probably as a result of the activity of the strongly developed stomodæal cilia. On retraction of the muscles, and subsequent diminution in size of the polypal cavity, the water is largely expelled, also through the mouth. In a colony where the cœlentera of all the polyps are in communication with one another, there seems no reason why water should not be abstracted from one region to another, so that the polyps in one part may be expanded and those in another retracted. The polyps of one area of a colony are often in a different state of expansion from those of another. If an expanded colony be suddenly lifted out of the water, flaccidity of the tissues almost immediately results, due to the loss of water, and the latter can be actually observed flowing from the internal cavity. On irritation of a single polyp in a fully distended colony the polyp readily retracts, and those around more slowly, the water issuing through the mouth as a distinct stream.

Polypal retraction is brought about by the united action of the musculature of the mesenteries, column wall, disk, and tentacles, the first mentioned being probably the most important. The longitudinal retractor muscles are always more or less well developed on one face of each mesentery, the mesoglœa being often folded to give increased area. By the contraction of these muscles the distal region of the polyp is drawn downward; at the same time the contraction of the circular endodermal musculature of the column wall aids in the shrinkage, and the same is to be said of the circular musculature of the disk.

From the comparative development and arrangement of the muscle fibrils throughout coral polyps, it is manifest that retraction is entirely dependent upon muscular contraction, while expansion is mainly due to the relaxation of the muscles, followed by the entrance of water.

The external appearance of corals varies greatly, according as the polyps are expanded or retracted, and it is only from a full knowledge of both conditions that a clear understanding of the relationships of the polyps to the corallum can be obtained. On complete retraction the superficial tissues come to lie more or less closely upon the upper part of the corallum, always separated, of course, from direct contact by the adhering skeletogenic tissues. In strongly retracted examples of most species the costæ and septa are seen through the polypal walls and stand out prominently, and the tissues over them are much thinner than the portions of the wall which occupy the intervening depressions. Where the edges of the septa or costæ are sharply spinous, as in *Isophyllia*, the points appear as if perforating the tissues; but it may be doubted

whether this ever occurs naturally, as sections reveal only a great thinning of the layers. Polyps of *Madrepora*, *Cladocora*, and *Astrangia*, having a tubular calice, are able to withdraw their upper parts so deeply within the latter as to render the disk and tentacles almost invisible. Most members of the Astraeidae also partly withdraw themselves within the calice, and at the same time, by the contraction of the sphincter muscle, the capitular region of the column wall is drawn, iris-like, over the disk and tentacles, leaving but a small central aperture through which the mouth and central part of the disk can usually be seen. In *Manicina* and *Colpophyllia* the columnar musculature is weakly developed, and when retracted the capitular region is partly drawn downwardly and inwardly, covering the tentacles, but leaving the middle discal area exposed. In *Madrepora*, *Porites*, *Siderastrea*, and *Agaricia* the column wall is very rarely overfolded; on retraction the disk and tentacles are merely drawn downward, coming to rest upon the corallum, and the tentacles, disk, and mouth remain exposed.

During full expansion the upper part of the polyp is elevated some distance beyond the corallum, and the perithecal portion of the gastro-coelomic cavity becomes swollen.[a] The column wall, instead of being folded horizontally or downward over the theca, now stretches nearly vertically from its line of union with the other polyps and skeleton as far as the tentacular zone. This alteration of form can be easily understood in the case of distinct polyps, but not so readily in species where the polyps are incompletely separated.

Manicina is a good example of the latter in which to compare the different appearances of polyps on expansion and retraction. In the latter condition the meandering disk rests upon the skeletal projections on the floor of the calice, and the upper part of the columnar expansion lies obliquely upon the upper edge of the septa, then folds over the margin of the theca, and is continued downward over the outside of the theca for a distance varying in different examples. On full distension the disk is raised several millimeters above the skeleton, becoming much broader and flattened, or even convex; the tentacles are arranged in a marginal zone, either overhanging or partly involved in the discal tissues. The column wall is elevated vertically, its lower margin being the line along which the superficial tissues pass into the tissues lining the skeleton, and this for the time being constitutes the lower fixed termination of the column.

Meandrina and *Colpophyllia* are somewhat more complicated. The living colony during the day usually exhibits a meandering system of columnar ridges and discal valleys; the column extends about half way within the calice, folded and slightly swollen as it terminates, and more or less hiding the rows of tentacles. Full distension completely reverses the relationship of the disk and column wall. The former now becomes raised from its depressed condition along the floor of the calice until it is some millimeters wholly above the corallum, and convex in vertical section; the adjacent column walls are also raised until they become nearly vertical, and are either pressing against one another laterally, or separated only by a deep, narrow groove, at the bottom of which lies the line of connection of the column wall to the skeleton. The former discal valleys are now the ridges, and the thecal ridges the bottom of the valleys.[b]

A few observations have been made with regard to the external conditions which seem to determine the state of expansion or retraction of coral polyps. As a general rule the polyps are not expanded to their full degree during the day, either on the reef or in the laboratory; but the process begins immediately after sunset, and full expansion is maintained for the greater part of the night. Thus on bringing into the laboratory, in the course of the morning, a collection of specimens, they usually remain retracted for the rest of the day, but after sunset (6.30 to 7.15 p. m. in Jamaica) the polyps begin to expand until they attain their full dimensions. The body cavity is greatly distended with water, and the column wall and disk become raised some

[a] Where the pericalicular continuation of the gastro-coelomic cavity has become broken up into irregular canals, as in *Madrepora*, the amount of distension is small; but even in this genus a marked difference is seen in the coenosarc, according as the canals are fully charged or nearly empty.

[b] Verrill (1863, p. 38), from an examination of alcoholic specimens of *Meandrina*, *Manicina*, and *Porites*, came to the conclusion that the polypal disk does not rise even level with the summit of the corallum. Also naturalists familiar with the Bahama and Bermuda corals have informed me that they have never seen many of the fissiparous species (e. g., *Isophyllia*) in an expanded state.

distance above the corallum, while the tentacles are erect or overhanging. The colonies remain in this state nearly all night, unaffected by any artificial light employed in observing them; even when the strong light from a condensing lens rests upon a polyp for some time there is no response. In the morning the polyps are again found retracted.

If injured too much in the process of collecting, as when a portion of a colony is with difficulty broken off a large mass, the polyps of most corals are unable to recover sufficiently to expand at night. The best specimens for laboratory study are the colonies found lying free on the sea floor, for these can be removed without much disturbance to the living animals.

On the reefs, *Maeandrina*, *Colpophyllia*, and *Orbicella* are found partly expanded during the day, only the tips of the tentacles and part of the disk being visible; *Manicina* will sometimes protrude its tentacles, but *Isophyllia* rarely so. On the other hand, *Madrepora* and *Porites* are usually fully expanded; colonies of both species are often met with *in situ* on which, by means of a water glass, all the polyps are seen protruding to their full extent.

The corals found in very shallow water in Kingston Harbor are mostly retracted during the day; but if collected with care, and placed in shallow glass vessels exposed to the full rays of the sun, such species as *Manicina areolata*, *Porites furcata*, *Siderastraea radians*, *Cladocora arbuscula*, and *Oculina diffusa* will expand fully. Further, when in the laboratory these species have been kept shaded from the sun during the early part of the morning and are then brought into its direct rays, they soon begin to expand, and remain so for some time. Also, on bringing corals which during the whole day have been kept in a cool, shaded place into the rays of the setting sun they nearly always respond to the change and expand fully. It may be that in such experiments it is not the strong light but rather the slight increase of temperature of the water which exercises some stimulating influence on the polyps.

The general experience is that if colonies are placed in shaded spots during the day the polyps respond to the change, and expand to a greater or less degree, but if exposed to full light they remain retracted.

Much difference is experienced in the readiness with which various coral species expand. In the laboratory *Agaricia* seems to open less freely than others; *Cladocora* and *Oculina* are among the readiest to open out. In some instances the polyps of the latter remained fully distended for two or three days together without ever retracting.

It may, therefore, be taken as a general rule that coral polyps expand to their full degree during the night, but that under artificial conditions they may respond to an increase of light and temperature. The whole question of their response to external conditions is full of interest, but can be solved only by a long series of observations and experiments.

That night expansion is not restricted to tropical corals may be gathered from the observations of Gosse (1860, p. 312) on *Caryophyllia Smithii*. This British species was also found to expand most freely at night.

Many sea anemones exhibit the same phenomena as coral polyps, though not to the same degree. Colonies of the Zoanthid *Palythoa* are found in plenty on the reefs; during the day the polyps are mostly in the retracted state, and in the laboratory night is always found to be the most suitable time for examining them in the fully distended condition.

In the course of his examination of the coral reefs of Funafuti, Rotuma, and Fiji, Mr. Stanley Gardiner (1898) found much the same results as regards the time of expansion of coral polyps; *Euphyllia*, *Symphyllia*, and *Mussa* were the only corals observed by Gardiner to be fully expanded in the daytime. He further states, as is also the case in West Indian waters, that only during the night is the tow net able to collect in any quantity the minute larvæ, eggs, and other small organisms which probably constitute the food of coral polyps. During the day such pelagic forms evidently sink to the deeper waters, reappearing nearer the surface at night, and becoming most abundant in the early morning.

It may be that night expansion and day retraction of the coral polyps are in some way connected with this distribution of their food, and it is not unlikely that the phenomenon may be associated with the strong local sea breezes which usually disturb tropical waters during the day, and produce a cloudiness some distance around the shores. At night and early morning, the

breezes having subsided, the waters are quieter and more favorable to the activities of delicate sessile animals.

Perhaps the activity of the unicellular commensal algæ, present in such great numbers in the endodermal tissue of nearly all species, may be associated with the changes. But fully expanded, more transparent tissues in the daytime, would manifestly be most favorable for the functional activity of their chloroplasts.

TENTACLES.

The tentacles of Madreporarian polyps exhibit a certain diversity of form and arrangement, though not to the same degree as the corresponding organs in the Actiniaria. They are mostly disposed around the margin of the oral disk, in two or more entacmæous, alternating cycles. In *Madrepora* and *Porites*, however, they appear to constitute only a single cycle. In living polyps the tentacles can usually be seen to correspond in position with the internal mesenterial chambers of which they are the external prolongations, and further to conform in position, and, as a rule, in number, with the internal skeletal septa. In nearly all cases they correspond exactly with the number of internal mesenterial chambers, both entocœlic and exocœlic. Tentacles arising from the entocœlic mesenterial chambers may be known as *entotentacles*, and those from exocœlic chambers as *exotentacles*. Where present the latter always constitute the outermost cycle, and all the inner cycles consist of entotentacles. In *Siderastræa* the exotentacles differ in form from the entocœlic members (Pl. XXII, fig. 151), while in *Agaricia*, and the fully developed apical polyps of *Madrepora*, exocœlic tentacles are wanting. Gardiner (1900, p. 365) also found the tentacles to be entocœlic only in *Canopsammia*.

In all coral polyps so far described only one tentacle arises from each mesenterial chamber. The number of tentacles therefore represents the actual number of mesenteries present, and, in general, the number of septa also. None of the species examined shows the stichodactylinous condition so prevalent among tropical Actiniæ.[a]

During extension the tentacles are usually elongated, broad below and narrow above, the walls thin and somewhat transparent. Most of the species studied are characterized by a white, opaque, knob-like apex, more or less distinct, and constituting a battery of nematocysts. The tentacular stems of coral polyps are rarely smooth throughout, but exhibit round, oval, or irregular opaque thickened patches, which, like the apical knob, are aggregations of nematoblasts. These are elevated a little from the general surface, but rarely show any spiral or other regular disposition. Such restrictions of the tentacular nematoblasts are very exceptional among Actinians, and in this group the knobbed condition is also unusual (*Corynactis*, *Corallimorphus*).

With the exception of *Siderastræa radians* and *S. siderea* the tentacles of all the species here described are simple, while in the genus mentioned the entotentacles become bifurcated toward their free extremity, but the exotentacles remain simple.

In the living polyp the tentacles assume varied positions. During retraction they are usually withdrawn within the calice, and completely hidden by the overfolding column wall; but in some genera, *Siderastræa* and *Agaricia*, they remain exposed under all conditions of retraction or expansion of the polyps. In *Porites* and other forms the tentacles may occasionally remain exposed on retraction of the polyps, though more usually hidden under the retracted column wall. Upon expansion of the polyp the organs stand erect or overhang, even to such an extent as to nearly hide the column wall; and on the same polyp different cycles may sometimes assume different attitudes, as where the inner cycle is erect and the outer overhangs. The tentacles of corals rarely display much independent motion when fully extended, compared with the activity exhibited by the long tentacles of anemones. The tentacles of *Cladocora* and *Siderastræa*, and probably others, possess considerable adhesive power, more especially at the apex; the distal part of the stem may also fold round any small object. When small annelids are placed

[a] The term is applied to polyps (e. g., *Corynactis*, *Discosoma*) in which the tentacles are arranged in radial rows, so that more than one tentacle communicates with a single mesenterial chamber. The character serves to distinguish the tribe *Stichodactylina* from other Actiniaria in which only one tentacle communicates with a mesenterial interspace.

upon living colonies of *Siderastræa* the tentacles of the expanded polyps at once close upon them and prevent their escape.

The detailed arrangement of the tentacles presents many differences in the various species studied. As seen externally, the twelve tentacles of *Madrepora* and *Porites* (Pls. I and IV) admit of no proper distinction into an inner and an outer series, though varying somewhat in size, and may therefore be described as acyclic or monocyclic; the apical polyps of the former genus bear only a simple cycle of six equal tentacles. Although forming only one cycle, the twelve tentacles in both genera represent two orders, constituted of six entotentacles and six alternating exotentacles. The tentacles of such genera as *Orbicella*, *Solenastræa*, *Oculina*, *Cladocora*, and *Astrangia*, whose asexual method of reproduction is by gemmation, usually exhibit a regular hexameral multicyclic arrangement, with the formula 6, 6, 12, 24, etc. Very often the first and second orders are arranged so as to form only one inner cycle of twelve members, with which the twelve members of the second cycle alternate; the third cycle of twenty-four alternates with both these, and so on, according to the number of cycles developed. Where only twenty-four tentacles are present they usually appear as an inner and an outer cycle.

Very often the hexameral sequence of the tentacles is not complete, especially in *Cladocora* and *Astrangia*. The total number of tentacles in mature polyps of *Cladocora arbuscula* varies from thirty-two to thirty-six, whereas the complete hexameral plan would require forty-eight as the next number after twenty-four has been reached. In describing below the development of the later tentacles of polyps, it is found that the organs do not arise a complete cycle at a time, but in simple or double pairs on each side of the median axis, and in many species a tentacular cycle once commenced is not always completed before the polyp attains its full size and growth ceases. In such a case it is clear that any intermediate number of tentacles between the commencement of a cycle and its completion may be present.

Whenever an entocœlic tentacle appears, a corresponding exocœlic member usually arises, either simultaneously or shortly after, so that the number of exotentacles comprising the outer cycle is always equal to the sum of the entotentacles of all the inner cycles. Hence in endeavoring to establish the cyclic scheme of any hexameral polyp, in which the number of tentacles may be intermediate between twenty-four and forty-eight, or forty-eight and ninety-six, incompletion must be looked for in the two outermost cycles, not in the outermost only. A polyp of *Cladocora* with thirty-two tentacles bears the cyclic formula 6, 6, 4, 16; one with thirty-six tentacles the formula 6, 6, 6, 18; with forty tentacles 6, 6, 8, 20, where the numbers 16, 18, and 20 represent the exotentacles. The exocœlic cycle thus increases by the same amount as the outermost entocœlic cycle. The order of appearance of the tentacles demonstrates that it is impossible to establish hexameral completion for all the cycles until the outermost is reached, and then relegate any omissions to this, as is usually attempted. Any omission due to hexameral incompletion affects both the exocœlic and the last entocœlic cycles.

The members of any tentacular cycle are nearly always alike in size, but the tentacles usually show a diminution in length in passing from the inner to the outer series, a condition expressed by the term entacmæous. The organs in *Madrepora* and *Porites* are exceptional in that they vary in size in a very definite manner in the same cycle, while *Orbicella radiata* offers a marked exception to the entacmæous order. The polyps of this species do not readily expand their tentacles, and hence are not always favorable for observation. When fully extended the different tentacular cycles are found to be widely apart, and the twelve members comprising the first cycle are much smaller than those of the next, and even less than the tentacles of the outermost cycle. The tentacular plan of a polyp of *O. radiata*, with three hexamerous cycles, is represented on the next page.

Usually the different cycles which constitute the crown of tentacles are closely arranged in a narrow marginal zone, so that basally the members of one cycle partly embrace those of the next. *O. radiata*, just mentioned, is again exceptional in that a wide discal interspace separates one cycle from the next, the tentacular crown being unusually broad, encroaching upon the peristome. The same feature is also characteristic of the polyps of *Siderastræa* and *Agaricia*;

the cycles are widely apart, and each individual tentacle is distant from the others. In these two genera the tentaculiferous area comprises nearly the whole of the exposed polypal surface (p. 427).

In polyps whose asexual method of reproduction is by fission, the hexameral plan, characteristic of larval polyps, and of adult polyps whose reproduction is by gemmation, is lost after fission is established, and even the cyclic arrangement becomes obscure. In *Favia*, *Isophyllia*, and *Manicina* individual tentacles belonging to several cycles can be made out, but not with any regularity all round. The tentacles in the young polyps are found to be arranged hexamerously, but this is altogether lost on mature colonies. Where fission is never or rarely completed, as in *Maeandrina* and *Pectinia*, the tentacles are arranged in meandering systems, and only two rows are developed, an inner entocoelic series and an outer alternating exocoelic series.

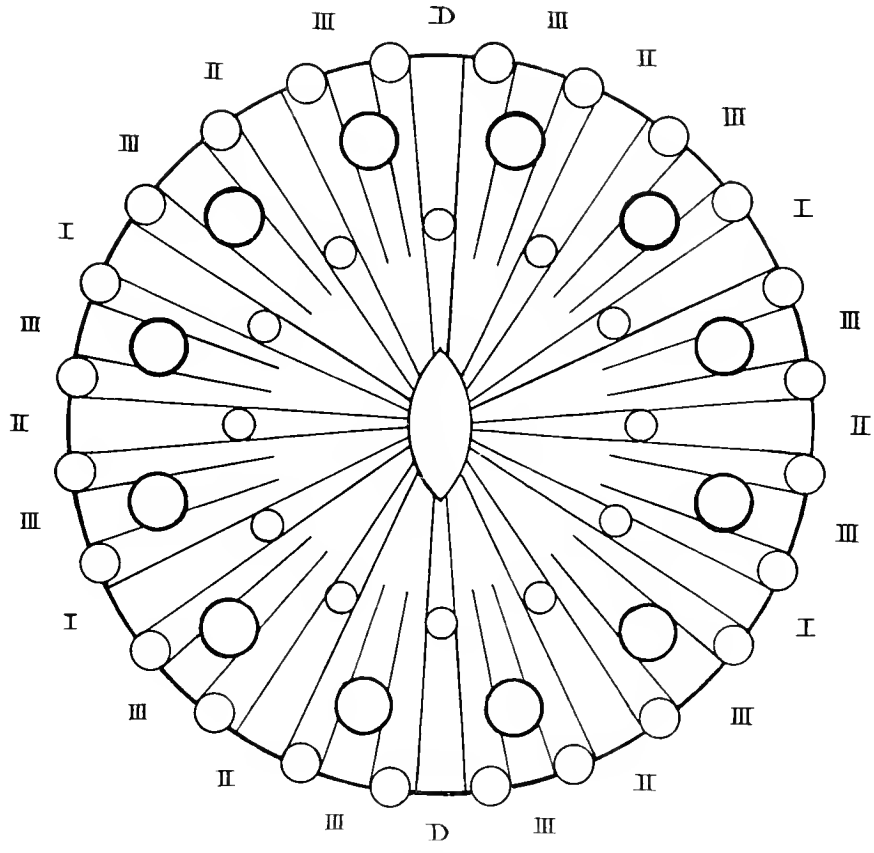

FIG. 1.

Tentacular plan of a polyp of *Orbicella radiata*. The Roman numerals indicate the orders of mesenteries; D, the directives. The innermost cycle of tentacles comprises twelve members which are the smallest of the series. They arise from the entocoeles of the first and second orders of mesenteries, which constitute the first cycle of twelve pairs of complete mesenteries. The second, middle cycle consists of twelve alternating tentacles which are the largest represented. They are outgrowths of the entocoeles of the third order of mesenteries, which form the actual second mesenterial cycle. The third or outermost cycle is formed of twenty-four tentacles, which alternate with the members of the two previous cycles, and arise from exocoelic chambers. The species is exceptional in that the members of the innermost cycle are the smallest of the series, and also in the wide distance apart of the cycles.

When the polyps retract, the tentacles do the same, and become greatly shortened. In addition, many species of corals exhibit the curious phenomenon of complete introversion of the tentacles, even during full expansion of the polyps, as well as on retraction. Both phases are clearly illustrated in the tentacles of *Porites* (figs. 30, 33, 40). At times the polyps in this genus will be expanded to their full degree, without any display of tentacles: twelve small, more opaque, circular areas, sometimes showing a central aperture, are all the external indications of their presence, while the local increased opacity indicates that they have become invaginated within the coelenteric cavity. At other times one or more individual tentacles of a polyp may be

protruded, while the rest are inturned. The process of introversion and subsequent extension has been actually observed on the expanded polyp. The movements of the tentacular walls, inwardly or outwardly, take place so slowly that they can be readily followed, the process somewhat resembling that seen when a glove finger is indrawn and afterwards pushed out. The alternations may be continued for some time. Likewise on retraction of the polyps the tentacles of *Porites* are, as a rule, introverted, instead of remaining merely exposed or covered by the column wall; and on preserved colonies very small apertures can be detected with a lens at the place of introversion. In longitudinal sections through such polyps the apical knob of the tentacle is deepest within the gastro-cœlomic cavity, and is directed outwardly, while with regard to the walls themselves, the ectoderm is internal and the endoderm external, a reversal of the ordinary condition. These conditions are clearly shown in fig. 40, representing a vertical section through a polyp of *Porites astræoides*. No overfolding of the column wall has taken place on retraction, so that the tentacles communicate directly with the surface of the colony. Three introverted tentacles (*t*) are present; the one to the left is divided radially, so that the section includes its aperture of communication with the exterior, while the two to the right are tangential sections, and therefore do not display the external opening. Again, in fig. 30, representing a transverse section through the stomodæal region of the same species, seven introverted tentacles are seen in section, almost completely occupying the mesenterial chambers, and exhibiting a reversal of the ordinary relations of ectoderm and endoderm. In other polyps sectionized a variable number of introverted tentacles has been met with. The apex of the introverted tentacle may extend as far inwardly as below the inner termination of the stomodæum, so that accompanying the introversion very little diminution in the length of the stem has taken place.

Among the living expanded polyps of *Madrepora* also complete tentacular introversion is often observed, in both apical and radial polyps. In the former six slight opacities around the margin of the transparent disk remain to indicate the tentacular area; later, the tentacles may be observed to protrude, either all together or successively.

During the retracted condition of the fissiparous genera *Faria*, *Manicina*, *Maeandrina*, and *Isophyllia* it is sometimes impossible to discover any tentacles externally. When sections are made, however, the organs are found to be introverted, occupying both the entocœlic and exocœlic mesenterial spaces.

In addition to actual introversion, in which all parts of the tentacles are still determinable, a condition is often presented in which the stem wholly disappears, becoming a part, as it were, of the discal wall.

Retracted tentacles of *Siderastræa* and *Agaricia*, for example, are usually represented by only a slight tubercular elevation of the disk, which is the knob or swollen apex, while the stems have wholly disappeared in the disk (Pl. XXIII, figs. 154, 155, and Pl. XXIV, fig. 163). In microscopic sections the former are displayed as mere ectodermal thickenings, charged with nematocysts, and no differentiated can be found whereby the tentacular stem can be distinguished from the discal wall.

Among the fully expanded polyps of *Orbicella annularis* the two cycles of short tentacles often wholly disappear. Here, again, it appears as if the tentacular tissues were not introverted, but rather have become involved in the greatly expanded margin of the disk; slightly raised, triangular areas, representing the apical swellings, are all that can be observed of the organs. On full extension of the adult polyps of *Manicina areolata* the tentacles likewise may be wholly wanting, their walls having become part of the expanded disk. Thicker, more opaque discal spots, which are the only evidence of their former presence, represent the nematocyst-bearing capitulum. In the young polyp of *Manicina* displayed in section on Pl. XIX, fig. 137, the tentacle appears only as a thickened, nematocyst-bearing area of the polypal wall. Occasionally in *Porites astræoides* tentacular disappearance, as contrasted with tentacular introversion, may be also observed.

Of previous observers, Fowler (1888, p. 11) has described and figured the introversion of the tentacles in *Seriatopora subulata*. Von Heider (1886, p. 158) has described in *Astroides calycularis* the opposite condition, in which the intertentacular portions of the disk have been

drawn within the mesenterial chambers of the polyp, while the tentacles remain directed normally outward. The introverted disk in von Heider's figures presents in transverse and longitudinal sections much the same appearance as the introverted tentacles of *Porites* in figs. 30 and 40, that is, the ectoderm is internal and the endoderm external. In many instances of strongly retracted polyps the tentacles are found greatly depressed or introverted as integral parts of the disk. Discal infolding is noticed more fully on p. 434.

From all these examples it is manifest that the phenomenon of tentacular introversion in both expanded and retracted polyps, and of disappearance in the discal wall of fully expanded polyps, are very general among corals. They probably serve to explain the statements of some of the older observers that tentacles are wanting in certain species of corals.

G. von Koch (1890, p. 399) has found in the contracted polyps of the Alcyonarian, *Rhizoxenia rosea*, that, in addition to the infolding of the disk and upper part of the column, the tentacles undergo invagination, but only for about half their length; the proximal half still preserves the normal relationship of outer ectoderm and inner endoderm. This is undoubtedly similar to the process described above, only the introversion is not continued to the extreme limit, as in *Porites*. In the living expanded polyps of the coral *Astroides calycularis*, von Koch has also observed that the terminal part of a tentacle is often drawn inwardly toward the basal part, and again pushed out, the movements somewhat resembling the drawing in and pushing out of a telescope tube, and continuing for some time.

An explanation of tentacular introversion does not seem readily forthcoming, for beyond the usual ectodermal longitudinal and endodermal circular fibers no special musculature is discoverable whereby the movements may be produced; further, a decided individuality is exhibited by the various members comprised in the cycles. One may surmise as a cause a difference in the hydrostatic pressure between the internal cavity and the exterior, owing to variations in the circulation of the nutrient fluid within the colony. But this would not account for the fact that the polyp itself may remain fully expanded, and only certain of the tentacles be invaginated, while the others remain extruded.

The disappearance of the tentacular walls in the discal tissues seems more easy of explanation. Structurally the tentacles in the Madreporaria are rarely the important differentiated discal outgrowths which they have become in most Actiniaria, and when the polyps attain their full expansion it can readily be understood how the tentacular walls may become involved in the discal expansion, and lose the distinctness of their walls, the thick apex only remaining to indicate their former presence. The tentacles are originally outgrowths of the disk, and can again become part of it, the thickened apical knob remaining as the only evidence of a special differentiation.

Histology.—Histologically the walls of the tentacles present few characteristics which do not occur in the column wall or disk. Such peculiar features as they display have reference to their function as stinging organs. Transverse or longitudinal sections of most species exhibit marked inequalities in the thickness of the ectoderm, the broader regions representing special nematocyst areas. The thickenings correspond with the more opaque areas on the tentacular walls in the living condition, and are best seen in sections made from tentacles in the expanded condition, as in the retracted examples the wider nematocyst regions tend to overlap the intervening narrow areas (Pl. VI, fig. 50; Pl. X, fig. 75). The largest battery of stinging cells is at the apex, and here the outermost zone is constituted almost wholly of nematoblasts. By focussing with a high power around the free edge of a nematocyst area, triangular or thread-like cnidocils can usually be discerned, especially in the living tentacle, and cilia may be present over the whole tentacular surface (Pl. II, fig. 10).

The nematocysts in the tentacles are mainly of the long, narrow, thin-walled form, with the spiral thread closely coiled (Pl. XVII, fig. 124*a*). Other thin-walled forms—small and oval, or large and oval with a loose spiral thread—may occasionally occur, but are never so characteristic as the former. In the deeper parts of the ectodermal layer, brightly staining, apparently homogeneous bodies are generally seen, which represent nematocysts in various stages of development. At first they are irregularly arranged at almost every angle with the surface, but as they reach

maturity they migrate to the periphery, and arrange themselves in a vertical direction, parallel with the other cellular constituents.

A weak longitudinal ectodermal musculature seems to be always present, the cut ends of the fibrils being displayed in transverse sections, and most pronounced toward the proximal extremity. In some species—e. g., *Cladocora*, *Madrepora*, and probably others—a distinct nerve layer also occurs, situated some distance from the mesoglœa (Pl. II, fig. 10 *nr. l.*). The ectodermal gland cells and supporting cells are practically the same as in the column wall, but the former are less numerous.

The tentacular mesoglœa is always a very thin layer, usually smooth on both surfaces, while the endoderm is comparatively broad with irregular internal limitations. The endoderm is generally richly supplied with zooxanthellæ, but the algæ are absent from *Phyllangia*, *Astrangia*, and certain of the tentacles of *Madrepora*. In all instances a weak circular musculature is developed, but the mesoglœa is rarely folded to afford it additional support, as in the larger tentacles of Actinians. The lumen is preserved, even in fully retracted tentacles.

The tentacles of several genera present so many peculiarities of form and arrangement as to call for special description.

TENTACLES OF MADREPORA AND PORITES.

The tentacles of the polyps of *Madrepora* and *Porites* are exceptional among the genera studied in that they are, with certain exceptions, only six or twelve in number, and in the adult usually exhibit constant variations in size. The tentacles of the apical polyps of *Madrepora* will be first described (fig. 1, *a*, *b*). In the most typical instances only six tentacles occur, all equal in size, and communicating with the entocœlic chambers. They are widest at their origin in the margin of the disk, where a considerable interval separates one from another, and terminate either acutely or in a rounded manner. The surface is smooth throughout, no urticating spots being visible.

Polyps with such a tentacular system are found at the apex of the long established branches of colonies of both the palmate and arborescent types of growth. On polyps at the ends of short, rapidly growing branches, rudiments of other tentacles also occur, alternating with the members of the first order. In regions of vigorous growth, as at the margin of palmate colonies, it is found that certain of the ordinary polyps, bearing the full complement of twelve tentacles, may become larger and assume an apical character, and among these the separation of the tentacles into an inner and an outer cycle can be recognized. Sometimes, only two or four of the six members of the outer cycle will be present, always much smaller than the entotentacles. All stages in the diminution in number and size of the outer exocœlic tentacles are, however, represented, according as the polyp has recently assumed or long maintained the apical position: at the same time, the six members of the inner cycle become larger and more equal.

From all the variations observed, it is clear that on any polyp taking on the axial condition the six exocœlic tentacles, present on all the radial polyps and smaller from the beginning, tend to completely disappear, and only the six entocœlic members ultimately remain, becoming at the same time larger and equal. Like the other regions of the axial polyp, the tentacles are perfectly colorless, owing to the absence of zooxanthellæ, and are not often seen fully expanded.

Among the fully developed radial polyps of *Madrepora* twelve tentacles occur; rarely, the number may be increased to sixteen, eighteen, or as many as twenty-four. The usual forms and arrangement are given on Pl. I, fig. 1 (*d.–a.*). The separation, as regards distance from the center of disk, into two alternating cycles of six each, is not clearly defined, but the members of one series are always larger than those of the other. The anterior or abaxial tentacle, adjacent to the nariform apex of the corallite, is longer and stouter than any of the others, and colorless, except toward its origin. It may be nearly twice as long as the others, and stands out very prominently; even in partly retracted polyps, when the tentacles are arranged vertically, it easily overtops the rest (*c.*). The opposite or axial tentacle—that is, the one adjacent to the stem—is the next in size, but differs very little, sometimes not at all, from the four large lateral

tentacles. These four, two on each side of the median plane, are approximately equal. Later, in describing the relationships of the mesenteries of *Madrepora*, it will be seen that the large anterior abaxial tentacle is dorsal or sulcular in position, while the opposite axial tentacle is ventral or sulcar as regards the polyp as a whole (p. 444).

Of the smaller alternating series of six tentacles the abaxial laterals (one on each side of the large abaxial tentacle) are always the smallest, and are generally colorless throughout. The middle laterals come next in size, and the axial laterals may be a little smaller than these. The difference in size between the middle and axial laterals is, however, often scarcely perceptible; but the four are always larger than the two abaxial laterals, and are more deeply colored. In polyps near the apex of growing branches all the tentacles may be colorless.

As far as can be made out in the living state, the tentacles of the very minute, intercalary polyps are uniform in size, and in regions where the corallites possess a circular, free edge the tentacles tend to become more uniform in size. The large abaxial tentacle is always best developed in polyps where the corallite has the most marked nariform projection, as in *M. cervicornis;* undoubtedly, there is a relationship between the form of the mouth of the corallite and the amount of inequality among the tentacles.

In L. Agassiz's Report on the Florida Reefs (Pl. XVIII) an outline figure of an expanded terminal polyp of *Madrepora cervicornis* is given, in which six large equal tentacles alternate with six much smaller tentacles, likewise equal. Such a stage is occasionally met with on young branches, but is to be regarded as transitional to the stage in older branches with only six equal tentacles. On the same plate are also outline figures of expanded lateral polyps from near the tip of a branch; as there represented the abaxial aspect is uppermost.

Prof. A. E. Verrill (1869) was the first to draw attention to this variation in the external characters of the axial and radial polyps of *Madrepora*, and regarded it as the only instance of dimorphism among the Madreporaria. The apical polyps are seen, however, to be derived by modification of the radial, and, as will be shown later, the internal anatomy of the apical and radial polyps presents no differences corresponding with those of the tentacles, so that the dimorphism is not very deep seated.

The tentacles in all the West Indian species of *Porites* are, like those of *Madrepora*, usually twelve in number. Developing polyps exhibit a less number, and others occasionally occur in which the number may be fourteen, sixteen, or as many as twenty-four. On the colonies no distinction is to be made between apical and radial polyps. The tentacles of all the polyps are extremely small, smooth-walled, and digitiform, rarely exceeding 1 or 2 mm. in length. Viewed with a lens, in their fully expanded condition, or even when introverted, they appear to constitute but one cycle, and very often differences in size are recognizable of the same character as in *Madrepora* (Pl. IV, fig. 32). The two tentacles in the longer oral axis are somewhat larger than the others, and one of these, corresponding with the abaxial in *Madrepora*, is somewhat longer than the other; the tentacles situated one on each side of the largest are likewise the smallest of the twelve. Both *P. clavaria* and *P. furcata* exhibit this bilateral arrangement, but in such minute polyps the differences are not so decided as on the larger polyps of *Madrepora*, and are not obvious on all the polyps of a colony. In *P. astreoides* the twelve tentacles are usually equal in size.

It is shown later (p. 431), that this regular variation in the size of the tentacles of *Madrepora* and *Porites* is to be explained as the retention in the adult of a well-known larval stage passed through in the development of the tentacles of certain Actiniaria, and is also associated with a primitive condition of the internal mesenteries.

TENTACLES OF SIDERASTREA AND AGARICIA.

The tentacles on the polyps of the genus *Siderastrea* are so small as to be scarcely distinguishable with the naked eye, especially when retracted; but by careful examination with a lens their disposition and character can be made out. Observations have been made upon the organs in both *S. radians* and *S. siderea*. Instead of being closely arranged in a narrow peripheral zone, as in most corals and anemones, the individual tentacles are widely separated from one

another, and occupy nearly the whole of the exposed polypal area (Pl. XXII, fig. 150). In the living condition each appears to arise either directly over or near the centripetal termination of the septum with which it corresponds. The cyclical arrangement is difficult to establish, and in many instances this would be impossible without the assistance from the septa which can be seen below through the soft tissues.

On full expansion the inner tentacles are found to consist of a short cylindrical stem, which bifurcates a little beyond midway, each half bearing a spheroidal enlargement at the apex; the outermost tentacles, however, are simple, consisting of a short stalk, terminated by a knob-like swelling (Pl. XXII, fig. 151). Thus in *Siderastræa* there is a true dimorphic condition of the tentacles, apparently the only instance of such among the Madreporaria, if we except the differences between the radial and axial polyps of *Madrepora*. In the course of the development of the young polyps (p. 533) it has been ascertained that the inner tentacles are at first simple, then afterwards another moiety arises over the same mesenterial chamber, and finally a common stem is produced, which bears the two halves at its extremity and raises them above the disk. Ontogenetically, therefore, the bifurcations represent distinct and separate formations, and only later constitute an entire tentacle.

Subsequent examination of sections confirms what would be expected from the external relationships, namely, that the bifurcated inner tentacles are all entocœlic in position, while the simple outermost tentacles communicate with the exocœles. In the nearly mature polyps of a colony, however, some of the entocœlic tentacles may be simple, but such are merely examples in process of development. The exocœlic members are never double.

On retraction of the polyps the disk and tentacles remain uncovered, the column wall in *Siderastræa* being incapable of overfolding. The tentacles are now represented by minute, simple and double tubercular enlargements, scattered over the greater part of the polypal wall. Microscopic sections reveal that the stems are no longer determinable as such, having become involved in the discal tissues, while the knobs remain as mere ectodermal thickenings (Pl. XXIII, figs. 154, 155). The apex of the exocœlic tentacles occurs as a simple swelling of the disk, directly overlying its corresponding septum, while the two knobs of the entocœlic tentacles are disposed one on each side of an entocœlic septal ridge, the two halves connected by a tissue similar to that of the disk, which manifestly represents the stem of the expanded tentacle. The ectoderm of the knobs includes a peripheral layer of long narrow nematocysts, and is thus easily distinguished from the rest of the disk.

Both *S. radians* and *S. siderea* are further characterized by the tentacles being apparently arranged in only approximate cycles, and by the occurrence of a comparatively wide interspace between one cycle and another. The imperfect cyclic disposition results from the presence of tentacles intermediate in position between the true cycles, and on the actual polyp it is often very puzzling, if not impossible, to say to which cycle some of the tentacles should be relegated. Polyps are found with from five to seven or eight tentacles, which, so far as their position is concerned, must be regarded as belonging to an inner cycle, and the remaining members seem to come in irrespective of any cyclic plan. In mature polyps of both species three more or less complete alternating cycles of tentacles are actually present, in addition to the outer single-knobbed cycle. The members of the latter being situated near the polygonal periphery of the polyp are rarely included within a circle.

When studied in conjunction with the underlying septa an approximate tentacular regularity can be established, as in fig. 150. The innermost cycle comprises six double-knobbed tentacles, separated by a wide interspace from the members of the second and third cycles, and these latter cycles are separated from the outermost cycle of single-knobbed tentacles. It is manifest from the figure that the tentacles correspond with the septa, and not all the twelve members necessary to complete the third cycle occur. *S. radians* appears to never complete its third cycle of mesenteries, tentacles, and septa, while in *S. siderea* it is occasionally reached or even exceeded. In fig. 150 only one member is wanting to complete the third cycle of entotentacles.

The apparent irregular disposition of the tentacles in this genus becomes explicable on a knowledge of the development of the mesenteries and their corresponding septa, or rather the

two illustrate the same fact. In both species studied six pairs of perfect mesenteries form the first cycle, six alternating pairs make up a second cycle, and there may be twelve pairs forming a third cycle. As just mentioned, however, this last cycle is rarely completed. Further, an examination of the macerated skeleton shows that in very few instances is the full complement of septa, viz., 6, 6, 12, 24, present. Usually in *S. radians* only a few pairs of the third-cycle mesenteries occur, the number varying with the size of the polyp, while in the larger *S. siderea* nearly all the pairs are present, and even some members of a fourth cycle.

This incomplete cyclic development in the case of the mesenteries is repeated in the last cycle of entocœlic tentacles, and, the organs being widely apart, the imperfection of the cycle becomes more pronounced externally. With few exceptions the hexameral plan can be traced only as far as the first and second cycles. The third cycle may comprise any number of members from one to twelve, while the outermost cycle of simple tentacles contains the sum of the members of all the three inner cycles. Further, there is a tendency in most species of corals for the two inner cycles to constitute but one cycle of twelve, in the same way that as the polyps increase in size the mesenteries of the second cycle tend to unite with the stomodæum, and the first two orders of septa form only one cycle.

A considerable discal space intervening between the different tentacular cycles in *Siderastræa*, as compared with most other corals, it is clear that the two conditions alluded to above find their outward expression in individual tentacles occurring at varying distances from the center of the disk, and thus giving rise to the characteristic irregularity. In a fully developed, long-established polyp, the cycles are more regular than in a young individual. Moreover, were the cycles of tentacles in other coral species to be separated by such comparatively wide discal interspaces, instead of being arranged closely in a narrow zone, similar cyclic irregularities would be more generally noticed.

The arrangement of the tentacles in *Agaricia* very closely resembles that characteristic of the genus *Siderastræa*, but the organs are never bifurcated, and are not distinctly stalked. They remain exposed during the retracted condition of the polyp, and during ordinary retraction can usually be seen as mere pointed or triangular tubercles, but when expanded they become more digitiform, with an opaque white area at the apex. They are often brightly colored by comparison with the rest of the polypal wall. In several colonies of the form I identify as *Agaricia fragilis*, I was unable to determine the presence of any tentacles in the living condition, even with the aid of a lens. In sections through the disk they are, however, recognizable as slight, nematocyst-bearing thickenings of the ectoderm (Pl. XXIV, fig. 163). The organs are better developed in *Agaricia agaricites*.

As in *Siderastræa*, the individual tentacles are widely separated from one another, and are distributed over nearly the whole discal area, one above the apparent centripetal termination of each of the larger septa. No tentacles occur over the members of the smallest cycle of septa, which transverse sections demonstrate as exocœlic. In this absence of exocœlic tentacles the genus *Agaricia* is unique among the forms here studied, with the exception of the axial polyps of *Madrepora*.

The majority of the tentacles are arranged so as to form an inner cycle, but the number composing it is variable, and the cyclic character is only approximate. Outside there are a few scattered examples at different distances from the center, suggesting no cycle relationship. The number in the inner cycle varies from five to nine, while the total number in any polyp may be from thirteen to twenty-four.

In *Agaricia* mesenterial increase appears to be in constant progress, corresponding with the growth of the individual polyp, though in no regular cyclic manner. Similarly with the tentacles: the inner cycle includes all the older tentacles, and outside this are the later-formed members which appear irregularly. Probably it is best to regard the tentacles as acyclic, no exotentacles being developed. Counting the tentacles of many polyps gives odd numbers as often as even, while in the case of species with exocœlic tentacles even numbers predominate. The irregularity in the disposition of the tentacles in *Agaricia* should be compared with the irregular arrangement of the mesenteries represented on Pl. XXIV, fig. 161.

G. C. Bourne (1887), in his paper: "The anatomy of the Madreporarian coral Fungia," refers to the disposition of the tentacles in that genus. His figure of *Fungia* (Pl. XXIII) shows a wide interspace between the different cycles of tentacles, as is found to be the case in the much smaller polyps of *Siderastrea* and *Agaricia*. Evidently, the character may be taken as of some diagnostic importance within the Section Fungacea. Bourne casts suspicion upon the accuracy of Dana's description and figures of *Fungia* (Zoophytes, Wilkes Exploring Expedition, and Corals and the Coral Islands), which represent an irregular distribution of the tentacles at intervals over the whole of the large disk, as does also the figure of Quoy and Gaimard in Voyage de la corvette l'Astrolabe. The results from *Siderastrea* and *Agaricia*, detailed above, prove that an irregular appearance in the disposition of the tentacles is by no means uncommon in the Fungacea. The regular cyclic disposition, when really present, can often be established only after a long acquaintance with the forms, and under favorable conditions of expansion or retraction.

The figures of the fully expanded polyps of *Siderastrea*, accompanying Agassiz's Florida Reefs (1880, Pl. XV., figs. 6, 7), indicate an irregular tentacular arrangement in both cases, and such would probably be assumed by any observer on a casual acquaintance with the polyps. The appearances given the tentacles in Agassiz's figures were rarely met with in Jamaican specimens, but the dimorphism is clearly shown on some of the members, and is referred to by Pourtalès in "Deep Sea Corals" (1871).

ORDER OF APPEARANCE OF PROTOTENTACLES.

In corals whose development has been studied sufficiently far, the first tentacles are found to make their appearance within a few days after the fixation of the larva. The number of tentacles first to arise corresponds as a rule with the number of internal mesenterial chambers already established, the tentacles being outgrowths from them. Generally, in coral larvæ, the twelve primary mesenteries, with their corresponding chambers, are developed either at the time of fixation or shortly after, and the twelve primary tentacles appear either simultaneously, one from each mesenterial chamber, or one cycle may arise in advance of the other. In the latter case the inner cycle of entocœlic tentacles usually appears first, and the exocœlic members next, but in *Siderastrea radians* this order is reversed (p. 533).

The establishment of the tentacles serves to delimit for the first time the larva into two regions—disk and column; and with this the larva may be considered to have become the polyp. The part of the polypal wall bearing the tentacles and mouth is the disk, and the region outside or below is the column. The former becomes more or less flattened, and constitutes the free oral extremity of the polyp, as opposed to the fixed or basal aboral extremity, while the column is vertical and remains more or less cylindrical.

The actual appearance of the primary tentacles has been observed as follows: The larvæ of *Astroides calycularis*, examined by Lacaze-Duthiers (1873), presented twelve tentacular prominences at a very early stage after fixation. During the development of *Cargophyllia cyathus*, G. von Koch (1897) found that in most cases the two primary cycles of tentacles appeared simultaneously, though some of his observations seemed to indicate a successive origin. Von Koch's figure (p. 760) of the young polyp, at the stage when the prototentacles are all developed, represents the members of the inner entocœlic cycle as smaller than those of the outer exocœlic cycle, but in the text the author states that they are larger. Lacaze-Duthiers (1897), in his recent paper on the corals of the Gulf of Lyon, gives many figures illustrating the early development of *Balanophyllia regia*. From the beginning two alternating cycles of large and small tentacles are indicated, and no reference is made to any intermediate stage. The same author (1894) mentions six tentacles as occurring at an early stage in the development of *Flabellum anthophyllum*, and later figures the complete twelve.

Young polyps of *Manicina areolata*, which I was able to rear to the stage with twelve tentacles, were also characterized by the simultaneous development of these organs. When first definitely recognizable under the microscope, after a period of fixation of about fourteen days, two cycles were present, nearly equal in size (Pl. XIX, fig. 135). In two or three young polyps, from

a batch of larvæ of *Fungia fragum*, only six primary tentacles appeared simultaneously, about four days after the larvæ were set free, and in other larvæ reared later the members of the inner cycle appeared in advance of the outer (Pl. XIV, figs. 106, 107).

So far as I can discover, *Siderastræa radians* is unique among both corals and Actinians in that the first tentacles to arise are the six exocœlic members. This relationship was established in scores of instances, and no exceptions whatever were observed, so that it must be regarded as characteristic of the species. The six members were developed simultaneously a few days after fixation of the larvæ, and two or three weeks elapsed before the members of the entocœlic cycle began to appear. These were situated central to the first cycle, and in most cases the six appeared together, but a few exhibited a successive order, though of no regular character. For a long time the newer tentacles remained smaller than the older, the usual entacmæous order being thus reversed.

On the completion of the prototentacular stage, the relationships of the tentacles and mesenteries are as follows: The twelve primary mesenteries only have appeared, eight of which are complete and four incomplete, and the tentacles are outgrowths from the twelve mesenterial chambers, one from each. The six larger tentacles constituting the inner cycle are situated over the six entocœles, and the six smaller tentacles of the outer cycle over the six exocœles.

The rule that the tentacular sequence is associated with the stage reached in the mesenterial development was first demonstrated by Lacaze-Duthiers (1872) in the larvæ of *Actinia equina*. The primary mesenteries in this species were found to appear in bilaterial pairs, according to a regular sequence, and the tentacles conformed to this. Thus from the dorsal chamber, the larger of the two produced on the appearance of the first pair of mesenteries, appeared a large tentacle, and from the ventral or smaller chamber a smaller tentacle, both in the axial plane. As the later pairs of mesenteries arose and chambers were formed, corresponding tentacles appeared in a bilaterial manner until the twelve were established. The primary tentacles in *A. equina* retained the bilateral symmetry for some time, but ultimately this was succeeded by the adult condition, in which the tentacles in any cycle are equal in size.

All corals so far investigated, however, are provided with twelve fully established mesenteries (eight complete and four incomplete) and mesenterial chambers before the tentacles begin to make their appearance. Hence, there is rarely any successive development in their tentacular outgrowths, but the members of one or both cycles arise simultaneously—one from each chamber. Where in Actinian larvæ less than twelve mesenteries are present, the number of tentacles shows a corresponding diminution. Thus in larvæ of *Lebrunia coralligens* only eight of the primary mesenteries were developed at the time of fixation, and but eight tentacles appeared in this case four large and four small. For nearly a week no increase of mesenteries took place, and the tentacles, though modifying their comparative size, remained of the same number. Some of the Actinian larvæ studied by Lacaze-Duthiers also showed only eight tentacles for some time, and Faurot (1895) has obtained similar results.

A few observations have been made upon the appearance of the tentacles in budding polyps. In the earliest stages determinable in buds of *Porites* and *Madrepora*, only six minute protuberances can be distinguished, two median and four lateral, differing somewhat in size. Older buds with eight or ten tentacles may also be found. Such instances merely suffice to indicate that the prototentacles of the bud do not arise simultaneously in the two genera mentioned, but in median and then in successive bilateral pairs. The buds, however, are so minute as not to permit of more detailed examination in the living expanded state, and scarcely anything can be ascertained from preserved colonies.

The bilateral condition of the tentacles in the adult *Madrepora* and *Porites*, already referred to, is full of suggestiveness from what is known of the tentacular development in the Actiniaria. Lacaze-Duthiers (1872) has shown that in *Actinia equina* an axial tentacle first appears, and that for a long time this remains larger than the others, which arise in successive bilateral pairs.[a] His

[a] Dr. A. Appellöf (1900, p. 79) doubts the accuracy of Lacaze-Duthiers' account and figures of the development of the tentacles in *Actinia equina*, which have been accepted almost as classic. Among hundreds of larvæ of this species investigated by him, Appellöf has never met with the succession and proportional size of the tentacles indicated by

figure of the larva, at the stage where twelve tentacles are present, should be compared with the figures of the tentacles in the adult polyps of *Madrepora* and *Porites*, on Pls. I and IV. It is seen how very closely they agree in the relative sizes of the tentacles, and especially in the prominence of one of the axial tentacles (the dorsal of Lacaze-Duthiers, the abaxial of *Madrepora*); also, the small size of the tentacle on each side of this. Since the publication of Lacaze-Duthiers results somewhat similar phases in the appearance of the prototentacles have been obtained in other Actinians. In the Actinian, *Lebrunia coralligens*, I have shown (1899) that a bilateral stage with a large dorsal or sulcular tentacle is assumed even after a primary tetrameral radial phase. Occasionally anemones are come upon in which the primary large tentacle is retained in the adult, and in certain Sagartids occurring in Kingston Harbor the organ displays remarkable motile powers.

All the facts go to prove that the adult bilateral condition of the tentacles in *Madrepora* and *Porites* is to be regarded as the retention of a larval stage occasionally passed through by Actiniaria.

METATENTACLES.

No description is available as to the manner of appearance of the tentacles in any young coral polyp beyond the two cycles of prototentacles. The few observations I have been able to make indicate that the metatentacles appear practically simultaneously with the metacnemes, an exocœlic and an entocœlic member together, as in *Solenastræa* (fig. 83); or the entocœlic tentacle may arise in advance of the exocœlic, as in the young polyp of *Faria* (fig. 109); *Siderastræa radians* is again exceptional in that its exocœlic metatentacles arise before the corresponding entocœlic organs.

Very definite accounts of the order of appearance of the tentacles in Actiniæ are given by Professor Lacaze-Duthiers (1872), and also by Dr. L. Faurot (1895). By these writers it has been shown, in numerous instances, that the tentacles beyond the two first cycles arise in pairs, of which one member is entocœlic and the other exocœlic. The entocœlic tentacle grows more rapidly than the exocœlic, surpassing indeed the members of the outer (exocœlic) cycle of prototentacles. The exocœlic metatentacle attains the same size as the exocœlic prototentacles, and when the former are all developed the two series together are comprised in the third cycle, the second cycle now being formed of the entocœlic metatentacles, which rank next in size to the entocœlic prototentacles.

The stages passed through will be best understood from the accompanying figures (fig. 2), taken from Faurot's "Études." The process is that followed in *Tealia felina*.

ORAL DISK.

The oral disk is the more or less flattened distal termination of the polyp. It includes and is bounded peripherally by the tentacular zone, and bears the oral aperture in the middle. In most species the cycles of tentacles are closely arranged, and comprised within a narrow marginal region, while the more central area of the disk, known as the peristome, is naked, and may be depressed, flat, or elevated in a cone like manner. The tentacles on the disk of *Siderastræa* and *Agaricia* are comparatively widely apart, and the naked area is correspondingly diminished; the tentacular zone in *Orbicella acropora* also occupies a large proportion of the disk (fig. 1, p. 423). The discal walls are often delicate and partly transparent, and permit of the septa being seen through; like the column wall, the external surface may be smooth or verrucose. Usually numerous radiating grooves occur, corresponding with the internal mesenteries; the grooves of the complete mesenteries extend as far as the center of the disk, while those representing the incomplete mesenteries stretch only part way.

Lacaze-Duthiers; usually eight tentacles arise, practically simultaneously and equal. Knowing the great variability often exhibited by Anthozoan larvæ, according to the developmental stage at which they are extruded, it seems to me not unreasonable to suppose that even the same species may present such wide variations as those given by Lacaze-Duthiers and by Appellöf. The agreement of Lacaze-Duthiers' figures of *A. equina* with those representing the tentacles of *Madrepora* and *Porites* is certainly suggestive.

In simple polyps, and where asexual reproduction takes place by columnar gemmation, the disk is circular or slightly oval, and bears only one central mouth; a complete tentacular system belongs to each individual, and forms a closed circle. But where increase takes place by incomplete fissiparity the disk becomes large and irregular in outline, and as a rule bears more than one oral aperture, the whole surrounded by a complex tentacular system. In genera like *Maeandrina* and *Meandrina* the disk is represented by irregular, meandering, flattened areas.

During the retracted state of the polyps the disk is depressed, its peripheral border resting upon the edges of the septa. On very strong retraction the interseptal discal areas may be drawn much below the level of the septal edges, and invade the polypal cavity as mesenterial funnels—"Septaltrichter" (see below). As a rule, the retracted disk is almost entirely hidden

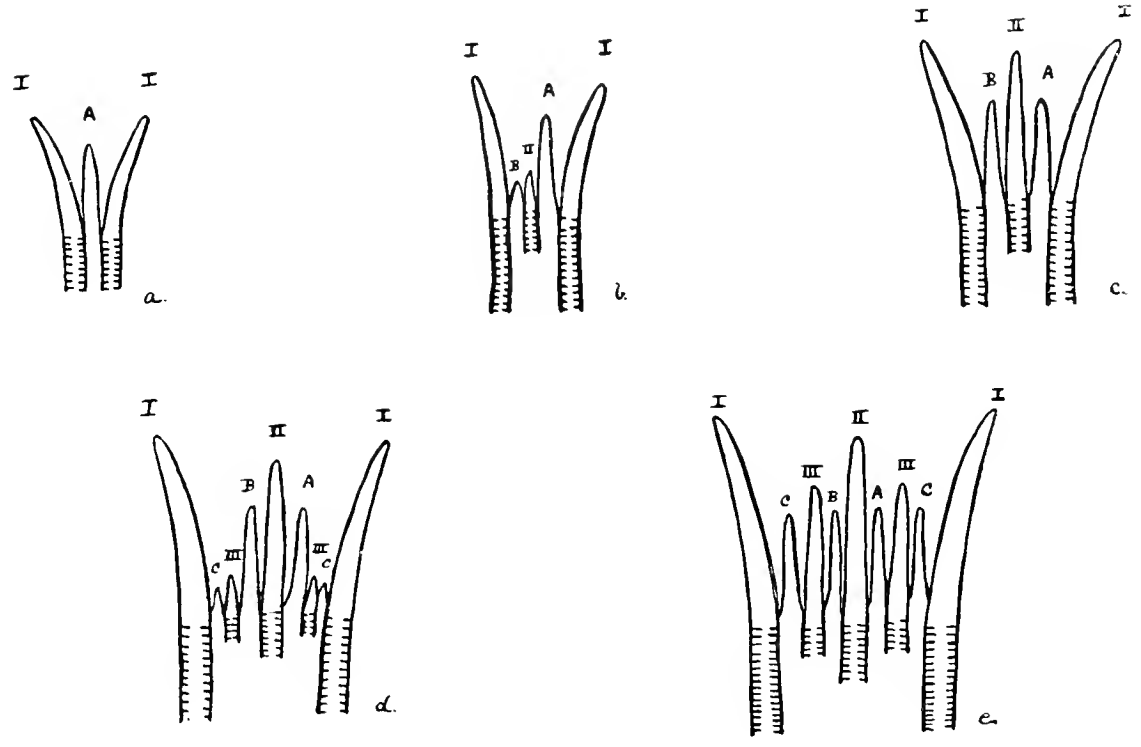

FIG. 2.

One of the six tentacular systems of an Actinian polyp, illustrating the order of development of the tentacles, from the stage with twelve to the stage with forty-eight tentacles, in their relation with the mesenterial chambers. *a*, Sextant with two entocoelic prototentacles (I, I) and one exocoelic prototentacle (A). *b*, Two rudimentary tentacles have appeared, one (II) from the entocoele and the other (B) from the exocoele of a new pair of metacnemes. *c*, The new entocoelic tentacle (II) has now become larger than either of the exocoelic tentacles, but is a little smaller than the entocoelic prototentacles (I), and constitutes the second cycle of tentacles, while the exocoelic tentacles (A, B) constitute the third cycle. *d*, Rudimentary tentacles (c, III; III, c) have appeared in association with the entocoeles and exocoeles of two new pairs of second-cycle metacnemes. *e*, The entocoelic tentacles (III, III), incipient in *d*, have now become larger than all the exocoelic tentacles, but are less than the member of the second cycle of tentacles, and constitute the third adult cycle of twelve tentacles. All the exocoelic tentacles (A, B, C, C), though appearing at different times, are now equal in size, and constitute the last or fourth cycle of the adult.

by the overfolding upper region of the column wall, but usually a small circular opening remains, simulating an oral aperture, and through it the middle of the disk can be seen below. On partial expansion also the disk may be sunk below the upper edge of the column, but on full expansion it usually becomes strongly convex, the middle area raised above the level of the column, and even of the tentacular zone. In *Favia fragum* the disk may project in this way as much as 5 mm., and the perioral region becomes extended in a dome-like manner, bearing the slit-like mouth at the apex. This is noticeable also in *Oculina diffusa* (Pl. XXII, fig. 149). In transverse sections through the disk thus produced only the complete mesenteries are usually included, as the incomplete members do not radiate far across (Pl. XI, fig. 83).

Histologically the disk differs but little from the tentacles or column wall. The peristome is generally very thin walled, and in nearly all cases is provided with weak radiating ectodermal and circular endodermal musculatures. Granular and clear gland cells are generally numerous, and nematocysts, somewhat similar to those in the tentacles, are sparingly distributed. In some cases a delicate ectodermal nerve layer can also be distinguished, but is never so pronounced as in the tentacles.

In fully retracted polyps of many species the discal wall is found partly introverted within the polypal cavity, somewhat in the same manner as already described for the tentacles (p. 423). Such a condition is often very confusing during the study of sections, and may seriously interfere with the determination of the relationship of the mesenteries to the stomodæum. In one important respect the invagination is distinguishable from the introversion of the tentacles; it is essentially mesenterial in position, while the tentacular inturning is intermesenterial. Pl. XVI, fig. 117, represents the appearance of the invaginations at different levels, as met with in a fully retracted polyp of *Dichocænia*. The indentations occur about midway along the radial extent of the disk, and vary greatly in extent, but in general diminish from above inwards. The one to the left extends at this level over three mesenterial chambers, the entocœlic septum being evidently notched, and thus permitting of the continuity of two really distinct tracts. The middle invagination occupies only one exocœlic chamber, while the upper is still smaller, both in width and radial extent. The discal ectoderm is exceptionally broad, being cut obliquely, and the radial muscle fibers are clearly seen. The tentacles themselves are also involved in the discal invagination, but only as part of the disk, not as distinct organs.

The depression of the discal wall results in the interruption of the mesenteries radially, so that the latter are seen only toward their insertion in the polypal wall and in the stomodæal wall.

On Pl. XIII, fig. 95*a*, taken from a retracted polyp of *Faria fragum*, a discal introversion is seen near its termination, about midway along the transverse length of the mesentery; a few sections below, the continuity of the mesentery is established. Such an appearance might easily be mistaken for some tubular organ connected with a mesentery, but the phenomenon can be readily explained as a result of the strong contraction of the mesenterial musculature. It is easy to see how on full retraction of the polyp the discal wall will come to rest upon the septal edges; then any further mesenterial contraction can draw the interseptal portion of the disk only downward, so that in transverse sections the latter appears as if actually inclosed within the polypal cavity, along the same radius as the mesentery.

As already mentioned, von Heider (1886) has described an invagination of the discal wall in *Astroides calycularis*, but in this case the wall passes into the mesenterial chambers, without in any way involving the mesenteries. It is evidently independent of the action of these organs, and von Heider endeavors to explain the occurrence as dependent upon the interaction of the tentacles and expulsion of the water during retraction of the polyp.

Dr. O. Carlgren (1899), in his paper, "Giebt es Septaltrichter bei Anthozoen," discusses Goette's view that the mesenterial funnels (Septaltrichter) found in the young of various Actinian species are to be regarded as distinct organs. In the larvæ of *Bunodes gemmacea*, Carlgren obtained appearances exactly similar to those figured by Goette, and shows conclusively that they are merely contraction phenomena. Carlgren's figures compare most closely with figure 117, Pl. XVI, and leave no doubt that the appearances are all due to the same cause, namely, unequal contraction of different regions of the polyps during preservation. The occurrence of fixed septa in corals renders it much easier to understand how the inequality is possible in this group than in the case of the wholly soft-bodied anemones or their larvæ.

It may be conceived that the peculiar canal-like modifications, described by Fowler (1887), as occurring in certain mesenteries of *Madrepora durvillei*, have been produced by invaginations during strong retraction of the polyp. There are however, some features in this case different from conditions yet met with in corals, but on the other hand the modification seems altogether at variance with our present knowledge of their morphology.

MOUTH AND STOMODÆUM.

The actual form of the mouth of corals depends much upon the condition of expansion or retraction of the polyp. In the retracted or partly retracted state the aperture, as a rule, is narrow and slit-like while the outline assumed on expansion may be nearly circular. Under certain conditions the mouth is closed all the way, with the exception of a small opening at each extremity. In practically all cases a longer and a shorter axis are determinable, thus giving a bilateral character to polyps which otherwise would be outwardly radial in symmetry. In genera like *Manicina* and *Maandrina*, with a meandering disk, bearing numerous small oral apertures, the longer axis of the latter is usually along the length of the disk, and the shorter axis is transverse. In branching colonies the longer oral axis is approximately in the axial-abaxial plane, while in the many polyps of compact flattened colonies it may be either radial or irregular in direction with regard to the middle of the colony.

The usual condition of living polyps is one in which the mouth is partly open, the white, smooth, depending walls of the stomodæum easily distinguishable through it. Rounded lips sometimes serve as a gradual transition from the disk to the stomodæum, but in deeply pigmented species the boundary between the disk and stomodæum is usually very sharply defined. When polyps are retracted, the mouth is generally in the same plane as the flattened disk, but on expansion it becomes more or less elevated along with the central part of the peristome (fig. 46).

The stomodæum is usually oval in transverse section, but may be circular. Its vertical extent, as a rule, is comparatively short, more so than is usually the case in Actinian polyps. In some species, the lower stomodæal edge can be easily discerned when the mouth is widely open, the organ suggesting a mere inturned flap of the disk. Sometimes the walls of the stomodæum are smooth, but in perhaps the majority of species they are thrown into deep vertical ridges and furrows, extending the whole length of the organ, and a little less marked in the fully expanded than in the retracted state. Generally the ridges are more noticeable on the living polyps than after preservation, and those of opposite sides alternate.

When the polypal tissues are partly transparent, the stomodæal ridges are seen to correspond in number and position with the attachment of the mesenteries to the inner or cœlomic surface of the stomodæum (Pl. XIX, fig. 131). To a limited extent, therefore, they serve to indicate the number of complete mesenteries. The ridges are found to be very variable in number in forms such as *Maandrina*, *Manicina*, and *Isophyllia*, which happen to be species in which they are best developed. In *Maandrina*, for example, only three or four ridges will be present on each side of the stomodæum where the oral aperture is small, while in others there may be seven or eight.

On transverse section the stomodæal ridges are seen to be formed by thickenings of the mesoglœa, and less so of the ectoderm, but the endoderm takes no part (Pl. XXII, fig. 147). In species in which the ridges are best developed the ectoderm of the elevations exhibits a slight histological distinction from that of the furrows; large nematocysts and gland cells occur among the supporting cells of the former, while they are practically absent from the intervening areas, which on their part are more strongly ciliated. At the inner termination of the stomodæum the ridges appear as if continued down the free edge of the complete mesenteries as the mesenterial filaments, and the histology of the two agrees very closely.

With the exception of the ridges and furrows, occurring only in certain species, the stomodæal walls are structurally uniform all round; in other words, true gonidial grooves or siphonoglyphs are absent from Madreporarian polyps. As met with in the Actiniaria, at the opposite ends of the stomodæum, the gonidial grooves are readily distinguished in the living condition by the greater thickness and firmness of the walls, and by their smooth free surface; histoiogically the ciliation is stronger than elsewhere, and usually nematocysts and glandular cells are more sparingly distributed. The grooves in anemones are invariably associated with a pair of directive mesenteries.

A gonidial groove at each end of the stomodæum is, with certain exceptions, present in all Hexactiniæ; and a single groove occurs in the Zoantheæ and Cerianthea. In the Zoantheæ the organ is ventral or posterior, while, according to Carlgren (1893, p. 243), it is dorsal or anterior in the Cerianthea. A ventral groove, first termed by Professor Hickson (1883) the Siphonoglyphe, is likewise found in nearly all Alcyonaria. It is, therefore, a little remarkable to find that such a typically Anthozoan organ has never been established for the Madreporaria, and it is absent from each of the twenty-six species here studied[a]. Its non-development is probably indicative of the more primitive character of coral polyps generally compared with most Actiniaria.

The suggestion may be offered that the grooves, already described as occurring all the way round the stomodæum in some species of Madreporaria, are to be regarded as the morphological and physiological equivalents of the two axial grooves in the Hexactinian polyps. Instead of a groove occurring only between each pair of directives, one is found between all the complete mesenteries. The same histological differences are found in each case, though not so pronounced in corals. No experiments have been made to determine whether the grooves in the Madreporaria have any special function in directing the inhalent and exhalent currents, and with such small oral apertures experiments of this character would be difficult to conduct.

In living polyps of *Cladocora arbuscula*, *Solenastræa hyades*, and others, the lateral portions of the lips and stomodæal walls have at times been observed to come into close contact, leaving a small aperture at each extremity of the mouth, through which currents of water enter or leave the gastric cavity. A similar approximation has also been recorded by different observers as occurring among the Actiniæ, but is there associated with the presence of gonidial grooves. In the Zoanthidæ, provided with only one gonidial groove, only one terminal aperture remains when the lips are approximated.

The inner stomodæal extremity may become reflected upwardly and outwardly, so that in transverse sections the stomodæal walls are cut through twice; or, if they are much folded in addition, they may appear several times in succession in the same section. The appearance of the reflection in longitudinal section is shown on Pl. VII, fig. 56, and in transverse section on Pl. VI, fig. 51. The stomodæum terminates internally at practically the same level all the way round, or the two axial extremities, with the directives attached, may extend a little below the lateral walls, but nothing comparable with the "Languettes" of Actinians has been observed.

Upon complete retraction of the polyp, the distal parts of the polypal tissues—upper column wall and disk—mostly come to rest upon the skeletal projections—septa, pali, columella; in consequence of which the stomodæum becomes flattened and more or less irregularly folded. As a result it is often with difficulty that transverse sections of the stomodæum, exhibiting the relations of the mesenteries, can be obtained, especially as the organ is comparatively short.

On retraction the stomodæal walls as a whole are sometimes thrown into a few deep vertical folds, which assume a symmetrical figure. This is especially the case in *Porites* (figs. 28, 30); the folds may be four or six in number, and approach so as to touch one another in the middle, practically obliterating the lumen. The stomodæal foldings of a bud of *Cladocora* likewise assumed a regular arrangement (Pl. VIII, fig. 60); Fowler (1888) also describes and figures a similar appearance in a transverse section of the stomodæum of *Seriatopora subulata*. No doubt it is a consequence of the strong contraction of the circular endodermal muscle.

The histological details of the stomodæal wall are practically alike in all Madreporarian polyps, and agree closely with those of the Actiniaria. The ectoderm is always a broad, strongly ciliated layer, comprised largely of supporting cells, the nuclei of which are closely arranged, and give rise in sections to a characteristic, brightly-staining zone. The ciliation is uniform throughout, and is nearly always persistent in preserved material. As a rule nematocysts of two or three kinds occur, while both clear and granular gland cells are numerous. The latter are particularly abundant in *Cladocora* (fig. 52*b*). In some cases, e. g., *Phyllangia*, distinct ectodermal nervous and muscular elements can be made out near the mesogloeal surface, but are

[a] Saville Kent refers to a siphonoglyp in a Barrier Reef *Fungia*, and Bourne adds one to his diagrammatic figure of a coral, on p. 62 of his article Anthozoa (1900).

never so pronounced as in the larger Actinian polyps. The histological differentiation where ridges and grooves are strongly developed has been alluded to above.

The ectoderm of the stomodæum terminates mesenterially in direct continuity with the mesenterial filaments of the complete mesenteries, and for some distance the histological details of the two are alike. The layer may be also partly reflected on the endodermal surface, and continued a short distance along the edge and both faces of the mesenteries (Pl. VI, fig. 51). This reflection of the stomodæal ectoderm plays an important part in discussions of the origin of the mesenterial filaments, and is again referred to on page 477.

The stomodæal mesoglœa is usually thin, and uniform in character all round. As a rule the endoderm presents no features which distinguish it from the same layer covering the whole of the upper part of the internal cavity.

COLORATION.

All descriptions of coral reefs allude to the great variety, richness, and beauty of color of the living coral. On any coral patch around Jamaica, the predominating colors are different shades of brown - light, dark, yellow, or green. This is largely due to the great abundance of colonies of *Madrepora*, *Millepora*, and *Meandrina*, all of which exhibit one or other of these brown tints. Adding variety to these are the rich yellows, greens, and blues of the different species of *Porites*. Of the less massive corals—*Solenastræa*, *Cladocora*, *Oculina*, and *Faria*—yellowish-brown is likewise the prevailing color. Even where the general coloration of the colonies is nearly black or steel gray, as in some species of *Orbicella* and *Isophyllia*, a closer examination, especially when the polyps are fully expanded, indicates that yellowish-brown is the fundamental color.

The prevalence of the yellow-brown color is easily understood when an examination is made of the polypal tissues. For in all instances in which it occurs, the endoderm is found to be more or less crowded with the so-called "yellow-cells" or zooxanthellæ, which are unicellular symbiotic algæ, the chromophores of which are yellow or yellowish-green. That these are the main cause of the external coloration may be readily proved from colonies of *Madrepora*. In this genus the polyps toward the apex of growing branches are nearly colorless, the white skeleton showing through the perfectly transparent tissues, and on a microscopic examination of the endodermal layer zooxanthellæ are found to be absent, while they are present in abundance in the endoderm of the older, strongly pigmented regions. When a contracted living tentacle is viewed under the microscope, the margin is quite colorless as far as the thickness of ectoderm, while on focussing within, the endoderm is found to be almost black and opaque. The interior of fully expanded tentacles is lighter, and the individual yellow cells can be seen.

In the few instances in which zooxanthellæ are nearly or wholly absent from a species, as in *Astrangia solitaria* and *Phyllangia americana*, the polypal tissues appear peculiar delicate, and are wholly colorless and transparent, except for the occurrence of delicate superficial colors, such as rose and green. The transparency of the tissue appears to be very general in the members of this group of corals. In the "Introductory Notice" of the anatomy of *Astrangia dana*, Fewkes (1889) also describes the color of the expanded polyps as "white, almost transparent, resembling an Edwardsia or small white Actinia: when contracted the color shows a green or bluish tinge." An examination which I have made of the tissues of this species reveals an absence of zooxanthellæ.

Again, the polyps on the under, unexposed surface of colonies living in shady places are nearly always devoid of color, although the individuals on the exposed area of the same colony are deeply pigmented. A remarkable instance of this occurs on the piles supporting the broad wharves at Port Royal. Numerous clumps of the corals *Oculina* and *Cladocora* grow attached to the piles: the outer exposed colonies are of the usual brown color, while those living on the inner pillars, which are cut off from the strong sunlight, are perfectly white, the corallum alone showing through the transparent tissues. It is manifest that a chlorophyll-bearing alga could not flourish under conditions where it is more or less deprived of light; but except for this absence of coloration the coral polyps appear normal. Colonies of *Agaricia*, which usually

are densely colored, are found to be quite pale when living in the shady places often selected by these forms. The presence of zooxanthellæ does not seem to be at all essential to the life of coral polyps, seeing that colorless individuals in the shade flourish apparently as well as those in fully exposed places.

The degree of aggregation of the yellow cells likewise determines the intensity of the coloration. The tissues of fully expanded polyps are generally lighter in color and more transparent, and under these conditions zooxanthellæ are proportionately less numerous in a given area than during the retracted condition. When the polyps retract strongly, the algæ become closely aggregated within the thicker endoderm, and the tissues are darker and less transparent.

During the early stages of maceration of corals such as *Madrepora*, within a white porcelain basin, the zooxanthellæ will separate freely from the tissues, and accumulate on the bottom of the dish, giving to it a distinctly yellow appearance.

When coral polyps are preserved in alcohol a brownish yellow or golden yellow pigment is first extracted, but after a few hours, if transferred to colorless alcohol, the liquid is colored in the same manner as by the green coloring matter of plants.

The column wall and disk of the species of *Isophyllia*, *Mæandrina*, and less so of *Manicina*, *Colpophyllia*, and *Orbicella*, are often characterized by the presence of small, superficial, opaque, granular spots and patches. These are recognizable by means of a lens on the living polyps, and persist for some time after preservation. When the polyps are retracted the exposed tissues are practically opaque, and seem dense in comparison with the nearly transparent walls of such forms as *Madrepora*, *Oculina*, or *Cladocora*. The opacity is, however, limited to the regions of the column wall and disk which are fully exposed during retraction; the infolding margin of the wall, the tentacles, and the peripheral region of the disk, which are non-exposed regions, seem thinner and are more transparent. Any other marked superficial colors which may be present in these genera are likewise practically restricted to the exposed areas.

Examination of the outer tissues of these genera, by means of sections and macerations, reveals the presence of much finely granular, colored, non-transparent matter. The granular matter is mostly concentrated in the deeper regions of the ectodermal layer, but at certain points extends throughout the thickness, strongly distinguishing the areas from the remainder of the layer. Occasionally, as represented in the section of the column wall of *Isophyllia* (Pl. XVII, fig. 122), the accumulation occurs at fairly regular intervals. On the other hand, some regions, such as the upper margin of the column wall, the tentacles, and the periphery of the disk, are without the granular cells, these being the more transparent areas in the living polyp.

The small dense spots, referred to above as seen on the living tissues, evidently represent the points at which the granular matter is most concentrated, so as to extend throughout the thickness of the ectoderm, while the general opacity of the tissues is due to its more diffuse distribution within the deeper parts of the layer.

On maceration the contents of the cells appear as a finely granular substance, usually yellowish in color, and unacted upon, or only very slightly, by stains and acids. The cells thus differ from the more usual granular gland cells of the Zoantharia, which are always best developed toward the free surface of the layers, and take up stains, such as hæmatoxylin and carmine, with great avidity.

It may be conceived that the opacity has for its function the regulation of the amount of light passing to the endodermal tissues in corals living in more shallow waters. Certainly the forms in which the granular cells are best developed are among the least active of the coral polyps, and the coloration is most dense over the exposed areas. The endoderm shows no peculiarities which can be connected with the ectodermal opacity; zooxanthellæ occur as numerously as in other species.

Manicina areolata affords some interesting variations in the presence or absence of its dense superficial coloration, which seem to indicate some connection with the depth at which the corals occur. In colonies inhabiting very shallow waters, such as those of Kingston Harbor and Bluefields Bay, the superficial pigmentation—yellow, brown, or dense opaque white—is strongly pronounced, and in small or large irregular patches; but in young polyps and large colonies from

the deeper water on the reefs this pigmentation is wholly wanting, and the tissues are of the more prevalent yellowish brown color, produced by the endodermal zooxanthellæ.

The superficial or ectodermal coloration of corals varies greatly within the same species, especially in different areas, and is of small importance for purposes of specific determination.

The polyps of *Dichocœnia stokesi* exhibit some exceptional conditions of coloration as regards the internal tissues. Within the ectoderm cells of the column wall are found highly refractive granules distributed throughout the layer with approximate uniformity. There is no evidence of the granules being aggregated within limited groups, nor of concentration toward the deeper regions of the layer. They are colorless in preserved material, but are green in the living polyp, and are no doubt the chief cause of the green color of the polyps, and the general opacity presented by the external tissues. On decalcification of preserved material the lower two-thirds of the embedded polypal tissues is also of a dark green color, contrasting strongly with the upper colorless walls. Microscopic examination reveals that, as usual, the lower skeletotrophic endoderm is greatly thickened, and densely crowded with granules of various sizes. Most of the particles, however, are a bright green, exactly recalling the chlorophyll granules in plants; in decalcified mounted sections the green color is still intense after two years. The granules in the gland cells of the lower region of the mesenterial filaments are also a strong green, and even the large nematocysts in the filaments have a green tinge.

Another form of pigment cell is found in the tissues of *Porites*. Some colonies of *Porites clavaria* are an intense bright yellow in their living condition, and a lemon color is often met with in living colonies of *P. astreoides*, while the polyps of *P. divaricata* as a rule exhibit only the pale brown due to the internal zooxanthellæ. Macerations and sections of polyps of the two first-mentioned species reveal that both the ectoderm and the endoderm are loaded with bright yellow, pigment-bearing cells, very variable in form and dimensions. So abundant are they in *P. clavaria* that in places it is almost impossible to make out any of the other histological elements; but in *P. astreoides* they are more sparsely distributed, and their relationships can be better determined. In general the chromophore cells are shorter than the supporting cells and gland cells of the ectoderm, and occur at all heights within the layer.

When the ectoderm is macerated the pigment cells separate somewhat readily from the other histological elements, and are very protean in shape, scarcely any two being of the same form. A few are represented on Pl. IV, fig. 37. The contents are very finely granular, and are scarcely affected by stains, but with borax carmine a very distinct nucleus becomes evident.

The chromophore cells occur most abundantly in the outer tissues, and in both ectoderm and endoderm, but are also met with sparingly throughout the polyp, including the epithelium of the mesenteries and communicating canals. Zooxanthellæ are found within the endodermal cells in their usual numbers. The polyps of the genus *Porites* vary in color more than any other form examined.

Another factor which probably influences the living appearance of many corals is the color given to the skeleton by the presence of perforating filamentous algæ, belonging to both the green and red groups. The coralla of all the species examined are found to be infested with boring algæ. After decalcification the filaments appear fresh and green near the surface, and contain protoplasm and chlorophyll granules, but are colorless and apparently dead in the more internal regions. So dense is the foreign growth that in some instances the superficial portion of the corallum is rendered bright green or pink by its presence, either wholly or in part. The skeletal color is best seen on freshly macerated specimens, as after a few months' exposure the coralla become more or less completely bleached. The upper superficial areas of the fresh corallites of *Orbicella* and extracalicular regions of *Colpophyllia* presented green patches of various sizes, while the color was usually more uniform in *Agaricia*, but almost any species of coral may exhibit large or small affected areas. Decalcification also proves that the perforating algæ may be present where a superficial examination of the corallum gives no indication.

By way of contrast with the more prevalent green color, the coralla of *Isophyllia dipsacea* after maceration of the soft tissues were a delicate pink, evidently from the presence of some red alga. This also gradually disappeared in the course of two or three months. *Siderastræa siderea*

and *Porites astreoides* likewise often exhibit a bright pink color immediately below the surface of the corallum. In the latter it is still obvious on dried specimens twelve months after collection."

Where the soft tissues of the polyps themselves are not densely colored, a green or reddish skeleton below must partly determine the general effect by reflection through the polypal wall. Lacaze-Duthiers (1897, p. 5) found the coralla of all the Mediterranean corals examined by him to be perfectly white when deprived of their soft tissues, hence concludes that the coloration is wholly polypal.

The surface of many polyps often presents a brilliant emerald-green color, arranged in streaks or patches. It is found mostly on the disk as a peristomial ring, but occasionally on the oral aspect of the tentacles. Such has been observed in *Siderastrea radians*, *Orbicella annularis*, *Agaricia agaricites*, and *Colpophyllia*, as an addition to the more usual colors. The phenomenon is wholly superficial, not intracellular in origin, for histological examination fails to reveal any structure which can be assigned as its cause. The bright green and reddish colors of the otherwise colorless and transparent *Phyllangia americana* and *Astrangia solitaria* are also of this character, and pigment granules are here absent from the ectoderm, as well as zooxanthellæ from the endoderm.

The causes of coloration in living corals may be thus summarized:

(1) *Ectodermal.*—Pigment granules in ectodermal cells: aggregated in more or less isolated patches (*Isophyllia*, *Meandrina*, etc.); generally distributed (*Porites*, *Dichocœnia*). Superficial.

(2) *Endodermal.*—Yellow cells or zooxanthellæ (nearly all corals); green granules (*Dichocœnia*); pigment cells (*Porites*).

(3) *Skeletal.*—Perforating green and red algæ.

MESENTERIES.

In all recent morphological studies, which have for their object the determination of the natural relationships of the Anthozoa, a greater significance is attached to the order of appearance and adult arrangement of the mesenteries than to any other polypal characteristic. These serve not only to limit the primary divisions of the group—Alcyonaria, Antipatharia, and Actiniaria, but in the Actiniaria the chief subdivisions—Hexactiniæ, Zoantheæ, Cerianthеæ, are likewise determined by the mesenterial features; and even for minor classificatory purposes the variations in the organs are often of great service. It will be found that a similar importance must be accorded the mesenteries in the Madreporaria, and dependent upon their arrangement is that of the tentacles and septa, as well as other less important relationships.

Among the adult polyps here studied, the simplest condition of the mesenteries is that occurring in the genera *Madrepora* and *Porites*. This is represented in transverse sections in the figures on Plates I and III, and, for the stomodæal regions, diagrammatically in the accompanying fig. 3. The latter will also serve as an illustration of the terminology to be employed, and also for certain cognate morphological considerations, which may be first considered.

In practically all the polyps of the two genera mentioned only twelve mesenteries occur, arranged in six pairs with regard to a median axis, which includes the longer diameter of the stomodæum. The four pairs reaching the stomodæum are known as complete mesenteries, while the two remaining pairs, not united with the stomodæum, are incomplete. The Roman numerals I–VI correspond with the established order of appearance of the pairs of mesenteries in coral larvæ to be described later.

The twelve mesenteries, characteristic of the adult *Madrepora* and *Porites*, occur also in the larval stage of genera of which the adults possess more than six pairs, and are strongly marked off by their mode of origin from the mesenteries subsequently developed; they serve, in fact, as the starting point for various types of mesenterial arrangement of the highest importance in Zoantharian studies. In 1900, I found it desirable to introduce some

"The subject of coral boring Algæ has been more fully dealt with in a paper: "Boring Algæ as Agents in the Disintegration of Corals." Bull. Amer. Mus. Nat. Hist., Vol. XVI, 1902.

term which would distinguish these mesenteries, either singly or as a whole, from the later mesenteries. The twelve primary mesenteries constituting the first cycle were designated "Protocnemes," and those appearing later "Metacnemes."[a]

The appearance of a mesentery in transverse sections is rarely the same on both surfaces. The cut surfaces of the longitudinal or retractor muscle fibers form a bead-like margin to the mesoglœa, which is highly refractive and stains deeply (Pl. XVIII, fig. 129). Usually the longitudinal musculature on one face is stronger than the oblique musculature on the other, and as a rule the mesoglœa becomes folded or plaited to afford an increased area for the support of the former. The oblique muscle fibers are on the opposite face, and in transverse sections are usually cut obliquely, and the mesoglœa is rarely plaited for their support. For purposes of orientation, when studying the internal anatomy of the polyp, the recognition of the retractor muscle fibers on one face or the other of a mesentery is of great importance.

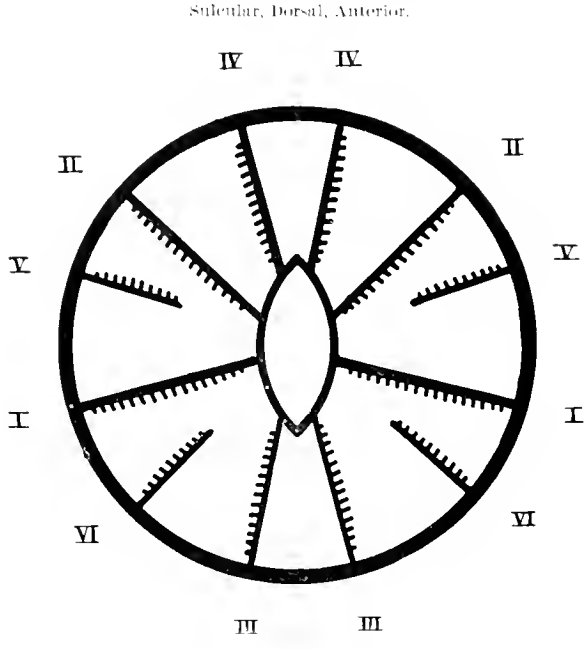

FIG. 3.

Plan of the mesenteries at the close of the protocnemic stage. The stage occurs in the growth of probably all larval and bud polyps, and is retained by most of the adult polyps of *Madrepora* and *Porites*. The Roman numerals (I-VI) indicate the order in which the mesenteries are found to appear in the larvæ of corals. The corresponding mesenteries on the two sides constitute bilateral pairs, and the adjacent mesenteries on each side in which the retractor muscles are turned toward each other (II, V; I, VI) constitute unilateral (anisocnemic) pairs, the members of the axial pair, III, III, are the sulcar or ventral directives, and the pair IV, IV the sulcular or dorsal directives. The vertical plane included within the two pairs of directives is the directive plane, and also the axial or median plane.

The mesoglœal plaitings for the support of the longitudinal mesenterial musculature are never greatly complicated in form in any of the coral species here studied. They may be quite simple, as on Pl. IV, fig. 38, or the folds may become secondarily plaited as in fig. 130. In the Actiniaria, on the other hand, the plaitings are often very finely subdivided in a dendriform manner, stretching along nearly the whole vertical face of the mesentery, or restricted about the middle to form a thick, broad, vertical band. The various figures given by Fowler, Bourne,

[a] The substantive "κνήμη"—a radius or spoke of a wheel—was first employed in Anthozoan literature by Haddon and Shackelton (1891, p. 626) in the course of their studies of the Zoanthese. In a foot-note with regard to it they write as follows: "We have tried hard to discover a short term for a mesentery, which would readily lend itself to combination with other words, but without success. The objection to the word 'cneme' is that it has reference to the appearance of a transverse section of an Actinian rather than to a mesentery as it actually exists. As the investigation of the Zoanthese, at least, must principally be made by means of transverse sections, this objection has not much weight."

and other students of the anatomy of corals indicate that in other genera and species the muscle plaitings likewise remain comparatively simple.

The degree of complexity attained by the mesogloeal foldings undoubtedly varies much with the state of expansion or retraction of the polyp, the plaitings being often scarcely recognizable in the former condition. Their character also changes in different regions of the polyp, and even in different parts of the same section (Pl. IV, fig. 38). The mesentery of *Orbicella*, represented on Pl. IX, fig. 68, shows remarkable differences in this respect, the peculiarities extending even to the face bearing the oblique musculature. In the diagrammatic and semidiagrammatic figures throughout the paper the retractor muscle is conventionally represented by simple processes from the face of the mesogloea.

From the figure on page 441 it is manifest that the paired character of the mesenteries may be regarded from two very different aspects. In the first place the corresponding mesenteries on the two sides of the median axis may be considered as pairs. These are known as "Bilateral pairs," and so far as concerns the first six pairs, this is the manner in which the mesenteries make their appearance in the larva. In bilateral mesenterial pairs the retractor muscle of each moiety is on the face turned toward the same aspect of the polyp. On the other hand, any two adjacent mesenteries in which the longitudinal muscles are on the faces turned toward each other – that is, toward opposite aspects of the polyp —may also be conceived as pairs, and, in contradistinction to the others, these may be known as "Unilateral pairs."

The two members of a unilateral pair may be either unequal (one complete and one incomplete, as in fig. 82) or equal (both either complete or incomplete, as in fig. 81). Considerations of much phylogenetic interest are connected with these conditions (p. 453). To distinguish a unilateral pair constituted of two equal mesenteries I propose the term "Isoenemic," and for a unilateral pair of two unequal mesenteries the term "Anisoenemic." In the majority of corals and anemones the metaenemes arise as isoenemic pairs, rarely, if ever, simultaneously by cycles, but bilaterally from one aspect of the polyp to the other (p. 459).

In most adult polyps the condition in which the longitudinal musculature of a pair is on the faces turned away from one another occurs only in the case of the two axial pairs, which by this means are distinguished as "Directives." Both from their origin and the disposition of the musculature, the directives are bilateral pairs, and are always isoenemic.

An attempt has lately been made to restrict the meaning of the nearly synonymous words "pair" and "couple," so as to imply whether the two moieties of a mesenterial pair are situated on the opposite side of the polyp, or whether they are close together on the same side of the polyp, their retractor muscles being vis-à-vis. Unfortunately, there is scarcely anything in the terms themselves to denote which should bear one special significance more than another, and already they are employed in a directly opposite manner by different Anthozoan writers. Thus Faurot (1895, p. 51), referring to the manner of appearance of the mesenteries beyond the primary twelve, writes: "Ces cloisons n'apparaissent pas par *couples*, comme dans la période précédente, c'est-à-dire, une d'un côté, une de l'autre côté de l'axe commissural de l'Actinie, mais par *paires* dans les interloges formées durant cette période. Il a été expliqué qu'une paire est constituée par deux cloisons voisines dont les faisceaux de feuillets unilatéraux se font vis-à-vis (les faisceaux unilatéraux des deux pairs commensurales faisant, seuls, exception) et que chaque pair forme une loge." Also van Beneden (1897, p. 21): "D'accord avec Faurot, j'estime qu'il y a lieu de réserver exclusivement le mot *paire* pour désigner deux closons voisines délimitant une loge; le mot *couple* pour dénommer l'ensemble de deux sarcoseptes symétriques, siègeant l'un à droite, l'autre à gauche du plan médian."

There can be not the slightest doubt as to the sense in which these authors employ the terms; a *couple* would be the arrangement corresponding with what is here termed a *bilateral pair*, and *pair* with what is here designated a *unilateral pair*. Yet Bourne, in the article "Anthozoa," in Lankester's "Treatise on Zoology" (1900, p. 39), in a foot-note adds: "It is convenient when speaking of the adult arrangement of the mesenteries to use the word 'couple,' when of their developmental sequence to use the word 'pair,'" thus signifying directly the opposite of Faurot and van Beneden.

Instead of adopting these familiar words, and giving to them a restricted meaning, and having to define whether the one or the other usage is to be attached to them, I prefer to speak of "unilateral pairs" and "bilateral pairs," according as the two moieties are situated on one side of the polyp, or are on opposite sides of the polyp. There can possibly be no ambiguity as to the character of the mesenterial pair indicated.

The portion of the gastro-cœlomic cavity included within a unilateral pair of mesenteries is, following the terminology proposed by Fowler (1885), known as an "Entocœle," while that between any two such pairs is an "Exocœle." Further, the polyp can be divided into sextants by six radii included within the primary entocœles, and the mesenteries or septa within each sextant are spoken of as constituting a "System."

A pair of directives occurs at each extremity of probably all sexually produced Madreporarian and Actiniarian polyps, but the regularity is often departed from in asexually developed polyps (p. 448). The vertical plane included within the two pairs of directives is known as the "Directive plane," and coincides with the axial or median plane of the polyp, as well as with the longer diameter of the stomodæum, and divides the polyp into symmetrical halves. Were the V and VI pairs of mesenteries to become complete, it is clear that a plane passing between the two pairs I and V would also divide the polyp symmetrically into equal halves, and include the shorter diameter of the stomodæum. Hence polyps at such a stage have two axes of perfect symmetry at right angles to each other. From the occurrence of directives, and of longer and shorter diameters of the stomodæum, perfect radial symmetry is not found in any of the present species, and where noticed elsewhere is probably a result of asexual methods of reproduction—not a fundamental characteristic.

Among animals like coral polyps and anemones, exhibiting a certain degree of radial symmetry, the terms dorsal and ventral and anterior and posterior, though adopted, have not the same significance as in the higher animals, where one aspect of the body is altogether different from the other. Moreover, the relationships, even as understood, are not readily established in adult polyps. To determine them it is necessary to select some morphological condition to which the disposition of the organs can be referred. The presence of directives enables a median plane to be established, to which the organs on each side of the polyp are symmetrically related, right and left, and such a mesenterial stage as that represented on page 441 also enables what may be termed upper and lower borders to be established. The aspect of the polyp toward which the faces bearing the longitudinal musculature of the two complete bilateral pairs of mesenteries I, II are turned has been designated by Haddon (1889, p. 300) the "Sulcar," and the opposite the "Sulcular." The terminology is based upon the fact that amongst Anthozoa where only one gonidial groove (sulcus) is present (Alcyonaria, Zoantheæ), the organ is on the aspect of the polyp toward which the faces of the two pairs of mesenteries, referred to as bearing the vertical musculature, are directed. As gonidial grooves, however, seem never to occur within the Madreporaria, this character is of no assistance for purposes of orientation, and the sulcar and sulcular relationships, as a rule, can only be determined from the order of development of the first cycle of mesenteries. Where, in Zoantharian polyps, all the six pairs of protocnemes are already complete, and either no gonidial grooves are present or both are equally developed, there is in ordinary cases no means of determining the sulcar and sulcular relationships. By most writers on the Anthozoa the sulcar border is regarded as ventral and the sulcular as dorsal.

Is it possible to determine an antero-posterior relationship in the polyps from the known facts of their development, such as shall be at all comparable with that in the higher animals? E. van Beneden (1891), from his study of the development of the Cerianthid *Arachnactis*, and E. B. Wilson (1884), from his investigations on the mesenterial filaments of the Alcyonaria, follow the suggestions of Sedgwick and Caldwell, and compare the gastro-cœlomic chambers of the Anthozoa with the cœlomic diverticula of the higher animals. On this theory the side of the Cerianthid polyp on which the sulcus and directive mesenteries are situated is regarded as anterior, while the side at which new mesenteries or segments are added is considered to be posterior. From the arrangement of the mesenterial musculature, Carlgren (1893) has shown that the sulcus of *Cerianthus* is situated at the opposite extremity of the polyp from its position

in the Alcyonaria and Zoanthidæ. If the sulcar aspect in all Anthozoa except *Cerianthus* be conceived as ventral, then in the latter it will be dorsal as well as anterior, and the ventral or sulcar aspect in other Anthozoa is posterior. It is shown later that the general succession of growth of the mesenteries in Madreporaria is also from the dorsal to the ventral aspect of the polyp, that is, they arise in an antero-posterior order. The septa have also been found to follow a like succession.

The relationships may be thus compared:

Hexactiniæ, Zoantheæ, Madreporaria	Sulcar =ventral=posterior.
	Sulcular=dorsal =anterior.
Cerantheæ	Sulcar =dorsal =anterior.
	Sulcular=ventral=posterior.

Where coral polyps present a definite relationship to the axis of a branch, as in most species of *Madrepora*, *Oculina*, and *Cladocora*, axial and abaxial positions are further determinable; and in the rounded colonies of *Orbicella*, *Solenastræa*, etc., inner and outer relationships, which correspond with axial and abaxial, are also distinguishable. Some importance underlies these determinations, for it will be found that the axial-abaxial and sulcar-sulcular relations are not always the same in corals.

The relationships of the strongly bilateral, radial polyps of *Madrepora* to the axis of the colony may be first determined. The transverse section on Pl. I, fig. 4, represents the polyp as situated in relation to the axis of the branch, but the lower side in the figure is inner or next the axis, and the upper is outer or turned away from the axis. Owing to the nariform growth of the corallite the skeletal tissue is more thickly developed on the upper than on the lower aspect. From the proportional development of the mesenteries, and the disposition of the longitudinal musculature, it is clear that the axial or inner aspect is the sulcar, and the abaxial or outer aspect the sulcular; or, in the terminology usually adopted, the former is ventral and the latter dorsal. The large anterior tentacle of *Madrepora* thus communicates with the sulcular, and the posterior tentacle with the sulcar entocœle.

Wherever in other corals it has been possible to determine the sulcar-sulcular relationships, as well as the axial-abaxial, to the colony as a whole, it is found that the relationships prevailing in *Madrepora* are reversed. Thus on Pl. VIII, fig. 61, representing a bud of *Cladocora* with the protocnemes in the *Edwardsia*-stage, the sulcar aspect of the polyp is abaxial or outward, and the sulcular is axial or inwards, in relation to the colony; similarly in fig. 62, representing another bud of the same species. In fig. 87, Pl. XII, taken from a young bud of *Solenastræa*, the sulcar side of the polyp is again outward (abaxial) and the sulcular is inward (axial).

Dr. G. H. Fowler (1887), in his studies of *Madrepora darvillei* and *M. aspera*, was the first to determine the axial-abaxial relationships of the mesenteries in the genus, and the year following (1888, p. 12) he showed that it was directly the opposite of that occurring in *Seriatopora subulata*, the polyps of which also permit of axial-abaxial determinations. The difference between *Madrepora* and other corals can best be appreciated by comparing the diagrams on page 445.

Dr. Carlgren (1896) has shown that in colonial Zoanthidæ the macro-directive mesenteries and the single gonidial groove are on the outermost side of the colony, or farthest from the mother polyp, while the micro-directive mesenteries and asulcular extremity of the stomodæum are toward the inner side of the colony, or nearest the parent polyp; the anterior (dorsal, asulcar) part is directed toward the axis of the colony, while the posterior (ventral or sulcar) is turned away from it (fig. *c*). The relationship of the individual polyp to the Zoanthid colony is therefore in strict conformity with that in Madreporaria, the genus *Madrepora* excepted.

The researches of Moseley, Hickson, and others on the Alcyonaria have also demonstrated that in this group the relationship of the polyp to the axis is the same as that in most Madreporaria. The so-called ventral aspect (sulcar) of the Alcyonaria is abaxial, the dorsal aspect (asulcar) is axial (fig. *d*).

The stage of mesenterial development with only four pairs of complete mesenteries usually serves the larvæ of Actiniaria and Madreporaria as a resting stage for a long period. Among the Actiniaria the only forms known in which the adult was thought to remain at this simple

stage are the Edwardsiæ. The resemblance between the mesenteries characteristic of this group, and those appearing in the course of the development of the Actinian larvæ, was recognized by Haddon (1889), and the stage was termed by McMurrich (1889) the "*Edwardsia*-stage." The eight complete mesenteries, comprising two bilateral pairs (I, II) and two pairs of directives (III, IV), are often spoken of collectively as the Edwardsian mesenteries.

Until recently the adult *Edwardsia* was supposed to have no other than these eight complete mesenteries, and in this respect was considered to be one of the simplest of the Actiniaria. As

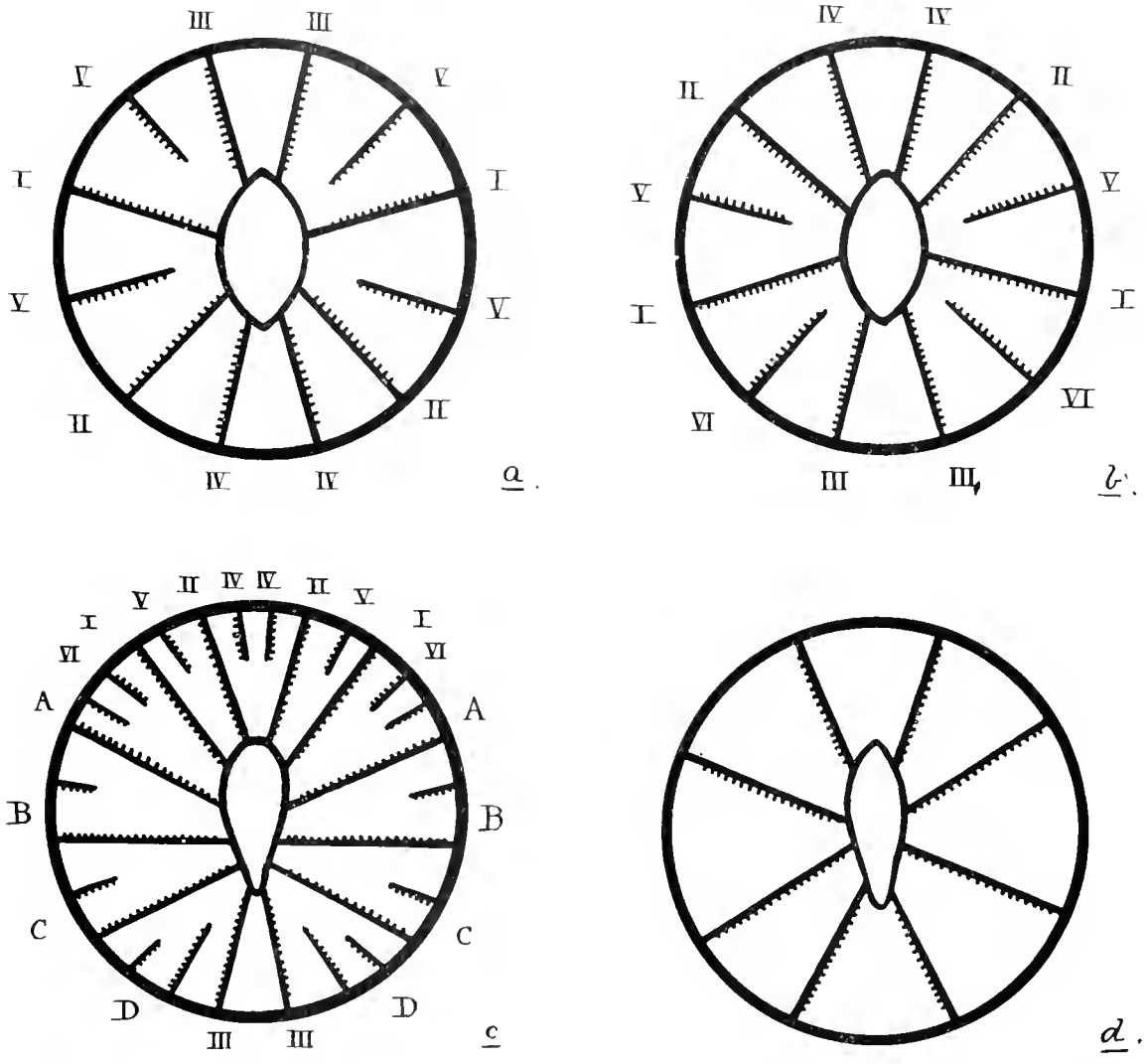

FIG. 4.

Diagrammatic figures showing the relationship of the polyps to the axis in various colonial Anthozoa. The upper side of the figure is supposed to be toward the axis (axial) and the lower is away from the axis (abaxial). *a*, *Madrepora*. The sulcar or ventral aspect of the polyp is axial and the sulcular or dorsal is abaxial. (The upper of the two bilateral pairs marked V, V should have been VI, VI.) *b*, Most other Madreporarian species. The sulcular aspect is axial and the sulcar abaxial. *c*, Zoanthids. The gonidial groove or siphonoglyph is abaxial, and all the metacnemes (A–D) are added at this aspect. *d*, Alcyonaria. The siphonoglyph is abaxial.

such it has been regarded by Boveri (1889) and McMurrich (1891) as the starting point for the diverse modifications occurring within the different Actinian groups. Lately Faurot (1895), by making transverse sections through the uppermost region of the capitulum of *Edwardsia beautempsi*, has shown that in this species sixteen and even twenty mesenteries are present, corresponding with the same number of tentacles. The eight additional mesenteries were found to be feebly developed, but arranged on the normal Hexactinian plan, and to extend vertically

only for about half a centimeter. Four of these, along with the eight complete mesenteries, constitute the six pairs of protocnemes, while the remaining four represent a pair of metacnemes within each dorsal or sulcular exocœle. Notwithstanding this discovery, it is deemed convenient to retain the term "*Edwardsia*-stage" for the condition in which only the first four protocnemic pairs are complete, whether other mesenteries are present or not.

The fewness of the mesenteries in *Porites* and *Madrepora* readily permits of their vertical order of appearance and disappearance being followed in serial transverse sections, but the same can be carried out also in more complex, multicyclic forms. In species with a large number of mesenteries the pairs are developed from above downward, as in *Porites* and *Madrepora*, so that the greatest number of cycles occurs in the more distal region of the polyps, and the members of the last-formed cycles often traverse but a slight vertical extent, compared with that of the oldest cycles. During the development of the mesenteries it is found (p. 454) that while the first two or three pairs arise at or near the uppermost extremity of the polyp, that is, around the oral aperture, the later pairs first appear some distance down the column wall, thence grow in both directions, upward and downward.

The mesenteries in adult corals as a rule terminate before the lower aboral extremity of the polyp is reached, hence this region is altogether unoccupied by any of the polypal tissues, except those lining the skeleton (Pl. IX, fig. 67). The organs rarely occur below the upper half or two-thirds of the vertical height of retracted polyps. Below, however, the septal invaginations extend farther centrally than above, and the skeletotrophic endoderm becomes enormously thickened, so that aborally the cœlomic cavity is greatly diminished in extent.

The restriction of the mesenteries in corals to the upper regions of the polyp should be compared with the extent of their course in Actinians. Here the principal mesenteries usually traverse the whole length of the column wall, and then extend across the basal disk toward the center, where they often meet. On the other hand, it must be remembered that the aboral extremity of the Madreporarian polyp does not altogether coincide with that of the Actiniarian polyp. In the former, part of the basal disk is greatly invaginated, and its peripheral border, where it passes into the column wall, is raised much above the actual extremity of the polyp.

Perithecally the mesenteries may extend the full length of the column wall or edge-zone (*Orbicella*, *Solenastræa*, etc.), or may terminate in advance of it (*Oculina*). In the latter case the attachment to the skeletotrophic tissue may be the first to cease, that on the column wall remaining, or the columnar attachment may be the first to disappear. In *Cladocora* the mesenteries rarely extend in a complete manner the whole length of the peripheral chambers, the skeletotrophic attachment ceasing first (Pl. VII, fig. 54).

The mesenteries in *Siderastræa* are characterized by a peculiar resorption of the peripheral extremities, so that in the more central part of the polyp the organs extend much farther vertically than in the peripheral region (Pl. XXIII, fig. 153).

The polyps available are generally so small as not to permit of the mesenteries being readily dissected out and viewed as a whole; but in serial transverse sections no interruptions suggestive of *mesenterial stomata* have been encountered. Hence there is good reason to suppose that mesenterial stomata are absent from Madreporarian polyps. The continual growth upward of the polyp, and the resorption of the mesenteries below, characteristic of most species, would in all probability preclude the formation of such characteristic Actinian features.

MESENTERIES IN GENERA REPRODUCING BY BUDDING.

The adults of all other polyps here described are provided with a greater number of pairs of mesenteries than the primary six of *Porites* and *Madrepora*. In the genera *Orbicella* (p. 423), *Solenastræa* (Pl. XI), *Oculina*, *Siderastræa* (Pl. XXIII), *Cladocora* (Pl. VI), *Astrangia* (Pl. VI), and *Phyllangia* (p. 464), which reproduce asexually by budding, the mesenteries are arranged in alternating hexameral cycles, and vary in size according to the cycle to which they belong. The designation "cycle" is employed to include all the mesenteries having the same radial extent, while the term "order" has reference to mesenteries which appeared at or about the same time; the first has reference to their insertion on or distance from the stomodæum, and

the second carries with it a developmental significance. Thus the members of the first order always appear before those of the second, the second before the third, and so on. Should the first cycle consist of twelve mesenterial pairs, as is sometimes the case, it represents the first and second orders. The members of the first order are known as primaries, the members of the second order as secondaries, the members of the third order as tertiaries, and so on.

In the genera above mentioned the first order or cycle of six pairs (protocnemes) includes the same mesenteries as those present in *Porites* and *Madrepora;* but usually all the pairs are complete and equal, and in each case they include two pairs of directives—sulcar and sulcular, which are bilateral, and situated at opposite extremities of the polyp; the other four protocnemic pairs, notwithstanding their origin as bilateral pairs, are now regarded as four unilateral pairs, two on each side, the retractor muscles of each pair being on the faces turned toward one another.

The second order of mesenteries in adult polyps also consists of six equal unilateral pairs, alternating with the pairs of the first order, and situated within their exocœlic chambers. In some cases the pairs of the second order may become complete throughout the whole or part of the extent of the stomodæum, as in the large polyps of *Orbicella cavernosa;* or some of the pairs of the cycle may be complete and the others remain incomplete, as in the polyp of *Phyllangia*, represented on p. 464.

When fully developed, the third order of mesenteries comprises twelve unilateral pairs, within the exocœles formed by the pairs of the first and second orders. The fourth order of mesenteries would contain twenty-four pairs, the fifth forty-eight, and so on, the mesenteries of the newer cycles always occurring in unilateral pairs within the exocœlic chambers of the previous pairs. The fourth-order mesenteries, however, never appear in any of the species here studied, except in *Phyllangia*, where occasionally a few members may occur (p. 465). Very often the mesenteries present in any mature polyp may be such as to leave the last cycle without the full number of pairs necessary to complete the hexameral sequence.

Although in the adult polyp the metacnemic pairs belonging to any cycle are approximately equal in size, it by no means follows that they were simultaneously developed, any more than in the case of the pairs of protocnemes; indeed, all the evidence from young polyps goes to show that the mesenteries arise successively. The order of appearance of the metacnemes is fully referred to on p. 455, *et. seq.*

The mature polyps of the species belonging to the genera enumerated contain, within narrow limits, a definite number of mesenterial pairs, which is characteristic of the species. As above mentioned, this number may or may not complete the hexameral multiple, so that the last cycle commenced may not be continued all the way round.

Increase in number does not continue indefinitely. *Orbicella acropora* has usually twelve pairs of mesenteries, six complete pairs of protocnemes, and six alternating incomplete metacnemes; *O. radiata* contains twenty-four pairs, the twelve pairs of the first and second orders complete and otherwise equally developed, and the twelve pairs of the third order incomplete (fig. 1, p. 423); the conditions are the same in *O. cavernosa*. The mesenteries of *Solenastræa* and *Oculina* are, like those of *O. acropora*, usually twenty-four in number, six pairs complete and six alternating pairs incomplete (Pl. XI, fig. 81).

Astrangia solitaria exhibits six pairs of complete mesenteries, and within each primary exocœle of adult polyps a pair of incomplete mesenteries always occurs, and in some instances two or three pairs (p. 463). In this latter case one of the pairs is slightly larger than the other and belongs to the second cycle of six pairs, while the smaller pair represents all that is yet developed of the third cycle; but in no instance has the full complement of twelve pairs constituting the third cycle occurred. In the closely allied species, *Phyllangia americana*, the number of mesenteries is always greater; but here also the incompletion of the final cycle of twelve pairs is very general. In one polyp sectionized transversely (p. 464), ten pairs of mesenteries reach the stomodæum. These consist of the six protocnemic pairs and four of the first-cycle metacnemes, the remaining two of this cycle not having yet reached the stomodæum. In the uppermost stomodæal region, however, one of the pairs becomes complete. An alternating cycle of twelve incomplete pairs occurs, but one or more pairs may be rudimentary or absent.

The adult polyps of *Cladocora arbuscula* always contain six pairs of complete mesenteries, constituting a first cycle, and six alternating pairs which remain incomplete and form a second cycle. Representatives of a third cycle are usually developed, but instead of consisting of twelve pairs, one in each exocoele between the previous twelve pairs, only four or six pairs are usually present, all on the same aspect of the older pairs (Pl. VI, fig. 49). Earlier stages in the development reveal that this is probably the sulcar aspect of each system (p. 458).

In *Siderastrea radians* six pairs of complete mesenteries are present, along with six alternating incomplete pairs, and a few pairs belonging to the third cycle may also occur; usually the third-cycle pairs are radially shorter than those of the second cycle, but at other times they nearly equal them in size. In the larger species, *S. siderea*, though more members of the third cycle are present, the whole twelve pairs necessary to complete the cycle are rarely present (Pl. XXIII, fig. 153).

The polyps of the seven genera described, all produced asexually by the process of gemmation, are thus characterized by the very regular disposition of the mesenteries in alternating hexamerous cycles. The first and second cycles are fully developed in all the adult polyps, while the third cycle may be only partly formed, but so far as it goes the members alternate regularly with the other pairs, according to the order of appearance established on p. 455 *et. seq.* In all the polyps two pairs of directives occur in the first cycle. So far as the mesenterial arrangement is concerned, there seems no difference between a polyp originating as a bud and one derived from a sexually produced larva; both follow the normal hexactinian plan.

Only the members of the first and second orders ever become inserted on the stomodæum in the species studied. The later orders never become complete, but retain a definite size characteristic of the species.

MESENTERIES IN GENERA REPRODUCING BY FISSION.

The asexual reproduction of the following genera takes place mainly, if not entirely, by stomodæal fission: *Agaricia*, *Isophyllia*, *Dichocœnia*, *Favia*, *Manicina*, *Meandrina*, and *Colpophyllia*. In the first four the polyps so produced may become more or less distinct from one another, each with its own system of tentacles and a column wall; in the remaining genera the separation is incomplete, and meandering discal, tentacular, and columnar systems are produced in place of distinct polyps, and only exceptionally are transverse walls developed, which separate one series of oral apertures from another. Sections have been made through polyps of each of the above genera, and reveal a mesenterial arrangement very different from that already described for genera where asexual reproduction by gemmation is the rule.

Transverse sections through two polyps of *Agaricia fragilis* are represented on Pls. XXIV and XXV, while the arrangements of the mesenteries of two different polyps of *Isophyllia* are diagrammatically shown on next page. Fundamental differences are at once apparent, compared with the mesenterial plans already described. No directive mesenteries occur in these nor in any of the other examples studied. Very rarely the number of complete pairs may be six, but is usually irregular, while the incomplete mesenteries vary greatly in number, size, and relation to the complete pairs. The hexameral plan is altogether departed from, and each stomodæum may have from ten to twenty-five complete mesenteries associated with it. A regular alternation of second and third cycle mesenteries is found in only one or two places, as at the upper right-hand region of fig. *b*; here and there a single unpaired mesentery may occur within an exocoele. Of the many polyps of each species examined no two display exactly the same number and relationship of the mesenteries.

A like absence of hexameral, or any other, regularity occurs in the polyps of *Dichocœnia* and *Favia* (Pls. XIII and XVI). Transverse sections reveal a variable number of pairs of perfect mesenteries from four upward, according to the size of the polyp, while the alternating incomplete pairs are rarely the same in number and size in any two exocoeles, and no directives occur.

In sections of mature colonies of *Manicina areolata* only two series of mesenteries can be generally distinguished, complete and incomplete, the latter rarely affording evidence of alternating

second and third cycles. The number of mesenteries associated with the stomodæal systems is very variable, and in any colony, however large, there are probably only two pairs of directives, situated at what may be regarded as the morphological extremities (p. 507).

Compared with the cyclical complexity in *Favia*, *Manicina*, etc., the mesenteries of *Meandrina* and *Colpophyllia* exhibit a remarkable simplicity of arrangement (Pl. XXI, fig. 141). Practically all the pairs are complete, and may be regarded as belonging to a single order; here and there alternating incomplete pairs are met with, but it is impossible to establish a regular succession of complete and incomplete pairs. Never more than one or two alternations occur together, while frequently six or seven consecutive complete pairs may be passed in review, all apparently of equal value, and all bearing filaments. The incomplete pairs in all probability represent new pairs in process of development, which will ultimately become complete like the rest. From eight to sixteen mesenteries may be inserted on each stomodæum, according to the size of the oral aperture; apparently there is no regularity in the number of mesenteries which upon fission may be apportioned to each daughter stomodæum. In the living colony a small oral aperture with only seven or eight complete stomodæal ridges, representing so many mesenteries, may appear as if just cut off from another large aperture with a dozen or more stomodæal ridges.

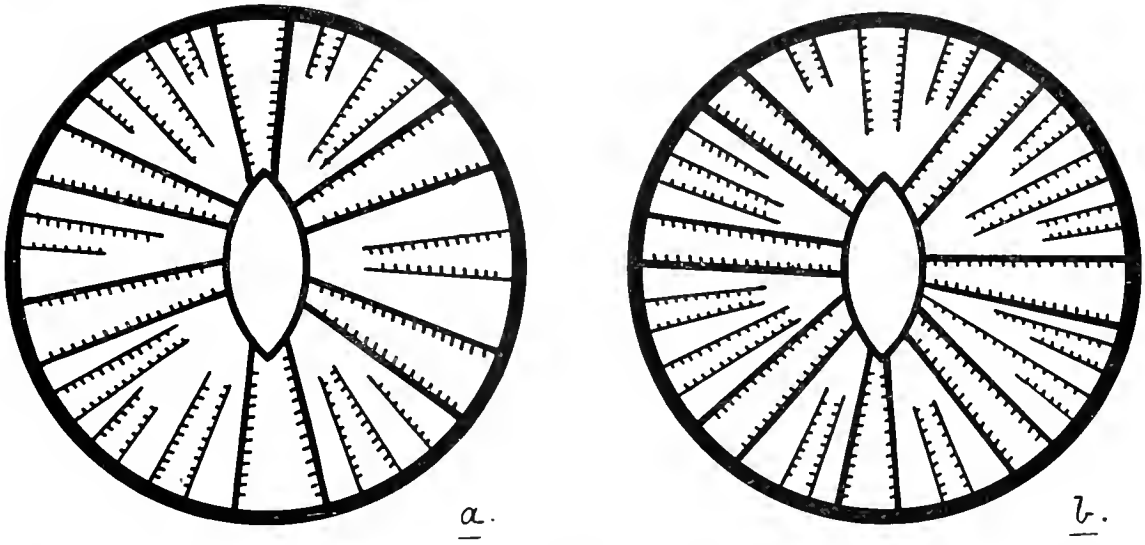

FIG. 5.

Isophyllia dipsacea.—Diagrammatic representation of the mesenteries in two polyps. The hexameral plan is departed from, the cyclic character is irregular, and no directives occur.

The mesenterial development of *Manicina* has been traced from polyps with only one oral aperture to small colonies with four stomodæal systems (p. 503, *et seq.*), and similar early stages have been followed in *Favia* (p. 508, *et seq.*). It is found that in simple polyps with only one oral aperture the hexameral cyclical character of the mesenteries is as regular as in any other sexually-produced polyp, or in adult polyps where columnar budding predominates; two pairs of directives also occur. It is only after fission has been established that irregularities begin to appear, and the hexameral plan is altogether lost. The subject of polypal fission is fully described, and from the manner in which the process takes place it can be easily understood how the above mesenterial irregularities come to be established.

It may therefore be taken as a general rule among corals reproducing by fission, that whether they give rise to distinct polyps, or form meandering systems, their mesenteries tend to lose the hexameral cyclical arrangement characteristic of the earliest stages, and probably never more than two primary pairs of directives are found in any colony, however large. Where the fission polyps are distinct, a cyclical disposition continues to be more or less recognizable, but where complex meandering systems are formed only a single order, including some developing pairs, can be established.

The results on the mesenterial arrangement in adult coral polyps may be thus summarized: The mesenteries in gemmiferous genera are regularly hexamerous, arranged in one, two, or more alternating cycles, and two pairs of directives are present; fissiparous genera are devoid of any hexameral mesenterial plan, are imperfectly multicyclic or acyclic, and without directives. Only the members of the earlier cycles become inserted on the stomodæum in the former, while apparently any of the pairs may become complete in the latter.

DEVELOPMENT OF PROTOCNEMES.

From the time of the publication of the classic researches of Lacaze-Duthiers (1872-73) onward, numerous embryological studies, upon both Actiniarian and Madreporarian polyps, have demonstrated that the twelve primary mesenteries always arise in bilateral pairs, but in an order which seems to vary somewhat in different species. The results of Lacaze-Duthiers were obtained by observation of the external appearances, apparently without confirmation by means of sections, while the latter has been the method more usually followed in later investigations.

In the Actinian larvæ studied by him, Lacaze-Duthiers found that the first mesenterial pair divided the cœlenteric cavity into two unequal compartments, known as dorsal and ventral. The second pair appeared in the larger or dorsal of the two chambers, cutting off a middle chamber; then within the primary smaller or ventral chamber the third pair was developed. According to Lacaze-Duthiers, the fourth pair appeared between the first and second pairs; but in most subsequent researches, among which are those of H. V. Wilson on the coral *Manicina areolata*, J. P. McMurrich on the Actinian *Rhodactis sancti-Thomæ*, and G. von Koch on *Caryophyllia cyathus*, the fourth pair has been found to appear in the dorsal chamber beyond the second pair, and its members become the dorsal or sulcular directives. The fifth and sixth pairs were found to arise nearly simultaneously within the middle and ventro-lateral chambers on each side.

According to the Hertwigs (1879), the fifth and sixth mesenterial pairs arise in *Adamsia diaphana* on opposite sides of the polyp between the first and second pairs. This has also been confirmed by Boveri (1889). In the light of subsequent results, such a condition must undoubtedly be looked upon as exceptional, having been met with in no other species, while the number of forms in agreement with the relationships given above is continually increasing in the Actiniaria, and is the only sequence yet met with in the Madreporaria. Appellöf (1900), in connection with his studies on the development of *Urticina crassicornis* and *Actinia equina*, discusses at some length the conclusions of Lacaze-Duthiers and later writers with regard to the mesenterial sequence of the primary eight mesenteries. In contradistinction to the successive development which Lacaze-Duthiers describes for *A. equina*, Appellöf found that the first eight mesenteries appeared for the most part simultaneously, and doubts the possibility of the order of appearance being determined by external observation alone without the assistance of sections. Sometimes only the strongly developed ventro-lateral pair of mesenteries would be visible from the outside, while transverse sections would demonstrate four pairs. His results on *Urticina* showed considerable variability in the mesenterial sequence. Reviewing the statements of different Actinological writers with regard to the appearance of the primary mesenteries, Appellöf (p. 55) comes to the conclusion: "Es ist wenigstens auf Basis des vorhandenen Materiales unmöglich eine bestimmte Regel auszufinden."

In comparison with the variable results obtained in the Actiniæ the protocnemic sequence in the Madreporaria appears to be very uniform.

Two most complete series of stages in the development of the protocnemes of Madreporarian polyps are already known, thanks to the labors of Prof. H. V. Wilson and Prof. G. von Koch. The former (1888) has traced their appearance in the West Indian coral, *Manicina areolata*, from the stage in the larva with but one pair of mesenteries to the young polyp with three cycles of mesenteries. His results as to the first cycle conform with those of Lacaze-Duthiers on various Actinian types, the second and fourth pairs being transposed.

G. von Koch (1897) also describes and figures the order of development in *Caryophyllia cyathus*, from the stage with two pairs of mesenteries to the completion of the first cycle. In this species the order of appearance, subsequent development, and union with the stomodæum

of the six pairs are in perfect agreement with Wilson's results. The arrangement on the completion of the six pairs represented in von Koch's fig. 1 exactly corresponds with that of the adult *Madrepora* and *Porites*, that is, four pairs are complete and two pairs incomplete.

My own results upon the larvæ of *Manicina areolata*, so far as they go, conform with those of Wilson. Stages with from three to six pairs of mesenteries have been obtained, the last (Pl. XIX, fig. 135), exactly reproducing the conditions of Koch's figure of *Caryophyllia*. The young polyps of *Manicina* remained for a week or two at the *Edwardsia*-stage, the first cycle of septa arising in the meantime. (See also p. 503.)

The various stages secured in the course of the development of *Favia fragum* serve to supplement the results of Wilson and von Koch on the two corals mentioned (Pls. XIII–XV, and p. 508). The earliest stage (fig. 112) is from non-extruded larvæ obtained from a decalcified colony. Three pairs of mesenteries are present, but only one of the pairs is yet complete, and this divides the cœlenteric cavity into two unequal chambers. In the larger or dorsal chamber a second pair of mesenteries occurs, the members of which, although incomplete, bear rudimentary mesenterial filaments. In the smaller ventral chamber the merest rudiments of another mesenterial pair are also seen. The middle pair, as is generally the case in Actiniarian and Madreporarian larvæ, extends almost the whole length of the cavity, the filaments being strongly developed all the way. The dorsal pair terminates some distance in advance of the aboral end, while the ventral pair has a very restricted course, disappearing vertically before the inner end of the stomodæum is reached, and centripetally never extending beyond the endodermal layer. Clearly, from the proportional extent of their development, both radially and vertically, the mesenteries have not appeared simultaneously, but represent the first, second, and third bilateral pairs in the sequence.

Sections of *Favia* larvæ which had been extruded for six hours reveal the next stage (fig. 113). Two pairs of mesenteries are here united with the stomodæum, and, by comparison with the previous figure, the additional complete pair is evidently the dorsal—the second in the mesenterial sequence. The ventral pair is scarcely better developed than in the former polyp, but in sections immediately below the stomodæum a new pair—the fourth—has appeared at the other extremity of the polyp, and dorsal to the second pair. A few sections below this are found the rudiments of another pair, situated between the first and second pairs (fig. 114). These represent the fifth pair in the mesenterial order and traverse only a few sections. As yet there are no indications of a corresponding pair between the first and third pairs.

Sections of another larva extruded at the same time present the conditions represented in fig. 115. The first three pairs now extend as far as the stomodæum, though the third pair ceases its connection in advance of the others. The fourth pair is more strongly developed, and rudiments of the fifth pair also occur at the stomodæal level, but are stronger below, where also an additional pair—the sixth, situated between first and third, is apparent (fig. 116). Incipient mesenterial filaments are present on the members of the third pair, while on the second pair they are fully developed, but do not extend so far as on the first pair.

Finally, in larvæ which had just settled, four mesenterial pairs have become complete, and the fifth and sixth pairs are well developed in the upper part of the column, but remain free from the stomodæum (fig. 105). All the complete pairs are provided with mesenterial filaments.

The series presented thus demonstrates that in regard to their proportional growth, both vertically and radially, the time of union with the stomodæum, and the appearance of the mesenterial filaments, a definite bilateral sequence is followed in the development of the protocnemes. The result is as follows:

(*a*) The first pair becomes the dorsal moiety of the ventro-lateral pair of mesenteries on each side of the adult polyp.

(*b*) The second pair becomes the dorsal moiety of the dorso-lateral pairs of the adult polyp.

(*c*) The third pair forms the ventral directives.

(*d*) The fourth pair constitutes the dorsal directives.

(*e*) The fifth pair becomes the ventral moiety of the dorso-lateral pair of mesenteries on each side of the polyp.

(*f*) The sixth pair becomes the ventral moiety of the ventro-lateral pairs of mesenteries on each side of the polyp.

Among the many larvæ sectionized very few irregularities have been met with. Sometimes one member of a pair will appear in advance of the other; in one larva only five complete mesenteries occurred, one member of the third pair having lagged behind. A young polyp settled for some time still presented only three complete pairs along with three incomplete pairs.

Although none of the other larvæ which have been studied present so complete a series as *E. fragum*, yet all the evidence from them goes to support the sequence just established. They each represent *Favia* at one or other of its developmental phases. Newly-hatched larvæ of *Isophyllia dipsacea* contain three pairs of mesenteries, the pairs differing greatly in the extent of their development (Pls. XVII, XVIII). The middle pair again extends nearly the whole length of the larva, and bears filaments which are strongly developed, especially at their lower extremity. Of the two smaller pairs, one is very rudimentary, while the other extends a short distance below the stomodæum. The stage very closely corresponds with that in the earliest available larva of *E. fragum* (fig. 112).

The non-extruded larvæ of *Porites clavaria* also reveal a phase with three pairs of mesenteries, while the mature polyps never get beyond the mesenterial stage with four pairs complete and two pairs incomplete—a stage represented by *E. fragum* at the time of fixation.

The larvæ of *Agaricia agaricites* on extrusion already possess the six pairs of primary mesenteries, all extending nearly the full length of the larva, but only the first four pairs are united with the stomodæum (Pl. XXV). Below the stomodæal region all the twelve mesenteries also bear well-developed mesenterial filaments. In this species, then, the stage reached by the larva on hatching is directly comparable with that in *Favia fragum*, *Manicina areolata*, and *Caryophyllia cyathus* at or about the time of fixation, as well as with the adult polyps of *Porites* and *Madrepora*.

The earliest larvæ of *Siderastræa radians* sectionized reveal eight mesenteries arranged in four bilateral pairs. The two lateral pairs, representing the first and second in the sequence, are united with the stomodæum, while the dorsal and ventral axial pairs, representing the directives, are free. Of the two directive pairs, the ventral pair (III) is slightly larger than the dorsal pair (IV), and in larva a little older the former becomes united with the stomodæm, while the latter is still free. In larvæ of about this age the fifth and sixth pairs make their appearance, and the dorsal directives uniting with the stomodæum the larva has reached the *Edwardsia*-stage of mesenterial development. At about this stage the larva undergoes fixation. Filaments do not appear on any of the mesenteries until their connection with the stomodæum has been fully established, but in most other species they are formed while the mesentery is still free.

The order of appearance and subsequent development of the primary twelve mesenteries, within the sexually produced larvæ and young polyps of the Madreporaria, thus appears to be very uniform, for no exception to the sequence first established by Wilson and von Koch has yet occurred. In the extent of its development, and also in its strong mesenterial filaments, the first pair to arise usually assumes predominance, and retains it until most of the other mesenteries become fully established. While the second and third pairs are scarcely apparent the first pair may have grown nearly the full length of the larva, each member tipped with the mesenterial filament all the way. The second, third, and fourth pairs follow one another in regular succession, uniting with the stomodæum in the order of their appearance.

In most Actinological studies the fifth and sixth pairs are stated to arise simultaneously, and H. V. Wilson observes the same for *Manicina*. Though such may often be the case, instances occur in which one pair appears in advance of the other, and where the same pair becomes united with the stomodæum before the other. Young polyps of a *Sagartia* from Beaufort, for which I am indebted to Dr. C. Grave, all show in section that the bilateral pair between the first and second Edwardsian pairs becomes inserted on the stomodæum in advance of the pair between the first and third Edwardsian pairs. Another such instance occurs in the bud polyp of *Cladocora arbuscula*, represented in transverse section on Pl. VIII, fig. 60. The polyp was preserved in a fully distended condition, the disk protruding in a cone-like manner above the zone of tentacles.

Transverse sections through the discal cone reveal five pairs of complete mesenteries, without any indications of others. The musculature is yet too feebly developed to allow of the paired character of the mesenteries being established by this means alone, but the larger interspaces and the examination of lower sections prove that the enumeration added is correct. In addition to the four Edwardsian mesenteries, the bilateral pair between the first and second pairs is complete, while the pair between the first and third, to be seen in the sections below, is still incomplete. In sections through the actual column wall, below the stomodæal region, the six pairs of protocnemes are equal in radial length, and six alternating pairs of metacnemes occur, the sulcar members a little in advance of the sulcular. In this instance the fifth pair is again complete before the sixth, and the first cycle of metacnemes is established before all the protocnemes are united with the stomodæum. In the bud of *Astrangia*, represented on p. 460, fig. 8*a*, the fifth mesentery on the right side is completed before the one on the left side.

In the section of the larva of *Fungia fragum*, represented in fig. 114, the pair between the first and second Edwardsian pairs is already represented on the larval wall, some distance below the stomodæum, by small mesogloal enlargements, but no trace of any such enlargement yet occurs between pairs I and II, where the sixth pair will be situated (*cf.* fig. 116).

From these examples there can be no doubt that though the fifth and sixth pairs may at times appear simultaneously, yet at other times an interval occurs. The pair of mesenteries between the first and second protocnemic pairs is to be regarded as the fifth in the sequence, and the pair between the first and third as the sixth or last in the development of the protocnemes. The enumeration of these two pairs in H. V. Wilson's figures of the mesenteries in an attached larva of *Manicina* (Pl. V, fig. 39) should therefore be reversed.

In all the instances yet referred to, the fifth and sixth mesenterial pairs remain free from the stomodæum, and in numerous cases it has been found that this condition is retained for a very lengthened period. In young polyps of *S. radians* completion was not attained within the course of four months, though the second cycle of mesenteries had appeared in the meantime. Likewise in the young polyp of *F. fragum*, with four pairs of metacnemes, they are still free (Pl. XIV, fig. 109). All coral larvæ appear to settle at or about the *Edwardsia*-stage, and the septa then begin to make their appearance.

No important resting stage, in the appearance of the protocnemes, seems to be indicated in any of the investigations yet conducted on the Madreporaria, though the comparatively strong development of the first pair must not be overlooked. With this possible exception, the development from the first to the sixth pair progresses with uninterrupted regularity, and the same may be said of the further growth of the first four pairs, as concerns their union with the stomodæum, but a prolonged interval separates the further development of the fifth and sixth pairs. Lacaze-Duthiers and others have endeavored to establish several resting stages in the appearance of the six pairs of primary mesenteries of the Actiniaria, but the Madreporaria afford little support for such.

The incompletion of the fifth and sixth protocnemic pairs is permanent in certain Zoantharia, and therefore this condition can not necessarily be looked upon as a developmental resting stage in the sense of Lacaze-Duthiers. Wherever these pairs appear in the Actinian family Edwardsidæ, they remain free from the stomodæum, and the same relationship holds for *Gonactinia*, etc. Throughout the Zoantheæ the fifth pair remains incomplete, and the sixth pair becomes complete only in macrotypic members of the group. In the West Indian *Aiptasia annulata* (Les.), I have found the pairs to remain free for the most part, although the second, third, and fourth orders of mesenteries were fully developed. They remain permanently free in *Madrepora* and *Porites*, even when an increase beyond the usual twelve takes place. Numerous other instances may be cited, all tending to show that some significance attaches to the incompletion of the fifth and sixth protocnemic pairs, as compared with the completion of the other four bilateral pairs. It is not merely a lagging behind in growth due to their later appearance.

My studies lead me to believe that the earliest corals and Actinians were characterized by anisocnemic pairs (excepting the directives), as compared with the isocnemic pairs of later corals and Actinians. To-day, the former condition is retained in the Zoanthids, and in *Porites* and

Madrepora, and as regards the protocnemes it persists for a long time in the growth of all others. The union with the stomodæum of the fifth and sixth protocnemic pairs is assumed after a time by forms characterized by cycles of isocnemic mesenteries; but they remain incomplete in Actinians and corals (Zoanthids, *Porites*, *Madrepora*) characterized by anisocnemic pairs throughout. Perhaps an earlier phylogenetic stage is represented by the Cerianthids and Alcyonarians, in which the incomplete moieties altogether fail to appear.

Much difference is apparent as regards the position at which the mesenteries first make their appearance. The first two or three pairs seem to arise in the angle between the stomodæal wall and the outer wall of the larva, and then to grow in both directions—that is, down the stomodæal wall and the larval body wall, the latter extension being the more rapid. This is very clearly shown in the figure of the living larva of *Isophyllia*, and in the sections through the oral region (Pl. XVII). While the members of the middle pair extend all the way down the stomodæal wall, and nearly as far as the aboral pole of the larva, the two smaller pairs pass scarcely at all down the stomodæum, and only for a short distance along the larval wall. The three first mesenterial pairs in *Fungia* probably arise in the same circumoral position, but the fourth pair is first apparent on the larval wall a little below the stomodæum (Pls. XIV, XV), and the fifth and sixth pairs arise still farther down.

Early bud polyps of *Madrepora* also illustrate the same relationship (Pl. III). Here the four primary mesenterial pairs are seen in the angle between the outer wall of the bud and the stomodæal wall. They extend the whole length of the stomodæum, and for some distance along the outer cœnosarcal wall. On the other hand, the rudiments of the fifth and sixth pairs are first seen on the outer wall, some distance removed from the oral aperture.

Probably in most Actiniaria and Madreporaria the fourth, fifth, and sixth protocnemic pairs arise independently of the stomodæum, and some way from the oral pole. When the appearance of the tentacles has established the topographical regions of disk and column wall, the metacnemic pairs are also found to arise somewhere on the latter, usually nearer the oral than the aboral extremity. Only later do they grow upward, and then inwardly along the discal wall, and in most cases ultimately reach the stomodæum and extend down it.

A marked distinction may thus be established in the place of origin of the different mesenterial pairs, the distance from the oral apertures varying with the relative age of the mesenteries; the earliest pairs arise circumorally, the later pairs are some distance removed. This further supports the contention that the Anthozoa are not primitively cyclical forms, but suggest an ancestry in which the organs appeared bilaterally, in an antero-posterior succession.

Several early stages, obtained in the development of bud polyps, suggest that in the asexual method of increase there is the closest agreement in the order of appearance of the mesenteries with that above described for the sexually produced polyps. The earliest stages have not been secured, and the evidence is therefore not so complete as in the larvæ. The youngest bud is one of *Cladocora arbuscula*, in which eight protocnemes are already present, all united with the stomodæum. Shortly below the stomodæum only four mesenteries remain, and bear mesenterial filaments; then two of these disappear, and the remaining couple are continued much farther, and bear filaments almost to their termination. The musculature at this stage is too weak to permit of the actual arrangement in pairs being determined by means of it, but from the greater length of one pair of mesenteries, and the stronger development of its filaments, it may reasonably be assumed that it represents the first pair of mesenteries, and that the order of disappearance of the others indicates their successive origin.

In other buds of *Cladocora* examined, all the protocnemes are already developed, the Edwardsian mesenteries complete, and the fifth and sixth pairs incomplete, just as in larvæ at or about the time of fixation (Pl. VIII, fig. 61). Buds of *Solenastræa* have also been secured, in which only four pairs of mesenteries are complete and bear mesenterial filaments, while the two incomplete pairs are without filaments, and disappear in advance of the other mesenteries (Pls. XI and XII). The bud polyp of *Astrangia*, whose mesenterial plan is represented on p. 460, indicates a somewhat later stage. In the very early bud of *Madrepora*, already referred to, all

the protocnemes are present, but their relative sizes are in conformity with those of the buds of *Cladocora* and *Solenastræa*, and may indicate a like successive origin.

Summarizing, we find: (1) That the twelve protocnemes arise as six bilateral pairs in a definite sequence, which is probably the same throughout the Madreporaria, and conforms with that characteristic of most Actiniaria. (2) The first two or three pairs arise at the angle between the stomodæum and the larval wall, while the later mesenteries first appear on the column wall, some distance from the oral aperture. (3) Two pairs of directives are always present, formed from the third and fourth pairs of the mesenterial sequence. (4) The first four pairs unite with the stomodæum in the order of their appearance (*Edwardsia*-stage), and a long interval elapses before the fifth and sixth pairs become complete; the fifth pair may develop somewhat in advance of the sixth pair. In some cases the fifth and sixth pairs are permanently incomplete. (5) The development of the protocnemes in asexually produced buds is in close agreement with that of sexually produced polyps.

FIRST CYCLE OF METACNEMES.

While much attention has been given to the order of appearance of the six pairs of protocnemes in the Madreporaria and Actiniaria, comparatively few observations have been recorded with regard to the order of development of the pairs of metacnemes. For the Madreporaria, the establishment of the latter becomes a matter of great importance, seeing that upon it is dependent the order of appearance of the septa, a question already much discussed by students of the hard part of corals, but with varying results.

The transition from the protocnemic to the metacnemic stage of Anthozoan development is one of the greatest morphological significance. Lacaze-Duthiers (1872) was the first to realize this in the Actiniæ, and in his résumé of the development of *Actinia equina* (p. 362) he writes:

"Le nombre, la grandeur, la position et la symmetrie des parties ne sont pas determines par les memes lois à toutes les epoques. Ainsi la loi qui préside à la multiplication des parties depuis l'origine jusqu' au nombre douze, n'est pas la même que celle qui régit la multiplication après que ce chiffre est atteint."

As regards sexually produced coral polyps, no previous accounts of the actual order of appearance followed by the metacnemes are available. The embryological observations of Lacaze-Duthiers, von Koch, and Wilson, so far as concerns the polyps themselves, practically cease with the protocnemic stage. Wilson describes the mesenterial condition in young polyps of *Manicina*, but gives no account of the sequence according to which the stages have been reached.

I have been fortunate in rearing young polyps of *Siderastræa radians* as far as the completion of the first cycle of metacnemes, and the various stages in the appearance of the latter have been obtained. Full details will be published later, but the diagrammatic figs. 6 (*a–c*) indicate the actual results. The polyps at fixation contained only the six pairs of protocnemes, as usual, four pairs complete and two pairs incomplete. The fact that the protocnemes retain this proportional development enables the dorsal and ventral, or sulcular and sulcar aspects, to be determined. The polyps remained thus for about a month, the first and second cycles of tentacles appearing in the meantime; then, in the largest specimens, a mesenterial pair was observed within the dorsal exocœle on each side, situated toward the aboral region of the column. A few days afterwards, a similar mesenterial pair appeared within each of the middle exocœles, the dorsal pairs at the same time extending higher up the column. Later, a mesenterial pair was formed within each of the ventral exocœles; so that six new isocnemic pairs were now present, diminishing in vertical and radial length from the dorsal to the ventral side of the polyp, according to their order of appearance. The fifth and sixth protocnemic pairs remained incomplete throughout.

The six unilateral pairs of mesenteries, of three different sizes, continued their growth *pari passu* with that of the polyps as a whole, and when the latter were about three months old became nearly equal in size, constituting a distinct second cycle. In time, the mesenteries, growing both upward and downward, extended the full length of the column and partly across the disk, but in

no instance did they stretch wholly across, and become united with the stomodæum. Subsequent examination, by means of sections, showed that in each pair the retractor muscles were disposed on the faces turned toward each other, thus resembling the unilateral pairs of the first cycle.

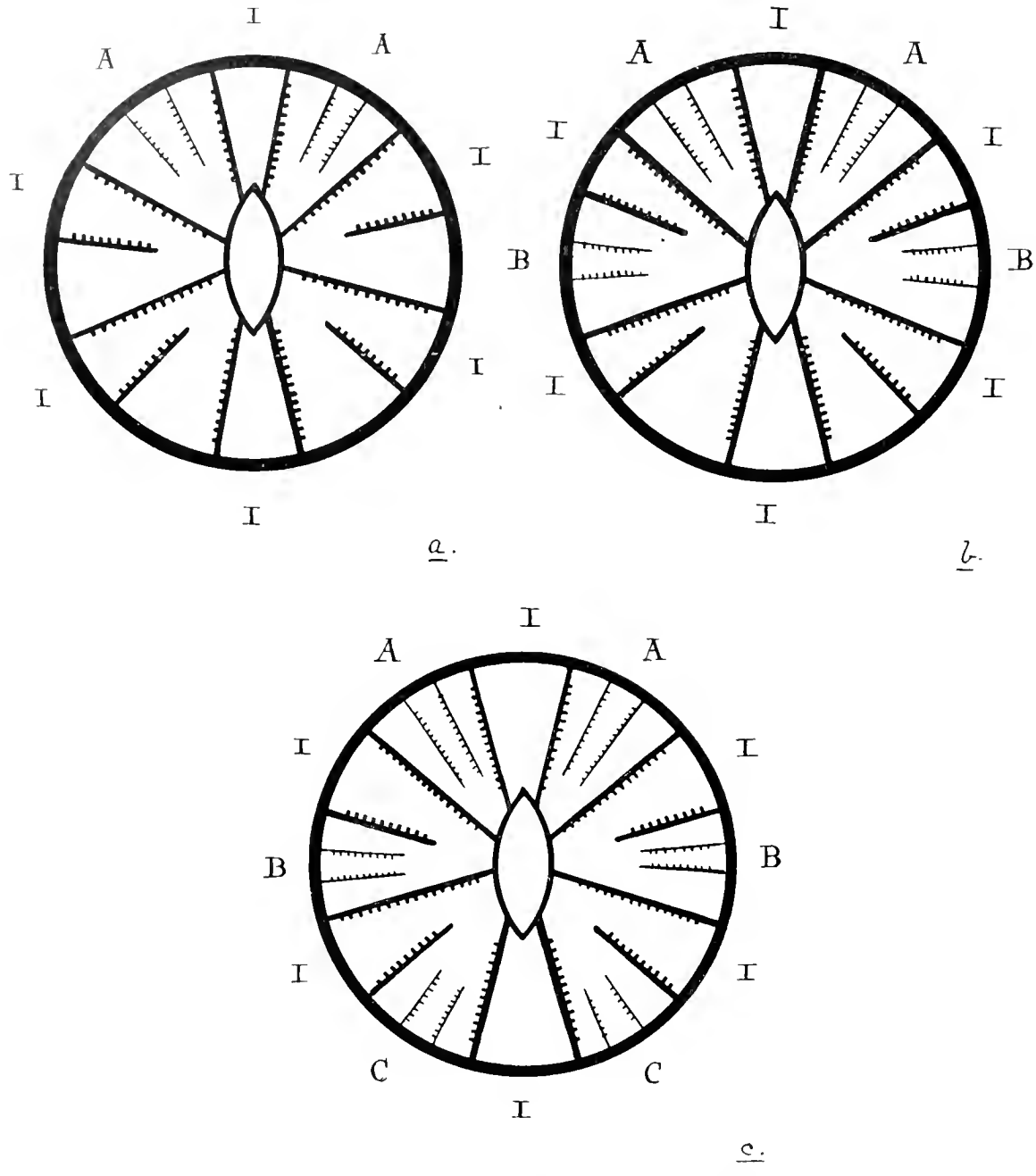

FIG. 6.

Sidrastræa radians.—Three diagrammatic figures illustrating the order of appearance of the first cycle of metacnemes in larval polyps. The Roman numerals I are opposite the protocneme pairs, and the letters A–C indicate the succession of the metacnemes.

While the actual mode of appearance of the mesenteries could be thus followed step by step in *Sidrastræa*, young polyps of *Favia fragum* were obtained with the mesenterial conditions shown on pp. 509, 510, and from these certain conclusions are warranted. Four pairs of second-cycle mesenteries are present in fig. 15*c*, in addition to the six pairs of protocnemes. Of the four metacnemic

pairs, the two larger are situated within the dorsal or sulcular exocœle on each side of the polyp, and the two smaller pairs are within the middle exocœle on each side (see also, Pl. XIV, fig. 109).

In addition to these two instances, a number of early mesenterial stages have been secured from young buds, and there is little doubt that the process of metacnemic development in these is exactly the same as that followed by polyps with direct larval predecessors.

Fig. 86, on Pl. XII, represents a transverse section through the stomodæal region of an expanded bud of *Solenastræa*. The protocnemes are in the *Edwardsia*-stage of development, and within each of the dorsal or sulcular exocœles a pair of metacnemes has appeared. Sections of the same bud, taken a little below the inner termination of the stomodæum, reveal, in addition, a rudimentary pair of metacnemes within the middle exocœle on the right side, though no trace of new mesenteries appears in the left middle exocœle; the sulcular pairs are also much further developed than in the upper region, and are much larger than the single middle pair (fig. 87).

The stomodæal region of another bud of *Solenastræa*, somewhat younger than the former, is represented on Pl. XI, fig. 82. Of the protocnemes, four pairs again are complete and two pairs incomplete. In this instance the first two pairs of metacnemes are very rudimentary, and appear within the middle lateral exocœles, not as before, within the sulcular exocœles. The new pairs are slightly better developed in sections somewhat lower, but no dorsal or ventral pairs were encountered.

In later buds of *Solenastræa* six pairs of metacnemes occur, a pair within each of the primary exocœles, and these exhibit a developmental succession from the sulcular (dorsal, axial) aspect to the sulcar (ventral, abaxial). In older buds all the pairs are equal in size, forming a regular hexameral second cycle, and this is the adult condition of most of the polyps in a colony (fig. 81).

The diagrammatic representation of the mesenteries of a young polyp of *Astrangia solitaria* on p. 460, also indicates a like dorso-ventral succession for the second order of mesenteries in this species.

Buds of *Cladocora arbuscula* reveal somewhat similar conditions in the appearance of the metacnemes (p. 458). Fig. 61, on Pl. VIII, represents a transverse section through a bud in which two pairs of mesenteries are present, in addition to the six pairs of protocnemes; of the latter only the Edwardsian mesenteries are complete and bear mesenterial filaments. The two pairs of metacnemes (A, A) are very rudimentary, and extend but a short distance down the column wall, and are devoid of mesenterial filaments. The proportional development of the protocnemes enables the dorsal and ventral aspects of the polyps to be determined, and serves to indicate that in *Cladocora* the first metacnemes appear within the ventral or sulcar exocœles, as compared with their dorsal or sulcular origin in *Solenastræa* (Pl. XII). Comparing fig. 87 with fig. 61, the sulcar aspect in both genera is seen to be the outer or abaxial with regard to the rest of the colony, while the sulcular is the inner or axial; therefore, in the two species the metacnemic succession proceeds from opposite aspects.

Pl. VIII, fig. 62, represents a transverse section through a somewhat older bud of *Cladocora*. The specimen is exceptional in that the dorso-lateral pair of protocnemes is missing from the left side, so that the polyp is pentamerous. Five alternating pairs of metacnemes also are present, and their interest in the present connection lies in the fact that they show a marked gradation in the extent of their development, in passing from the outer to the inner aspect. Mesenterial filaments occur on the pairs in the sulco-lateral exocœles, and the longitudinal muscular fibers are also determinable. This latter character is apparent on the metacnemes in the middle lateral exocœles, but no trace of mesenterial filaments occurs. The single pair in the sulculo-lateral exocœle is very rudimentary. The proportional development indicates the same relationship as fig. 61, namely, that the metacnemic sequence is from the abaxial to the axial border of the polyp. At a little later stage the polyps of *Cladocora* consist of six protocnemic pairs, all the members complete, and of six alternating metacnemic pairs, all incomplete and equally developed. Many polyps in a colony are found in this condition.

The manner of appearance of the first cycle of metacnemes in asexually produced coral polyps is thus in closest agreement with that in larval polyps. In both cases they arise as isocnemic pairs within the six primary exocœles, and in bilateral order from one aspect of

the polyp to the other, the aspect varying, however, in different species. In *Siderastræa*, *Solenastræa*, *Favia*, and *Astrangia* the succession is from the dorsal to the ventral side, in buds of *Cladocora* from the ventral to the dorsal. The exceptional succession in the latter may be in some way dependent upon the more rapid growth which takes place on the abaxial side of the buds, as compared with the axial. Before it can be regarded as actually characteristic

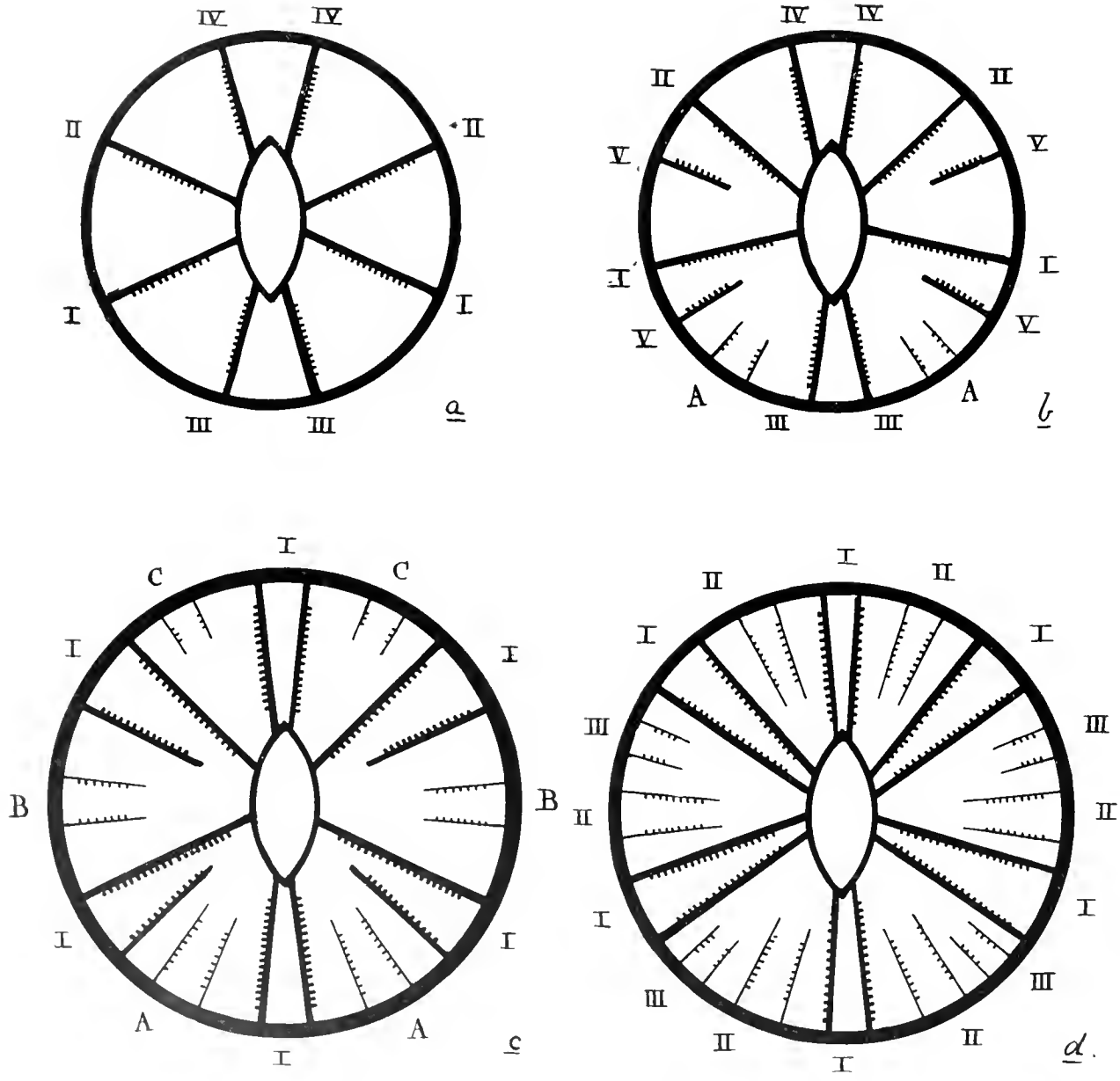

FIG. 7.

Cladocora arbuscula.—Four diagrammatic figures illustrating the order of appearance of the mesenteries in bud polyps (*cf.* Pls. VI–VIII). (In *b* the lower bilateral pair marked V, V, should have been lettered VI, VI.)

of the species, it will be necessary to follow the sequence in polyps reared directly from larvæ, as in the case of *Siderastræa*. Until such is carried out, it may be taken as a general rule that the development of the second order of mesenteries is from the dorsal to the ventral aspect of the polyp; that is, from the anterior to the posterior border.

A wide distinction in their manner of appearance thus separates the members of the second order of mesenteries from those of the first order. The primary mesenteries appear in *bilateral pairs*, in a succession which is first toward one aspect and then toward the other aspect of the polyp, and so on, and only later do they constitute unilateral pairs, in which the musculature is on the faces turned toward each other. With the exception of the directive pairs, the two members of each unilateral pair arise at different times, the dorso-lateral pairs being constituted of mesenteries II and V, and the ventro-lateral pairs of mesenteries I and VI, in the protocnemic sequence; and for a long period the lateral pairs are anisocnemic. The secondary mesenteries also arise in a bilateral manner, but are in *unilateral (isocnemic) pairs from the beginning*, and in any polyp they are formed in only one succession, from the dorsal to the ventral aspect, alternating with the primary pairs, and situated within the primary exocoeles. In mature polyps the secondary mesenteries are all equal, except perhaps in their vertical extent, and are arranged around the polypal wall with perfect hexameral radial symmetry, all traces of their bilateral succession being lost.

Where coral polyps attain considerable size, as in *Orbicella cavernosa* and *Phyllangia americana*, the members of the second order of mesenteries often become united with the stomodæum. In doing so they follow the same antero-posterior succession as that characteristic of their order of appearance in the young polyp (see fig. 9*h*, p. 464).

SECOND CYCLE OF METACNEMES.

The order of appearance of the second cycle of metacnemes, or third order of mesenteries, may now be considered. These, when complete, consist of twelve equal pairs, a pair within each of the exocoeles between the protocnemes and the first-cycle metacnemes. The succession has not been followed upon any coral polyp reared directly from the larva, but sufficient evidence is forthcoming from the asexually produced polyps of several species to indicate in a general way the manner in which it is carried out.

Mature polyps of *Cladocora arbuscula* and *Astrangia solitaria* usually contain a certain number of second-order metacnemes, but apparently never the full complement of twelve pairs. It is therefore possible to obtain from these certain intermediate stages in the establishment of the cycle. Pl. VI, fig. 49, represents a section through the stomodæal region of a polyp of *Cladocora* with sixteen pairs of mesenteries. Of these the six complete pairs are protocnemes, the six alternating pairs are first-cycle metacnemes, and the four pairs remaining are the only representatives of the second-cycle metacnemes. The latter are but feebly developed, and without mesenterial filaments. The fact of greatest importance, in connection with the four new pairs of mesenteries, is their restriction to only one exocoele within each of the six primary systems; they are not developed in both the exocoeles within the two ventral systems, as considerations of symmetry would suggest. It will be also observed that in each case they occur within the exocoele on the dorsal aspect of the second-order mesenteries (*cf.* p. 458).

The polyps of *Cladocora arbuscula* very rarely pass beyond the stage with sixteen mesenteries, which corresponds externally with thirty-two tentacles. For the further mesenterial sequence therefore other species will be employed.

All the members of an isolated group of eight separate polyps of *Astrangia solitaria* were decalcified and sectionized, and the stage reached in the mesenterial development of each is diagrammatically represented in figs. 8 (*a–g*). Camera lucida drawings of a transverse section from two different individuals are also given on Pls. V and VI, figs. 43, 47. The seven diagrammatic figures reveal that no two polyps in the group were alike in their mesenterial arrangement, so that the series may be taken as affording a fairly complete representation of the order of mesenterial development generally followed in this species.

Fig. 8*a* is taken from the smallest of the polyps. In this instance three members of the protocnemes are still incomplete, and only four pairs of metacnemes have yet appeared, situated within the dorsal and the middle primary exocoeles. The sequence of the first-cycle metacnemes is evidently similar to that of the polyps of *Sidrastræa* above described (p. 456). In the next

largest polyp (fig. 8*b*) the first two cycles of mesenteries are fully established, a pair of metacnemes having appeared within each of the six primary exocœles.

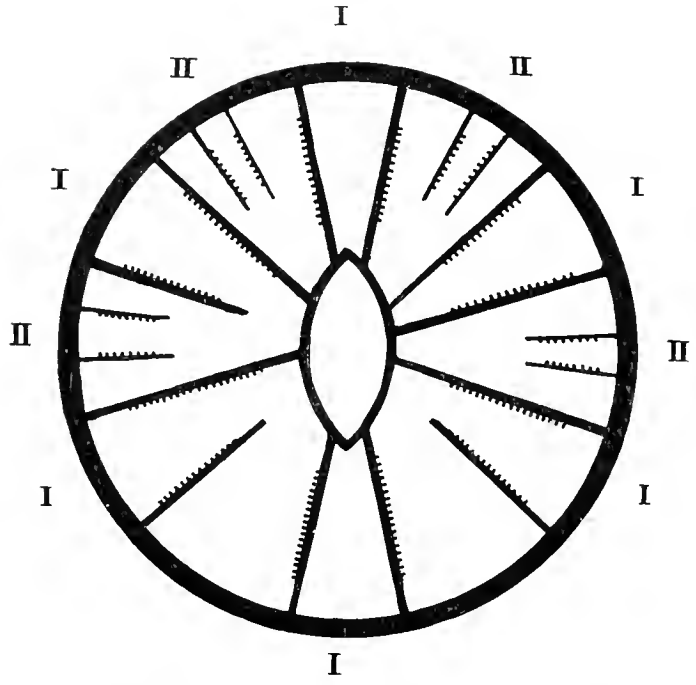

FIG. 8*a*.

Astrangia solitaria.—Fig. 8. Series of diagrammatic figures (*a–g*) illustrating the order of appearance of the mesenteries of the first and second cycles of metacnemes. *a*, Four isocnemic pairs of the first cycle of metacnemes are present (II), while three of the protocnemes are not yet united with the stomodæum.

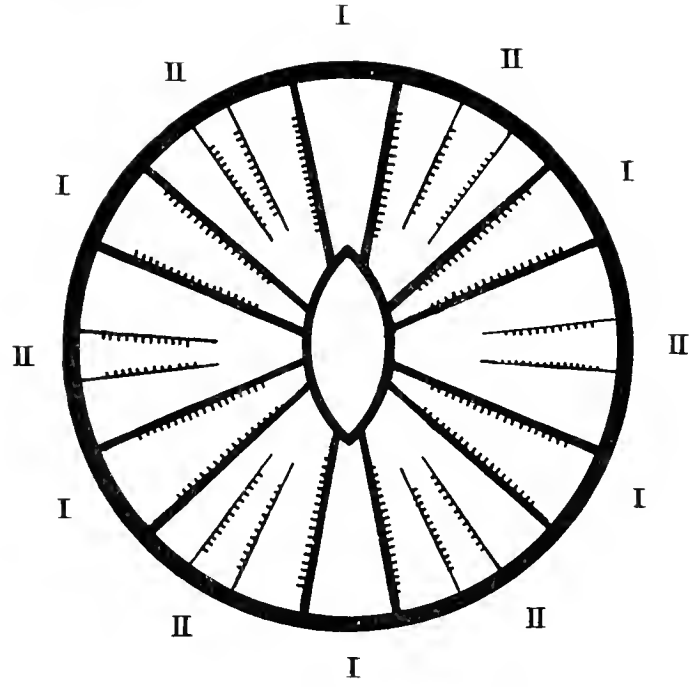

FIG. 8*b*.

Astrangia solitaria.—The protocnemes are all complete, and the six pairs of first-cycle metacnemes have all appeared.

Fig. 8*c* presents the first appearance of the third-cycle mesenteries or second-cycle metacnemes, which are to be especially studied. A new pair of mesenteries has appeared within the exocœle

on each side of the dorsal directives and the pair of dorsal second-cycle mesenteries, and a similar pair within the left middle system III.

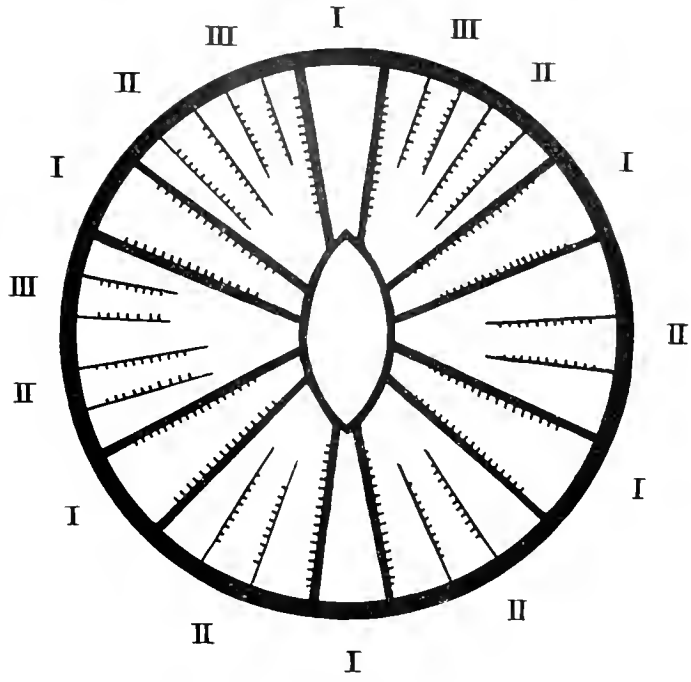

FIG. 8*c*.

Astrangia solitaria.—Three pairs of second-cycle metacnemes (III) have arisen toward the dorsal aspect of the polyp.

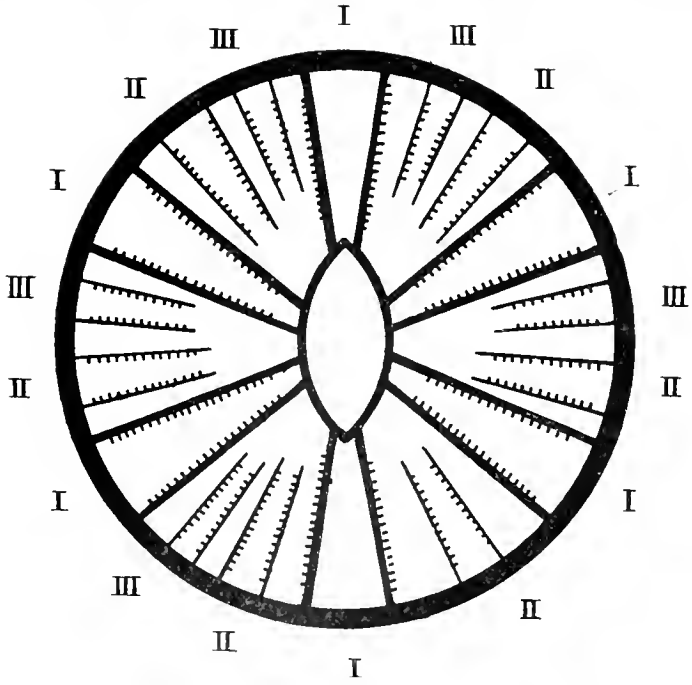

FIG. 8*d*.

Astrangia solitaria.—Two additional pairs of second-cycle metacnemes have appeared: as yet only a single pair of second-cycle metacnemes is contained within each primary exocœle.

In fig. 8*d* two additional pairs occur, one in the right middle system, and one in the left ventral system. Two other polyps sectionized from another colony exactly correspond with fig. 8*d*.

The polyp from which fig. 8*e* was taken contains a like number of mesenteries, but the right middle system includes only one pair of mesenteries, while the right ventral has two.

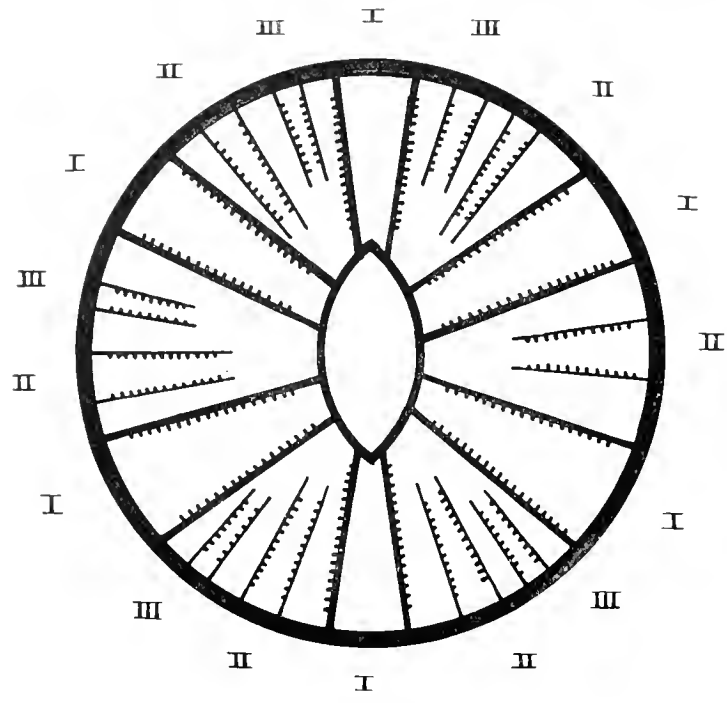

FIG. 8*e*.

Astrangia solitaria.—The development of the mesenteries within the ventral exocœlic chambers is exceptional in that it is in advance of that in the right middle exocœle (*cf.* fig. 47, Pl. VI).

In fig. 8*f*, from another polyp, a third-cycle pair occurs in each of the six primary systems.

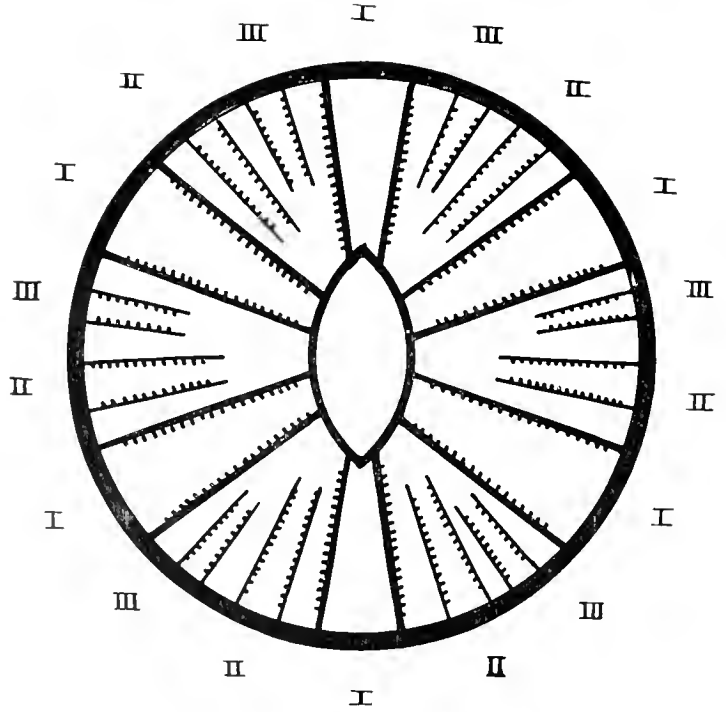

FIG. 8*f*.

Astrangia solitaria.—A pair of second-cycle metacnemes now occurs within each primary exocœle.

So far the series serves to demonstrate the important fact, first suggested by *Vaughan*, that in the establishment of the third order of mesenteries only a single pair first arises within each of the six primary systems, not two pairs—one in the exocœle on each side of the second-cycle pair—as might have been expected. Further, the pairs do not appear simultaneously, any more than do the members of the first and second cycles. They present evidence of a general, though not rigid, succession from one border of the polyp to the other. What this aspect is, whether dorsal or ventral, can not be determined in polyps at this late stage, seeing that the protocnemes are all complete. In isolated polyps apparently no means is available for such an important determination; the relative sizes and vertical extent of the second-cycle mesenteries are of no assistance. The latter are now practically of the same size, and any variation they may present is of very uncertain value. However, as in most species the succession of the second-cycle mesenteries is found to be from the dorsal to the ventral aspect, I have disposed the figures in such a way that they indicate a like succession for the first six members of the third cycle.

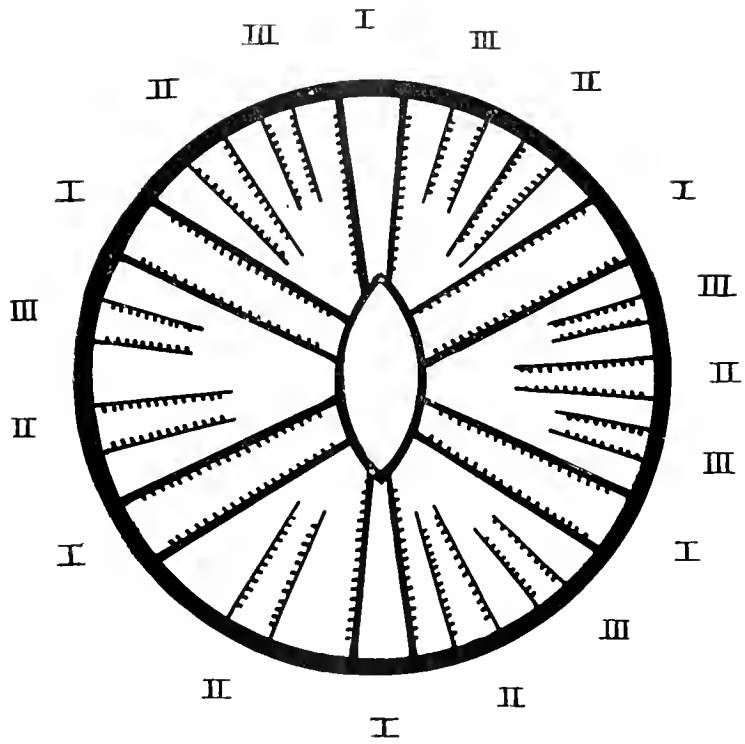

FIG. 8g.

Astrangia solitaria.—An additional pair of tertiary mesenteries has appeared within the right middle exocœle (*cf.* fig. 43, Pl. V).

In some instances (fig. 8*c*) the growth is more rapid on one side than on the other, and in fig. 8*e* the right middle pair has lagged behind. In *A. solitaria*, at any rate, a certain amount of individuality in growth is exhibited by each sextant, and mesenteries may appear in one irrespective of the condition in other divisions.

Clearly, in order to complete the third cycle of mesenteries according to the hexameral plan, a second pair of mesenteries must now arise in each of the six primary systems, and within the exocœle on the ventral aspect of each of the second-cycle mesenteries.

Such has already taken place in fig. 8*g* in connection with the right middle system, but a lagging behind occurs in the left ventral system, as only a single mesenterial pair is yet developed.

Polyps of *Astrangia solitaria* rarely exhibit more than seven or eight third-cycle mesenteries; no specimen with the full twelve pairs has been met with. The further stages necessary to complete the third order may, however, be obtained from the larger polyps of the closely allied *Phyllangia americana*.

Fig. 9*h* represents a transverse section through a polyp of *P. americana*, in which ten pairs of mesenteries are complete; six pairs represent the protocnemes, while the other four pairs belong to the second order. The remaining two pairs of secondaries are still incomplete. The full complement of twelve tertiary pairs is present, except for one pair in the dorsal exocœle of the two ventral primary systems. Here, as before, it will be understood that the dorsal and ventral aspects were not actually determinable.

Fig. 9*i*, from a still larger polyp of *Phyllangia*, reveals twelve pairs of complete mesenteries belonging to the first and second orders, and twelve alternating pairs of incomplete mesenteries representing the third order. At the dorsal extremity a few pairs of mesenteries of the fourth order have also appeared. Polyps of *Phyllangia* rarely contain more than this number of mesenteries, so that it has not been possible to follow the method of growth of the fourth order. All that can be asserted from fig. 9*i* is that the mesenteries of the fourth order begin to

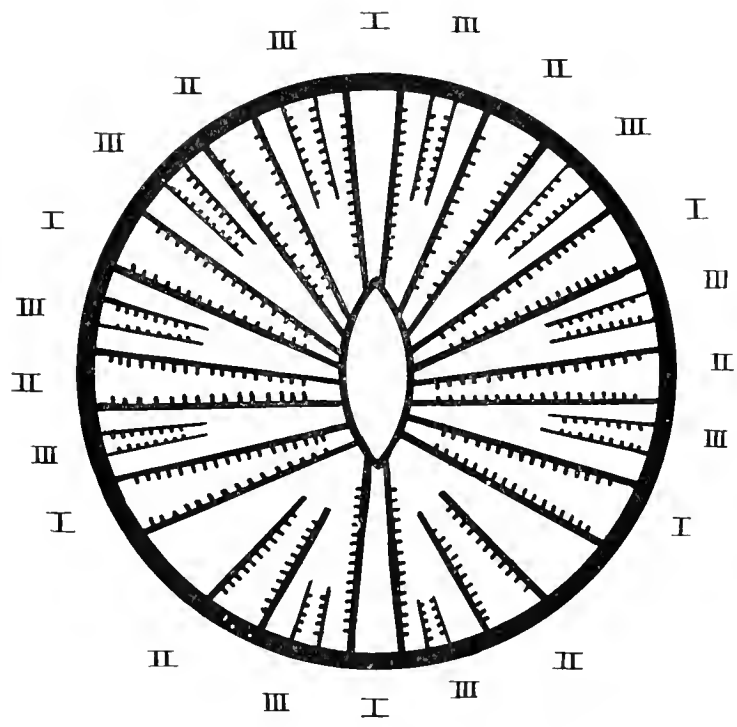

FIG. 9*h*.

Phyllangia americana.—Order of appearance of the metacnemes continued. Other pairs of second-cycle metacnemes (III) are present, and four pairs of the first-cycle metacnemes (II) are now united with the stomodæum. The succession of growth is from the dorsal to the ventral aspect.

make their appearance at one extremity of the polyp, which is probably the same as that at which the members of the second and third orders first arise.

The sections of the polyps of *Faria fragum* represented on page 510, and of *Manicina areolata* on page 504, reveal that in these species the order of appearance of the third-cycle mesenteries follows a succession closely comparable with that in *Cladocora*, *Astrangia*, and *Phyllangia*.

The order in which the twelve pairs of tertiary mesenteries are developed may be thus summarized:

The members of the third order of mesenteries arise in successive isocnemic pairs, after the establishment of the secondary mesenteries, within the exocœlic chambers between the pairs of the first and second orders of mesenteries. In a general way, two stages of growth are distinguishable: First, a single pair arises within each of the six primary systems, that is, within only one of the two exocœles, the succession being from one aspect of the polyp to the

other; second, another pair appears within each of the remaining exocœlic chambers, the different members of the series of six pairs following the same succession as the first series of six pairs. The regularity is by no means strictly adhered to; growth in one sextant of the polyp may be in advance of growth in another, independently of the general dorso-ventral succession. Part or all of the twelve pairs necessary to complete the order may be characteristic of any species. Ultimately all the tertiary pairs attain the same radial extent, which is less than that of the secondaries.

APPEARANCE OF MESENTERIES IN POLYPS REPRODUCING BY FISSION.

All the examples referred to above, as attaining a cyclical disposition of the mesenteries in the adult polyp, are species reproducing asexually by gemmation. A perfect regularity, as regards the radial length of the mesenteries of the different cycles, obtains in these, exactly as in sexually

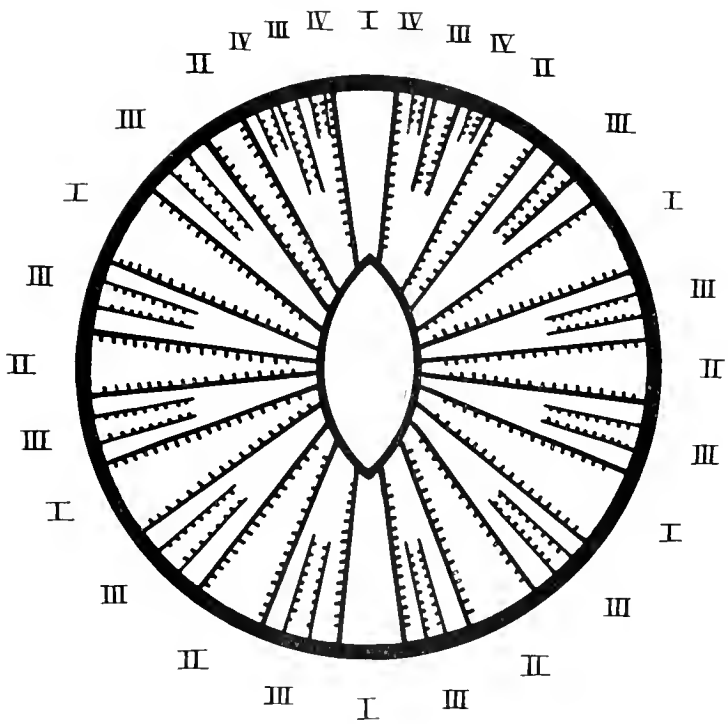

FIG. 9*i*

Phyllangia americana.—All the secondary mesenteries are now united with the stomodæum, and along with the members of the first order (protocnemes) constitute the first cycle of mesenteries. Four pairs of third-cycle metacnemes (fourth-order mesenteries, IV) have appeared on the dorsal side.

produced polyps. The organs do not continue their growth indefinitely until reaching the stomodæum; only the members of the first order of six pairs, or, in larger polyps, those of the second order also, become united with the stomodæum. The remaining orders extend for definite radial distances from the body wall, uniform for the members of any one cycle, and in the main characteristic of the species. The adult arrangement has been shown to be otherwise with species in which asexual reproduction by oral fission prevails; and this whether the new polyps become distinct, each with its own tentacular system, or whether they remain incompletely separated, and give rise to meandering tentacular and discal systems (p. 448).

In describing the mesenterial arrangement in the genera *Mæandrina* and *Colpophyllia* (p. 449), it was found that the mesenteries at most are divisible into only complete and incomplete pairs, but that the alternation is by no means constant. Sometimes several complete pairs are found without any intervening incomplete pairs, while, when the latter do occur, they are very

variable in the extent of their development. One pair may extend nearly as far as the stomodæum, while another may be merely incipient; further, the complete or incomplete pairs belonging to opposite sides bear no bilateral relation to one another.

In these genera, therefore, the mesenteries manifestly arise in single exocœlic pairs at almost any region of the colony, though more freely in the regions of forward growth. The new pairs, however, do not continue as a separate incomplete cycle, but become larger and larger, and ultimately come into union with the stomodæum, while other new pairs appear in the meantime.

Similar relationships of the mesenteries are also described for *Isophyllia*, *Favia*, *Agaricia*, and others. In transverse sections mesenteries of all sizes are found, representing different stages of growth, but without any regular alternation of small and large pairs; the Roman numerals only approximately indicate any ordinal relationships of the pairs. Here again, one can only assume that the different pairs arise for the most part independently of any cyclic plan, and that each pair continues to increase in size, and may ultimately become complete. If the polyp be in an actively growing condition, fission will again step in, the mesenteries which before were incomplete now become complete, and new pairs continue to arise in the daughter polyps in the same irregular fashion.

When the very regular cyclic arrangement of young polyps of *Manicina areolata* is compared with that after fission is well established (p. 503, *et seq.*), it is seen that the order of appearance of the mesenteries is becoming fundamentally altered. It is manifest that single pairs arise at any point, and grow independently of the others already present, so that in different primary exocœles they may be one, two, three, or even four incomplete pairs.

It may therefore be accepted as a general rule, that in genera reproducing by fission, the mesenteries are not developed according to any regular cyclical sequence, once fission has become established; but they arise as isolated exocœlic pairs, in regions of most forward growth, and each and all the pairs may ultimately become complete. This is more fully illustrated under fission in *Manicina* and *Favia* (p. 502, *et seq*).

INCREASE OF MESENTERIES IN PORITES.

As already mentioned, the tentacles and mesenteries in the genus *Porites* are always twelve in number, and larval in the extent of their development, the Edwardsian mesenteries alone being complete. Very exceptionally polyps are met with in which these organs may be increased to fourteen, sixteen, or even twenty-four, the polyps maintaining a circular form, like that of the ordinary polyp, only larger. Similar numerical increases are likewise occasionally found in the septa of individual corallites. A study of transverse sections of these larger polyps reveals that the increase in the number of mesenteries proceeds in a manner different from any yet described in the Madreporaria. The diagrammatic figures 10 and 11, and the camera drawings on Pl. V (figs. 41, 42), will serve to explain the various sequences followed.

In fig. 41, and 10*a*, is represented a transverse section through the stomodæal region of a polyp in which fourteen mesenteries are present, that is, two beyond the usual number. The twelve primary mesenteries are easily determinable from the arrangement of the retractor muscles, and retain their original condition, that is, four pairs (I–IV) are complete and two pairs (V, VI) are incomplete. Within the sulcar or ventral entocœle, however, another complete pair (A, A) has been added, and the sulcar directives are pushed farther apart. The retractor muscles on the newly added pair are on the faces of the mesenteries turned toward each other, so that each forms with the adjacent directive mesentery a unilateral pair, in which the retractor muscles are on the mesenterial faces turned from one another as in directives proper.

The next stage (fig. 10*b*) obtained is one in which eighteen mesenteries occur: fourteen are in the same condition as in the previous polyp, and the four additional members are situated within the entocœle of the seventh pair. The bilateral pair, B, B, is very rudimentary at this level, but becomes proportionally better developed a short distance below the stomodæal region; each member forms with the adjacent moiety of pair C, C a unilateral, anisocnemic pair, in which the retractor muscles are vis-a-vis. A similar stage is represented in the next figure (fig. 10*c*), except that an unpaired complete mesentery is added within the entocœle of the last bilateral

pair C, C. In the polyp from which fig. 10*d* was taken a pair of complete mesenteries occurs, in place of the unpaired member of the previous polyp. Below the stomodæal region, the members of pair D, D are found to belong to the smaller series, corresponding in size with pair B, B.

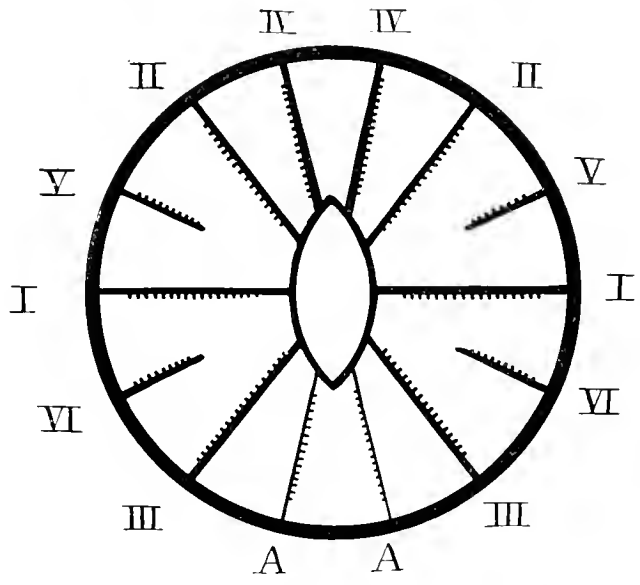

FIG. 10*a*.

Poritæ.—Fig. 10. Increase of mesenteries beyond the protocnemic stage, as exhibited by various polyps. The six pairs numbered I-VI and represented by thicker lines are the protocnemes. *a*, An additional bilateral complete pair (A, A) occurs within the exocœle of the ventral pair of directives.

All the additions thus far are within the entocœle of the ventral pair of directives, but in fig. 11 the new mesenteries are disposed within the entocœle of the dorsal directives. In 11*a*,

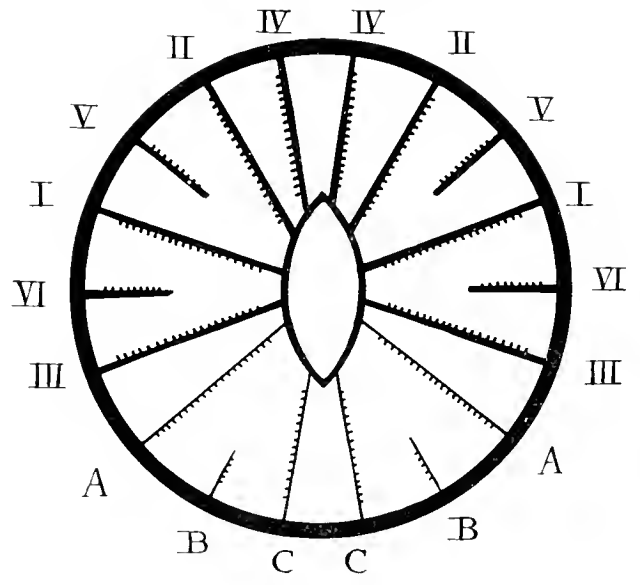

FIG. 10*b*.

Poritæ.—Two further bilateral pairs have been added; one (B, B) incomplete, and another (C, C) complete. Mesenteries III, A, on each side form unilateral isocnemic pairs, in which the retractor muscles are on the faces of the mesenteries turned away from each other, as in directives; mesenteries B, C, on each side constitute unilateral anisocnemic pairs.

three bilateral pairs are represented, all the members of which are attached to the stomodæum. The retractor muscles are so disposed that, as in the previous instances, the members of the first

new pair form with the adjacent members of the primary directives an isocnemic pair of directives on each side, and the moieties of the next two bilateral pairs form a pair on each side, in which the muscles are turned toward each other.

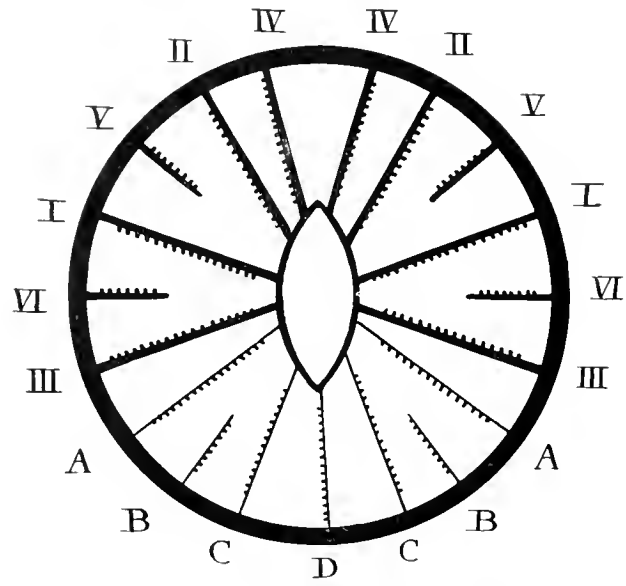

FIG. 10c.

Porites.—A single additional mesentery (D) has appeared without a corresponding member to form a pair.

Fig. 11*b* is the diagrammatic representation of fig. 42, Pl. V, which is taken from a section of an enlarged polyp of *Porites*. The figure of the section will give some idea of the difficulties involved in unraveling the relationships of the various mesenteries to one another. It is only by deter-

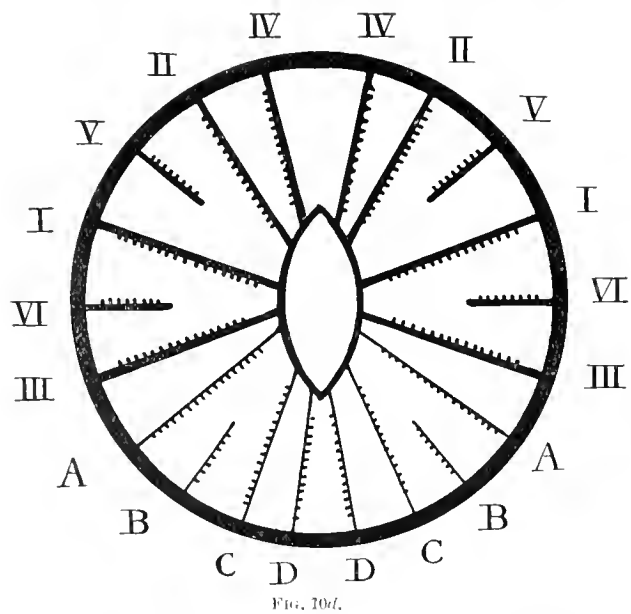

FIG. 10d.

Porites.—Four additional bilateral pairs are present. The pair D, D is united with the stomodæum, but below this region is shorter than pair C, C, showing that it belongs to the microcnemic series.

mining the faces of the mesenteries bearing the retractor muscles, and the proportional sizes of the mesenteries, that the primary and the later mesenteries can be established in their relations to one another. Comparing fig. 11*b* with fig. 42, it is seen how the pairs in the actual section

correspond one by one with those in the diagrammatic plan. It is further manifest that no other arrangement of the pairs than that offered would represent the primary mesenteries with the characteristics they present in ordinary polyps. In the region here figured, the dorsal directives

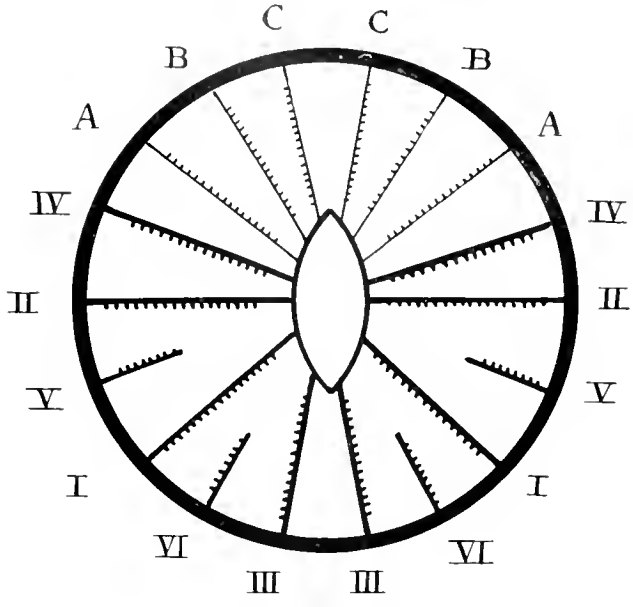

FIG. 11*a*.

Porites.—Fig. 11. Increase of mesenteries continued. All the additions occur within the dorsal directive entocœle. *a*, Three new pairs (A, C) occur, all of which are united within the stomodæum.

belong to the smaller series of mesenteries as well as the new bilateral pair next to them, and as in the previous figure the adjacent moieties of each pair constitute a pair of directives. The

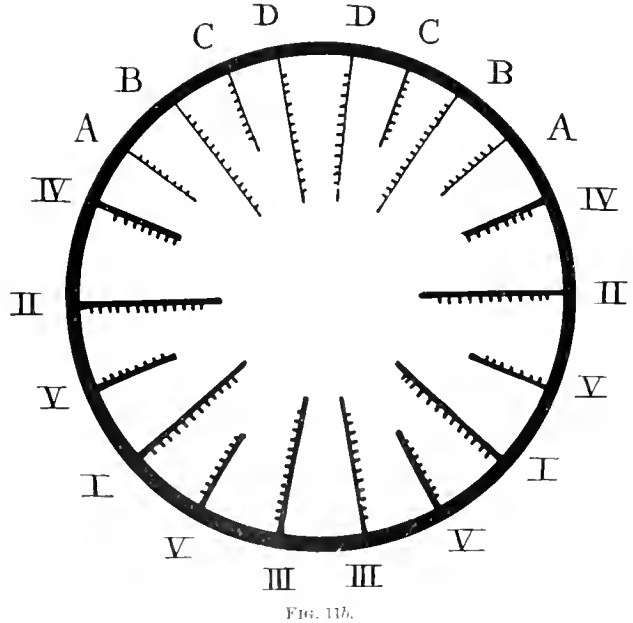

FIG. 11*b*.

Porites.—Section of another polyp, below the stomodæal region. Mesenteries IV, A, on each side constitute microdirectives, and B, C are anisocnemic pairs (cf. Pl. V, fig. 42).

next two mesenteries on each side form a unilateral pair in which the ventral moiety is large and the dorsal small.

Fig. 11*c* is from a transverse section through the stomodæal region of a polyp in which twenty-four mesenteries are present, arranged in twelve bilateral pairs. The primary dorsal directives (IV, IV) are incomplete at this level, as often happens in ordinary polyps. The unilateral paired arrangement of the six new pairs of mesenteries, as regards the complete and incomplete moieties, is exactly the reverse of that of the primary mesenteries. In the former, the incomplete members have their musculature on faces directed ventralwards, while in the latter it is toward the dorsal aspect. Four isocnemic pairs occur in which the retractor muscles are on the faces turned away from one another (directives), and eight anisocnemic pairs in which the musculature is on the faces turned toward each other.

Of the many living polyps examined, none showed a stage beyond that represented in fig. 11*c*. In one or two instances where twenty-four mesenteries occurred, the stomodæum was found to have undergone fission in the dorso-ventral or directive plane, and with each stomodæal tube were associated six pairs of mesenteries, arranged exactly as in ordinary polyp. Of the six pairs in each fission polyp, three belong to the primary series of mesenteries, and three to the later formed pairs (p. 514).

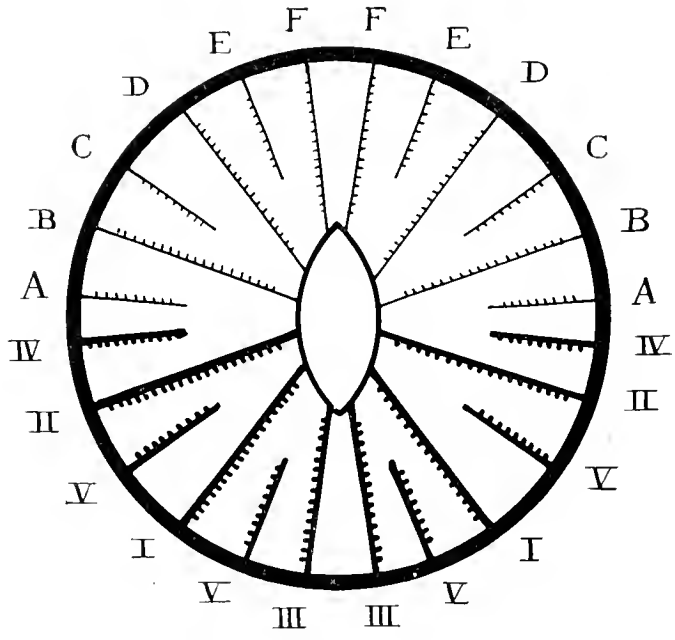

FIG. 11*c*.

Porites.—six new mesenterial pairs have appeared, equaling in number and corresponding in arrangement, only in reverse order, with the protocnemes.

The results may be summarized as follows:

1. In *Porites* new mesenteries beyond the primary six pairs are added at only one region, which is within either the dorsal or the ventral directive entocœle.

2. The additional mesenteries appear successively in complete or incomplete bilateral pairs, the latest formed arising within the entocœle of the previously formed pair. Sometimes the moiety of a pair on one side may arise a little in advance of the moiety on the other side.

3. The longitudinal muscles on the mesenteries are so arranged that the members of the first additional pair constitute with the sulcar or sulcular directives, as the case may be, two isocnemic pairs, in which the musculature is on the faces turned away from one another. In the succeeding bilateral pairs, the musculature is alternately on opposite faces, so that the eighth and ninth bilateral pairs on each side form a unilateral pair in which the muscular faces are turned toward each other, and likewise the tenth and eleventh pairs. On the twelfth bilateral pair the retractor muscles are on opposite faces, as in directives proper.

4. Below the stomodæal region both the primary and additional pairs consist of alternately

longer and shorter mesenteries (anisocnemic), with the exception of the directives, which, whether lateral or axial, consist of equal moieties (isocnemic).

5. When the number of mesenteries in a polyp reaches twelve pairs, stomodæal fission may take place, in such a manner that six primary and six new mesenteries are associated with each stomodæum.

A great distinction is thus established between the manner of appearance of the metacnemes in *Porites* and that in other coral polyps. In the former, the additions are shown to take place in bilateral pairs at only one region, and within an entocœle, while in the latter it has been shown that the additions are made in unilateral pairs all round the polyps, within the six primary exocœlic chambers. In *Porites*, the unilateral pairs consist of a larger and a smaller moiety (anisocnemic), without the formation of hexameral cycles, while in other Madreporaria the members of a pair are alike in size throughout (isocnemic), and in the end the different pairs constitute cycles.

Later results suggest that the additions in *Porites* are to be regarded as stages in the process of fissiparous gemmation. (See foot-note, p. 496.)

INCREASE OF MESENTERIES IN MADREPORA.

In a recently published paper,[a] I have fully described the peculiar manner in which the increase of mesenteries beyond the protocnemic stage takes place in *Madrepora*. The process is again alluded to on p. 515, in connection with fission in *Madrepora*, and is illustrated by three diagrammatic figures (fig. 18*a-c*). Fundamentally, the increase takes place in the same manner as in *Porites*, that is, by bilateral pairs, which are disposed within the directive axial entocœle. But in any one polyp of *Madrepora* additions are made at both extremities, whereas, in *Porites*, they are restricted in any one polyp to either the dorsal or the ventral directive entocœle. Six new pairs seem to rise simultaneously in *Madrepora*, as against the successive order in *Porites;* for some time one or two of the pairs may be united with the two stomodæal tubes, without any connection with the column wall.

MESENTERIAL FILAMENTS.

The edges of all the complete mesenteries, after ceasing their connection with the stomodæum, are provided with the Anthozoan structures known as mesenterial or gastric filaments, and likewise the free edge of most of the other mesenteries, which at no time extend transversely so as to reach the stomodæum. In dissected polyps the filaments appear as dense, white, thread-like organs, connected with the mesenteries, usually straight and vertically descending in the upper region, but greatly convoluted below. In the living condition, they are frequently extruded through the mouth and polypal wall, as white coiled threads, along with the portion of the mesentery to which they are attached. They are generally strongly marked off from the rest of the tissues in microscopic preparations, on account of the brightly-staining character of their cellular constituents.

On the incomplete mesenteries, the filaments, as a rule, commence a short distance from the uppermost region of the polyp, and terminate below somewhat in advance of the mesentery; occasionally they are absent from the last cycle of mesenteries, or remain incipient. On the other hand, the filaments are borne by the complete mesenteries only after ceasing their connection with the stomodæum. At first they are straight, but soon become greatly convoluted, on some mesenteries more than on others.

Structurally, the filaments display the same essential characters in all the species examined, and are simpler than the corresponding organs in the majority of Actiniaria. Throughout the Madreporaria, so far as yet known, the actual filament consists of only a single median lobe, in contrast with the trilobed condition of most Actinian filaments. In transverse sections the organs appear as cordate or disk-like expansions of the edge of the mesenteries. In addition to the actual terminal filament, the mesenterial epithelium immediately behind is usually much swollen on each side, and is either sharply rounded off from the rest of the endoderm or passes

[a] "The Morphology of the Madreporaria.—II. Increase of Mesenteries in *Madrepora* beyond the Protocnemic Stage." Ann. Mag. Nat. Hist., Ser. 7, Vol. X, 1902.

gradually into it. Figs. 14, 39, 44, 45, 57, and 69 will give some idea of the variety of form presented in transverse sections.

Histologically, a filament differs in passing vertically from one region of the polyp to another, and also exhibits a variety of cellular constituents in different parts of the same section. In the complete mesenteries the actual boundary between the stomodæal ectoderm and the mesenterial filament is by no means well defined. As shown on Pl. VI, fig. 51, the deeply-staining ectoderm of the stomodæum, at the termination of the latter, appears to pass around and for some distance along both sides of the mesenteries, and as the latter become free they are capped with the ectoderm. In transverse sections (fig. 57*b*) the filament at first is cordate, the mesoglœa bifurcating and supporting the lateral wings. The anterior and lateral borders of the filament differ in no respect histologically from the stomodæal ectoderm, while the posterior borders are ordinary mesenterial endoderm. The first part of the filament in most corals is of this character, but continues thus for a longer distance in some form (*Cladocora*, *Astrangia*) than in others. The stage is never represented in the filaments of mesenteries which are unconnected with the stomodæum. It passes gradually into the next stage, which represents the longest part of the filament (fig. 57*c*). The anterior or inner portion of the filament is constituted mostly of narrow nematocysts, clear and granular gland cells, and supporting cells, while laterally and behind the cells become shorter, supporting cells predominate, and the ciliation is stronger than elsewhere. The mesoglœa of the mesentery passes but a short distance into the filament, and there bifurcates, each half being directed forward, horizontally, or backward, and quickly thinning out. Immediately in front of the mesoglœal expansion nervous elements are usually recognizable, and less often muscular fibrils. The latter may also be present along the hinder mesoglœal border, as a continuation of the mesenterial muscle layer (*cf.* also figs. 44, 45, Pl. V.)

Passing to the lower regions of the polyp, the filaments usually become broader in transverse sections, and large, oval, thin-walled nematocysts, with a very distinct spiral thread, are the chief feature. So abundant are the stinging cells that in some cases they make up by far the greater proportion of the whole filament, the supporting cells serving as a kind of matrix (Pl. VII, fig. 58; Pl. XIII, fig. 94)[a].

The swollen mesenterial endoderm, immediately behind the filament, must in no ways be confounded with the two lateral lobes of the trilobed Actinian filament. In these the three lobes are very distinct structures, both as to their form and histology, and each is supported upon a separate mesoglœal axis. The apical part of the middle lobe (Drusenstreif) is mainly glandular in character in the upper region of the polyp, and a few small nematocysts usually occur. On their antero-lateral borders, the two lateral lobes are constituted wholly of ciliated supporting cells, being known as the ciliated bands or Flimmerstreifen. Between the glandular streak and the ciliated bands is found a patch of tissue, which as a rule bears a close resemblance to undifferentiated endodermal epithelium, and has been termed the intermediate streak.

Comparing the coral filament with that of the Actinian, it is manifest that the organ in the former is represented by the middle lobe of the latter, and there is nothing which corresponds morphologically with the lateral lobes. The lateral lobes of coral polyps never contain a separate mesoglœal axis, and histologically they bear the closest resemblance to the ordinary mesoglœal epithelium. In Actinians the lateral ciliated lobes disappear aborally, and also distally on the incomplete mesenteries, while in certain genera (*Corynactis*, *Rhodactis*) the lateral lobes are altogether wanting, when the filament is essentially like that of the Madreporarian polyp.

Histologically the postero-lateral region of the coral filament, especially in *Madrepora* (p. 474), closely recalls the ciliated streak of anemones, and its strong ciliation also suggests a similar function.

The filaments on the imperfect mesenteries often remain in a rudimentary condition, and afford instructive stages in the development of the organ. The free edge of the mesentery is

[a] None of the mesenterial filaments examined ever show the nematocysts partly extruded, in the manner described and figured by Bourne for *Fungia* (1893, pl. XXIV, fig. 28), and by Pratt for *Nephelia* (1900, pl. LXIII, fig. 8c); but in the polyps of certain Pacific corals I have observed the phenomenon noticed by these authors.

capped by a tissue which stains brightly, and consists mainly of ciliated supporting cells, but is not sharply separated from the unmodified mesenterial epithelium. The mesoglœa is not swollen or bifurcated, and the endoderm immediately behind never becomes lobed. Such incipient filaments occur on the secondary mesenteries of *Orbicella* and *Cladocora* (fig. 57*a*), and a somewhat further stage is represented by *Solenastræa* (fig. 85). The figures should be compared with the early stages in the development of the filament met with in larvæ (Pl. XV), and also in *Porites* (fig. 38). There is the closest resemblance between the two phases, leading to the conclusion that phylogenetically they represent similar structures, whether continuous with the stomodæal ectoderm or remaining free from it.

GLANDULAR MODIFICATIONS.

The filaments of many species of corals undergo a peculiar histological modification, the organs within restricted limits becoming almost wholly glandular. In the fresh tissues, the alteration is indicated by the part being of a golden yellow color, instead of the usual dull white; while in preserved material the same parts are much darker than the rest of the filament, above and below. A transverse section through one of these modified regions, taken from *Orbicella annularis*, is represented on Pl. IX, fig. 69. The filament has become enlarged in diameter, and its cellular constituents are remarkably uniform in character. The latter are long, clearly defined, columnar cells, radiating in a fan-like manner from the expanded mesoglœal base. Each cell is filled with a finely granular substance, and on staining a nucleus is rendered visible. The free margin presents no indication of ciliation, but, in places, globules of some liquid appear in the act of oozing out, while the organ is enveloped in some secretion, evidently issuing as the polyp was preserved. The secretion is of a faint yellowish color, slightly different in refraction from the Canada balsam in which the sections are mounted. The same filament, as it appears in a partly tangential section, is represented in fig. 70. The cells in the middle are cut transversely, while peripherally they are seen more lengthways. The well-defined polygonal outline of each cell in transverse section is very characteristic.

After maceration, the preparations (fig. 71) reveal that the filament comprises only two kinds of cells: (*a*) long, columnar gland cells, of the same diameter throughout, and charged with granular matter; and (*b*) equally long, narrow supporting cells. Nematocysts are altogether wanting. The modification extends over a very restricted vertical range, for on following the sections of the filament, both upward and downward, the normal, more complex structure soon appears.

The actual presence in some cases of a secretion surrounding the filament, and the character of the cells themselves, leads to the conviction that the structure represents a purely glandular organ. Such a histological specialization is very exceptional among Zoantharian tissues. One of the functions of the ordinary mesenterial filament is deemed to be the production of a digestive secretion, and it is manifest that in these special filamental regions an increase in size and number of the secretory cells has taken place, to the exclusion of nematocyst and other cells, with the exception of the ever present supporting cells.

A comparison with the section through the unmodified region of the same filament, represented in fig. 72, at once suggests the manner in which the alteration has taken place. The portion of the mesentery included in the figure is at first very narrow, but just behind the filament its epithelium and mesoglœa become swollen, and as the latter enters the filament it is flattened, terminating in a branch to each side. The boundary between the filament and the swollen mesenterial endoderm is clearly defined. The comparison of fig. 69 and fig. 72 renders it evident that in the former the whole of the filament has taken on the glandular character, while the unmodified basal area is the swollen mesenterial epithelium, now, however, so closely apposed to the filament, as to be distinguished only histologically.

Intermediate stages in the production of the glandular organ from the normal filament are afforded by the filaments of *Maandrina* (Pl. XXI). A transverse section of one of these is represented in fig. 144: the right side of the filament presents the usual histological details, while

to the left side most of the cells have become enlarged and glandular. In lower sections the whole of the filament takes on this latter character, becoming at the same time much larger (fig. 145).

The glandular cells in *Maeandrina* differ from those in *Orbicella* only in the fact that the contents of the cells are a brighter yellow in color; being unaffected by stains, they stand out as very conspicuous areas in microscopic preparations. In *Favia fragum* also the contents are bright yellow.

The glandular modification appears to be somewhat generally distributed, having been found in *Orbicella acropora*, *Maeandrina labyrinthica*, *Favia fragum*, and *Colpophyllia gyrosa*. Its occurrence appears to be somewhat sporadic. Only a few of the filaments in any one polyp undergo the alteration, and its vertical extent is always very limited. In *Orbicella* and *Favia* two or three mesenteries, out of the usual twelve pairs, are thus distinguished, and in *Maeandrina* the proportion is much the same. In one instance, in a portion of the brain coral, the two mesenteries of a pair were thus altered.

A still further development in the same direction is presented by the filaments of *Maeandrina* (fig. 145). In transverse sections of ordinary filaments, the endodermal lobes immediately behind are not sharply marked off from the rest of the mesenterial epithelium; the cells are exceptional in the amount of vacuolization, and the comparative paucity of the zooxanthellæ, but are not essentially different from the ordinary mesenterial endoderm (fig. 143). Where the glandular alteration has taken place, the cells, not only of the filament, but also of the mesenterial epithelium for some distance behind, are nearly all of a uniform character, and the elongated nuclei of the supporting cells are arranged in a zone. In fig. 145, three, coarsely granular, gland cells are represented, the granules staining very deeply, but the remainder of the cells are filled with an extremely fine granular matter, which stains but slightly. The nuclei of the cells are oval, and distributed through the tissue with an approximate uniformity, and perfectly clear gland cells are altogether absent. Instead of the filament being separated from the mesentery by a distinct groove on either side, as is the case elsewhere, its cells are directly continuous with those of the mesenterial epithelium, and these latter have undergone a like glandular modification for some distance, passing gradually into the ordinary mesenterial endoderm.

Thus the elements of two different tissues—filamental and mesenterial endoderm—may assume a like specialized character.

MESENTERIAL FILAMENTS OF MADREPORA AND PORITES.

The histological characters of the mesenterial filaments of *Madrepora* are such as to call for special note. A transverse section of one of these is represented on Pl. II, fig. 14. The mesogloeal lamella from the mesentery enters a short distance into the base of the filament, and there bifurcates; the two halves are directed backward into the lateral regions, where they thin out and are lost. The filament thus becomes divided into three distinct areas, a larger antero-lateral area, and two smaller posterior crescentic regions, each characterized by special histological elements. In front the cells consist of long, narrow, supporting cells, amongst which are numerous clear and granular cells, and a few small thick-walled nematocysts, though the latter are plentiful only in the proximal region. The cells of the posterior crescentic areas are all of one kind—narrow, ciliated, supporting cells, with the deeply-staining nuclei wholly restricted to the inner two-thirds of the cells (fig. 13*b*); the ciliation is also stronger than anteriorly. Though some such differentiation between the middle and posterior areas of the filaments is found in other coral polyps, the distinction is rarely so marked as in *Madrepora*. In sections stained in borax carmine the posterior regions are an intense red, and present a sharp contrast with the rest of the filament.

The middle region corresponds in histological detail with the glandular streak of the middle lobe of the Actinian filament; while histologically the crescentic areas most distinctly recall the ciliated bands of the lateral lobes of the Actiniæ. In these latter the ciliated bands are constituted wholly of ciliated supporting cells, and the condition in *Madrepora* serves to

demonstrate how similar, highly specialized tissues may recur in different regions. The marked development of the lateral ciliated area in *Madrepora* may be conceived as associated with the complex circulatory system of the porose corals, but the weakness of the filaments in the allied genus *Porites* scarcely bears out such a suggestion.

Mature polyps of *Porites* usually contain four pairs of complete mesenteries in the upper region, but the dorsal directives often become free before the lower termination of the stomodæum is reached (figs. 30, 41). Mesenterial filaments, however, are found on only the three remaining pairs of mesenteries, I, II, III; the free edge of pairs IV, V, VI is covered with the ordinary mesenterial epithelium (Pl. III, fig. 29). For a short distance below the stomodæum the tips of the older mesenteries are provided with a deeply-staining tissue, in no ways distinguishable from the stomodæal ectoderm with which it is continuous (Pl. IV, fig. 38); and no sharp boundary line here separates the filament from the rest of the endodermal epithelium. Some distance below the stomodæal region, however, the filament takes on the normal character, and lateral endodermal lobes may be formed on the first and second pairs (fig. 39), though they persist for a very short vertical distance.

The limited development of the mesenterial filaments in *Porites*, on only two or three of the pairs of the mesenteries, is in close agreement with the results of Fowler (1888) upon polyps of *Seriatopora*. In *S. subulata* Fowler found the mesenterial filaments to be well developed on only one pair of mesenteries, the two marked 3 and 10 in the author's notation, and corresponding with the pair marked I, 1 in the present paper; the mesenteries numbered 1, 5, 8, 12, corresponding with pairs II, III, were generally devoid of any "filamentar" thickening. The proportional development of the filaments thus corresponds with the order of appearance of the mesenteries.

EXTRUSION OF MESENTERIES AND FILAMENTS.

In corals reproducing by gemmation the filaments are rarely so strongly developed as in fissiparous species. In the latter, certain of the filaments are more important than others, and become greatly folded and convoluted, attached to the free edge of the mesentery all the way (Pl. XXII, fig. 148). The mesenteries bearing such strongly developed filaments are capable of partial extrusion through the walls of the polyp, either upon irritation or injury to the latter, sometimes in such quantities as to nearly hide the surface of the colony. Extrusions may appear at any part of the column wall or disk, as well as through the mouth. In the living polyp the mesentery and filament sent out are easily distinguished one from the other; the former is usually thin, colorless, and transparent, while the latter is opaque white, and disposed in irregular loops and coils. The extruded mesenteries in some species are faintly green in color, perhaps due to the large number of zooxanthellæ in the endodermal epithelium. In polyps preserved with the mesenteries thus partly extruded, some of the filaments are also found displaced within the upper polypal regions, and even within the chambers of the edge-zone. In *Cladocora* the filaments have been observed to enter the tentacular cavities, and occasionally they are found in the peritheeal continuations of the polypal cavity.

The phenomenon takes place most readily in fissiparous genera, upon strong irritation or after rough handling of the colony, and the extrusions are more copious in these forms than in genera reproducing by gemmation, but probably there are few corals in which it may not occur occur to a greater or less degree. It has, however, never been observed in the numerous colonies of *Siderastræa* kept under observation.

Examination of the column wall and disk of the polyps, under ordinary conditions, fails to reveal any apertures comparable with the "Cinclides" of the Actiniaria, through which it may be supposed that the filaments can pass. The absence of cinclides, and the irregular disposition of the extrusions over any part of the column wall and disk, make it evident that the openings are merely temporary, and capable of formation at any point, structural continuity being again established when the mesenteries are indrawn. On examining the surface of the column wall, immediately on withdrawal of the filaments, the apertures could be observed, and have been found to remain open for a short time; gradually, however, they close over, and all evidence of their former presence is lost.

On Pl. VIII, fig. 64, is given a section through the infolded apical region of *Orbicella*, in which the filament, and the mesentery to which it is attached, are shown in the act of passing through an actual perforation of the column wall. The extra-polypal portion of the filament is charged with numerous, large, thin-walled, oval nematocysts, and the disrupted column wall reveals no histological peculiarities.

The extrusions from coral polyps can scarcely be compared with the ejection of "Acontia," a phenomenon characteristic of the Sagartinæ among the Actiniaria. Acontia are thread-like structures, which are but feebly attached to the mesenteries, and pass through permanent apertures (cinclides) in the column wall of the polyps, or through the mouth, the mesentery in no ways following. If not wholly liberated from the polyp, the acontium can be indrawn. The extruded filaments of corals, on the other hand, still retain their normal position along the contorted edge of the mesentery, and a portion of the latter passes out along with them. The function of both is probably the same, as in each case the organs are strongly charged with nematocysts, and less so with gland cells.

ORIGIN OF MESENTERIAL FILAMENTS.

Probably there is no subject affording greater diversity of opinion among writers on the Anthozoa than that of the ectodermal or endodermal origin of the mesenterial filaments. In the Alcyonaria the problem has been made the subject of special study by E. B. Wilson (1884); in the Actiniaria, by McMurrich (1891); while H. V. Wilson (1888) has made it the object of lengthy notice in the coral *Manicina*.

The actual facts of the case are briefly as follows: In the adult polyps of all three groups, the stomodæal ectoderm is in absolute continuity with the mesenterial filaments of the complete mesenteries, as the latter become free at the lower termination of the stomodæum, and the two agree closely enough in their histological detail to suggest a common origin. Further, the filament differs markedly in structure from the mesenterial endoderm, and would thus appear to have no connection with this layer. Likewise in very early larval stages, the same unbroken passage from the stomodæal ectoderm to the filament is often found to exist, though rudiments of the filaments may be present on the primary mesenteries before or independently of their union with the stomodæum. Were the complete mesenteries only to be taken into account, as in the Alcyonaria, the problem would be much simplified, but in both Madreporaria and Actiniaria exactly similar filaments to those on complete mesenteries are found on the incomplete mesenteries, which remain free from the stomodæum, and hence are never in continuity with its ectodermal lining.

The independence of the filamental and stomodæal tissues within the early larva or bud, along with their histological difference, led E. B. Wilson to regard the six ventral filaments in the Alcyonaria as endodermal; on the other hand, the apparent continuity with the stomodæal ectoderm of the two dorsal filaments from the beginning, and the closer histological resemblance of the two structures, caused Wilson to regard these as ectodermal.

From evidence of a like character, McMurrich, in 1891, came to the conclusion that the Drüsenstreif or glandular streak on the middle lobe of the Actinian filament is of endodermal origin, while the ciliated bands on the lateral lobes are ectodermal. Returning to the controversy in 1899, McMurrich, from his investigations of the mesenterial filaments in *Zoanthus sociatus*, again concludes that the ciliated bands must be conceived as ontogenetically distinct from the glandular streaks. Regarding the ectoderm and endoderm of the Cœlentera as representing but an approximation to the diblastic condition of the higher groups, McMurrich is constrained to regard the distinction between an ectodermal and endodermal origin of any of the organs as of relatively little moment. With this understanding, he concludes: "the ciliated bands are probably in all cases ectodermal, and that in some mesenteries at least, the glandular streaks are endodermal, yet I am prepared to accept as correct the ectodermal origin of the glandular streaks in other mesenteries." The "intermediate" epithelium of the trilobed Actinian filament McMurrich is inclined to regard as ectodermal; my own observations, on species where it is favorably developed for study, lead me to consider it as endodermal.

The structural uniformity of the filaments in all Madreporaria, and the absence of lateral lobes bearing ciliated bands, simplifies the matter somewhat in this group, as compared with the Actiniaria. From its relationships to the mesentery, its form and histological structure, the Madreporarian filament for the greater part of its course undoubtedly corresponds with the middle lobe of the Actinian filament. In the simple condition of the latter, the organs are indistinguishable in the two groups, and without doubt a common phylogenetic origin must be assigned them.

In connection with the origin of the filaments, H. V. Wilson was the first to attach importance to a reflection of the stomodæal ectoderm, which takes place at the inner termination of the stomodæum. This occurs in both adult and larval polyps. On Pl. VI, fig. 51, representing a transverse section through the terminal stomodæal region of an adult polyp of *Cladocora*, the ectoderm is seen to line not only the outer surface of the wall, but has also become folded round the edge of the stomodæum, and comes to occupy the inner or endodermal surface of the organ, thence passing for some distance along both faces of the complete mesenteries, and seeming to give rise to the mesenterial filaments as the mesenteries become free. Similarly, on the left side of fig. 56, a vertical section through the stomodæum of *Cladocora*, the ectoderm becomes folded at the termination of the wall, and is then continuous with the mesenterial filament. The right side of fig. 2 shows the same relationship in *Madrepora*.

On Pl. XIV, fig. 112, a transverse section through an early larva of *Fungia*, also displays a tissue on the endodermal surface of the stomodæum, in all respects resembling that of the stomodæal ectoderm. Separated by the first pair of mesenteries, it forms a distinct, deeply-staining lobe, in both the larger and smaller primary chambers, and differs greatly from the surrounding endoderm. In sections a little higher, the reflected ectoderm is wholly wanting, and the stomodæal lining is purely endodermal (*cf.* figs. 126, 127).

The stomodæal ectoderm, reflected in this way around the lower edge of the stomodæal wall, occurs to a greater or less degree in probably all Madreporaria. Invariably, the mesenterial filaments of the complete mesenteries seem as if they took their origin from it, and the histological resemblance is very close. The extent of the reflection along the cœlomic surface of the stomodæum, and also outwardly along the mesenterial faces, varies much with the amount of retraction or expansion of the polyps, for in the latter condition the stomodæal wall and edge of the mesentery come to be almost in the same vertical straight line, and no reflection is then apparent.

Wilson, in his studies of the early larvæ of *Manicina*, found the stomodæum to be applied to the column wall, and its ectoderm appeared to pass down the inner surface of the wall, even before the first pair of mesenteries had appeared. In later stages the ectoderm of the stomodæum was reflected up the endodermal surface, and all the primary mesenteries, except the first pair, were considered to receive their filamental tissues from these ectodermal tracts, though some filaments were found to be present on the mesenteries before the union of the latter with the stomodæum had been effected. With regard to the origin of the filaments on the mesenteries which never reach the stomodæum, probably few students of the embryology of the Anthozoa will be prepared to follow Wilson in his suggestion (p. 220) that these receive their ectoderm from a reflection along the entire length of the cœlomic surface of the stomodæum and peristome (the epithelium *x*, of Wilson's figs. 50 and 55). Its acceptance, in the case of the incomplete mesenteries of some species, would demand that the inner lining of nearly the whole of the upper region of the polyps should consist of ectodermal tracts.

A typical example of the condition of the filaments found in larvæ is presented by the transverse sections of the larva of *Fungia fragum* represented on Pl. XIV. For the greater part of its length the inner (cœlen'teric) layer of the stomodæum resembles the rest of the endoderm, but toward the internal end it begins to assume a histological character more nearly resembling that of the ectodermal lining. The cells are now narrow and closely arranged, and the numerous brightly-staining nuclei form a definite zone, marking off the region very distinctly from the ordinary endoderm. This is the so-called "reflected ectoderm" of Anthozoan literature. In *Fungia* it passes along the first pairs of mesenteries for a short distance, and as these sever

their connection with the stomodæum they are tipped with a tissue of like nature. Increasing in extent, it is continued as the mesenterial filament along the edge of the first pair of mesenteries, almost as far as their termination at the aboral end of the larvæ, ceasing on one mesentery a little in advance of the other (*cf.* also Pls. XVIII, XXV).

At this early stage the mesenterial filament is not sharply marked off, except histologically, from the rest of the mesenterial epithelium. Its numerous nuclei stain brilliantly in borax carmine, and structurally it is indistinguishable from the stomodæal ectoderm. This resemblance, combined with the absolute continuity of the two at the commencement of the filaments, would seem to remove all doubt that the two—stomodæal ectoderm and the mesenterial filaments—are of one and the same origin.

But the conclusion becomes less certain when the incomplete mesenteries are taken into account, for along their free edge is a tissue of exactly similar nature; yet the mesenteries are in no way connected with the stomodæum, and there is no apparent means by which the incipient filament can have been in unity with its ectoderm.

The early appearance of the filaments on the second pair of mesenteries is represented in fig. 112, from a section taken a little above the termination of the stomodæum. At first only one mesentery displayed any marginal modification, but in the figure the filament has appeared on the other member of the pair, while below it is as strongly developed on both as on the first pair of mesenteries, but disappears in advance of the filament of the latter. In some of the sections coming below that represented in fig. 112 there is the feeblest hint of the filament on the mesenteries of the third pair, which scarcely extend beyond the endodermal lining.

It is manifest therefore that the filaments on the second pair of mesenteries originate quite independently of any connection with the stomodæum and of the reflected ectoderm. From a study of the conditions in both the third and the second pairs it is inconceivable how at any earlier stage, say before the middle embryonic tissues had broken down, that any such connection could have been established. The reflected ectoderm passes backwardly but a short distance along the cœlomic surface of the stomodæum, and there is no possibility of its working its way upward, across what represents the disk, and then downward along the free edge of the mesentery. The presence of filaments on the second pair of mesenteries before union with the stomodæum would imply that a similar development may also take place on the third pair of mesenteries before their union, and sections reveal that such actually occurs. It is also manifest from the sections, that before the union of the mesenteries with the stomodæum is effected, there is no means by which the free margin of the former can have come into contact with the reflected ectoderm.

From the conditions represented in the larvæ of corals generally, the conclusion is reached that the mesenterial filaments may originate independently of any connection with the stomodæal ectoderm, and may therefore be assumed to be endodermal.

The filaments on both the complete and incomplete mesenteries at the early stages of larval development present but little histological differentiation, except in the case of the filament on the first mesenterial pair. They consist mainly of supporting cells, and stain much more deeply than the ordinary endodermal lining, but gland cells and nematocysts are scarcely determinable. Similar details are often presented by the edge of adult mesenteries, which always remain free from the stomodæum, showing that in the orders beyond the primary the filaments originate in the same manner. In these cases the filaments may never become fully developed, but remain in an incipient or rudimentary condition. This is illustrated by the mesenteries of *Orbicella acropora*. The six pairs of mesenteries of the first cycle are complete, and filaments are well developed below; similar filaments appear on the mesenteries of the second cycle, which fail to reach the stomodæum; but on the third cycle of twelve pairs the mesenteries are merely tipped with a deeply-staining tissue, which is indistinguishable from that on the filaments of larvæ. Further, some mesenteries bear incipient filaments only in their upper course, while the organs are fully developed below. *Cladocora arbuscula* also affords similar illustrative examples (Pl. VII). The edge of a mesentery in its upper course is represented in fig. 57 *a*, and the filament is seen to be quite rudimentary; below the stomodæal region, however, the filament on the same

mesentery is fully formed (fig. 57 *c*). If the filaments of the incomplete mesenteries originate from a reflected tract of stomodæal ectoderm, it might reasonably be expected that they would be best developed in the uppermost region of the polyp, whereas, as a matter of fact, they are here absent or only incipient, even when fully developed below.

All the evidence seems to favor the view that in the Madreporaria the mesenterial filaments first appear independently of any connection with the ectodermal lining of the stomodæum, but that in the case of the complete mesenteries such a continuity is early established, while with incomplete mesenteries the separation is permanent.

When describing the adult mesenteries, it is shown that the first part of the filament differs in form and structure from that below, and histologically is indistinguishable from the stomodæal ectoderm, with which it is in direct continuity. It is manifest, therefore, that between the actual stomodæal termination and the commencement of the true filament there is a tract which partakes more of the nature of the stomodæal ectoderm than of the filamental tissue. It forms the connecting link, as it were, between two tissues which may be considered as wholly distinct both phylogenetically and ontogenetically. Such, it may be conceived, is the significance of the "reflected ectoderm" as seen in corals. It is the stomodæal ectoderm passing along the mesentery to establish structural continuity with the upwardly growing filament.

The strongly ciliated character of the stomodæal ectoderm marks out the layer as specially concerned in the circulation phenomena of the polyp, and the same must be affirmed to a less degree of the upper part of the mesenterial filament. For the proper carrying out of this it is manifest that a close histological continuity should be maintained between the two structures, and it can be conceived that in establishing this the stomodæal ectoderm passes some distance down or along the mesenterial edge to meet the upgrowing filament proper.

The mesenterial filaments on the incomplete mesenteries are the homologue of those on the complete filament, but the latter are in more or less direct histological continuity with the stomodæal ectoderm by a downgrowth from the latter, while the others are free throughout.

In his recent paper (1900, p. 73), Appellöf contends for the ectodermal origin of the whole Actinian filament, his fig. 25 showing a distinct passage of the stomodæal ectoderm down the free edge of the mesentery. The occurrence of an interval of endoderm between the stomodæal ectoderm and early filament, such as McMurrich (1891) and I (1899) have found in other larvæ, Appellöf would explain as the result of a more or less accidental severance of continuity upon retraction of the larvæ. Such a suggestion would scarcely be applicable to the conditions already described in the larvæ of *Fungia*, for the first indications of the filamental tissue occur at very different levels on the various mesenteries, in some instances at a considerable distance below the stomodæal termination. On the view presented above, the appearances which Appellöf describes in *Urticina* are not directly concerned with the formation of the filament; the downward growth of the ectoderm from the stomodæal wall is merely the means of establishing continuity with the true filament which will appear independently below.

BASAL DISK, SKELETOTROPHIC OR SKELETOGENIC TISSUES.

Under these terms will be included the three Cœlenterate layers—ectoderm, mesogloea, and endoderm—which everywhere cover the surface of the skeleton in the living portion of a coral. G. von Koch (1882) has fully demonstrated that the ectoderm alone is the true skeletogenic layer, and is actually adherent to the corallum; but it is convenient to study along with it the associated mesogloea and endoderm. The early stages in the growth of the young polyp after fixation (Pl. XIX) reveal that the basal disk only is concerned in the formation of the skeleton, and therefore all the subsequent foldings, invaginations, and evaginations of the skeletotrophic tissues are but so many extensions of this region of the polyp, produced *pari passu* with the deposition of the calcareous particles. The theca, septa, costæ, columella, and all the teeth, spines, etc., connected with them, represent so many foldings of the basal disk, for all take their origin from the same continuous layer, and their surface remains covered by it so long as they belong to the living parts of the polyp.

In most instances, and especially in the perforate corals, the skeletotrophic layers comprise the greater proportion of the soft parts of the colony upon decalcification. The superficial tissues as a whole—column wall, tentacles, and disk—are always much less in superficial area than the skeleton-covering tissues. The polyps, as a rule, extend a little more deeply within the skeleton than is the amount of their expansion above.

To study with any degree of success the skeletotrophic tissues of a coral, it is necessary that decalcification be carried out. Lining the corallum so very closely, it is impossible to make a minute examination of the polypal layers *in situ* with the thinness to which sections of the skeleton can be ground. In the process of dissolving away the skeleton by means of acids, scarcely any distortion of the tissues appears to take place if the latter have been properly hardened, and the same may be said of the histology of the skeletogenic layer.

The polypal region set free by decalcification is very complicated in its detailed characters, and varies greatly for each genus. An exact representation may be obtained by making a plaster cast of the surface of any dried coral, and then dissolving away the latter. The superficial tissues seen in the living or preserved colony are found to represent but a small proportion of the polyp. The space formerly occupied by the thecal wall is now free, and in the case of gemmiferous species each polyp presents much more individuality than under ordinary conditions, while in fissiparous genera, like *Mæandrina* and *Colpophyllia*, the polypal systems stand out as very distinct, continuous ridges, separated laterally by deep grooves formerly occupied by the collines. The septal and columellar projections are now represented by so many deep lateral and vertical inturnings of the polypal tissues, and their arrangement can be studied in detail, though adding little to what is obtainable from the skeleton itself.

The height of the decalcified polyp gives the depth to which in the living condition the soft tissues extend downward within the corallum, revealing how comparatively superficial in every case is the living portion of a colony. For example, after decalcification the polypal tissues in *Porites astræoides* vary from 3 to 5 mm. in thickness; the polyps of *Siderastræa radians* are 3 mm. in height when freed from the skeleton, and those of the larger *S. siderea* are 6 mm. Polyps of *Orbicella acropora* scarcely extend for 1 cm. within the skeleton of the colony, and the same is the case even with the polypal systems of the large colonies of *Mæandrina*.

In the upper region of decalcified polyps the skeletotrophic walls as a rule present a different structural appearance from those below. Above, they are more transparent and delicate looking, but as the lower region is approached the walls gradually become firmer in character, white, and strongly opaque. This structural alteration is seen in nearly all the forms examined, and is evidently due to the pronounced histological change, referred to below, which takes place in the endoderm in passing from above downward.

Histologically the three skeletotrophic layers differ much among themselves, and also in different regions of the polyp. They will now be described as seen in sections.

ENDODERM.

In the upper part of any polyp the skeletal endoderm, as a rule, closely resembles that of the column wall, disk, and mesenterial epithelium; or, as in Pl. XVIII, fig. 129, it may be somewhat narrower, being represented by a very simple columnar epithelium. Gland cells of various kinds, supporting cells, and scattered zooxanthellæ are the usual constituents, but no trace of any muscular fibrils nor of a nerve layer has been found.

As the more proximal regions of the polyps are approached, the layer begins to undergo a peculiar modification. It becomes much broader and is highly vacuolated, exhibiting in sections a delicately reticular structure, the individuality of the cells being wholly lost (figs. 129, 73), while the chief constituents—nuclei, cytoplasm, zooxanthellæ, and the contents of the few granular gland cells—are mostly accumulated in a marginal zone. The differences in character between the endoderm in the upper regions and below are represented by figs. 44, 45, and 73, 75. In *Orbicella* (Pl. X, fig. 73) the layer is 0.1 mm. broad below, while above it is about 0.03 mm. in thickness (Pl. IX, fig. 68).

In some species the thickened endoderm is crowded throughout its extent with granules of various size, which render the layer dense and nearly opaque in sections. This is especially characteristic of *Astrangia solitaria* (Pl. V, figs. 44, 45) and *Dichocœnia stokesi*. The granular particles are usually non-staining, and are thus distinguished from the nuclei which are also present, situated near the margin. In *Dichocœnia* the granules are green (p. 439). Very rarely they are arranged as if constituents of an oval cell; more usually they are scattered uniformly through the whole or part of the layer, without any suggestion of being contained in special gland cells. The condition in the lower skeletal endoderm of *Solenastræa*, represented on Pl. X, fig. 79, is somewhat intermediate; large cells full of coarse granules occur, and in addition to these are many isolated granules.

The thickened skeletotrophic endoderm of the fissiparous genera *Meandrina*, *Manicina*, *Colpophyllia*, and also *Orbicella* has very few contents; a few small scattered nuclei, here and there a zooxanthella, and perhaps a few granules, are all that can be made out, the layer being vacuolated in either a rounded or irregular manner. In the porose genera *Madrepora* and *Porites* practically no modification occurs; the skeletotrophic endoderm is much alike in character in all parts of the polypal cavity, as well as in the canalicular outgrowths. Also in *Siderastræa* scarcely any difference is apparent between the upper and lower skeletotrophic endoderm (Pl. XXIII, fig. 156). This genus is further exceptional in that the calicoblast ectoderm remains a broad layer throughout.

The great thickening of the endoderm sensibly diminishes the mesenterial loculi below; while the comparative fewness of the nuclei, their small size, and the sparse protoplasmic contents would indicate that the cellular activity is much diminished compared with the upper regions of the polyp.

Wherever the calicoblast layer is in an active condition the endoderm overlying it presents a corresponding state. In the upper parts of polyps, where skeletal growth is proceeding as a result of the activity of the calicoblasts, the endodermal cells overlying the latter are highly protoplasmic, stain deeply, and present all the evidence of functionally active cells. A marked instance of this occurs in connection with the aboral termination of the interseptal loculi. It is here that from time to time the dissepiments are formed which cut off the polyp from the lower portion of the corallum; below the last dissepiment the skeleton may be considered as dead, while above it is covered with the soft polypal tissues. The production of dissepiments must be constantly taking place in a vigorously growing coral, hence the calicoblasts at the actual base remain in a more or less permanent condition of activity, as represented on Pl. X, fig. 73. The figure shows that the columnar character of the cells is limited to the actual flat base of the chambers, the calicoblasts being insignificant along the lateral walls. Fig. 73 is also specially instructive as showing how the endoderm immediately overlying the active calicoblast layer differs from the layer on the lateral walls, where the calicoblasts are non-active. The endoderm has become much thinner, the cells are fully charged with protoplasmic contents, and stain deeply.

The skeletotrophic endoderm overlying the upper parts of septa which may be supposed to be in a growing condition, is also much thinner than that lining the wall of the calice and inner parts of the septa at the same level. This diversity is very marked in fig. 129, Pl. XXIII, representing a mesentery of *Meandrina* with the skeletotrophic tissues associated with it.

It is manifest that the outer calicoblasts can obtain their nutriment and the calcareous salts wherewith to form the dissepiments only in so far as these pass through the overlying endoderm and mesoglœa; hence wherever the former are in a functionally active condition the endoderm would be expected to show a corresponding modification, as compared with regions where it overlies non-functional cells.

MESOGLŒA.

The mesolgœa of the skeletotrophic tissues is nearly everywhere a thin lamella, but, as a rule, it thickens a little along the line of attachment of the mesenteries to the corallum. At this place, and more or less scattered over the whole surface, are found peculiar cone or wedge-shaped

structures which appear as processes of the mesoglœa. In sections the processes are striated toward their free extremity, which in methyl blue and in carmine always stains much more deeply than the remaining mesoglœa. Their function would seem to be to bind the soft tissues to the corallum. Where the insertion of a mesentery on the column wall is seen in longitudinal section the processes appear as represented in fig. 95, Pl. XIII.

The nature and origin of the mesogloeal processes has been specially studied by Bourne (1899). He shows that they are formed from special ectodermal cells which he terms *desmocytes*. These take their origin from certain cells in the calicoblast layer, and become secondarily attached to the mesoglœa. The processes thus formed may be known as desmoidal processes, though Bourne employs the term desmocyte for them, as well as for the cells by which they are produced.

The desmoidal processes may occur at any part of the outer skeletotrophic tissues, but are most numerous in areas along which the tissues may have to withstand, as it were, the strain of any muscular activity of the polyp. The attachment of the mesenteries to the skeletotrophic tissues represents such areas, and here desmoidal processes usually occur in numbers.

Also, as shown in fig. 67, Pl. IX, they are specially developed in colonies along the line of separation of one polyp from those adjacent. It is obvious that at the point *des. pr.* the polyp upon expansion will tend to raise the skeletal covering from its adherence to the edge of the calice; hence to meet this the skeletotrophic tissues are provided with a special development of desmoidal processes. However fully expanded a polyp may be, it is never able to detach its basal wall from its adherence to the corallum.

The whole manner of distribution of the desmoidal processes fully supports Fowler's (1899) suggestion that the structures are special devices for maintaining the adherence of the polypal tissues to the skeleton. Their purpose in many ways is comparable with that of the ligaments in the higher animals. They do not occur over the actively growing regions of polyps: the skeletotrophic ectoderm is here a continuous epithelium (Pl. II, fig. 8).

ECTODERM OR CALICOBLAST LAYER.

The basal ectoderm or calicoblast layer is of much importance in studies of the morphology of the Madreporaria, seeing that by it is produced the entire skeleton, or coral as popularly understood. The nature of the layer, and the mode of formation of the skeleton by it, have been the subject of much controversy, with which the names of Milne Edwards and Haime, A. R. von Heider, G. von Koch, Miss Ogilvie, and G. C. Bourne are associated. Bourne (1899) has recently summarized the various views as to the structure and formation of the skeleton, and has made a very thorough study of the process as it takes place in different genera of Anthozoa. With regard to the Madreporarian skeleton he finds, with von Koch, that the calicoblast layer is everywhere a simple epithelium, the cells rounded, columnar, or fused together, and that the calcareous matter is laid down wholly external to the polyp. He thus differs from von Heider and Ogilvie, who concluded that the calicoblast ectoderm was a multilaminar layer, and that the skeleton resulted from calcification within the cells. The calicoblasts described by von Heider are shown to correspond with the desmocytes of Bourne, and are not concerned with the secretion of the skeleton.

The results from the present study fully confirm those of von Koch and Fowler as to the unilaminar condition of the calicoblast layer and the ectoplastic formation of the skeleton. Usually the layer is only well developed within regions of active growth, as toward the uppermost part of the corallites (Pl. II, fig. 8), or aborally, where dissepiments are in course of formation (Pl. X, fig. 73). Elsewhere the calicoblasts form an extremely flattened layer; in *Siderastraea*, however, the structure is the same practically throughout the whole of the skeletal area (Pl. XXIV). As a rule desmocytes are wanting where the calicoblasts are well developed, but are plentiful where the cells are nonactive, especially along the line of attachment of the mesenteries to the basal wall.

In some instances (*Madrepora*, fig. 16) the skeletogenic ectoderm shows distinct cell limitations, as in ordinary columnar epithelium; but generally these are lost, and the contents are arranged in a continuous manner and largely vacuolated.

Between the calicoblast layer and the actual skeleton, Bourne has found what he terms a *limiting membrane*, separating the polypal wall from the calcareous matter. This occurs wherever decalcification of properly preserved material is carefully carried out, but to my mind represents the remains of the colloidal matrix in which the skeleton is deposited. At the growing apex of *Madrepora* a continuous ground substance remains after decalcification, and fills the whole of the space occupied by the corallum, behaving toward reagents exactly like the mesoglœa between the ectoderm and endoderm. It presents a striated, scale-like appearance, altogether similar to that of the calcareous fibers of the skeleton of *Madrepora* (figs. 18, 19). The striæ have manifestly been produced by the calcareous skeleton laid down within a perfectly homogeneous substance. This latter is evidently secreted by the calicoblasts, but only under the most favorable conditions, as near the actual tip of rapidly growing branches, can it be found persisting throughout the skeleton. Elsewhere the organic matrix has either wholly disappeared, or is so insignificant as not to persist in a continuous form on decalcification. Stages in its disappearance can be easily followed in *Madrepora*, in passing downward from the apex of branches, and it becomes obvious that the mesoglœa-like covering on the outside of the calicoblast layer is but the densest, most recent part of the matrix, which is persistent, and within which calcareous fibers will be deposited.

The skeletotrophic tissues of *Siderastræa* and *Madrepora* will be described in somewhat more detail.

The skeletotrophic layers of *Siderastræa* present certain features which distinguish them from most corals (Pl. XXIV, figs. 157, 160). The endoderm broadens but little in passing from above downward; it is strongly vacuolated throughout, and contains numerous granules and a few zooxanthellæ, but all traces of cellular divisions are lost. The skeletotrophic mesoglœa is everywhere thin, forming only a mere dividing line between the ectoderm and endoderm. The skeletogenic ectoderm has practically disappeared where the mesenterial mesoglœa unites with the body wall, and the mesoglœa has become swollen in a triangular manner, and is finely striate, giving rise to desmoidal processes. The latter are found only in association with the mesenteries, where these unite with the calicinal wall, or more frequently where perforated by synapticula (fig. 159).

The calicoblast layer of *Siderastræa* is remarkable in that it persists as a broad, uniform layer throughout the polyp, even in regions where the corallum may be assumed to be in a less active condition, as along the lateral surface of the septa. Its usual appearance is represented in figs. 157, 160. It is strongly vacuolated, with numerous fine granules which stain deeply, and seem as if constituting a matrix in which the vacuoles are formed. The ectoderm nowhere presents the characteristics of a columnar epithelium; cell limitations are indistinguishable, and larger, deeply-staining bodies among the granules are probably nuclei. Where decalcification has been carefully carried out, fragments of the homogeneous organic ground substance, within which the skeleton is deposited, remain behind, closely adherent to the calicoblast layer.

Sections of decalcified material of *Madrepora* through the growing region at the apex of branches, usually show a broad, columnar calicoblast epithelium, much broader than the ciliated endoderm of the canal system (Pl. II, figs. 8, 16). Cell limitations are more or less clearly indicated, and the cells are largely vacuolated, the protoplasm being finely granular, and more concentrated toward the periphery of the layer. The nuclei are rounded and arranged mostly along a middle zone, but are not as regular in position, nor as numerous, as in the columnar cells of the endoderm. There is no indication whatever that the layer is more than one cell thick, or that transverse cell division ever takes place.

In the first few sections through the actual apex, where the spaces left by decalcification are very narrow, the calicoblast layer is even a little broader than in the sections represented, and the vacuolization is not so pronounced. In sections some distance from the apex, the layer begins to narrow, and soon it is represented by flattened cells which are often scarcely perceptible. This is the condition for the most part throughout the colony, and is inconsistent with much functional activity.

In the most actively growing regions of the colony, where the calicoblast layer forms a broad columnar epithelium, the mesogloea appears as a uniformly thin layer, entirely free from any connection with the corallum (figs. 8, 16); but in other areas, when decalcification has been carried out slowly, the middle layer displays numerous desmoidal processes on its skeletal surface (figs. 7, 17). The most perfect forms of desmoidal processes are conical or pyramidal, the base projecting outward; usually they are seen in longitudinal section, but occasionally in transverse section. Toward their free edge the processes stain much more deeply than elsewhere, and are very finely striate, the striæ being practically parallel and of equal length. The actual edge of the desmoidal processes is usually jagged, as if torn from some attachment.

Elsewhere the mesogloeal lamella exhibits smaller, less regular elevations, which are similarly deeply stained and striate. When a process is cut through transversely, either radiating striæ are presented at all the levels, or a punctate appearance is revealed. Nuclei are scattered about the origin of the processes, but are never found within it. The processes are undoubted outgrowths of the thin mesogloeal lamella, the actual continuation being readily observed; but the deeply-staining character toward the free edge indicates that some structural alteration has taken place.

Madrepora offers special advantages for a study of the nature and relations of the skeletal matrix, as, owing to the rapid growth taking place at the apex of the branches, the admixture of ground substance and calcareous deposit is here better preserved than in many corals. In apical polyps, which have been hardened in chromic acid, and slowly decalcified by means of weak acetic acid, the organic matrix of the skeleton is obtained *in situ*. It presents exactly the appearance of a striated mesogloeal substance, and behaves toward reagents in the same way, and is wholly devoid of nuclei. The fine striæ are arranged in a scale-like manner (fig. 18). The matrix is best developed at the terminal region of the corallites, and is densest toward the polypal surface, gradually thinning toward what would be the primary center of calcification within the branch. In most preparations it is shrunk from the calicoblast layer.

Looking at fragments of the corallum under a low magnification (about 60) the surface has the appearance of minute imbricating scales. They are somewhat polygonal in outline, and the free edge is directed obliquely forward, the whole indicating a spiral arrangement, most pronounced in the smaller branches. Under a higher magnification, however, each of the apparent scales is seen to be but the exposed terminal portion of an obliquely arranged fiber, proceeding from the deeper regions of the corallum, and the superficial scale-like appearance is produced by the overlapping of the numerous fibers. This is also seen in sections of the skeleton starting from the surface, but the distinction between one fiber and another practically disappears a little below the surface. The free edge of each fiber is often slightly jagged, not rounded and smooth, as if torn from some other connection. Viewed by transmitted light, each fiber has an indistinct, delicate, fibrillar appearance, with alternating lighter and darker transverse bands, somewhat recalling a striped muscle fiber (fig. 19).[a] The matrix left upon decalcification is thus closely repeated in the microscopic characteristics of the newly formed skeleton.

In studying the relations of the corallum to the soft tissues, sections have been made through the apical region of branches in which decalcification has but partly proceeded. It is found that the middle portion or center of calcification is the first to disappear by the action of the acid, the periphery, where most organic ground substance occurs, being last.

[a] Dr. Ogilvie (1896, p. 217) also gives a figure of the enlarged calcareous fibers of *Madrepora*, terminating in what she considers to be calicoblast scales. According to the view there presented, the scales are calcified calicoblasts, but as shown above the polypal tissues afford no support for such a conclusion. The organic matrix referred to by Miss Ogilvie is proved to be a homogeneous, jelly-like substance secreted by the calicoblast layer, within which the calcareous fibrillæ are laid down in a scale-like manner.

GASTRO-CŒLOMIC CAVITY.

The term gastro-cœlomic is applied to the whole of the internal, endoderm-lined cavity of coral polyps, including any outgrowths or continuations which it may possess. In some ways the designation is preferable to the terms gastro-vascular cavity or cœlenteron, generally employed for the polypal cavity in Anthozoa. For from the considerations of van Beneden (1891), and E. B. Wilson (1884), there seems some evidence to support the view that the space but incompletely inclosed by the mesenterial filaments is the morphological equivalent of the gastric cavity, or enteron, of the higher Metazoa, while the remainder of the internal cavity, partitioned by the mesenteries, is the morphological representative of the cœlom of the Enterocœla.

Among colonial corals the gastro-cœlomic cavities of all the polyps in actual union with one another are in communication, and the nutrient fluid can pass from one to the other. This is a persistence of the conditions consequent upon asexual development, whether this takes place by gemmation or by fissiparity. In gemmation new polyps arise wholly or in part from the column wall of other polyps, and the internal cavities of the two are common for a time. Thus the developing bud of *Madrepora*, shown in the series of figures on Pl. III, arises altogether from the cœnosarcal wall of the colony, and its cœlomic cavity during the primary stages is represented by one of the superficial canals of the colony. In the developing polyp of *Solenastræa*, represented in section in Pl. XII, fig. 87, a distinct partition wall, lined with endoderm on both sides, now partly separates the bud from the parent; but interruptions occur at more or less regular intervals, which permit of a circulation between the two cavities.

The mode of communication of the various polypal cavities in a colony varies somewhat in different forms. In genera like *Porites*, *Siderastræa*, and *Agaricia*, in which the polyps are separated from one another merely along a common calicinal wall, intermesenterial apertures remain along the line of union, while the polyps are partitioned mesenterially. In *Siderastræa* septal partitions also occur, at any rate during retraction; for peripherally the column wall comes to rest directly upon the septal covering, so that only a very narrow space is left on each side between the mesenterial and the septal wall (Pl. XXIII, fig. 156). The channels of communication of four adjacent polyps of *Porites* over the thecal edge are represented on Pl. III, fig. 31, taken from a section through the superficial region of a colony in which the polyps were in a retracted condition. The fragments of the corallum seen are the slightly exsert septa, and the canals pass over and around them.

Adjacent polyps of *Orbicella* and *Solenastræa* are also placed in communication intermesenterially at the superficial line of union of the polyps. During retraction the apertures are not connected directly with the main cavity, but through the intermediation of its perithecal prolongations. The same method of superficial intermesenterial communication holds for the contiguous rows in the genera reproducing by incomplete discal fission, e. g., *Meandrina* (Pl. XX, fig. 138), *Colpophyllia*, *Manicina*, *Isophyllia*. In these, however, the polyps which are united in the same discal system have no independent cavity, the one continuous chamber is shared in common. The polyps do not attain true individuality; they can best be understood as so many mesenterial and stomodæal systems within a general cavity.

The numerous polyps constituting a colony of *Madrepora* are likewise in communication by means of the superficial canals, which are continuous over the thecal edge with the main gastric cavity (Pl. I, fig. 2); but in the great group to which *Madrepora* and also *Porites* belong—the Porosa—there is another and more complicated system of communication than that afforded by the superficial canals. Anastomosing radial canals are given off by the basal (skeletotrophic) part of the body wall, in such a way that they appear as if penetrating the corallum which separates one polyp from another, and thus place the different cœlentera in union; in *Madrepora* they further come into communication with the superficial canals.

The radial canals are given off very closely in both *Porites* and *Madrepora*, and are disposed both mesenterially and intermesenterially, without any apparent regularity. As many as five or six may be seen in a single transverse section (Pl. I, figs. 3–6). They are not so numerous in the

upper region of the apical polyps of *Madrepora* as below. In fig. 2, representing an apical polyp, no radial openings occur on either side, though an uninterrupted continuity of the corallum for such a distance appears to be somewhat unusual. The superficial canals in exsert corallites of *Madrepora* are mostly longitudinal in direction: but transverse connections occur, and the canals may be also interrupted by skeletal growths. Decalcified preparations show that the canal system does not as a rule prolong the gastro-cœlomic cavity at the aboral end of the polyps; in both *Porites* and *Madrepora* the polyps and their canals are abruptly truncated.

The internal canal system in the Porosa is morphologically basal in origin. For it is established that the whole of the skeletotrophic tissue is derived from the primary basal disk, and all its evaginations and invaginations are but so many foldings and complications of the walls of this region of the polyp. The canals of the perforate corals may therefore be compared with the basal communicating canals of colonial Actiniaria, such as those of *Palythoa* among the Zoantheæ. Though exerting a profound influence on the character of the corallum, the canal system of the Porosa has but little morphological significance, and in any natural classification of corals appears altogether unworthy of the importance which has been assigned it by systematists.

The fundamental difference between colonial non-perforate and perforate corals may be thus stated: In the Aporosa the gastro-cœlomic cavities of the component polyps of a colony are in communication only by superficial apertures along the common line of union of the column wall and base, while the Porosa have in addition a means of communication by basal anastomosing canals.

Compared with that of the Actinian polyp the gastro-cœlomic cavity of the Madreporarian polyp is much more subdivided and intruded upon, both radially and peripherally, particularly in its lower region. In addition to the mesenterial partitions, shared in common with the Actiniaria, a like number of radiating septal invaginations usually occurs, while columellar, spinous, and synapticular productions still further break it up centrally and peripherally. Moreover, the calicinal wall itself is often produced upward as a peripheral, circular wall, and, so far as it extends beyond the line of union of the column wall and base, divides the cœlomic cavity, as well as its mesenterial partitions, into inner and outer moieties, the latter constituting the cavity of the edge-zone or Randplatte.

During expansion the upper part of living polyps is elevated for some distance wholly beyond the corallum, and in distinct polyps the free portion is cylindrical, in form closely recalling an Actinian polyp (figs. 46, 48). Here the subdivisions of the gastro-cœlomic cavity are only mesenteric, and are arranged peripherally into entocœlic and exocœlic chambers in a strictly Actinian fashion. The fleshy parts of fissiparous genera likewise become extended for several millimeters, the oral disk appearing as a meandering platform fringed by the zone of tentacles, and the column wall on either side as a nearly vertical sinuous parapet; the cavity is divided into entocœlic and exocœlic chambers, but not with any cyclic regularity.

In retracted polyps not only is the oral region withdrawn within the calice, but the perithecal wall becomes more nearly apposed to that immediately covering the skeleton, and closely reproduces the outer corallar form, thus largely obliterating the intervening gastric space.

Proximally the polypal cavity extends some distance within the corallum, or rather the corallum has intruded within the polyp; and in these lower regions the cavity becomes subdivided in a most complex manner by skeletal ingrowths. In addition, the skeletotrophic endoderm becomes greatly thickened proximally, and further encroaches upon the chambers, but apparently the mesenteries always cease before the lower termination of the polypal cavity is reached.[a]

[a] Nothing like the peculiar obliteration of the polypal cavity which Sclater (1886) describes in *Stephanotrochus* has been encountered. In all cases the cœlomic cavity persists as far as the proximal floor of the polyp. According to Bourne (1893, p. 219), the polyp in *Fungia* does not desert the lower part of the calice, but remains adherent to the basal plate. Yet even here Bourne finds that the primary and secondary mesenteries are carried upward as growth proceeds, and are confined always to the upper moiety of the calice; the lower moiety consists only of chambers lined with endoderm and undivided by mesenteries.

In the upper region of the calice the septal invaginations as a rule stretch but a short distance radially into the gastro-celomic cavity, the portion of the polypal cavity included between one septum and another being spoken of as an interseptal chamber or loculus. As the lower regions are approached, the septa extend farther and farther centrally, subdividing the cavity more and more, until ultimately they unite in the middle to form or share in the columella. Where such central fusion takes place, the gastro-celomic cavity is divided into interseptal chambers, which in transverse section are wholly distinct from one another, laterally and centrally (figs. 55, 84). If the septa of all the cycles, both entocoelic and exocoelic, extend as far as the center of the polyp, each chamber is simple, and includes within it only one mesentery (*Solenastræa*, fig. 84); but when younger cycles extend only part way toward the center, each chamber is incompletely subdivided, and may contain two or more mesenteries (figs. 54, 55). All stages toward the complete isolation of the septal chambers are represented in passing a series of transverse sections in review, from above downward, the primary septa being the first to unite centrally. Where the septa do not completely fuse centrally, in other words, where they do not form a solid columella, the interseptal polypal chambers remain in open communication at the middle throughout the polyp (*Meandrina*, Pl. XXI, fig. 142).

The actual manner in which the interseptal chambers terminate proximally is best studied in entire, decalcified polyps. In some species they narrow gradually in an oblique manner, while in others they terminate abruptly. Where the chambers are oblique, the polyps gradually diminish in transverse area as the lower region is approached, the newer chambers ceasing in advance of the older. This is characteristic of the genera *Oculina*, *Favia*, *Agaricia*, *Meandrina*, *Manicina*, and *Isophyllia*. In *Orbicella*, *Solenastræa*, *Siderastræa*, *Cladocora*, *Astrangia*, *Porites*, and most *Madrepora*, the polypal chambers are of practically the same sectional area from beginning to end, though the truncation of the newer chambers may occur a little in advance of that of the older. In mature polyps of the last series of genera, the basal floors of the mesenterial chambers may all occur at practically the same level, as if all had been cut off by dissepiments formed simultaneously.

Pl. V, fig. 42, representing transverse sections through *Porites*, shows how the central cavity is encroached upon by the spine-like, columellar projections; according to the level at which the section is made, they may be either distinct or in continuity with the septa. The presence of synapticula results in a similar encroachment on the outer regions of *Siderastræa*, at the same time leading to a disappearance of the peripheral portion of the mesenteries (Pl. XXII).

The extent to which the gastro-celomic cavity may be prolonged over the edge of the calicinal wall, before it terminates at the line of communication with the adjacent polyps, varies greatly in different species. In the older regions of colonies of *Oculina*, the interval between one polyp and the next may be a centimeter or more; the mesenteries may, however, cease before the spiral line of union of contiguous polyps is reached. In *Cladocora* the outside of the theca may be covered for 5 or 6 mm. by the fleshy tissues, and the mesenteries subdivide the inclosed chamber for practically the whole distance (Pl. VII, fig. 54). The calicinal wall in *Orbicella* and *Solenastræa* is prolonged but a short distance above the level at which the contiguous polyps are united with one another. Just as the calicular portion of the polypal cavity is partitioned and intruded upon by skeletal growths, so is the narrower extracalicular space; the mesenterial continuations divide it into vertical chambers, and costal ingrowths usually alternate with the mesenteries, corresponding with the septa internally. In *Madrepora*, where no perithecal mesenteries occur, the space is broken up by costate ridges, which are more numerous than the septa within. Here, however, the skeletal ridges actually come into contact with the superficial wall and support it, and were it not for transverse communications the perithecal cavity would be typically represented by a series of distinct vertical canals.

SYNAPTICULA.

Synapticula are solid calcareous bars of various form which unite adjacent septa across the interseptal loculus. They are formed by the enlargement of granulations on opposite faces of adjoining septa, growth continuing until the projections meet in the middle of the interseptal

space and fuse, without the presence of any intervening soft tissues. Intermediate stages in the formation of indentations of the skeletotrophic walls lining the interseptal spaces are presented by corals in which the septa bear only granulations. The complete skeletal fusion necessarily leads to the piercing of the skeletotrophic tissues originally covering the granulations, and by means of which the calcareous additions are made. The mesentery contained in the interseptal chamber is likewise perforated as a result of the skeletal growth across the chamber containing it.

Much discussion has arisen as to the systematic value to be assigned a synapticulum, according as it is completed by the simple enlargement of two granulations, or by the intercalation of one or more additional centers of growth. The former have been termed by Pratz (1882) "False synapticula," and the latter "True synapticula." The polypal tissues themselves show no distinction, according as one method or the other is followed, and for discussion as to their importance in skeletal morphology the works of von Koch (1896, p. 259), Ogilvie (1896, p. 184), and Vaughan (1900, p. 47) among others may be consulted.

The genus *Siderastraea* is especially favorable for a study of the relationships of the polyp to these characteristically Fungid structures (Pls. XXII, XXIII). In the corallum of *Siderastraea* the synapticula are seen as vertical rows of short, thick, nearly circular bars, stretching from one septum to another across the interseptal space, and mainly restricted to the peripheral region of each corallite.[a] Upon decalcification of a polyp the soft tissues remaining are found to be made up of a large number of radiating vertical lamellæ. In the upper region these are united centrally, but are mostly free from one another below, and all terminate at about the same level. The complete separation of the lamellæ results from the fact that in the lower region of each corallite the septa extend all the way from the calicinal wall to the central columella, and, uniting with the latter, wholly cut off one septal loculus from another. In its natural state each lamella is separated basally from the lower part of the corallum by a delicate horizontal dissepiment, exactly as in other corals, except that the dissepiment in its course may encounter the synapticula. The lamellæ thus represent the interseptal polypal tissues freed by decalcification; each consists of two lateral walls which lined adjacent septa, and above contains a single mesentery, while below it is empty.

A surface view of an isolated interseptal lamella, slightly enlarged, is represented on Pl. XXII, fig. 152. The edge to the right is central in regard to the polyp. For nearly the whole of its length the lamella is perforated toward its peripheral border by three rows of round or oval apertures. Smaller lamellæ may bear only two rows of perforations, while again there may be four more or less complete rows in some of the larger polyps. The apertures in the lamellæ represent the spaces which before decalcification were pierced by the skeletal synapticula, and in each corallite the increase takes place above and centrally.

Various sections of polyps of *S. siderea* are represented on Pl. XXIII, and from these the relations of the fully formed synapticulum to the polyp as a whole can be ascertained. In both transverse and vertical sections each interseptal chamber appears as if composed of several wholly distinct segments, the skeletal matter which separates them representing the synapticula. Some of the chambers are wholly or in part occupied by a mesentery, while others are empty; in the few instances in which the section of a chamber does not include a perforation, or rather a synapticulum, the loculus is complete from center to periphery. A consideration of the varied appearances which would result from sections at different levels through the complete lamella (fig. 152) will aid in an understanding of the appearances presented by the different interseptal chambers. The synapticula never wholly isolate any portion of the internal cavity, though they must interfere with the effectiveness of the peripheral circulation.

The sections further demonstrate that a gradual atrophy of the mesenteries takes place in the lower and peripheral parts of the polyp as these become invaded by the synapticula. In the uppermost polypal regions all the mesenteries are attached to the column wall and disk, and six pairs extend inwardly as far as the stomodæum; but a little below the level of the stomodæum the peripheral attachment becomes lost, while in the lowest sections no part of the mesenteries whatever remains.

[a] For excellent representations of the synapticula in *Siderastraea* see Miss Ogilvie's paper, 1896, pp. 180–182.

All stages in the resorption of the lower parts of the mesenteries can be observed. Where the action is in progress the peripheral edge is free and tapering, although the mesentery was originally attached by this to the wall (fig. 158). The mesoglœa is seen to break up into distinct pieces, and the endodermal epithelium is in different stages of disorganization; terminal fragments appear as if about to break off, and occasionally free particles are met with. The mesenterial débris thus set free is evidently injested by the endodermal epithelium lining the chambers, for the layer is here of exceptional thickness and the large cells are crowded with granules and irregular fragments, which closely recall those given off from the disintegrating mesentery.

Fig. 153, taken from a retracted polyp, reveals that the mesenteries do not extend as far as the most peripheral chambers, although the region represented is no lower than the stomodæum. In some cases a fragment of the mesentery may persist in the second chamber, but its imperfect character indicates that it is about to disappear; even where the section does not actually encounter a synapticular interruption the peripheral tissue is atrophied.

In the tangential section, fig. 156, the mesenteries all extend vertically beyond the first transverse rows of synapticula, but in the chambers below they begin to exhibit the various stages in absorption.

That the mesenteries are actually pierced by the synapticular formations is manifest from the preparations. When serial sections are passed in review, it is seen that the mesentery wholly surrounds the upper and more central perforations left by the removal of the synapticula, and frequently the mesenterial mesoglœa becomes swollen, and presents striated areas, such as are formed by the desmocytes where a mesentery is inserted on the calicular wall (fig. 157).

Miss Ogilvie has attributed an altogether different origin to the synapticula, in her account of these structures in *Fungia* and *Siderastræa*. Commenting (p. 170) upon Bourne's description of the synapticula in *Fungia*, she states: "The important point is that they *neither 'interrupt' nor 'pierce' the mesenteries.*" Further, it is assumed all along that the body wall is specially invaginated from below to produce them[a]. Had an examination of the actual polypal tissues been made it is impossible to see how any support could have been adduced for such statements, any more than would be forthcoming for the production of simple tubercles on the septa.

Professor Bourne, in his paper, "The Anatomy of the Madreporarian coral *Fungia*" (1887), also describes somewhat similar mesenterial relationships in the genus *Fungia*, only here the synapticula are in single vertical or oblique bars, not in vertical rows, as in *Siderastræa*. In the upper regions of the interseptal chambers there are no synapticula, and the mesenteries are free to radiate across the whole space between the stomodæum and the periphery of the disk, but in the lower portions of the loculi the continuity of the mesenteries becomes interrupted by the synapticula. Owing to the much larger number of vertical bars across the broad septa of *Fungia*, the intersynapticular cavities in sections greatly outnumber those of *Siderastræa*, and the mesenteries do not extend wholly across any segment, being represented by a small projection at each extremity of the chamber (Bourne's figs. 13, 15). Bourne's explanation (1887, p. 19) of the significance of the synapticula, that "physiologically they seem to serve as stays or buttresses, giving solidity and coherence to the corallum," is probably the most correct of any yet offered. From the disappearance of the mesenteries below, almost *pari passu* with the development of the synapticula, the circulation of the digestive fluids and functional activity within the synapticular region becomes diminished, and it is very doubtful if, as Miss Ogilvie (p. 171) suggests, the main advantage is that "an increased endodermal surface is afforded within the visceral cavity."

[a] Acting upon this suggestion of Miss Ogilvie, Delage and Hérouard, in their "Traité de Zoologie Concrète, Tome II, pt. 2, Les Coelentérés," 1901, have constructed two ingenious diagrammatic figures (pl. 62, figs. 1, 2), attempting to show how the basal infolding of the soft wall of the polyp proceeds in the formation of both bar-like and lamellar synapticula. The polyps of *Siderastræa* give no support whatever for such a conception. From the interseptal lamella represented on Pl. XXII, fig. 152, it is manifest that each synapticulum is formed independently of the others, not from a continuous infolding of the basal part of the skeletogenic layer, as Ogilvie and Delage & Hérouard assume.

Where the mesenteries are pierced and fixed by synapticula it is manifest that their retractile power will be lost; hence, only centrally and above will they still be able to extend and retract. With this, perhaps, may be associated the fact that the polyps of both *Siderastræa* and *Agaricia* are able to expand above the corallum the least of any species coming under observation. Colonies of the former have been kept in aquaria for months, and the polyps raise themselves but little above the corallum.

COLUMELLA.

If the aboral surface of a coral polyp be examined after decalcification, either as a whole or by means of sections, its middle affords certain indications as to the nature of the columella. If the calcareous tissue in the center of the corallite be elevated and solid, it intrudes, as it were, into the central basal part of the polyp, just as the septa intrude radially, and upon its removal a conical chamber remains. The soft tissues of the interseptal loculi are then wholly distinct from one another, for a greater or less vertical distance from the base, and in transverse sections the loculi are separated both laterally and centrally (figs. 55, 84). The calcareous deposit in these cases extends radially from without the boundary of the polypal tissues to the central deposit. If, on the other hand, the middle of the corallite be occupied by a spongy or merely convoluted calcareous mass, irregular chambers remain, which represent so much of the gastro-cœlomic cavity of the polyp, and serve to maintain the different interseptal loculi in communication (fig. 142).

The details represented by polypal sections, however, afford no evidence as to how the columella has been produced, whether as an upgrowth of the floor of the corallite, or by fusion of the free edges of the septa, or by both combined. This can best be ascertained from an examination of the skeleton itself.

ORDER OF APPEARANCE OF SEPTA.

PROTOSEPTA.

In accordance with the division of the mesenteries into Protocnemes and Metacnemes, the septa appearing in association with them will be described as "Protosepta" and "Metasepta" respectively. The protosepta will include the six primary septa appearing within the primary entocœles, and the six septa which appear within the primary exocœles; all the succeeding septa, arising within the entocœles or exocœles of the later mesenteries, will be metasepta. The septa within the directive entocœles are known as "Directive Septa," and are axial in position. Sometimes, as in *Madrepora*, these can be distinguished from the other protosepta by their greater or less size, and thus give a marked bilateral character to the calices.

Prof. H. de Lacaze-Duthiers (1873) was the first to observe the origin of the primary septa in coral larvæ, his researches being conducted upon the simple, perforate coral, *Astroïdes calycularis*. The description and figures indicate that twelve independent septa appeared simultaneously, one in each mesenterial chamber, while the young polyp was at the protocnemic stage of development. Apparently from the beginning each septum was constituted of three pieces, arranged in a Y-shaped manner, the bifurcated end being peripheral. Prof. G. von Koch (1882) subsequently obtained similar results for this species, at the same time fully establishing the ectodermal origin of the skeleton. In a paper, "Evolution du Polypier du *Flabellum anthophyllum*," Lacaze-Duthiers (1894) refers to young specimens of this species with only six septa and six tentacles, and in later coralla, where twelve septa occur, the members of the second cycle are much smaller than those of the first. G. von Koch (1888) had previously demonstrated, by means of serial sections of adult coralla, that *Flabellum* at its earliest stage is provided with only six septa, and that an alternating cycle of six appears later.

In one of his last works on corals, Lacaze-Duthiers (1897) makes further important contributions to our knowledge of the early stages in the development of the septa, so far as the process can be followed by observations on the living polyp and macerated coralla. A very complete series are given, illustrating the appearance of the septa in *Balanophyllia regia*, as well as notes

on those of *Caryophyllia* and other forms. The corals *Leptopsammia* and *Cladopsammia*, in addition to *Astroides* and *Balanophyllia*, were found with twelve primary septa appearing simultaneously.

Prof. G. von Koch's paper (1897), on the development of *Caryophyllia cyathus*, indicates that in this imperforate coral the six entocœlic septa are the first to appear, and are early attached to the theca, which arises a little later and independently of the septa. The alternating exocœlic septa appear somewhat later than the entocœlic, and like them are uniform in size, but shorter in their radial extent. The basal plate preceded the development of the septa, appearing at first as six independent, somewhat triangular, calcareous deposits, which afterwards fused with one another. Here, again, the protocnemes alone are developed, and only as far as the *Edwardsia*-stage, the fifth and six pairs being incomplete.

My results on the origin of the septa in the fissiparous coral *Manicina areolata*, so far as they go, coincide with those of Lacaze-Duthiers and von Koch. The septa appeared as upgrowths of the basal plate, covered on both sides by the basal wall of the polyp (fig. 137). The first six septa appeared simultaneously, within the entocœles of the larva at the *Edwardsia*-stage of mesenterial development (fig. 135); on the other hand, no exocœlic septa had arisen when the young polyps were preserved, although an interval of over a week had elapsed since the appearance of the entocœlic members. There is good reason to suppose, however, that the primary exocœlic members never appear in *Manicina*, as exocœlic septa seem to be absent from the adult.

In numerous polyps of *Siderastræa radians* reared from larvæ, the six members of the primary cycle of septa appeared simultaneously, within the six primary entocœles, three or four days after fixation of the larva, and in practically all cases were equal in size. Each septum was at first a simple lamella, with the upper edge distinctly serrated, and the lower edge flat and adherent to the glass to which the polyp was affixed. A day or two after the formation of the first cycle of entosepta, the six exosepta began to make their appearance, in some cases practically simultaneously, but in others in successive bilateral pairs from the dorsal to the ventral aspect of the polyp (p. 492). Thus in fig. 12*c*, a septum occurs in each of the two dorsal exocœles, a rudimentary member in each middle exocœle, while in the ventral chamber no skeletal formation is yet apparent. Figs. *b*, *c*, although representing different stages, were taken from two different polyps of the same age.

The young polyps of *Siderastræa* in the end presented two complete cycles of protosepta, a primary cycle consisting of six equal entosepta, and a secondary cycle of six equal exosepta, the latter series having appeared later and remaining a little smaller than the former. The protoseptal stage was completed within the first fortnight after the extrusion of the larvæ. In the later growth of the septa the peripheral extremities assumed a Y-shape, the additional portions appearing in some instances as distinct formations, and in others as continuations of the primary simple septum.

The above examples all agree in the fact that the six entocœlic septa arise simultaneously at the developmental stage marked by the presence of six pairs of mesenteries, and with the Edwardsian mesenteries alone complete. Lacaze-Duthiers' figures of *Balanophyllia regia* indicate that when the septa appear all the twelve mesenteries are united with the stomodæum, but no microscopic sections were made to confirm this. In *Astroides*, *Balanophyllia*, and others, the exocœlic septa appear along with the entocœlic, but an interval elapses in *Caryophyllia*, *Flabellum*, and *Siderastræa* before this takes place, while in *Manicina* they are wholly wanting. Where exosepta are developed, the six members usually appear together, but in certain polyps of *S. radians* a decided dorso-ventral succession in bilateral pairs was followed.

The simultaneous appearance of the cycle or cycles of protosepta in corals, and their uniformity in size, are in marked contrast with the successive order of development followed by the pairs of protocnemes. In no case do the septa appear until the six primary pairs of mesenteries are fully established, and then the six members of the cycle arise together. The septal sequence most nearly conforms with that of the tentacular, in which the members of a complete cycle, or both inner and outer cycles, appear together.

It must be borne in mind that the protocnemes are practically established at the time the larva settles, and that no skeletal formation takes place before the sedentary stage is assumed. During the subsequent growth of the coral, the new septa (metasepta) are found to arise in a dorso-ventral succession, approximately *pari passu* with the pairs of mesenteries, and it may be conceived that if the larvæ settled with only a few pairs of mesenteries developed then the primary septa would show a corresponding succession in their appearance.

In most adult polyps of *Porites* and *Madrepora* the protoseptal stage is retained, six entocœlic members and six exocœlic forming a larger and a smaller cycle. Very often some of the twelve septa are wanting, and usually one or both of the directive septa are much larger than

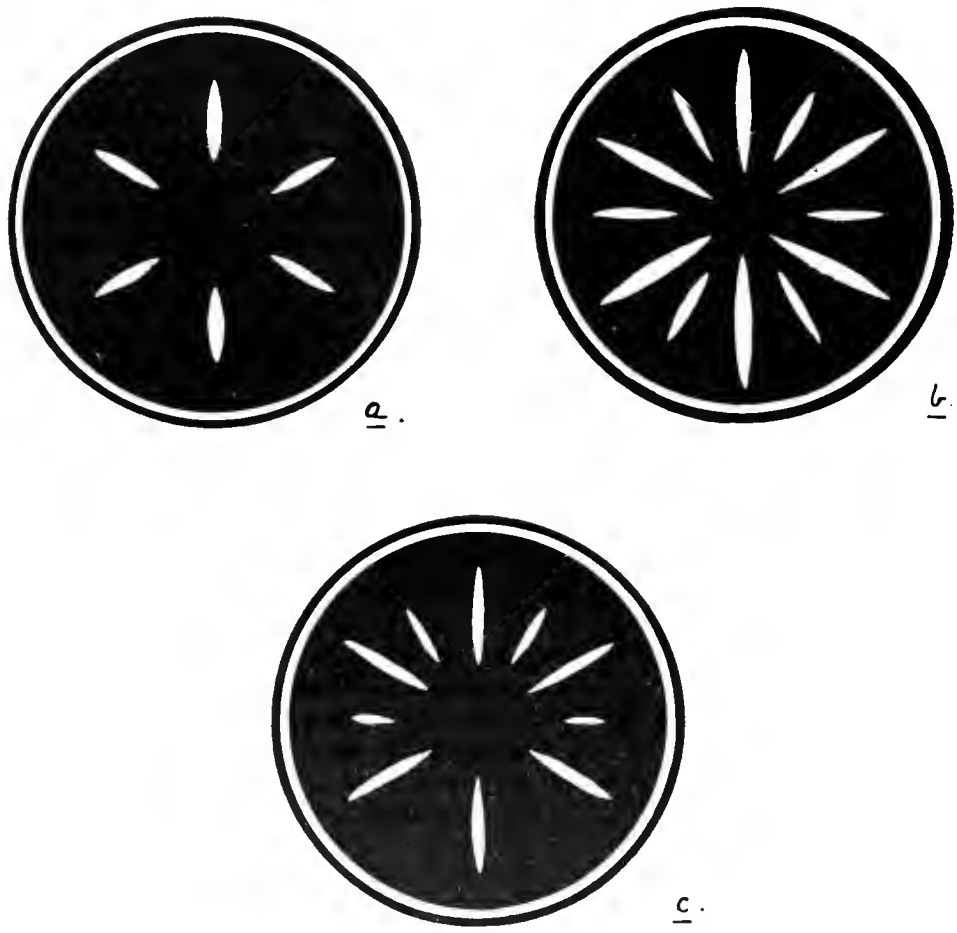

FIG. 12.

Siderastrea radians.—Series illustrating the development of the protosepta in larval polyps. The outer white ring represents the epitheca. *a*, Six equal entosepta are present, developed simultaneously. *b*, Six equal smaller exosepta now occur, also developed simultaneously, and alternating with the six primary entosepta. *c*, Successive appearance of the exosepta from the dorsal to the ventral aspect of the polyp, observed in a few cases.

the lateral, thus exhibiting a bilateral symmetry, corresponding with that of the mesenteries and tentacles.

The young bud of *Madrepora*, represented in section on Pl. III, proves that in asexual growth all the protocnemes may make their appearance before septal development commences, so that it seems not improbable that the protosepta may arise simultaneously in bud as well as in larval polyps.

It is manifest from the examination of buds of other genera that the septa occur in accordance with the number of the mesenteries at any particular stage, or at any rate their downward extension is in conformity with the mesenteries present. It is found that as the mesenteries

disappear downward so do the septa: or conversely, as the pairs of mesenteries increase in number the septa follow. This is well shown in the series of sections of the bud of *Solenastræa* on Pl. XII. In the transverse section, represented in fig. 89, nine protocnemes are present, and the same number of alternating septa, the latter indicated by the septal invaginations. Only one representative of the incomplete fifth and sixth pairs (V) occurs at the stage, and with it is associated a smaller septum. This mesentery disappears a few sections below, and then the septa become octameral, in correspondence with the four pairs of mesenteries remaining: as others of the mesenteries disappear the septa are found to follow, and in the last section obtained (fig. 90) only six mesenteries and six septa occur.

Whatever be the arrangement of the septa in adult corals, all the evidence seems to indicate that either six or twelve protosepta constitute the fundamental plan for all Madreporaria, whether recent or extinct. Thus, by means of serial sections, Prof. G. von Koch (1889) has proved that the coral *Caryophyllia rugosa*, which Moseley (1881), from his studies of the adult, first described as octameral, is really hexameral in its early stages. At first, six septa of the primary cycle are present, then six septa of the second cycle, and it is only with the appearance of a third cycle that modifications are introduced which lead to the production of the adult octameral condition. Lacaze-Duthiers (1894) refers to the eight or ten systems of septa exhibited by *Flabellum*, yet the early stages are typically hexamerous.

Lindström's results in regard to the coral *Duncania* are also of the same character. Pourtalès (1871) regarded this in the first instance as a living member of the order Madreporaria Rugosa. With regard to the tetramerism of its septa, Lindström, as quoted by Pourtalès, writes:

"There seems to be no reason to class this species, Duncania, among the Rugosa, which commonly are considered to have four septa of the first order. In making a thin section of the apex of a Duncania I distinctly saw six septa of the first order, which met in the center."

There is also evidence, from the results of Ludwig and Pourtalès, that some of the Palæozoic Tetracoralla exhibit a like hexameral primary condition.[a]

Solenastræa hyades is hexameral as far as the third cycle of septa, but the additions beyond this take place in such a manner as to wholly destroy such symmetry. The septa of adult polyps of *Manicina* and *Fungia*, which reproduce by oral fission, exhibit no hexameral plan, yet the early stages have been found to be of this type, and such can probably be assumed of fissiparous corals generally.

The instances are sufficient to show how little importance can be attached to the disposition of the septa in the adult coral, when discussing the broad relationships within the group. The whole history of any form must usually be known before its true nature can be determined, or any great importance assigned its adult peculiarities. The soft parts afford the surest guide for morphological comparison, from the greater certainty with which the relationships can be determined, owing to the many structural details available for correct orientation.

It has already been shown that, as regards the appearance of the twelve protocnemes, there is evidence of practical uniformity throughout the Actiniaria and Madreporaria: the several divergences in the later mesenterial sequence, distinguishing the great groups, make this their starting point. As regards the septa, also, there is good reason to expect that the six or twelve protosepta will be found characteristic of both living and extinct corals, and that all the numerous types of metaseptal sequence likewise make this their point of divergence. The distinctive characters of the principal divisions of the Zoantharia are not manifest from the beginning, but from the completion of the protocnemic stage.

METASEPTA.

The endeavor to establish the order of appearance of the septa beyond the primary stage presents many difficulties: no uncertainty can possibly arise as far as the protoseptal stage, but

[a] The subject is further discussed in a paper: "Relationships of the Rugosa (Tetracoralla) to the living Zoantheæ." Johns Hopkins Univ. Circ., vol. xxi, no. 155; also, Ann. Mag. Nat. Hist., ser. 7, vol. x, May, 1902.

it is doubtful if the next step in septal development is yet fully understood. Milne Edwards and Haime (1857) first attempted with any degree of thoroughness to determine the law governing the septal sequence of corals, and gave expression to their general results in the well-known figure on Pl. A5 of the Atlas accompanying the "Historie." Their investigations, however, were conducted almost exclusively upon adult coralla, the determining factors being the comparative sizes and radial extent of the different septa. The relative size and extent of the septum were conceived to indicate the order of appearance; the largest, most developed septa, were the oldest or first formed, the smallest were the last formed.

Prof. G. von Koch, in the course of his wide and thorough studies of coral morphology, has investigated the laws governing the order of appearance of septa more fully than any other writer. His results are largely founded upon the order of appearance and relative magnitude of the septa in serial sections of fully developed coralla, a method far more likely to yield reliable results than an examination of only the superficial characters of the calice. He concludes that in the main the law of Milne Edwards and Haime expresses the actual facts of the case—a new septum always appears between two older septa, and as a rule a perfect cycle is present before the septa of the next cycle arise.

Unfortunately, there is no account available of the order of development of the first metasepta in their relation to the mesenteries, and yet it is only upon this relationship that the problem can be satisfactorily solved. Both Lacaze-Duthiers and von Koch describe such early stages in the formation of the corallum, but in no case is the relationship of the mesenteries indicated.

One of the facts frequently emphasized in the present investigations is that the formation of the septa follows very closely upon the appearance of the mesenteries. In ordinary cases, whatever be the number of mesenterial pairs present, an entoseptum and an exoseptum are associated with each. This is clearly shown in the serial sections of the young bud of *Solenastrea* (Pl. XII); the polyps of *Astrangia* (fig. 47), *Phyllangia*, and *Cladocora* (fig. 49) are also very instructive in this respect. The correspondence in the number of mesenteries and septa at all stages can be established with the greatest certainty: if any mesenterial cycle is incompletely developed so is the septal. In *Manicina* (fig. 132) and *Petinia* septa appear as a rule only within the entocœlic chambers, but one corresponds with even the youngest of the mesenterial pairs.

Transverse sections of *Manicina* sometimes reveal septal invaginations within the exocœlic chambers, as in fig. 132, although by far the majority are entosepta. On following the sections toward the distal region, however, mesenterial pairs are usually encountered which correspond with the apparent exocœlic septa seen below. Thus the latter are really entosepta which in their downward growth exceed that of the mesenterial pair within whose interspace they occur. H. V. Wilson (1888) states that the septa of *Manicina* may for a time be exocœlic, but it is doubtful if higher sections would not have revealed the corresponding mesenteries. Bourne (1893) also found a few exocœlic septal invaginations in *Fungia*, though only entosepta are the rule; here, again, it is likely that the more distal regions of the polyp would have revealed the corresponding mesenterial pairs.

From an examination of a large number of stages in the growth of various species, it becomes manifest that the sequence of the septa beyond the protoseptal stage follows very closely that of the mesenteric succession. Knowing then the order of appearance of the mesenteries, that of the septa can be determined also. The metacnemes have been shown to appear, not a cycle at a time, but in successive bilateral pairs from one aspect of the polyp to the other, and the septa must follow a like sequence. Although in the end the mesenteries and septa of any one cycle become practically equal in size, yet the early stages render it evident that adult size does not conform with order of appearance.

A difficulty arises, however, in connection with the exosepta. It has been established throughout that the exosepta, like the exotentacles, always constitute the last or outermost cycle; the entosepta form all the internal cycles, the sum of the entosepta corresponding with that of the exosepta. But at all stages in the development of most corals, from the protoseptal stage onwards, exosepta occur. The important question therefore arises, whether the exosepta

of the early stages become the entosepta of the later or adult stage, or whether the exosepta remain exosepta throughout their existence. It is clear that whichever method is followed will lead to very different fundamental results in formulating the law of septal sequence.

The former condition appears to be very generally assumed. According to this, the six primary exosepta are considered to represent the second order of entosepta found in the developing coral in which the primary and secondary orders of mesenteries have appeared. The outermost cycle of twelve septa, constituting the third cycle, would be exosepta, and represent new formations, alternating with the twelve older septa. The twelve pairs of tertiary mesenteries on their appearance would include these third-cycle septa within their entocoeles, and thus the exosepta of a previous stage would become the entosepta of a later stage. The next cycle of septa would consist of twenty-four exocoelic members alternating with the first, second, and third cycles, and on the appearance of the quaternary mesenteries these would likewise become entosepta, followed by a fifth cycle comprising only exosepta.

My investigations so far give support to the view that the exosepta remain exosepta throughout, and that new entosepta arise with the new pairs of mesenteries. The results, however, are not yet sufficiently complete to fully establish the method. Such a relationship agrees with what actually takes place during the growth of the different cycles of tentacles; an exotentacle remains an exotentacle throughout the life of the polyp, those appearing early being displaced by the later entotentacles.

ASEXUAL REPRODUCTION.

By far the majority of corals are colonial in habit, and in nearly all cases the colony is produced as a result of the non-sexual or vegetative reproduction of an original, sexually-formed, simple polyp. It follows that in any study of the Madreporaria much attention must necessarily be given to the various methods of polypal increase other than by larvae.

Some few instances are known in which colonies are formed by the direct union or aggregation of individuals originally distinct. For these G. von Koch (1890, p. 376) employs the term "Aggregated Colonies," to distinguish them from colonies produced by the budding or fission of a single polyp. Von Koch describes such aggregated colonies in the usually simple coral, *Balanophyllia regia*, and shows that in all probability they have been produced from originally free and distinct larvae which settled near one another, their skeletons afterwards becoming fused in a common deposit. Lacaze-Duthiers (1899) describes the production of somewhat similar aggregations, "boquets," in certain specimens of *Caryophyllia* obtained from Port Vendres. In the process of fixation of the larvae of *Siderastrea radians* I have actually observed such aggregations taking place, and have followed the formation of colonies therefrom as far as the production of the tentacles and early stages in the appearance of the skeleton.[a]

The foregoing, however, are only exceptional instances of colony formation, and need not be further noticed in any general consideration of the subject.

The manner in which polypal increase is brought about, whether by budding, or by fission, or both combined, varies greatly in different species, and is the main cause of the immense variety of form assumed by colonial corals. So far as the resulting types of growth can be studied by observation of the skeleton alone, they have been described by writers such as Dana, Milne Edwards and Haime, and Duncan, and an extensive terminology has arisen in connection therewith. Dr. A. Ortmann (1890), in his paper "Die Morphologie des Skelettes der Steinkorallen in Beziehung zur Koloniebildung," has summarized the methods of colony formation in a very detailed manner, and at the close of the account applies the results in part toward a classification of the Madreporaria. Von Koch, in various contributions, has also given much attention to the process of coral budding, especially as revealed by means of serial sections of the corallum. As the earliest stages in the production of any new polyp must necessarily take place within the soft tissues of the parent, the study of these should yield results of fundamental importance.

So far as the species of corals under observation are concerned, all the methods of asexual polypal reproduction can be reduced to two types, which result in very different morphological

[a] "Aggregated Colonies in Madreporarian Corals." Amer. Nat., vol. xxxvi, 1902.

conditions. I recognize vegetative growth only by *budding* and by *fission*. The differences manifested within each division are mainly such as are dependent upon the position and method according to which the process takes place, and these do not in any way modify the essential distinctions between the two types.

When studying the mesenteries of adult polyps, two great divisions were determinable. In one section, including the genera *Orbicella*, *Solenastræa*, *Oculina*, *Cladocora*, *Astrangia*, *Phyllangia*, and *Siderastræa*, the mesenteries of all the polyps in a colony were found to be arranged according to the regular, hexameral, cyclic plan, with two pairs of directives; while in the other section, embracing the genera *Faria*, *Dichocœnia*, *Isophyllia*, *Manicina*, *Mæandrina*, and *Colpophyllia*, the mesenteries have lost their hexameral cyclic regularity, including the directives, and little more than a distinction into complete and incomplete pairs can be established. It was further found that the first-mentioned group comprises genera whose asexual growth is by gemmation, while fissiparity is characteristic of the latter. In whatever position the buds are produced, whether on the disk, upper part of column wall, intercalary, marginal, apical, cœnosarcal, or stolonic, matters not; the polyps retain a hexameral disposition of the organs. Also, whether the products of fission assume an individuality, or remain as constituents of a complicated system, makes little difference as regards the irregularity of the arrangement of the mesenteries, tentacles, and septa.

This fundamental difference in the adult polyps of the two groups seems to be determined by the fact that in gemmation the polyp as a whole is formed practically as a new individual, whereas, in fissiparity, some parts at least of the essential organs of the new polyp are obtained fully formed from a parent polyp. In the one case the polyp as a whole is free to develop according to a definite plan characteristic of the species, while in the other new organs are to be added and adapted to parts already formed, and fissiparity may again take place before any second regularity has been established. Growth in the one is altogether new, and in the other it is patchwork—some regions new, some regions old.

It has not been possible to determine whether in every case of gemmation the mesenteries are formed wholly independent of those of the parent. In some instances they certainly are, and in others it seems very probable. In very young buds the mesenteries are already found to be wholly cut off from those of adjacent polyps, and the bud is free to develop as symmetrically as any sexually-produced polyp.

Either one or the other method of growth is in the main characteristic of any species; sometimes a case of simple fissiparity may be found in a species where gemmation prevails,[a] as in *Madrepora* and *Porites*, but the converse has never been found—that is, the production of buds where fissiparity is the rule.

Intermediate stages are not wanting which seem to indicate how the passage from the one mode of colonial growth to the other has been brought about. In corals like *Cladocora* and *Oculina* the buds usually arise toward the upper extremity of the column wall, and it is easy to understand how gemmation may overstep, as it were, the usual boundary and occur on the discal wall. Such apparently happens, for occasionally polyps of *C. arbuscula* and *O. diffusa* are found in which two oral apertures are inclosed within one system of tentacles, and a common column wall and theca occur. In such cases the two polyps may be equal, or one may be larger than the other. Microscopic examination of these shows that the normal hexameral regularity of one of the polyps, along with the presence of two pairs of directives, has in no way been disturbed, and the other polyp is either perfectly hexameral, or evidently on the way to become so. Such double polyps can certainly not be regarded as fission products, at any rate not according to the plan followed where fissiparity prevails. They seem best understood as discal buds, or as examples of fissiparous gemmation (see foot-note).

It is but one step from discal budding to oral fission, or perhaps the conception may be

[a] The occasional instances of simple fission in corals reproducing by gemmation have since been found to be a modified form of budding, which I have termed "Fissiparous Gemmation"; the products are altogether different from those in ordinary fissiparous growth, being cyclical, hexamerous polyps, with two pairs of directives. This discovery greatly strengthens the separation between the two groups of corals. "Morphology of the Madreporaria.—IV. Fissiparous Gemmation." Ann. Mag. Nat. Hist. (In press.)

simplified by regarding the latter as stomodæal budding; but, as already stated, the step involves an important morphological distinction. Although the stages in division of the mouth or stomodæum have not been actually observed, the results to be detailed below prove conclusively that in fission the stomodæal wall is actually divided into two equal or unequal parts, and that the complete mesenteries inserted on each part go along with it, and help to form the new or daughter polyp. The plane of fission is entocœlic, and usually at right angles to the directive plane and longer oral axis; hence, only one pair of directives is retained by each of the two primary daughter polyps (p. 505). Were fission to proceed no further in all probability the mesenteries in their later growth would assume the hexameral plan, and the polyps would only differ from a larval or bud polyp in having but one pair of directives. In most instances, however, the daughter fission polyps are again subjected to fission, so that they never attain a truly regular cyclic character.

The process of polypal gemmation and fissiparity, as revealed by individual species, will be briefly described. *Madrepora*, *Solenastræa*, and *Cladocora* will serve as examples of the former, and *Manicina* and *Favia* as illustrations of the latter phenomenon.

BUDDING IN MADREPORA.

Madrepora is a favorable form on which to study extratentacular gemmation, in a region in which there is no perithecal continuation of the mesenteries (cœnosarc). The early stages are reproduced on Pl. III, figs. 22–27, taken from longitudinal sections of a very young bud, a little below the apex of a branch.

All the sections represented are from the left side of the median axis of the bud, but the sections on the other side exhibit the same details. The right end is upper in relation to the axis of the branch on which the bud was situated, and the left end is lower. Fig. 22 is from the median dorso-ventral plane passing through the stomodæum and the axial entocœles. The polyp is yet scarcely raised above the general surface of the cœnosarc; the ridges above and below (right and left in figure) probably indicate the commencement of the axial entocœlic tentacles, and the included depression the central part of the oral disk. Compared with that of the colony generally, no histological difference is yet presented by the outer ectoderm. Communication between the exterior and the superficial canal system has just been definitely established, the mesoglœa of the cœnosarc passing directly into that of the stomodæal wall. The stomodæal walls hang freely within a superficial longitudinal canal, differing in no important respect from the others around; but as the sections are taken in a longitudinal direction, the canals appear much longer than in the case of transverse sections (Pl. I, figs. 2–6). The endoderm of the canal has undergone a marked alteration from that lining the canals and gastric cavity of the polyps. It is broader, more strongly ciliated, non-vacuolated, and zooxanthellæ are practically absent, though present in the surrounding canals; long, narrow, supporting cells, with abundant protoplasmic contents, are the chief constituents. As best shown in figs. 23 and 24, the endoderm of the canal becomes thinner and more normal toward the periphery of the chamber; the inner and outer layers –ectoderm and endoderm– of the stomodæal walls are histologically alike.

The stomodæal wall for a few sections beyond that represented in fig. 22 appears as a projection from the superficial wall of the colony, hanging freely within the canal; the periphery of the projection exhibits four vertical mesoglœal strands, connected with a lower transverse strand. Later, as shown in fig. 23, three central cavities appear and separate the ridges into four distinct components. The lower transverse connecting strand is the horizontal continuation of the stomodæal wall, and the vertical strands represent the mesenteries, not yet separated from one another. The stomodæal wall is continued, as it were, along the free edges of the mesenteries, as often happens in adult polyps. In the next section, fig. 24, the upper and lower (right and left) projections have become free, but the two inner are still united by the stomodæal prolongation.

The two inner mesenteries afterwards, fig. 25, become free, and now the uppermost of the four is united with the boundary layer of the canal, and in the later sections ceases to exist. Immediately below the uppermost mesentery is a slight projection of the cœnosarcal endoderm

surrounding a mesogloeal axis, which represents a rudimentary mesentery; and a few sections beyond, another rudimentary mesentery is revealed. Thus the six mesenteries of one side of the adult polyp of *Madrepora* are accounted for, four large and two small. The upper and lowermost of the four complete mesenteries now begin to diminish in size, and in fig. 26 have disappeared at the place at which the skeletotrophic layer of the canal is united with the cœnosarc; the uppermost of the two rudimentary mesenteries has likewise passed away. There now remain only the two middle mesenteries of the larger four, and the lower of the rudimentary two, and of the former, the upper is much larger than the lower. The difference is more marked in fig. 27, where the lower mesentery is disappearing, again at the union of the skeletotrophic layer with the superficial wall; the rudimentary mesentery has already disappeared. A little later, the remaining mesentery has united with the skeletotrophic layer, and is soon lost in sections beyond.

The series of sections illustrates, in the clearest manner, that buds of *Madrepora* arise along the superficial wall of a simple external canal, independently of any structural connection with the other polyps, though in communication with them by means of the canal system. The six pairs of mesenteries are fully established before the tentacles appear, and the septa are as yet wholly unrepresented. The rudimentary stage of the bud as a whole would indicate that very little time elapses between the development of the different pairs of mesenteries, if, indeed, they do not appear simultaneously. Four of the pairs of mesenteries unite early with the stomodæum, probably originating along with it; the two remaining pairs are independent of the stomodæum throughout. The complete and incomplete nature of the mesenteries thus early indicated is retained in the adult polyp; for a short distance the four larger complete mesenteries are already united with the skeletotrophic tissues, but the others have a free course from beginning to end.

The musculature at this stage is too rudimentary to afford any assistance in determining which are the directive mesenteries. But comparing the arrangement with that in transverse sections of *Madrepora* (Pl. I), there can be no doubt that the four pairs of mesenteries inserted on the stomodæum represent the eight complete mesenteries, which in the adult extend along the stomodæum, and that the two pairs of rudimentary mesenteries correspond with the free pairs, V and VI, of the adult. The outer mesenteries, right and left, will be the directives III and IV, and the two inner pairs, I and II, will be the first and second bilateral pairs. The right end of the sections being upper or axial, and the left end lower or abaxial, in relation to the colony, it is clear that the axial-abaxial relations of the complete and incomplete mesenteries are exactly as in an adult polyp.

Each of the complete mesenteries, on becoming free from the stomodæum, is somewhat club-shaped in section, but no sharp distinction yet exists between the filamental portion and the epithelium along each face, or, indeed, from the endoderm of the outer wall generally. On Pl. II, fig. 20, is represented the mesentery from another bud, at a somewhat later stage, showing the early development of the filament. The terminal region stains a little more deeply than the lateral, owing to the greater closeness of the cells, and consequent greater number of nuclei, but the tissue passes into that of the mesenterial endoderm by an insensible gradation. The gland cells and nematoblasts, characteristic of the adult filament, are not yet distinguishable.

The strong ciliation of the whole endoderm in the bud, in the earliest stages of development, is probably to be associated with the greater need of bringing an extra supply of nutrient fluid to the rapidly growing parts, while as yet the polyp is unable to take in food for itself through the oral aperture. It is only later, when direct communication with the exterior has been established for some time, that the different polypal functions become more restricted to special regions, and these exhibit corresponding histological modifications.

The subsequent development of the *Madrepora* bud takes place by an upward growth beyond the general surface of the colony. In radial polyps the lower (sulcular) region grows more rapidly than the upper (sulcar), so that the former comes to lie outside and the latter on the

inside in regard to the axis of the branch. In this way the axial and abaxial relations are established.

Dr. G. H. Fowler (1887, p. 12) has contributed some brief notes upon the budding of *Madrepora aspera* (Dana), founded upon an examination of the soft tissues of the developing polyps at the apex of the branches, while G. von Koch, in his paper "Die ungeschlechtliche Vermehrung (Knospung und Stockbildung) von Madrepora," 1893, has made an important study of the same subject, but more particularly with regard to the skeleton. The short account of Fowler indicates that the stomodæum is invaginated to a considerable depth into the future polyp cavity before it is perforated, and also apparently before any mesenteries arise. The first mesenteries, already bearing filaments, are formed from the walls of the canals, apparently independently of the rest of the polyp, the connection with the stomodæum being established later. The process of gemmation in Fowler's species is thus altogether different from that in the West Indian *Madrepora*.

Many attempts have been made to obtain the early stages in the gemmation of *Porites*, but without any material results. Sections through polyps with six or eight tentacles show a corresponding number of complete mesenteries, but the remaining members necessary to make up the normal six pairs are also present, though not developed to the same degree as in older polyps. It may be that in *Porites*, as in *Madrepora*, the full complement of twelve protocnemes is produced at a very early stage and before the tentacles make their appearance.

BUDDING IN SOLENASTRÆA.

Among Astræan colonies, such as *Orbicella* and *Solenastræa*, new polyps may be either intercalary or marginal in origin. By means of the latter the colony spreads laterally, while the intercalary buds serve to occupy the larger superficial area as the colony rises in height.

The earliest marginal buds observable in colonies of *Solenastræa* are already separated from adjacent polyps on the inner side by an external groove, while the outer side, forming the periphery of the colony, is necessarily independent of other polyps. Sections made through one of these marginal buds, preserved in the expanded condition, reveal at different levels the details represented on Pl. XII, figs. 86–90.

Through the transparent tissues eight perfect mesenteries were seen to be already developed, but no tentacles were yet apparent. Fig. 86 is from a transverse section through the free stomodæal region of the column wall. All the protocnemes are present, but only the eight Edwardsian mesenteries are yet complete, while in the exocœle on each side of the dorsal directives the rudiments of a pair of second-cycle mesenteries (A, A) are visible.

The section represented in fig. 87 reveals the conditions at the level at which the bud is connected with the mother polyp on the inner side, but is free on its outer aspect: from the arrangement of the mesenteries the outer side is seen to be the sulcar or ventral aspect, and the inner the sulcular or dorsal border. The eight Edwardsian mesenteries alone bear mesenterial filaments, and the retractor muscles are sufficiently well developed to enable the pairs of directives to be determined. The pairs of metacnemes within the sulculo-lateral exocœles are better developed than in the previous figure, and another pair (B) has appeared in the left middle lateral exocœle, but the corresponding pair on the right side is undeveloped, and at this stage mesentery V has nearly disappeared on the same side. The boundary wall between the bud and the fully developed polyp is perforated in a number of places, and by this means communication between the gastro-cœlomic cavity of each is permitted. The portions of the skeleton of the adult polyp, added on the upper part of the section, represent the exsert septa, the polyp being in an expanded condition; the entocœlic septa are large and the exocœlic small. No continuity between the mesenteries of the bud of the adult polyp are represented in this or any of the sections. To the right, at the angle between the wall of the bud and the adjacent polyp, are the first indications of another bud.

Fig. 88 is taken from the region of the polyp wholly embedded in the corallum, except for a limited area on the right upper side; the bud polyp is now entirely separated from that

adjacent. On the right upper side of the directive axis the fifth and sixth protocnemes, incomplete from the beginning, have now disappeared, as is also the case with the pair of metacnemes on the same side. Mesenterial filaments are no longer present on the dorsal directives (IV, IV), and the pair of metacnemes has also disappeared from the middle exocœle on the left side, but the dorsal pair (A), though very feeble, still persists.

The arrangement of the septal ingrowths, present as yet only on the left lower side, is very instructive. The largest occur within the entocœle of the pairs of directives; two are found between the left dorsal mesentery and the mesentery of the first bilateral pair (IV–II); two between this last mesentery and the mesentery of the second bilateral pair (II–I), while only one appears between this and the left ventral directive (I–III). Three of the septal invaginations are exocœlic, the exocœle of the dorso-lateral pair of protocnemes (II, V) is provided with one, but the septum of the exocœle of the ventro-lateral pair (I, VI) is as yet undeveloped. The entocœle of the persistent pair of metacnemes (A) also contains an invagination.

In the section from a still lower region, represented in fig. 89, fully developed filaments are retained only on the first three bilateral pairs of protocnemes. Only nine mesenteries are present, the mesentery remaining in addition to the Edwardsian mesenteries is the fifth member of the left side. A septum occupies each chamber between any two mesenteries, whether the two constitute a pair or not; the septum in the entocœle of the left dorso-lateral pair is small, and soon disappears along with mesentery V. The skeletal fragments within the middle of the gastro-cœlomic cavity represent the first appearance of the columellar projections.

In fig. 90 only mere traces of six of the mesenteries persist, the first pair being the strongest; the number of septa is also six, corresponding with the number of mesenteries. With one exception the septa are all united in the middle, otherwise the gastro-cœlomic cavity is divided into as many separate chambers as there are septa.

Another bud of about the same age presents a different condition with regard to the appearance of the first two pairs of metacnemes from that just described (fig. 82). The protocnemes are at the *Edwardsia*-stage, and within each of the median lateral exocœles are the rudiments of a bilateral pair of metacnemes (A, A), which are somewhat better developed in sections below the stomodæum.

The tentacles in the bud have already appeared, and exhibit an interesting stage. Fig. 83 is taken from a slightly oblique section, the upper half through the free portion of the tentacles, and the lower through their attachment to the periphery of the disk. The polyp was expanded to such a degree that the peristome projected in a cone-like manner beyond the zone of tentacles, and, as seen in the middle of the section, the Edwardsian mesenteries extend as far as the stomodæal walls. Ten of the tentacles show a regular alternation of large and small members, and, superposing the section on that in fig. 82, the tentacles arising from the entocœles are seen to be the larger, and those from the exocœles the smaller. In place of the single median lateral prototentacle on each side are three tentacles, as yet incompletely formed. These will be found to correspond in position with the incipient pair of metacnemes in the median lateral exocœles, and serve to establish that the metatentacles arise practically simultaneously with the metacnemes, an entocœlic and an exocœlic member together.

A third bud, somewhat older than either of the two described, was also studied, and the details of its lower region are represented on Pl. XIII, fig. 91. The upper right side is the border toward the centre of the colony, and the lower left side is the outer aspect. The relationships of the mesenteries, as before, show the inner border to be the sulcular aspect, and the outer border the sulcar. In the stomodæal area six pairs of protocnemes and six pairs of metacnemes occur, and of the former all the pairs are complete on one side, but the members of the fifth and sixth pairs are incomplete on the other side.

In the region represented only four pairs of the metacnemes occur, the two pairs on the upper left side having disappeared some distance above. Mesenterial filaments occur on the Edwardsian mesenteries, but not on the fifth and sixth bilateral pairs; and septal invaginations, both entocœlic and exocœlic, appear within practically all the mesenterial spaces.

The lower sections demonstrate the same relation as in the previous bud, namely, that as the

mesenteries disappear, so do the corresponding septal invaginations; the metacnemes disappear first in unilateral pairs, the protocnemes in bilateral pairs. In the anterior part of the section is seen the beginning of another polyp.

Two somewhat older buds sectionized presented the following conditions: In one only ten pairs of mesenteries were developed, five complete and five incomplete, in regular alternation; in the other eleven pairs occurred, six complete and five incomplete.

The results thus briefly indicated may be summarized:

(1) The polyps of *Solenastræa*, produced asexually by gemmation, pass through the *Edwardsia*-stage of mesenterial development, in which four pairs of the protocnemes are complete and two pairs incomplete, just as in larval polyps.

(2) The metacnemes begin to make their appearance before this stage is passed over, that is, before the union of the fifth and sixth pairs of protocnemes with the stomodæum takes place.

(3) The first metacnemes appear along the polypal wall, at about the level of the inner termination of the stomodæum, as isocnemic pairs within the dorsal or sulcular primary exocœles, but in one case within the median lateral exocœles.

(4) In relation to the colony as a whole the dorsal or sulcular side is inner (axial), and the ventral or sulcar outer (abaxial). The succession of the metacnemes is therefore dorso-ventral, antero-posterior, or from the axial to the abaxial side of the bud.

(5) The mesenterial filaments and mesenteries disappear below inversely as the order of their development: first, the metacnemes in unilateral pairs, then the protocnemes in bilateral pairs.

(6) In the same transverse section the growth on one side of a polyp may be slightly in advance of the growth on the other side.

(7) The metasepta and metatentacles, both entocœlic and exocœlic, arise practically *pari passu* with the mesenteries.

BUDDING IN CLADOCORA.

The young buds in *Cladocora arbuscula* generally occur singly toward the upper part of the column wall of the terminal polyp of the sub-colonies. What seems to be discal budding has also been found to take place, when both the parent and daughter polyps are surrounded by a continuous system of tentacles and a single column wall; but the extratentacular buds seem rarely to arise above the level of the corallite. The reproductive power of any polyp is very limited, for as a rule not more than three or four polyps are connected in a sub-colony, and among these is rarely more than one immature example. Each polyp in its turn may give rise to buds, either before or after becoming distinct from the rest of the sub-colony. At a very early stage the growth of the lower abaxial aspect of the bud is in advance of the upper or axial aspect, thus giving rise to the obliquity of the polyps to one another.

Numerous extratentacular buds of slightly different sizes have been studied, and in most specimens eight complete and four incomplete mesenteries are already present, their arrangement and musculature agreeing with that of the protocnemes in larvæ of the same stage. In one case the fifth and sixth developmental pairs were absent, and, following the sections downward, only four mesenteries were present a short distance below the stomodæum; then two of these disappeared; the two remaining, which represented the first developmental pair of mesenteries, were continued much farther, and bore mesenterial filaments almost to their termination. At this early stage none of the mesenteries were in any way connected with the extrathecal continuations of the mesenteries of the parent polyp, so that evidently the buds arise on the column wall quite independently of any of the other organs of the parent, as happens in *Madrepora*, and as appears to be also the case in *Solenastræa*.

Pl. VIII, fig. 61, represents a transverse section through a bud in which two pairs of metacnemes have appeared, in addition to the six pairs of protocnemes. Owing to the difference of level at which the corresponding details occur on the inner and outer surface, as a result of the obliquity of growth, it is usually impossible to obtain all that is desired in one section: the figure is therefore a combination of the inner and outer regions of sections at slightly different levels. Above the bud is a portion of the edge-zone of an adjacent polyp.

The sulco-sulcular axis is a little to the side of the axial-abaxial plane. Only the eight Edwardsian mesenteries bear mesenterial filaments, and these alone are complete. A pair of metacnemes (A) have made their appearance in the exocœle on each side of the sulcar directives; they are feebly developed, and extend for only a few sections below the termination of the stomodæum. The three septa—two entosepta and one exoseptum—already developed at the upper side of the bud are seen to be continuations of the costæ of the adjacent polyp.

Fig. 62 is taken from a bud at a somewhat later stage, preserved in a partly expanded condition, so that sections could be obtained almost independently of the skeleton. The specimen is exceptional in that only five pairs of protocnemes are present, instead of the usual six. The directives lie in the axial-abaxial plane, and development is most forward on the outer abaxial aspect of the bud. Five alternating pairs of mesenteries, belonging to the second cycle, have made their appearance within the primary exocœles, and the pairs exhibit a progressive order of development from one aspect of the polyp to the other: the two lower pairs are the largest, the musculature is well developed, and mesenterial filaments occur at their free edge; the middle pairs are smaller and without any trace of filaments, while the uppermost pair is quite rudimentary. Sections through five exsert septa are shown at the lower border, and are both entocœlic and exocœlic.

The section is of interest as indicating the tendency to irregularities in the early formation of the bud, but more particularly as exhibiting the progressive development of the metacnemes and their filaments from one side of the polyp toward the opposite side, and the appearance of both entocœlic and exocœlic septa in connection with the metacnemes, *pari passu* with the growth of the latter.

The section represented in fig. 60 is through the protruding cone-like disk of a fully expanded young polyp, and is of importance as showing that the fifth developmental pair of protocnemes may become complete in advance of the sixth pair. On the left side is seen the outwardly reflected lower edge of the stomodæum passing along the three lateral mesenteries, and the ectoderm of the stomodæum has assumed a very symmetrical form. Below the stomodæum the six pairs of protocnemes are equally developed, and the six pairs of the first cycle of metacnemes have also made their appearance.

Extratentacular gemmation in *Cladocora* proceeds therefore exactly as in *Solenastræa*, except in the one important fact, the metacnemic succession is reversed. In the latter it is from the dorsal to the ventral surface, while in the former it proceeds from the ventral to the dorsal. However, before this exceptional sequence in *Cladocora* can be regarded as established, it will be necessary to confirm it on polyps arising directly from larvæ.

Transverse sections were made through a double polyp of *Cladocora*, that is, one where two oral apertures are surrounded by only a single system of tentacles and the two polyps have only a common column wall. One polyp was normally hexamerous, having two orders of mesenteries, not much differentiated in size, and including two pairs of directives; it differs in no essential respect from a normal simple polyp. A small polyp to the left is evidently a bud which has arisen on the discal wall of an older polyp, and as yet is imperfectly developed, having only seven pairs of mesenteries, including one pair of directives. In the stomodæal region four of the pairs are complete and two incomplete.

If the sections be compared with those of the fission polyps of *Meandrina* and *Favia* (p. 505, *et seq.*) most important distinctions are at once manifest. In the two latter a normally hexamerous polyp has become divided through the stomodæum into practically equal halves, each half having only a single pair of directives, while in *Cladocora* a new polyp is growing by the side of another, which still retains the primary arrangement of the mesenteries, including two pairs of directives."

FISSION IN MANICINA.

Manicina areolata is one of the most favorable corals on which to study the process of continuous fission, on account of the readiness with which small colonies provided with only a

"The morphological significance of such double polyps in *Cladocora* and other corals has since been fully discussed in a paper on "Fissiparous Gemmation." See foot-note, p. 496.

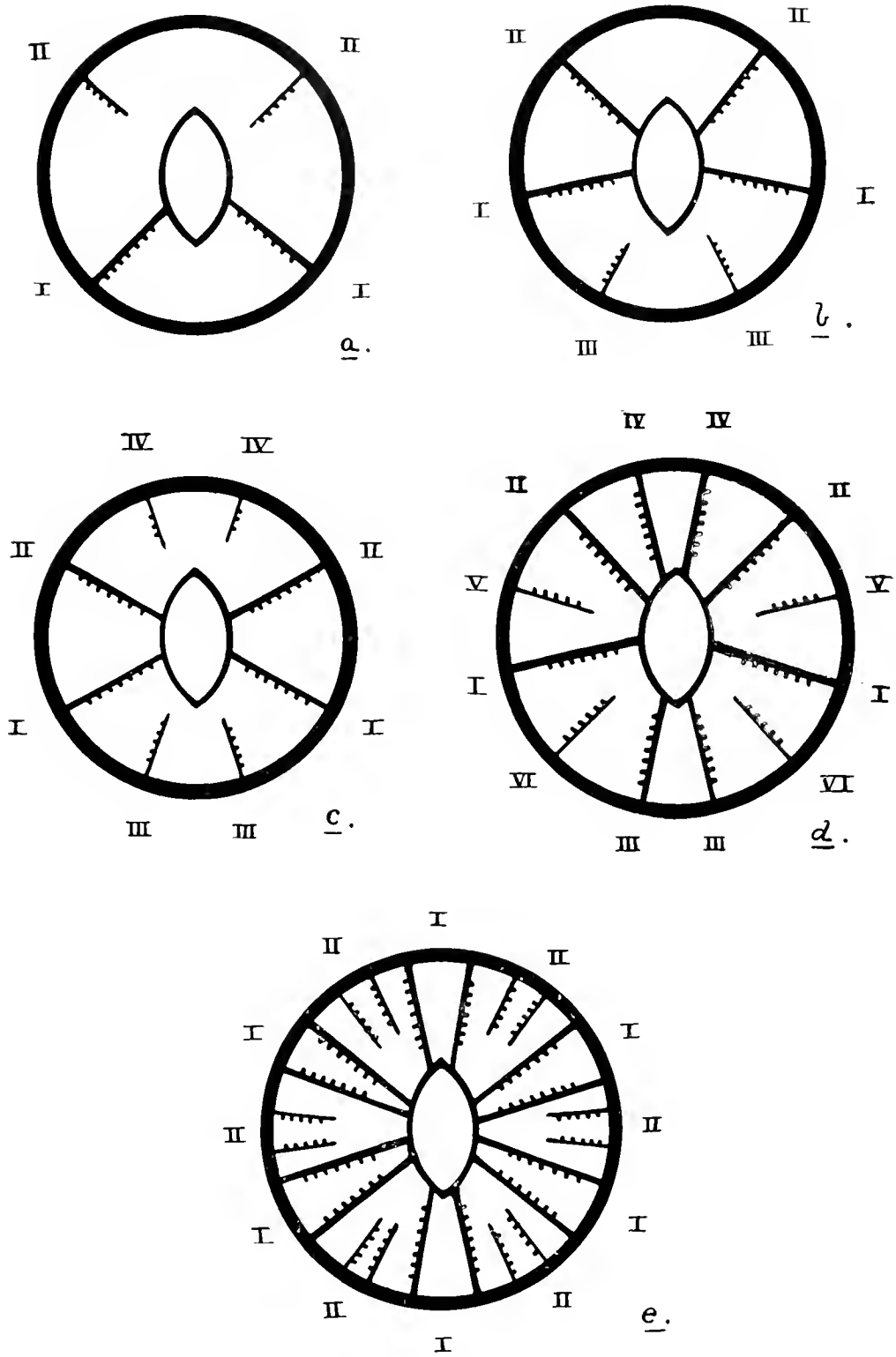

FIG. 13 (*a–e*)

Manicina areolata.—Figs. 13. Series of diagrammatic figures illustrating the mesenterial sequence in larvæ and larval polyps. *a, b* are taken from H. V. Wilson's (1888) account of the development of this species. *a*, Stage with two pairs of protocnemes, one pair of which is united with the stomodæum (*cf.* Wilson's fig. 18). *b*, Stage with three pairs of protocnemes, two pairs united with the stomodæum (*cf.* Wilson's fig. 27). *c*, Stage with four pairs of protocnemes (*cf.* Pl. xix, fig. 134). *d*, *Edwardsia*-stage. The larva is now fixed and remains at this stage for a considerable time, during which the six entocœlic septa are developed, and also the two cycles of tentacles (*cf* Pl. xix, fig. 135). *e*, Stage with six pairs of protocnemes, all united with the stomodæum, and the first cycle of metacnemes.

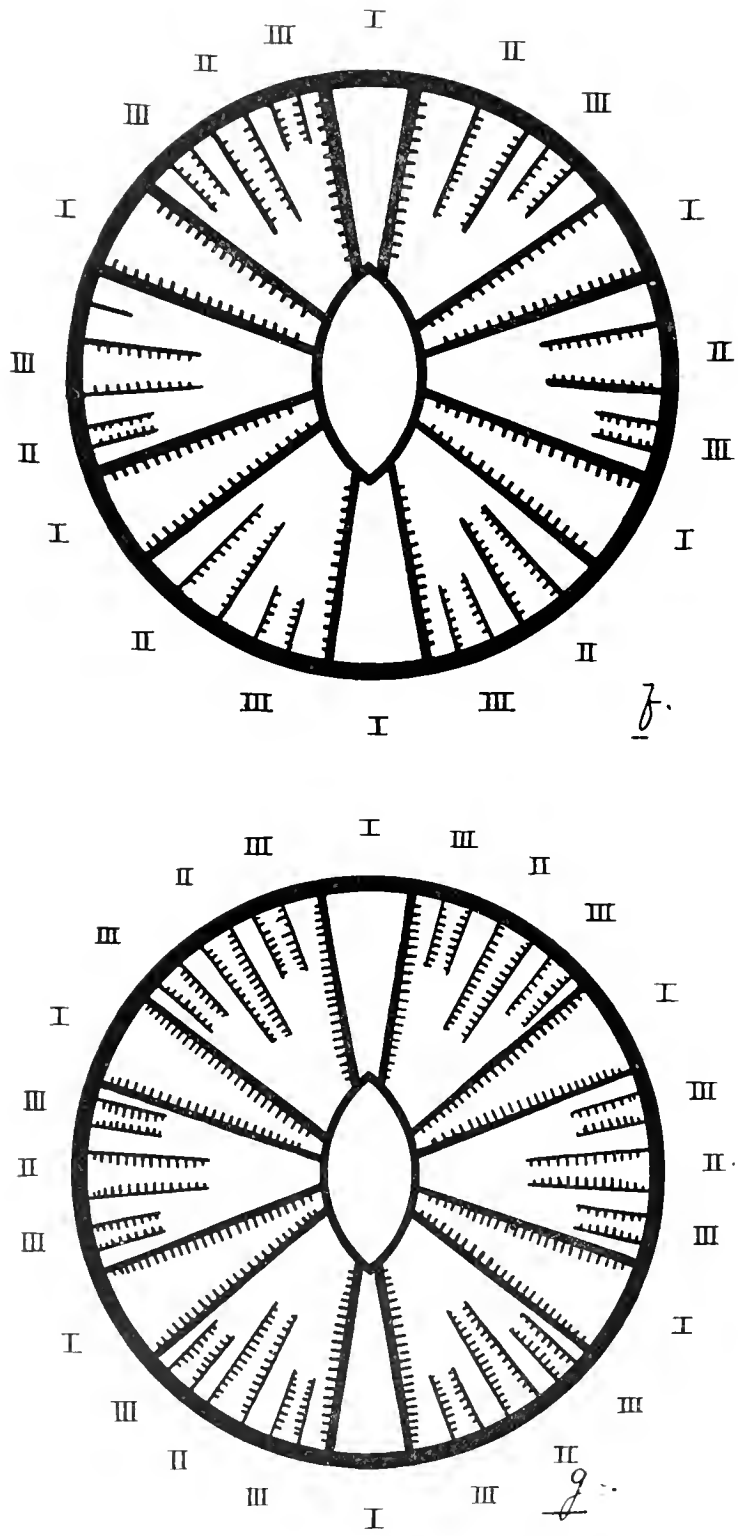

FIG. 13 (*f*, *g*).

Manicina areolata.—Mesenterial development in larval polyps continued. *f*, Seven pairs of metacnemes of the second cycle have now appeared. *g*, Stage with second cycle of twelve pairs of metacnemes complete. The young polyps now very rarely exhibit perfect regularity, the development being more advanced in some regions than in others. The members of the first cycle of metacnemes at this stage begin to unite with the stomodæum.

few oral apertures, and of a size suitable for sections, can be obtained. H. V. Wilson (1888) has traced the development of the primary mesenteries in the larvæ of this species, from the first to the sixth pairs, and has also shown that in young polyps, provided with only one oral aperture, the mesenteries are arranged in three hexamerous cycles. The first cycle comprises twelve pairs of complete mesenteries, two pairs of which are directives; the second cycle also contains twelve alternating pairs; and the third twenty-four. At this early stage the polyps of *Manicina* therefore correspond exactly, so far as regards the mesenterial arrangement, with any normal hexactinian Madreporarian or Actiniarian polyp. The diagrammatic figures on pp. 503, 504 represent most of the stages in the appearance of the mesenteries of *Manicina*. The earlier sequences have been already described (p. 450), so that attention need be directed only to the later stages, which illustrate the phenomena of fissiparity. In Kingston Harbor young polyps of *M. areolata*, with the disk bearing only one, two, or four oral apertures, are not infrequently found, fixed to older colonies of the same species, or to other corals or small pebbles.

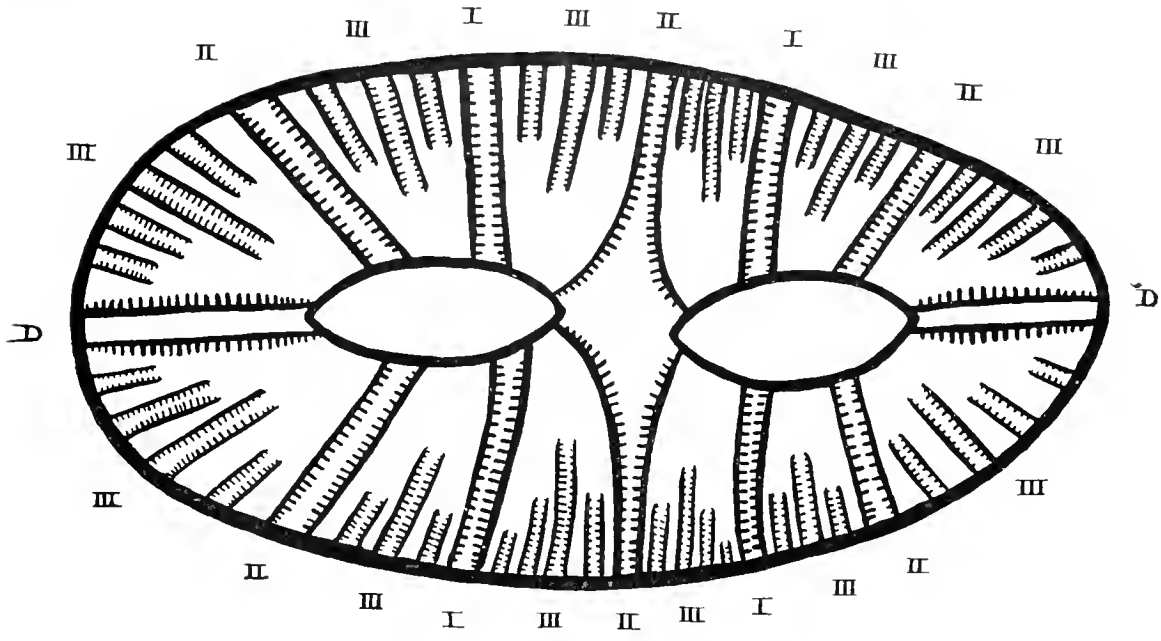

Fig. 14*a*.

Manicina areolata.—Figs. 14. Diagrammatic figures illustrating fission. *a*, Polyp with two oral apertures, twelve pairs of complete mesenteries (I, II), twelve alternating second-cycle pairs (III), twenty-four third-cycle pairs, and a few members of a fourth cycle. Associated with each stomodæum are six pairs of mesenteries, three pairs of which are protocnemes, a pair of directives being at opposite extremities. The plane of fission is within the entocœle of the middle pair of complete mesenteries on each side.

Fig. 14*a* represents the conditions in a transverse section of *Manicina* through the stomodæal region of a polyp with two oral apertures. The twelve pairs of complete mesenteries, including the two pairs of directives, represent the first and second cycles of fig. 13*g*, and comprise two alternating orders, primary and secondary, each of six mesenterial pairs; the twelve pairs of large incomplete mesenteries constitute the third order, the twenty-four next in size a fourth order, while here and there, at regions of most forward growth, occur rudimentary pairs, which are the first indications of a fifth order. The originally simple stomodæum has become divided into two, and half the complete mesenteries of the primary polyp are now associated with each stomodæum. The plane of fission passes through the entocœle of the middle lateral pair of complete mesenteries on each side, and a single pair of directives at the opposite extremities of the polyp remains attached to each stomodæum. The plane of fission is thus at right angles to the directive plane, which is also the plane including the longer oral axis of the simple polyp.

Were the separation of the disk and column wall to be completed at this stage, across the plane of fission, it is clear that two similar daughter polyps would be produced. In each case one moiety of the middle mesenterial pair of one side would form with the corresponding mesentery from the other side a pair, attached to the side of the stomodæum opposite the directives. But the longitudinal muscles of the two mesenteries in each pair would be arranged so as to face one another, instead of turning from one another, as in the case of the directives; in other words, the complete mesenteries of each polyp would include only one pair of directives, and five pairs in which the retractor muscles are vis-a-vis. The six pairs of complete mesenteries attached to each stomodæum would then constitute a first cycle, the six large alternating pairs a second, the twelve next a third cycle, and the odd pairs would represent the commencement of a fourth cycle.

The almost perfect regularity in the number, arrangement, and extent of development of the mesenteries found in the above example appears to be rather exceptional, for other specimens of *Manicina* sectionized reveal many irregularities. Fig. 14*b* represents the mesenterial arrangement in a second polyp, also bearing two oral apertures. The details are those presented by a single section toward the lower termination of each stomodæum. The hexameral regularity has been altogether lost, or perhaps was never reached. But here again the plane of fission passes through the entocœle of two opposite pairs of complete mesenteries, at right angles to the direc-

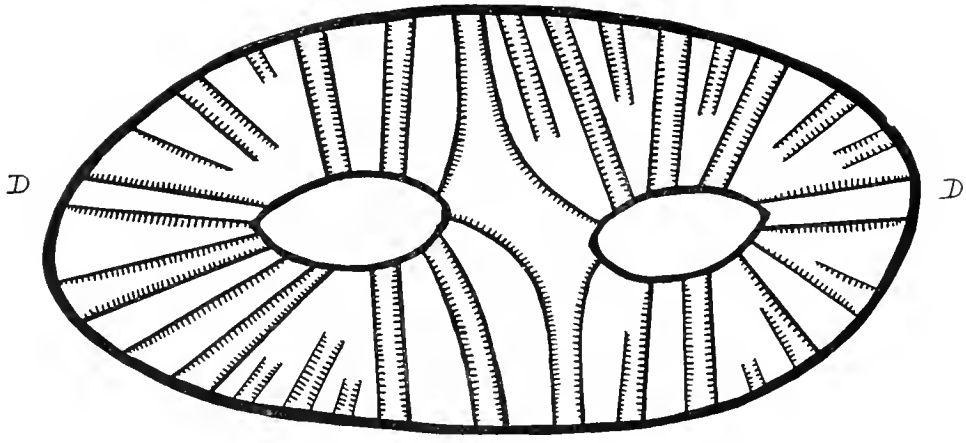

FIG. 14*b*.

Manicina areolata.—Another polyp with two oral apertures. The mesenteries have entirely lost their hexameral cyclic regularity, and of the protocnemes only the directives at opposite ends can be determined with certainty.

tive plane, and one of the two pairs of primary directives is found at each extremity. More than six pairs of complete mesenteries are united with each stomodæum, and only in two or three regions of the polypal wall are any members of the second and third cycles developed; the hexameral cyclic plan will be entirely lacking in the daughter polyps as in the original, and two or more complete mesenterial pairs may occur in succession, without any alternating incomplete members. In the sections higher than the one represented other pairs of small mesenteries occur, but do not in any way assist towards the production of the hexameral regularity. At the left end of the polyp two single large mesenteries occur, without any corresponding member to complete the pairs; higher sections demonstrate that one moiety has simply disappeared in advance of the other.

In a third bi-oral polyp studied the alternation of first, second, and third cycles of mesenteries was a little more regular than in the last example, but was by no means perfect all round; one stomodæum was provided with six pairs of complete mesenteries, while to the other eight pairs were attached.

Young polyps of *Manicina* with three oral apertures are not so plentiful as specimens with two or four apertures. It seems not unlikely that after the first division into two, each stomodæum is again divided at about the same time, and thus the stage with three apertures would rarely occur.

Fig. 14*c* is a diagrammatic representation of the mesenteries in a *Manicina* colony with four oral apertures. The longer axis of any one stomodæum is now in a different plane from that of others, and the two primary pairs of directives are widely separated, but still situated at the opposite extremities of the colony; the two middle stomodæa have no directive mesenteries inserted on their walls. The plane of separation of each stomodæal system with one exception passes through two entocœles. The rule holds so far as the divisions on the lower side are concerned, but on the left upper side the division plane is exocœlic, a condition which is probably to be regarded as an individual irregularity.

The number of mesenteries connected with each stomodæum is inconstant; the stomodæum at the right extremity bears twelve, the next fourteen, the third twelve, while that at the left end has seventeen. The alternating incomplete pairs are still more irregular. In one or two

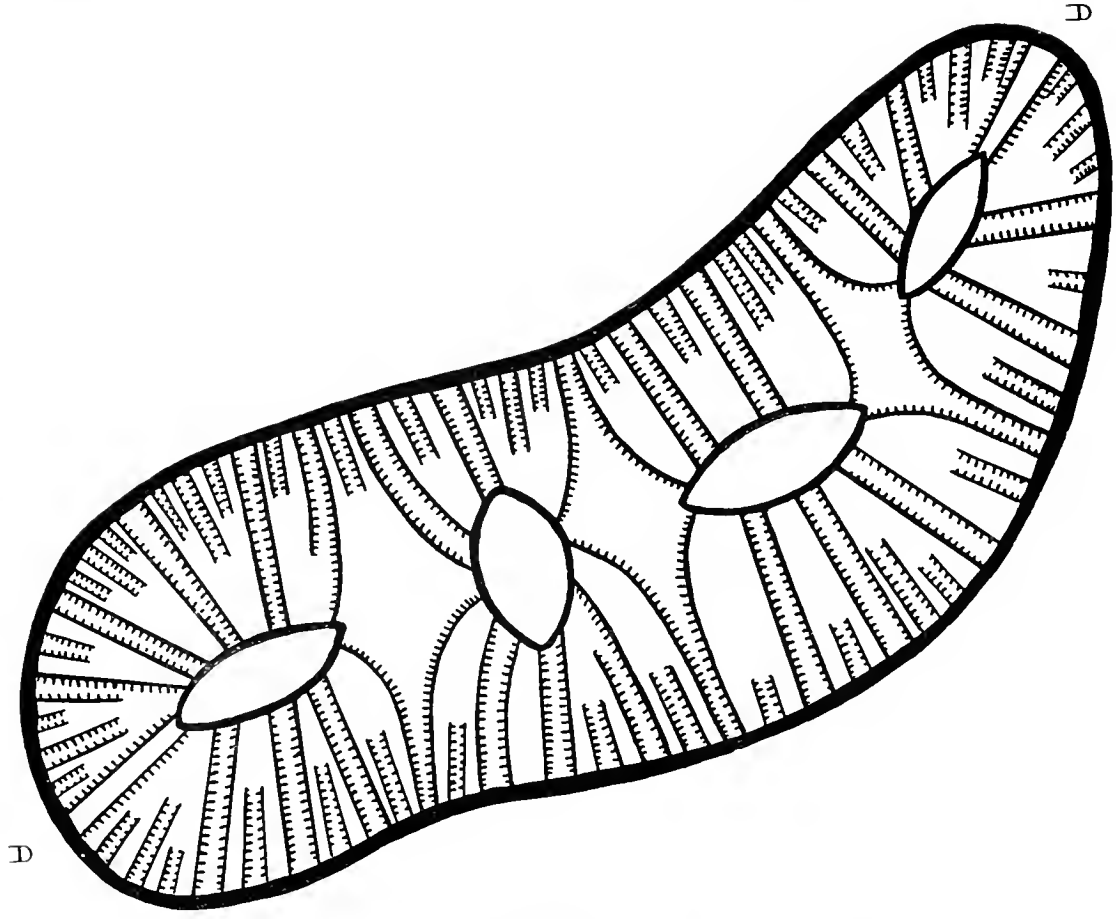

Fig. 14*c*.

Manicina areolata.—Polyp with four oral apertures. The mesenteries exhibit a tendency to an arrangement in alternate complete and incomplete pairs. The regions of most vigorous growth are at the opposite ends, where also the primary directives are still situated The fission planes are entocœlic, except for the irregularity at the upper left hand corner.

cases they are wholly absent from the exocœle between two pairs of complete mesenteries; in many others only one pair occurs; while in a few chambers two or three pairs, representing the second and third cycles, are developed. As in the previous figure, the tendency in the older regions is toward a system of alternating incomplete and complete pairs, and only at places of most forward growth are the third and fourth cycles represented. The incomplete mesenteries further exhibit great variation in the extent of development at one and the same level; some pairs are nearly as large as the complete mesenteries, while others are rudimentary. The variability is such as to indicate that when the members of the younger orders increase in size they may ultimately unite with the stomodæum, and newer pairs appear in their exocœles. Under such circumstances it is scarcely possible to determine a cyclical plan.

The phenomena presented by the early divisions of *Manicina* clearly prove that fission actually takes place in a plane at right angles to the long axis of the mouth and stomodæum; otherwise the regular distribution to each daughter stomodæum of six complete pairs of mesenteries, derived from the primary twelve pairs, with one pair of directives only at opposite extremities, would be inconceivable. Although among the many living colonies which have been examined, examples in which the oral aperture or stomodæum was in the actual process of division have not been observed, yet frequently two small mouths are found in close proximity, suggesting that they have arisen from the splitting of a single larger aperture.

The later divisions in *Manicina* reveal that the fission of the stomodæum, along with its associated mesenteries, is not always median, or results in the production of equal halves. Sometimes in living polyps a very small aperture will be found, as if cut off from a larger, and only a few mesenteries are associated with it compared with the number united with the latter.

FISSION IN FAVIA.

Favia fragum occurs in some abundance on the reefs throughout the West Indies, forming small, convex, hemispheroidal or irregular colonies, usually four to five centimeters in diameter.

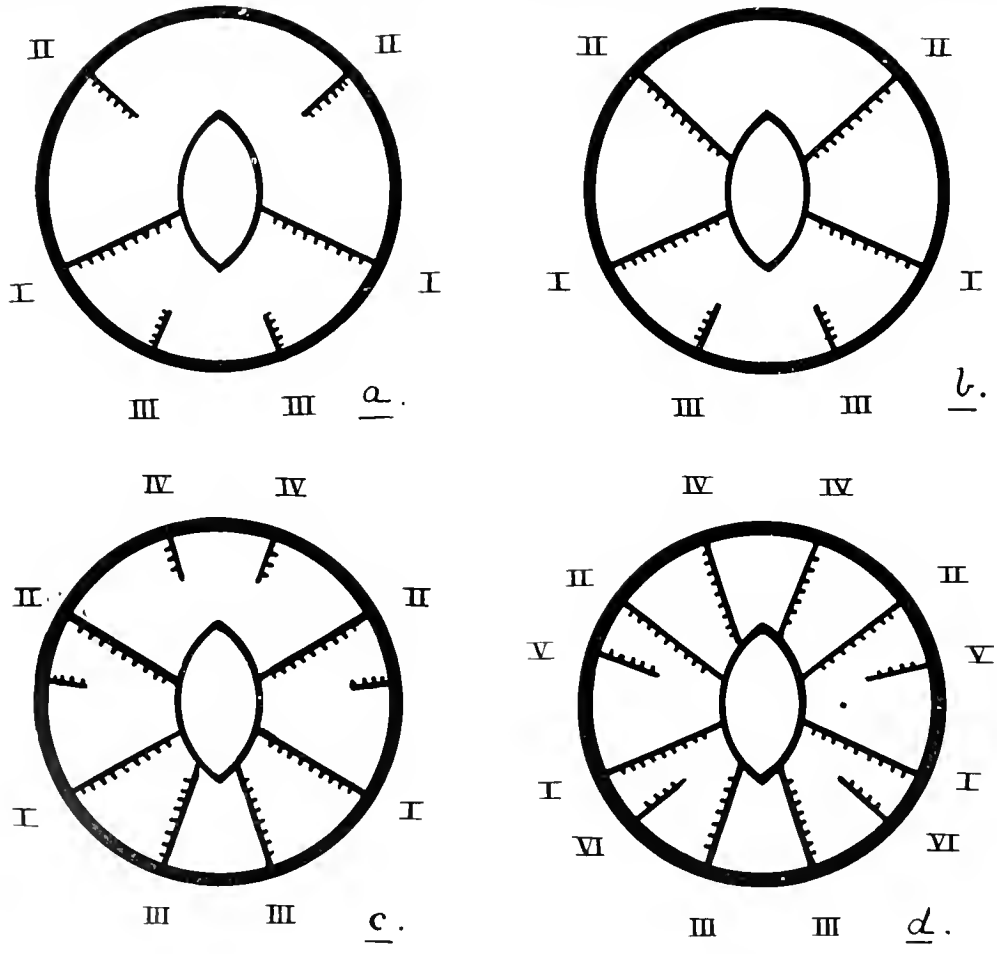

FIG. 15 (*a–d*).

Favia fragum.—Figs. 15. Diagrammatic figures illustrating the mesenterial sequence and fission in larvæ. *a*, Larva with three pairs of protocnemes, of which only one pair is complete (*cf.* Pl. XIV, fig. 112). *b*, Larva with three protocnemic pairs, of which two are complete (*cf.* Pl. XV, fig. 113). *c*, Larva with five pairs of protocnemes, of which three pairs are complete and two pairs incomplete (*cf.* Pl. XV, fig. 115). *d*, Larva at stage of fixation, with Edwardsian mesenteries complete and fifth and sixth pairs incomplete.

New polyps are added to the colony by division of the older polyps, apparently never by budding. A polyp sometimes exhibits two or three oral apertures on a single elongated or triangu-

lar disk, surrounded by a single system of tentacles; and in the different polyps of any colony all stages can be traced in the separation of the results of fission. It is therefore a very favorable species for the study of polypal fission. G. von Koch (1890) has already described the process as it occurs in the corallum of the nearly allied species, *Favia cavernosa*.

Fortunately, also, in *F. fragum* a complete series of stages illustrating the development of the mesenteries within the larva and young polyp is available, a series extending from the larva with only one pair of complete mesenteries to polyps with such a number as results in fission. The oldest stage reached by the mesenteries of the simple polyp is represented in fig. 15*g*, but the earlier stages may be briefly noted (figs. 15 *a*–*f*).

The twelve primary mesenteries are all developed at or shortly after the time of settling, when the larva exhibits the conditions represented in fig. 15*d*, four pairs of mesenteries complete and two pairs incomplete. Free swimming larvæ, extruded from mature polyps, are readily obtained, but can with difficulty be induced to settle, and development proceeds very slowly.

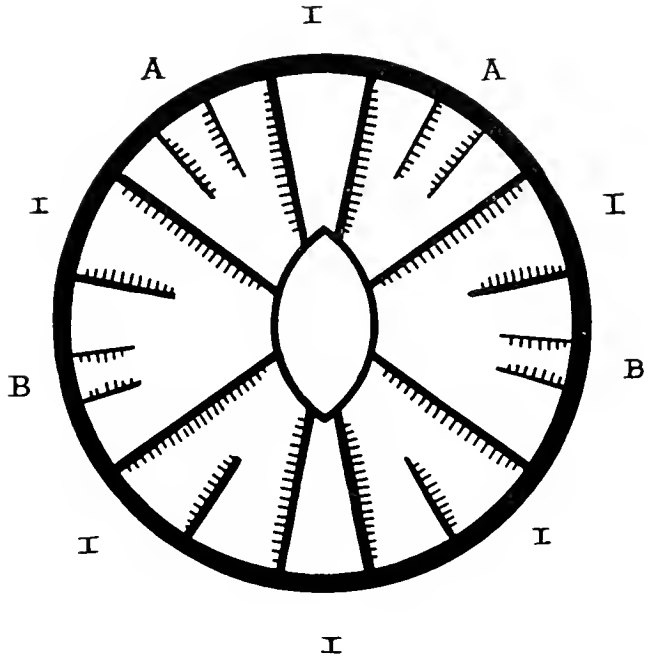

Fig. 15*c*.

Favia fragum.—Young polyp with four pairs of metacnemes (A, A; B, B). The succession of the second-cycle mesenteries is bilateral, from the dorsal to the ventral aspect (*cf.* Pl. xiv, fig. 109.)

However, on foreign objects, such as dead coral or old shells, to which the mature colonies are adherent, young polyps are sometimes found in different stages of development. These have grown from larvæ which on extrusion settled around the parent, and it was from such larval polyps that the stages represented in the text figures were taken.

Fig. 15*c* is from a young polyp in which four isocnemic pairs of mesenteries are present, in addition to the primary twelve. In the upper stomodæal region all the latter are inserted on the stomodæal wall, but the fifth and sixth pairs become free before the termination of the stomodæum is reached, and at this place the protocnemes are in exactly the same condition as in fig. 15*d*. The four pairs of new mesenteries are situated within the dorsal and middle primary exocœles on both sides of the polyp, and the dorsal pairs are somewhat further developed than the middle pairs.

Fig. 15*f* represents the mesenterial condition obtained from a transverse section through the lower part of the stomodæum of another decalcified polyp. The six protocnemic pairs are now

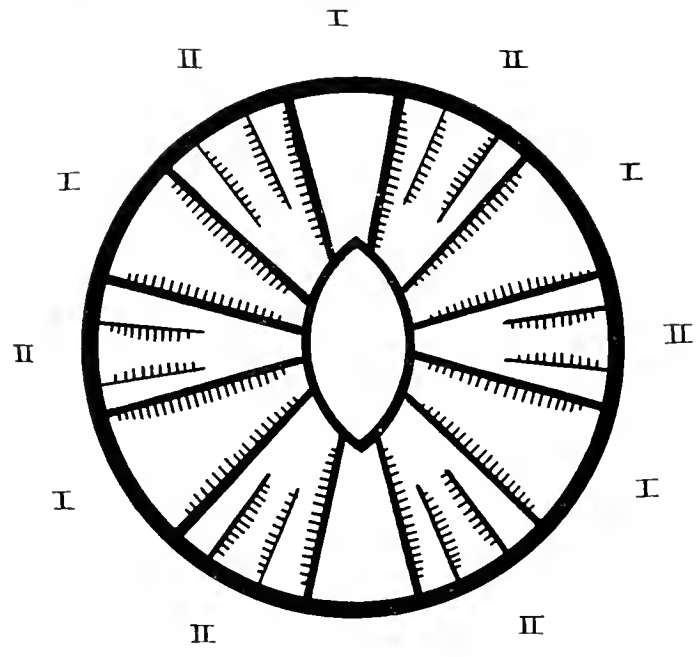

FIG. 15*f*.

Favia fragum.—Young polyp in which all the pairs of protocnemes (I) are united with the stomodæum, and the six pairs of first-cycle metacnemes (II) are developed.

all complete, and six alternating pairs of metacnemes are fully established as a second cycle. The next figure, from a somewhat larger polyp, shows the commencement of the third cycle of

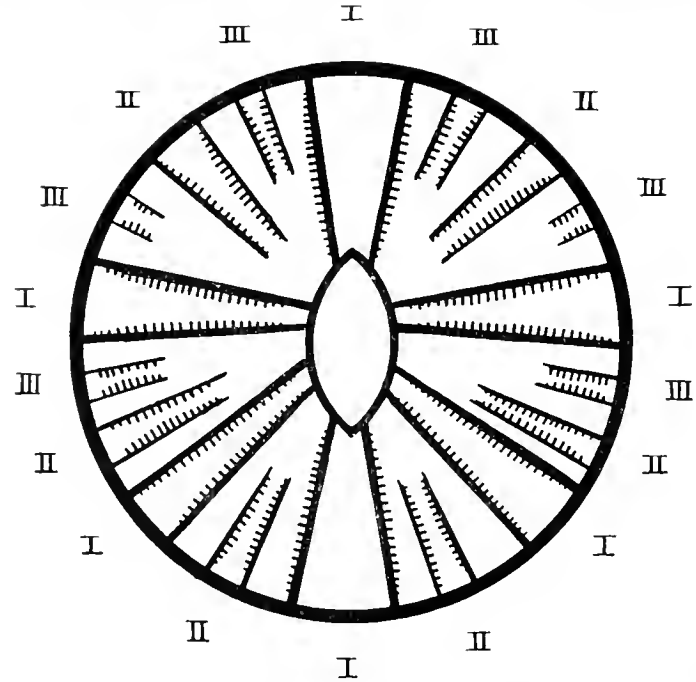

FIG. 15*g*.

Favia fragum.—Polyp with six pairs of second-cycle metacnemes (III). The succession is from the dorsal to the ventral aspect.

mesenteries (fig. 15*g*): its development also is proceeding by isocnemic pairs in a dorso-ventral or antero-posterior order.

The polyps of *Favia* growing directly from larvæ are thus seen to follow a very definite sequence in their mesenterial growth, a sequence which bears the closest resemblance to that characteristic of other larval corals which have been examined. Each is provided with two pairs of directives, and the mesenteries are arranged in two or three radial cycles, according to the usual hexameral plan. It is at about the stage represented by fig. 15*g* that fission is introduced.

Two larval polyps were secured, each provided with two oral apertures, but still surrounded by only one system of tentacles and a simple column wall. They thus represent the earliest stage in fission. At such a stage the polyps are very short, and rather irregular in form when preserved, so that it is practically impossible to secure in one section the complete arrangement of the mesenteries around the stomodæum. The diagrammatic figures are therefore constructed by combining the relationships of the mesenteries in the various serial sections. In each polyp the stomodæum has been divided throughout its length into two distinct tubes, and a definite number of mesenteries is associated with each.

The mesenterial system of one of the double polyps is represented by fig. 16*h*. Compared with the stage in fig. 15*g* two additional pairs of mesenteries have become complete, so that four pairs are inserted on each stomodæum. Instead of the two new complete pairs arising as a pair on each side of the directive plane, as considerations of symmetry would suggest, both are situated on one side of the angulated directive axis of the polyp, though from the section alone

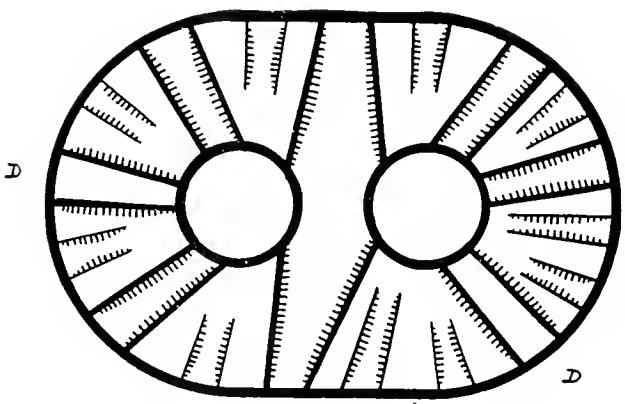

FIG. 16*h*.

Favia fragum.—First stage of fission in a larval polyp.

it is impossible to say which of the four pairs actually represent the additions. The members of the second cycle include only a single pair of mesenteries in each exocœle, except in the two exocœles adjacent to the right pair of directives, where third-cycle pairs are developed.

The two polypal halves are thus nearly alike, the original single stomodæum having been divided practically down its middle, so that half the mesenteries are attached to each moiety. The plane of fission crosses the directive axis, passing through the entocœle of two lateral pairs of complete mesenteries on opposite sides. Growth is taking place more rapidly at the upper right side than elsewhere, and the pair of directives has thus been pushed to one side of the median plane, so that the directive plane no longer divides the polyps into equal halves.

Were the halves to be completely separated at this stage, it is clear that a pair of mesenteries would be formed in each new polyp, by the approximation of a mesentery from the two opposite sides, the musculature in the two moieties being on the faces turned toward each other; an ordinary pair of mesenteries would be thus produced, and each polyp would have but one pair of directives. Thus, from the beginning, an important difference in the nature of the mesenteries would be established between fission polyps and single polyps reared directly from larvæ; the distinction between the orders to which the mesenteries primarily belonged also begins to be lost.

Fig. 167 represents the mesenterial plan in the second bioral polyp. In the living condition one oral aperture was much smaller than the other, appearing as a mere perforation in the disk, and sections reveal that a less number of complete mesenteries are associated with it than with the larger. In the diagram the smaller stomodæum is to the left, but is represented equal with the other. In the actual transverse sections it displays eight strongly marked vertical ridges, corresponding with the eight mesenteries attached to its inner side, while the large stomodæum bears ten. Here, again, it is seen that the plane of fission passes through the entocœle of two opposite pairs of lateral mesenteries, and growth is proceeding more rapidly at one region—to the lower right—of the polyp than at another, so that the directive axis does not coincide with the longer diameter, but is turned toward the dorsal surface.

Attention may now be directed to the fully developed polyps constituting a colony of *Furia*, in order to ascertain what are the results of fission upon these. As already remarked, the mature polyps are found to exhibit very varied conditions with regard to the stage of fission. They are rarely circular in contour, but polygonal or greatly elongated, and at times deeply angular; in the majority of adult polyps only one oral aperture is surrounded by a tentacular system, but sometimes two or three mouths occur on a single disk.

A transverse section of a decalcified polyp is represented on Pl. XIII, fig. 93, and indicates much variability and irregularity in the disposition of the mesenteries, differing greatly from

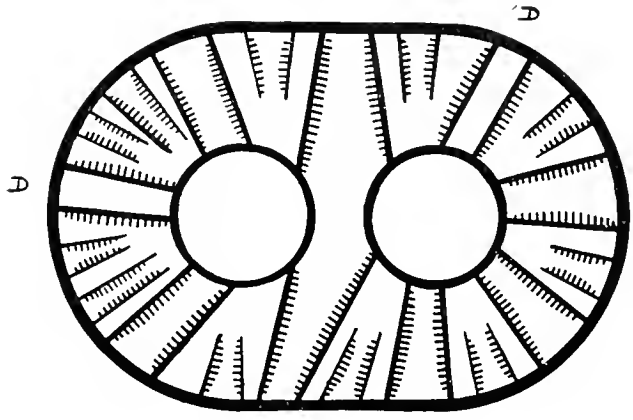

Fig. 167.

Furia fragum.—First stage of fission in another larval polyp.

the perfect regularity of the early larval polyps. The organs are paired throughout, but no regular hexameral cyclic arrangement can be established. Different stages of growth are represented in different regions; in some places there is an indication of a tricyclic plan, but more often only a dicyclic arrangement is manifest, and at times this is obscured by three or four pairs of mesenteries of equal ordinal value occurring together.

In the upper part of the stomodæum all the mesenteries may be complete, except a pair here and there in process of growth, but in passing downward some pairs become free in advance of others, indicating that they are not all of the same ordinal value.

The mesenterial pairs are always isocnemic, and the retractor muscles are invariably on the faces turned toward one another; in transverse sections of over a dozen polyps examined no directives occurred.

Adult polyps of the genera *Isophyllia* (p. 449), *Agaricia* (fig. 161), *Maandrina* (fig. 141), *Colpophyllia*, and *Dichocœnia* (fig. 149) display a like irregularity of mesenterial arrangement and absence of directives. The actual stages in fission have not been traced in these, but from their prevailing mesenterial arrangement it is manifest that the process proceeds in the same way as in the young polyps of *Manicina* and *Furia*.

Several Actiniæ also exhibit the phenomenon of fissiparity, and certain investigations have been made as to its influence upon the mesenteries and other organs. Dr. G. H. Parker (1899) has

given an account of the longitudinal fission in the common Actinian, *Metridium marginatum* Milne Edwards, and shows that the asexually formed polyps do not reproduce all the features characteristic of the sexually produced individuals. In some of the specimens examined, Parker found that fission of the stomodæal tube was still incomplete, the organ being Y-shaped, a single inner end opening into the gastro-vascular cavity, and the two outer ends opening each through a distinct mouth on a single disk. Generally in the fission specimens each mouth was monoglyphic (provided with only one gonidial groove), instead of diglyphic, as in normal forms; and with the monoglyphic condition was associated only one pair of directives. No evidence was forthcoming as to the formation of new siphonoglyps or new directives in fission polyps, while there were practically twice as many non-directive mesenteries in double specimens as in single ones. In any given case the assumed plane of division passed through either two primary exocœles or two entocœles, never a primary entocœle on one side and a primary exocœle on the other. The production of regular hexamerous diglyphic specimens by non-sexual methods was not observed; such specimens were found to number about one-fifth of the total collected, and are with good reason assumed to be the products of sexual reproduction.

The West Indian stichodactylinous anemones, *Actinotrya sancti-Thomæ* Duch. and Mich., and *Ricordea florida* Duch. and Mich., also reproduce by discal fission, and frequently more than one oral aperture is present within a single tentacular zone. In the latter species as many as seven mouths have been found on a single disk, thus recalling such a coral form as *Manicina*. Professor McMurrich's (1889*a*) anatomical studies of these two species, and also mine (1900), have shown that the mesenteries in both species are irregularly arranged, and in some polyps no directives occur, while in others only one pair is present.

The results on polypal fission in corals may be thus summarized:

1. The larval polyps of fissiparous species develop for a time like other hexamerous species. Before the introduction of fission the mesenteries are regularly arranged in two or more alternating hexameral cycles, and two pairs of directives are present.

2. The first fission plane passes through the entocœle of two lateral mesenterial pairs, approximately at right angles to the directive plane and longer oral axis, and divides the stomodæum and the mesenteries attached to it into practically equal halves, so that only one pair of directives is inserted on each stomodæal tube.

3. For a time the products of simple fission continue their development according to the regular cyclic plan, but before long fission is repeated, and each stomodæum and the mesenteries associated with it may be again divided into equal halves, or one part may be larger than the other. In probably every division the fission plane is included within two opposite entocœles. At an early stage in the development of fission polyps growth may proceed more rapidly at one region than at another, and thus introduce irregularities in the cyclic plan.

4. Beyond the two primary pairs no new directive mesenteries are ever introduced, so that in any fissiparous colony, however large, only the protocnemic directives occur, situated widely apart, at what may be regarded as the two morphological extremities of the colony.

With such results before one, it is clear that care must be exercised in attempting to establish relationships from the absence of one or both pairs of directives in mature polyps of both corals and Actinians. The history of the individual polyp must be taken into account before such an occurrence can be regarded as a specific peculiarity. As a general rule, one would be justified in assuming asexual reproduction by fission for polyps with only one or no directives, especially if accompanied by irregularities in mesenterial growth.

FISSION IN PORITES.

Polyps displaying a bioral disk are very rare on colonies of *Porites*. After an examination of scores of living colonies of all the West Indian species, only a single example exhibiting this condition has been found, although polyps showing an increase of tentacles beyond the usual twelve are by no means scarce; from these all stages in the development of the mesenteries beyond the primary six pairs are readily secured. These proportions present a marked contrast

with those of the closely allied polyps of *Madrepora*; enlarged polyps are frequently found on colonies of *Madrepora*, provided with two oral apertures, and twenty-four mesenteries are already present at one stage or another of their development.

For the most part, the enlarged polyps of *Porites* are circular in section, and any increase in the number of tentacles merely results in the enlargement of the polyp, without altering its outline. The polyp with two oral apertures had, however, assumed an oval form, but the tentacles remained disposed in a single cycle, as in ordinary polyps.

In a former paper (Johns Hopkins Circulars, June, 1900), and again on p. 446, it is shown that in *Porites* the increase of mesenteries beyond the protocnemic stage takes place axially, by the addition of bilateral pairs within either of the directive entocœles, and that in the end they constitute both isocnemic and anisocnemic pairs. In some polyps the new mesenteries are added within the dorsal entocœle, and in others within the ventral entocœle, but never within both chambers in the same polyp. All stages from the occurrence of a single pair of new mesenteries to six pairs have been already described.

Serial transverse sections of the *Porites* polyp displaying the bioral condition were prepared, and by studying these at different levels the arrangement of the mesenteries represented in

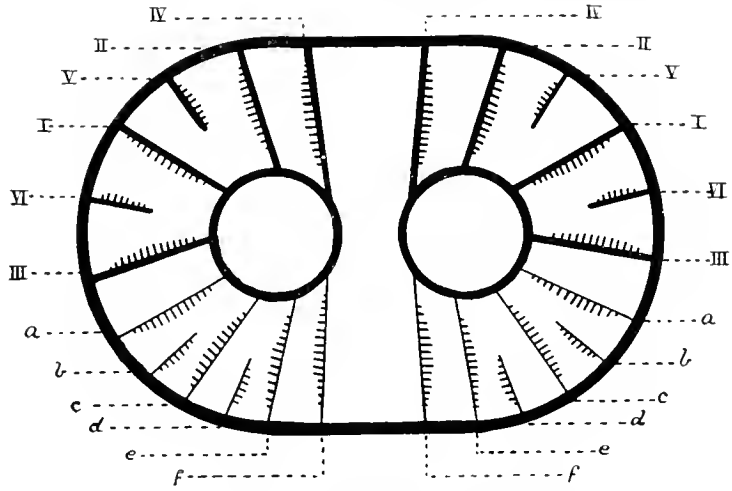

FIG. 17.

Porites.—Diagram illustrating polypal fission in a bud polyp. Within the entocœle of the ventral pair of directives (III, III) six bilateral pairs of mesenteries (*a-f*) have appeared, and the stomodæum has been divided into two distinct tubes. The complete and incomplete pairs of mesenteries and the musculature are so arranged that when the two polypal halves separate, each polyp will have six pairs of mesenteries arranged as in ordinary polyps.

fig. 17 has been established. Two stomodæal tubes are distinct throughout their length, and twelve pairs of mesenteries are present, six pairs associated with each stomodæum and arranged as in a single polyp. All the additional mesenteries have been added within the ventral entocœle, the inclosing directives (III, III) of which have been pushed widely apart. The figure should be compared with fig. 11*c*, on p. 470, representing the arrangement in a polyp also with twelve mesenterial pairs, but in which only one stomodæal tube occurs.

From the figure itself (fig. 17), it would be difficult to determine within which of the two directive entocœles the increase has taken place, or which half is primary and which half secondary. In the actual sections the mesenteries on the ventral aspect are closer together, and disappear first in passing from above downward. From the sections of the various polyps at intermediate stages, it is clear that polypal fission in *Porites* is effected only after the successive addition of six bilateral pairs of mesenteries, the complete and incomplete members alternating in such a way that the moiety of the six new pairs on one side resembles the moiety of the six primary on the same side. When the two fission polyps are completely separated along the axial plane, a pair of directives will be formed for each polyp, by the approximation of one of the members of the primary dorsal directives (IV) and the corresponding member of the last-formed ventral pair (*f*).

The plane of fission coincides with the primary directive plane which passes through the primary dorsal and ventral directive entocœles and longer oral axis, and divides the enlarged polyp into equal halves with twelve mesenteries to each; of these, six are the protocnemes and six are new formations.

As the order of appearance of the mesenteries beyond the protocnemic stage in *Porites* differs from that in other coral polyps, so its method of fission is altogether different. In most corals the plane of fission is at right angles to the directive or median axis of the polyp, whereas in *Porites* it is along the directive plane; each of the two primary daughter polyps in ordinary fission has only one pair of directives, but in *Porites* the mesenteries are arranged exactly as in the larval polyp, and each fission polyp bears two pairs of directives. (See foot-note, p. 496.)

FISSION IN MADREPORA.

When describing, in a recent paper[a], the method of addition of new mesenteries in *Madrepora*, beyond the protocnemic stage, the process of fission was also noticed, so that for the present purpose it is only necessary to briefly reiterate the facts there brought forward. On examining most colonies of *Madrepora* with a lens, a few polyps are found which are slightly larger than the others, and bear more than the usual twelve tentacles, any even number from sixteen to twenty-four being represented. The tentacles form, however, only a single cycle, as in ordinary polyps (Pl. I, fig. 1 *l*.). Such polyps seem to occur anywhere over the surface of a colony, wherever vigorous growth is in progress, but have not been found in the oldest parts of colonies, nor on the under surface of palmate colonies, where conditions of growth are not very favorable.

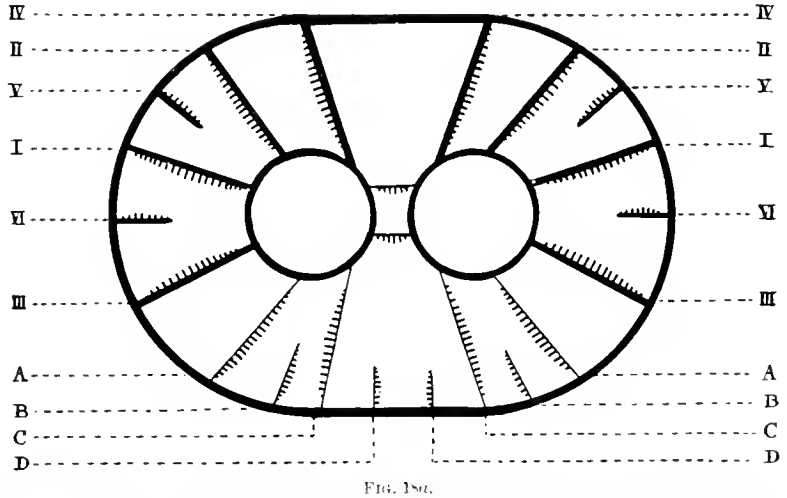

FIG. 18*a*.

Madrepora.—FIGS. 18, series of diagrammatic figures illustrating polypal fission and the manner of increase of the mesenteries beyond the protocnemic stage. Two stomodæal tubes are present from the beginning, either connected by one or two mesenterial strands or altogether distinct. *a*. Four new bilateral pairs (A–D) are present within the ventral directive entocœle, and two others connect the two stomodæal tubes.

Most of the larger polyps are strongly oval, the longer axis being at right angles to the axial-abaxial plane. Out of forty or fifty enlarged polyps examined, only one or two did not already display two oral apertures, and of nearly thirty specimens sectionized transversely each bore two distinct stomodæal tubes. Compared with the enlarged polyps of *Porites* those of *Madrepora* are therefore characterized by the early production of the bioral condition.

Transverse sections reveal that in practically every case twenty-four mesenteries—that is, double the number in ordinary polyps—are already developed, though in different examples they exhibit somewhat different relationships. Sixteen complete mesenteries occur, and the remaining eight are incomplete, the paired arrangement agreeing with that of simple polyps.

[a] "The Morphology of the Madreporaria.—II. Increase of Mesenteries in *Madrepora* beyond the Protocnemic Stage." Ann. Mag. Nat. Hist., ser. 7, vol. x, 1902.

The different polyps studied exhibit one or another of three successive stages toward complete fission. These are diagrammatically represented in figs. 18 (*a–c*). The primary mesenteries are indicated by thicker lines, and are numbered from I to VI; the new mesenteries are denoted by the letters A to F, no successive order in their appearance being assumed thereby.

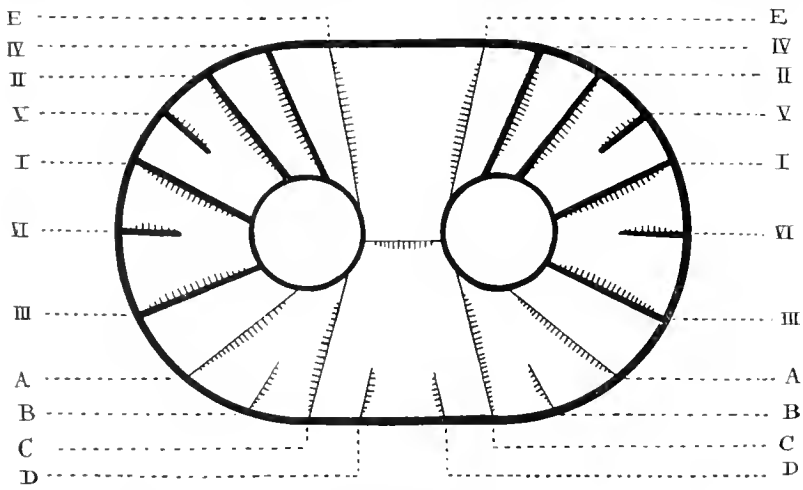

FIG. 18*b*.

Madrepora.—Fission continued. The same number of mesenteries are still present within the ventral directive entocœle, and a single pair (E, E) occurs within the dorsal directive entocœle, while only one mesenterial strand connects the stomodæa.

The figures reveal that new mesenteries are added in bilateral pairs, disposed axially in both the dorsal and ventral entocœles. No stage in which less than twenty-four mesenteries were present has been found.

Special interest attaches to the mesenteries in figs. 18*a*, 18*b*, which connect the two stomodæal

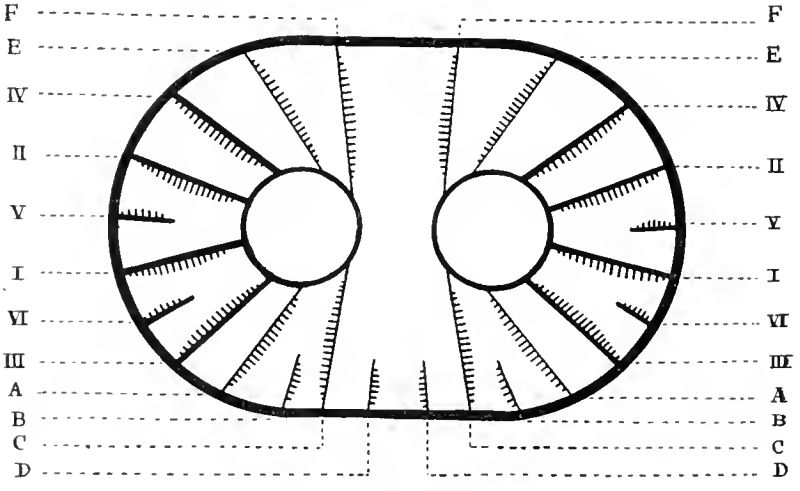

FIG. 18*c*.

Madrepora.—Fission continued. Two mesenterial pairs (E, F) now occur within the dorsal directive entocœle, and the stomodæal tubes are wholly disconnected. The macrocnemes and microcnemes and arrangement of the musculature on the faces are such that if the polyp were divided into two halves along the median axis the mesenterial arrangement in each polyp would be the same as in an ordinary polyp with only six pairs of mesenteries. (*cf.* Pl. I, fig. 1.)

tubes. In fig. 18*a* two of these are present, in fig. 18*b* only one, while in fig. 18*c* the connection has ceased altogether. In the paper already mentioned, it has been shown that these connecting mesenteries are a result of the practically simultaneous division of the primary stomodæum and the appearance of the new mesenteries. The adjacent mesenteries, situated between the two

stomodæal tubes, for a time retain this connection throughout the length of each stomodæum. Serial transverse sections indicate that later the middle portion of each connecting mesentery begins to grow radially across the disk, and that when it reaches the vertical column wall it divides into two distinct mesenteries, which constitute a bilateral pair. The division extends all the way from the upper to the lower termination of the stomodæal tubes, the successive stages in the process being easily followed. As shown by fig. 18*b*, the dorsal connecting mesentery becomes divided and stretches to the column wall in advance of the ventral member.

That no earlier stages, exhibiting a sequence in the appearance of the six pairs of new mesenteries, have been met with, such as are described for *Porites*, seems strongly to suggest that the additional six pairs arise practically simultaneously, in all probability *pari passu* with the division of the primary stomodæum. In the earliest bud polyp of *Madrepora* which has been obtained, representing a stage before any tentacles appear, all the twelve mesenteries are already present, and the oral perforation appears to have been just established (p. 497). It would also seem that in the formation of new polyps by fission a like simultaneous development takes place, and thus no intermediate stages between the twelve and twenty-four mesenteries are to be expected.

The results from the two methods of asexual reproduction in coral polyps—budding and fission—may be thus contrasted:

(1) Polyps arising as buds pass through the same stages as regards the order of appearance of the tentacles, mesenteries, and mesenterial filaments as the larval polyps of the same species, and the adults of both are alike.

(2) Excepting *Porites* and *Madrepora*, polyps originating by discal fission, whether completely or but partly separated, never wholly resemble the sexually-produced polyp. No new pairs of directives are formed, and the mesenteries do not assume a hexamerous or other regular cyclical arrangement.

(3) Polyps of *Porites* and *Madrepora* arising by fission resemble larval polyps in having two pairs of directives and four anisocnemic pairs of mesenteries. (See foot-note, p. 496.)

SEXUAL REPRODUCTION.

DISTRIBUTION OF GONADS.

Although the asexual method plays such a prominent part in coral growth, yet the production of sexual elements, for the formation of entirely new individuals, appears to be quite as important as in other groups of animals where sexual reproduction alone prevails. In West Indian waters, colonies of *Favia fragum*, *Manicina areolata*, *Siderastræa radians*, and *Porites clavaria* seem to be nearly always fertile, while species of *Madrepora*, *Orbicella*, and *Cladocora* are, as a rule, found without sexual cells.

Several observations upon the distribution of the gonads in the Madreporaria have been recorded by other writers, but, as in the Actiniaria, no general rule is apparent with regard to the monœcious or diœcious character of the polyps. Thus Moseley (1882) found *Seriatopora* to be unisexual; Fowler mentions the occurrence of ova only in *Madrepora durvillei*, *Turbinaria*, sp., and in *Sphenotrochus rubescens*, while *Pocillopora brevicornis* is monœcious. H. V. Wilson merely states that *Manicina areolata* is hermaphrodite. Gardiner (1900, p. 367) found all the polyps of *Cænopsammia* which he examined to be female, without any trace of male generative cells.

In the course of the present studies many instances of fertile polyps have occurred. A portion of a colony of *Meandrina labyrinthica* sectionized bore gonads on almost every mesentery, and in this case ova and spermaria were closely associated. In a few instances both kinds of sexual cells are found on the same mesentery (Pl. XX, fig. 140), but usually they are developed on separate mesenteries, the number of male mesenteries being greatly in excess of the female. The merest suggestion of an alternation of male and female mesenteries is manifest; thus, one member of a pair may bear spermaria and the other ova, but at other times two or three ova-bearing mesenteries are intercalated between a number of sperm-bearing

mesenteries. Four to eight spermaria may be present on a single mesentery in section; but the number of ova is much less, usually one or two, rarely reaching four or five. In the hermaphrodite mesenteries the ova are invariably situated toward the fixed end of the mesentery, and the spermaria nearer the free edge, that is, more central.

Furia fragum is likewise monœcious, and in this species also the two kinds of sexual cells may occur on the same mesentery, though more often they are on different mesenteries within the one polyp. In one large colony examined, the cavity of practically every polyp was crowded with larvæ, all at the same stage of development. In addition to these the mesenteries were swollen with spermaria and ova, all apparently at a similar stage toward maturity—the ova having a large nucleus and nucleolus, and the spermaria with the tails of the spermatozoa already developed.

On a colony of *Porites clavaria* most of the individual polyps contained several free larvæ, again all at about the same stage of development. In this instance, ova only were present on the mesenteries, usually one large egg to each, and of numerous polyps examined from the same colony none bore male sexual elements. In transverse sections of a polyp of *Madrepora palmata* a single ovum occurred on three of the four lateral complete mesenteries, but not on any of the directive mesenteries.

Female gonads were moderately developed in a colony of *Isophyllia dipsacea*. In transverse sections some of the mesenteries exhibited three or four ova, restricted in their distribution toward the insertion of the mesentery in the body wall. Most of the mesenteries of a polyp of *Orbicella radiata* also contained ova, again situated toward their insertion in the polypal wall; likewise polyps of *Siderastræa siderea*. In the last the ova were greatly distorted and irregular in form, as if adapting themselves to the very narrow interseptal loculi.

From the above examples, it is impossible to say how far sexual differentiation has proceeded within Madreporarian polyps. In all instances where a unisexual character would be indicated, only female cells have been found, and then somewhat sparsely. Spermaria have never been found alone, but always in association with large numbers of ova.[a] It may be that coral species are mainly monœcious, but that ova are first developed (protogynous), and later spermaria, either on the same or different mesenteries. Further, the ova are, as a rule, restricted toward the fixed or peripheral margin of the mesentery, while in Actiniæ generally they are disposed about the middle of the radial length of the mesentery.

Apparently very little importance can be attached to the particular mesenteries on which gonads may occur, for where present in numbers they are found on practically all the mesenteries, both complete and incomplete. In *Orbicella radiata* any of the mesenteries of the three cycles may bear ova; as shown on Pl. IX, fig 68, ova occur on a small incomplete mesentery, while they are not developed on the larger complete member. In Actinian studies the distribution of the gonads on particular mesenteries is considered to be of some importance for systematic purposes, but manifestly the production of a few sexual cells on certain mesenteries can not be of much significance, when in riper polyps they may possibly be found on all the organs.

Within its lifetime a polyp may give rise to more than one series of ripe sexual cells, for individuals charged with fully developed larvæ also contain numbers of nearly ripe eggs, still within the mesoglœa of the mesentery.

Viviparity would appear to be the rule among corals, though Wilson records the extrusion of eggs and semen from *Manicina*, and I have also found this to happen in *Furia*. It may be doubted whether such occurrences take place under normal conditions, as in both instances highly developed larvæ have also been found within the gastric cavity. Similar promiscuous extrusions of sexual cells are likewise found to take place among anemones. From *Rhodactis sancti-Thomæ*, *Aulactinia stelloides*, and others unfertilized eggs and semen have been found to be extruded in abundance, while from both species mentioned larvæ at an advanced stage of development have also been obtained.

[a] Miss Pratt (1900) describes *Nichelia* as probably monœcious, spermaria only being present.

From the few records yet available, it is impossible to determine how far the different species of corals have any regular breeding season; such would scarcely be expected under the uniform conditions of temperature characteristic of tropical waters. During the month of July four or five different colonies of *Siderastræa radians* were collected, all having polyps charged with free larvæ, while other collections made at different times from the same locality never yielded fertile colonies. From another locality larvæ of this species were secured during the middle of March.

Most of the larvæ to be here described were collected in the early months of the year (March, April); but larvæ of *Manicina areolata* and *Favia fragum* seem to be extruded nearly the whole year round.

SPERMARIA AND OVA.

In their detailed structure, the spermaria and ova of corals are much like the corresponding elements in the Actiniaria. A mesentery bearing two spermaria, in addition to three ova, is represented on Pl. XX, fig. 140, taken from *Mæandrina*. The fertile portion of the mesentery is greatly swollen, and the mesoglœa is thin and surrounds each ovum and spermarium as a very delicate sheath. The mesenterial epithelium has undergone certain modifications; toward their base the cells are much vacuolated, and without any recognizable protoplasmic contents. Cell limitations are not obvious, and the nuclei are arranged in a very definite zone toward the margin, along with the other protoplasmic contents of the cells.

The spermaria are crowded with deeply-staining, spheroidal, sperm cells, each with several still more deeply-staining particles or nuclei. A similar stage has been figured by Professor Hickson for *Alcyonium* (1895), and also described by Ashworth (1899) for *Xenia*. Occasionally a central cavity containing a coagulum is already developed, and here and there this is filled with the projecting tails of the spermatozoa. Without any doubt the ova and spermaria are developed from the mesenterial epithelium, as in other Anthozoa, and the cells wander into the mesoglœa and become encapsuled by it, but none of the earliest developmental stages have been found.

The spermaria from another colony of *Mæandrina*, instead of being nearly spherical, are narrow, and extend along the transverse length of the mesentery for some distance, and display constrictions, as if made up of four or five fused spermaria.

On one occasion, ripe spermatozoa were observed in the act of extrusion from a polyp of *Favia fragum*, the process taking place by the same jerking motion as when larvæ are liberated. They were of the same form as those of *Actinia equina*, described and figured by Lacaze-Duthiers, that is, a pear-shaped head with a laterally fixed tail.

A mesentery bearing two large ova is represented in fig. 146, again taken from *Mæandrina*. The eggs contain a large amount of vacuolated, finely granular yolk. The vacuolization is very uniform except peripherally, where the ovum stains more deeply, owing to the greater concentration of the protoplasm. In the same region deeply-staining granules are also numerous. The germinal vesicle is large and homogeneous in structure, and is unaffected by carmine stains, but readily takes up aniline blue. The germinal spot is usually situated close to the margin of the germinal vesicle, and differs from the latter in staining intensely in borax carmine.

White, spheroidal, unfertilized eggs were extruded singly from *Favia fragum* on several occasions, after floating around in the gastric cavity for several hours. Examined under the microscope, the ova underwent a great variety of irregular movements for about an hour, sending out lobate processes, first from one region and then rapidly from another.

The experiences of von Koch, Wilson, Haddon, and those here recorded render it manifest that the eggs in coral polyps are ripened in batches, not a few at a time, and that the larvæ develop equally; for in all cases where larvæ have been obtained from any polyp they occurred in numbers, and practically of the same age, while many far advanced eggs were present in the mesenteries preparing for another series. This is usually the case in the Actiniaria, but exceptions may occur, as where larvæ at all stages have been secured from the same polyp at one time. Fowler (1888, p. 13) states that the ova in *Sphenotrochus rubescens* were in various stages of maturation.

LARVÆ AND POSTLARVAL DEVELOPMENT.

In all corals yet observed, the segmentation of the ovum and early stages in the development of the larva take place within the internal cavity of the polyp, and are therefore not easily accessible for study. The extrusion of a few eggs and semen, which sometimes occurs, appears to be fortuitous in character, and is not to be regarded as the normal method of sexual reproduction. It is a little remarkable, that in the many sections of adult polyps which have been prepared, none of the intermediate stages between the egg and the fully developed larva have been secured, though fertile polyps, and others containing free advanced larvæ, are by no means rare.

Probably by keeping under observation, for a lengthened period, colonies which are known to be fertile, it would be possible to secure the earlier embryonic stages; polyps which are charged with advanced larvæ often contain in addition nearly ripe eggs, from which another batch of larvæ might soon be expected.

From the colonies of *Manicina areolata*, which H. V. Wilson had under observation for a period of several months, eggs, semen, and larvæ in very different stages were extruded. The first specimens of coral poured forth eggs and semen on the 15th and 17th of March, while on the 20th the polyps had given birth to larvæ a little more advanced than the planula. After this date only larvæ were ejected, their stage of development becoming much more advanced as the Bahama season progressed.

Among Actinians also the larvæ are usually ejected in an advanced stage of development; but unfertilized eggs and semen are extruded from a few forms—*Urticina crassicornis*, *Metridium marginatum*, *Sagartia parasitica*, and *Cerianthus membranaceus*, so that different investigators have found it possible to follow the segmentation and early embryonic stages of these.

Manicina areolata is the only coral in which the segmentation and formation of the germinal layers has hitherto been followed. But the early stages of development, as far as the formation of the skeleton, seem so completely alike in the Madreporaria and Actiniaria that the fuller details obtainable within the latter group may be considered to hold for the former. Appellöf (1900), in his admirable paper, "Studien über Actinien-Entwicklung," has followed very completely the early stages in the development of the Actinian *Urticina crassicornis*, and at the same time reviews the results of other workers throughout the Zoantharia in the light of his own.

The following account will be restricted to a description of the larvæ either upon extrusion or shortly after, and as far as their subsequent development has been traced. During the course of the present investigations numerous larvæ of the following species of corals have been obtained: *Manicina areolata*, *Favia fragum*, *Siderastræa radians*, *Porites clavaria*, *Isophyllia dipsacea*, and *Agaricia agaricites*; not always, however, under circumstances in which their future history could be followed. In some cases it has been possible to trace their growth through various stages, but in others only the larvæ themselves are available for study. Some of the larvæ were preserved directly in corrosive acetic, and others in formol. The former method gives the best results. During preservation mucus was often extruded from the unicellular ectodermal glands, resulting in the adherence of foreign particles to the larval wall; often also the larvæ collapsed when transferred to the preserving medium.

Where the superficial tissues of viviparous polyps are partly transparent, the larvæ can be seen moving about within the gastro-cœlomic cavity, coming into view above and then disappearing below. Very often they enter the tentacles, and may remain there for some time, so that when the polyps retract they give rise to small protuberances of the surface. Whether the motion within the polypal cavity is due to the larva's own ciliary activity, or is brought about as a result of the general circulation of the internal nutrient fluid, is not readily ascertained; certain larvæ are provided with cilia and able to swim about immediately on extrusion, while others remain motionless for a short time, showing that cilia are not yet active.

The actual extrusion of the larvæ seems always to take place suddenly, not with the slow convulsive movements more usual in parturition in other groups. In *Manicina areolata* the larvæ were ejected through the mouth in batches, a dozen or so at a time, by a peculiar jerking motion of the adult; but in *Porites clavaria*, *Favia fragum*, and *Siderastræa radians* they

appeared singly, or only two or three at a time. Probably the larvæ are able to made their exit through the tips of the tentacles, as well as through the mouth, though owing to the rapidity with which the process takes place I have never been able to assure myself of this method, even when, as in the case of *Siderastræa*, colonies have been watched for hours. Von Koch states (1897) that the larvæ of *Caryophyllia cyathus* pass through the tips of the tentacles. The various polyps of a colony continue to give out larvæ for several days, or even for a week or two, and then the supply ceases, or for some time one or two individuals may appear at long intervals.

Development appears to proceed equally within most of the polyps in any colony. In the fertile colonies of *Favia* or *Siderastræa* the majority of the polyps contained larvæ all at the same stage, and in *Porites* such was the case with most of the polyps within any restricted area.

On first extrusion the larvæ of corals are spheroidal, oval, pear-shaped, or elongated rod-like bodies, varying from 1 to 3 mm. in length, the outer surface uniformly ciliated throughout. The various forms assumed by the different larvæ of *Favia fragum*, extruded about the same time, indicate the more usual shapes (Pl. XIII, figs. 96–100). Lacaze-Duthiers (1873) figures the larva of *Astroides calycularis* as elongated and assuming a spiral form, von Koch (1897) that of *Caryophyllia cyathus* as pear-shaped. The individual larva, however, often manifests the power of retraction and of altering its shape, so as to be at different times oval, pear-shaped, spheroidal, or flattened and cake-like. In the majority of cases, one end, usually the anterior during progression, is much broader than the other, though when the larva has been extruded for some time these relations are frequently reversed. Thus, the pear-shaped larva of *Favia fragum* has at first the broad end at the aboral forward pole, but later the broad end is oral or posterior and the narrow end is aboral. A similar alteration of form has been noticed in *Siderastræa radians*, but most of the larvæ of this species have a narrow aboral and a swollen oral pole from the beginning. Twin larvæ, with two oral extremities and one aboral, have been extruded by polyps of the species just mentioned. No coral larva has yet been described in which the aboral extremity bears the tuft of larger, less mobile cilia sometimes met with in Actinians.

Coral larvæ are able to swim about either immediately on extrusion or shortly after. For the first few minutes they may remain motionless, either at the surface of the water or on the bottom of the vessel, then, cilia having been formed, active movements of both rotation and translation commence. Some gyrate throughout the depth of the water, coming to rest from time to time; others remain nearer the surface or accumulate around the sides of the vessel. Within one to three days a few of the more vigorous examples would become attached to the sides of the glass vessel or other object, and remain thus for some time, then become active again, and afterwards refix themselves. But the great majority seemed unable ever to settle, and continued alive for days or weeks, without much motion, and apparently without undergoing further development. If fixation did not take place during the first two or three days it was never found to occur after, though some of Wilson's larvæ of *Manicina* settled after swimming around for three weeks.

When first extruded, coral larvæ are dense and opaque, and either colorless or slightly brown; afterwards they may become slightly distended, and as a result the wall appears thinner and more nearly transparent. Occasionally the larvæ are set free in a distended form, when they are more transparent from the beginning. The alteration from the opaque to the more transparent condition is brought about by an important change in the internal endodermal tissue, described below. Under the microscope the colorless or nearly colorless outer ectoderm can be distinguished from the inner endoderm, and in all species examined the latter bears zooxanthellæ, which give a yellowish color to the internal mass.

The oral pole, whether narrow or broad, is usually darkly colored externally. Examination of the living larvæ under the microscope, and also by means of sections afterwards, reveals that the color is due to the presence of numerous zooxanthellæ or yellow cells toward the oral end. Usually these occur within the ectoderm cells, but sometimes, as in *Isophyllia dipsacea* (Pl. XXV, fig. 165), they crowd the endoderm cells around the oral extremity, and the ectoderm contains comparatively few. In both cases the zooxanthellæ are densely aggregated toward the apex, which in consequence is the darkest area. In general the algæ are sparingly distributed

throughout the endoderm, and thus give rise to the faint brown color of the larvæ as a whole. Only rarely do they occur beyond the oral region of the ectoderm.

From time to time the zooxanthellæ are seen to be set free from the ectoderm cells, and in the end they wholly disappear from the outer layer, the larva becoming uniformly colored. Occasionally they persist for a short time within the perioral area after the larva has become fixed.

The presence of numerous symbiotic zooxanthellæ within such a restricted region of the larva during its interpolypal existence, and their disappearance shortly after the larva is set free, are phenomena upon which no explanation has yet been offered. In no adult corals are zooxanthellæ found within the ectodermal cells; it is wholly a larval condition.

When the larvæ are first extruded, the oral aperture is usually indeterminable, but a very minute opening appears shortly after, often situated a little to one side of the actual apex, and later the wall immediately around the mouth becomes slightly depressed. Extrusions of zooxanthellæ, and what seem to be yolk granules in a mucus-like mass, have been observed to take place from time to time through the newly formed mouth. This phenomenon commences shortly after the larvæ are set free, and continues for some time. Lacaze-Duthiers (1873) has figured the ejection of waste material actually taking place in the larvæ of *Astroides*, and it is also found to be a common occurrence in Actinian larvæ. It is manifest that this is the larva's method of getting rid of the surplus zooxanthellæ, yolk, and cell débris remaining after the formation of the narrow endodermal layer from the original nearly solid internal tissue. Sections of late larvæ are generally found to contain free zooxanthellæ, and what seem to be cells in process of disintegration (fig. 112), while in early larvæ the interior may be wholly filled with a compact vacuolated tissue (Pl. XXV).

Some time after their extrusion, the larvæ may enlarge a little, and begin to lose their opacity, or this may not take place until they settle. Through the more transparent walls the internal attachment of the mesenteries can be seen, and their number and course determined. Usually three or four pairs of mesenteries are indicated at this stage, one or both of the lateral pairs generally extending as dark, thickened bands farther down the polyp than the two axial pairs (Pl. XVII, fig. 125).

In nearly all cases sections of the freshly extruded larva reveal an almost solid interior, into which the very narrow stomodæum has pushed, as it were, its way; also three or four pairs of mesenteries are more or less developed (Pls. XVIII, XXV). Afterwards the four pairs of mesenteries seem to grow quickly, so that by the time of settling all may be united with the stomodæum, two additional pairs—the fifth and sixth developmental pairs—having appeared in the meantime; the latter, however, never unite with the stomodæum for a long time after fixation. All the six pairs of protocnemes were already present in freshly extruded larvæ of *Isophyllia dipsacea*. Tentacular protuberances seem never to make their appearance before the fixation of the larva, nor has any trace of skeletal matter been observed during the free swimming stage.

Within a day or two after extrusion the individual larvæ settle by the forward aboral pole, on any suitable surface which presents itself, and usually independently of one another. Should the aboral extremity of the larva be narrow, it rapidly flattens after fixation; the larva as a whole shortens greatly, swells laterally, and for the first time the differentiation into basal disk and column is established.

Fixation may take place in close proximity to the parent colony, and in such cases probably directly after liberation. It is a common occurrence to find a few young polyps adhering to the lower, dead surface of colonies of *Manicina* and *Favia*. Lacaze-Duthiers (1899) has also shown that in the *Caryophyllia* obtained from Port Vendres "bouquets" of the coral have been produced, evidently by the larvæ fixing themselves on the exposed region of other corallites, and, thus attached, growing to their full dimensions and giving a semblance of budding or fissiparity to the usually simple coralla. Von Koch (1890) also describes "aggregated" colonies in *Balanophyllia*, which could only have originated in the same manner.

A still more remarkable instance of colony formation, from the union of individuals originally free and distinct, occurred during the fixation of the larvæ of *Siderastræa radians*. The larvæ settled in groups in such close proximity that when expanded the polypal walls pressed against

one another, and produced angulated outlines. In one instance a colony thus produced consisted of thirty-two primarily free larvæ, in another twelve larvæ associated themselves, in a third seven, while several groups of three or four polyps were formed. Some of these colonies lived in small aquaria for three or four months, during which time the tentacles and skeleton appeared. To all appearances they would, under natural conditions, have given rise to actual colonies, indistinguishable from ordinary colonies produced by gemmation. (See foot-note, p. 495.)

Of the numerous larvæ extruded by corals comparatively few seem to settle, and in aquaria the greatest difficulty and uncertainty are experienced in securing permanently fixed individuals. Sometimes a number will become fixed, while under what appear to be exactly similar circumstances fixation seems impossible. In addition to the somewhat unnatural conditions under which the larva may be placed in aquaria, it seems not improbable that the ripeness of the larvæ for settling may also be a factor. In my experience, if fixation be not effected within two or three days after extrusion, it does not take place afterwards. The larvæ will then remain resting or slowly swimming about for an indefinite time, apparently undergoing no development whatever. Larvæ of *S. radians* have been kept thus for a period of twenty days.

Different measures were employed to provide the larvæ with suitable surfaces for fixation, and at the same time permit of their examination later. Glass dishes and small pebbles were placed in the vessels, and cover glasses floated vertically by means of pieces of cork. These provisions, however, were of little service. The most favorable position appeared to be the sides and bottom of the glass vessels in which the colonies were living. The larvæ being properly settled, the vessel was broken with care, and the fragments bearing the larvæ distributed to other vessels in which coral colonies were already established. Many larvæ were secured in this way, fixed to transparent pieces of glass, and could be taken out at any time, and examined in small glass dishes as transparent objects under the microscope.

Once the larvæ were fixed, they appeared quite vigorous and hardy, and continued their growth even under unfavorable conditions; while larvæ which remained unfixed, though kept alive and active for several weeks, never increased in size or underwent development in any way.

Ectoderm.—The larval ectoderm is very broad compared with the same layer in the adult polyp. In section the ectoderm of the larva of *Agaricia* measures 0.1 mm., and that of *Favia fragum* 0.08 mm. Most of the usual Anthozoan cellular elements are already differentiated at or before extrusion; gland cells, nematoblasts, supporting cells, and nervous elements occur, but no muscular fibrils have been recognized. No observations have been made on fresh macerated material, but the various cells separated somewhat freely from certain of the specimens preserved in formalin.

Both transverse and vertical sections of the ectoderm exhibit certain zones characterized by differentiations in the cellular constituents (fig. 165). The greater number of the nuclei are aggregated about the middle of the layer, and inwardly they occur in diminished numbers as far as the mesoglœa. By reason of the deeply-staining character of the nuclei their zone of distribution stands out strongly in moderately thick sections, and macerations show that it comprises the nuclei belonging to the supporting cells; the more deeply situated nuclei are those of the gland cells, developing nematocysts, and nervous elements.

The outer half of the ectoderm comprises the swollen portion of the gland cells and the mature nematocysts, embedded, as it were, in a matrix of supporting cells; the margin frequently shows the swollen bases of the cilia, which stain very strongly in methyl blue.

The inner zone is not well defined, and in early larvæ is usually characterized by the presence of large numbers of developing nematoblasts. These stain deeply, appear nearly homogeneous, but with a nucleus to one side, and are arranged irregularly at all angles to the other constituents; as they mature they migrate peripherally, and become arranged at right angles to the surface of the layer.

The gland cells are a very important constituent of the larval ectoderm, and their contents are nearly always finely granular, and usually remain unstained. Sometimes the vacuolar part extends nearly, if not altogether, across the layer, and on preservation the larvæ often throw out large quantities of mucus, when the cells become clear.

As already mentioned in describing the external characters, the ectoderm cells may contain zooxanthellæ, mainly restricted to the oral pole, but at times occurring sparsely throughout.

At the aboral extremity of all the larvæ examined the ectoderm undergoes an important alteration: nervous elements become developed to such a degree as to suggest that the region represents a special sensory organ. The general features of the differentiation are much the same in each species (Pl. XXV, fig. 165). From the narrow mesoglœa a number of delicate fibrils extend parallel with one another and at right angles to the layer, and unite in a reticulum which in sections seems largely made up of the cut ends of nerve fibrils. The nerve layer may be very broad, and on the outer side is continued into the ectoderm cells. The latter are usually more elongated, and more compactly arranged; the mucous cells are greatly diminished in numbers, and the nematocysts and supporting cells have undergone a corresponding increase.

The special nervous development is not restricted to the actual aboral pole, but extends some distance up the wall, gradually becoming weaker and weaker, until ultimately, a little below the middle of the larva, it is scarcely distinguishable.

I have described the occurrence of a similar sense organ at the aboral pole of the larva of *Lebrunia coralligens* (1899), and Professor McMurrich (1891) has found the same in the larva of *Rhodactis sancti-Thomæ*. It is suggested that the organ is in some way associated with the forward position of this end of the larva in swimming, and disappears when the larva settles by this extremity. Appellöf (1900) has found a less marked ectodermal modification at the aboral pole of the larva of *Actinia equina*, but in this species no special nerve layer is developed. The layer is clearer than elsewhere, and the cells are long and extraordinarily fine, and some even seem to terminate in two or more fine fibrils, while on the outside a group of longer, less mobile cilia occurs. Appellöf observed no corresponding differentiation in the aboral ectoderm of *Urticina*.

Mouth and Stomodæum.—When the larvæ are first extruded an oral aperture as a rule is indeterminable, though a few hours afterwards a small circular opening can be made out, and later the wall around may be partly depressed. Transverse and longitudinal sections through the oral pole of freshly extruded individuals also indicate that for a time the mouth and stomodæum are not functionally active, and the ectoderm at the entrance to the interior often appears without any break. In sections through the stomodæal tube an extremely narrow lumen occurs, but the condition of the canal does not suggest that ciliary activity has been established, any more than the nearly solid interior of many of the larvæ would permit of the circulation of a nutrient fluid. The stomodæal ciliation is not always distinguishable, yet when fully active the cilia here are the strongest in the whole polyp. The deeper parts of the ectodermal epithelium at this stage contain the developing stages of many nematocysts, and the nuclear zone so characteristic of the stomodæal ectoderm in adult polyps is not yet strongly differentiated.

The ectoderm never stops short all the way round at the actual inner termination of the stomodæal tube, but is partly reflected along the endodermal surface, and thence becomes continuous with the mesenterial filaments, passing down the free edge of whatever mesenteries are wholly complete (Pl. XVIII, fig. 127). In endeavoring to establish the homology of the mesenterial filaments, much significance has been attached to this reflected ectoderm, and to the apparent passage of the stomodæal ectoderm on to the mesenteries (p. 477).

Endoderm.—Much variation exists as to the condition of the interior of the larvæ when the latter are newly hatched. In some instances it is filled with a highly vacuolated tissue, so that the larva is a nearly solid mass of spheroidal cells; other larvæ are hollow toward the middle, but provided with a broad endodermal lining. A comparison of the figures on Pls. XV and XXV will give an idea of the different internal conditions which have been encountered.

The vacuolated tissue filling the cœlenteric cavity appears as if made up of distinct spheroidal or polygonal cells, each with a definite boundary, and having a nucleus applied to the wall. Each cell is occupied almost completely by a large vacuole, but around the walls are granules of different sizes which do not stain. The appearance of the tissue is the same throughout, in whatever direction the sections may be made. Zooxanthellæ are numerous and may be uniformly

distributed, or, as in *Agaricia*, are more restricted toward the oral extremity and periphery (fig. 165).

In larvæ of *Agaricia* and *Isophyllia* the endodermal tissue is in its most compact condition, and in both transverse and longitudinal sections slits or lines of demarcation are present, which limit one portion of the tissue from another. Along the margin of the slits the cells have more contents, and the boundaries of the mesenterial filaments and more central part of the mesenteries are also shown, the tissue appearing as a matrix in which these organs are embedded. The slits thus serve to delimit a parietal, mesenterial, stomodæal, and middle endodermal tissue (Pl. XVIII). In some larvæ the slits are represented by wider, more definite spaces, especially in the stomodæal region, while below the stomodæum the middle endodermal tissue can be seen in process of breaking down. Only the middle tissue, however, undergoes disorganization; that lining the wall and mesenteries persists as a thickened mass for a long time. Where the process has continued for some time the middle of the larval cavity is occupied by organic débris, comprising granules of various kinds, fragments of cell walls, and zooxanthellæ (Pl. XIV, fig. 112). This is afterwards extruded by the larvæ shortly after the establishment of the oral aperture (Pl. XIII, fig. 96).

For a long time the parietal and mesenterial endoderm remains enormously thickened, arranged in high vertical ridges, all the cells of the same vacuolated character, in both respects differing from the epithelium of the mature polyps. G. von Koch (1897), in his paper on the development of *Caryophyllia cyathus*, and later in "Das Skelett der Steinkorallen," has drawn particular attention to the parietal thickenings of the endoderm in larvæ of this and a somewhat later stage. As a rule the endodermal thickenings assume a definite form and relation with the mesenteries, which varies as the latter increase in number. In the section of the larva of *F. fragum*, represented in fig. 116, they are ten in number, two axial thickenings and four bilateral pairs; at a later stage another pair will be formed, and ultimately a thickening will occur in each of the twelve mesenterial interspaces. Von Koch (1896) has found similar endodermal swellings in the corals *Astroides*, *Balanophyllia*, and *Caryophyllia*, and in the Hydroids *Coryne* and *Tubularia;* Haddon (1890) figures exactly similar structures in the larva of *Euphyllia*.

The thickenings correspond with the positions which later will be occupied by the calcareous septa, and von Koch has applied to them the term *Prosepta* (Vorsepten). It is not to be assumed that they in any way represent the septa, or are concerned in their formation, for they are just as well developed in Actinians, e. g., *Lebrunia*, which never form a skeleton. From their structure and arrangement, von Koch supposes that in the larva the endodermal thickenings function as elastic supporting organs; that they are the physiological predecessors of the septa. Morphologically they are seen to be the remnants of the vacuolated endoderm, which, at an earlier stage, practically filled the interior of the larva.

When the larva settles the thickenings still persist in the lower region, and extend intermesenterially along the base and for some distance up the column, as shown in the section of *Manicina* (fig. 137). The septal invaginations of the ectoderm arising later are formed within the prosepta, so that the skeletotrophic endoderm is greatly thickened from the beginning.

Apparently in the larval prosepta we have the precursors of the enormously thickened vacuolated skeletotrophic endoderm, already described as characteristic of the lower aboral region of a great number of corals.

The prosepta are thus the persistent representatives of the endodermal tissue, which at an earlier stage completely occupied the internal cavity of the larvæ. The middle portion of this tissue becomes disintegrated, and the débris extruded from the larvæ, while the peripheral portion persists, becomes associated with the skeletal ingrowths, and undergoes more or less histological alteration.

In the larva of the Actinian *Lebrunia* (1899) I have already described a somewhat similar, nearly solid condition of the interior, and in this case the tissue of the earliest larvæ showed definite narrow spaces, which were regarded as indicating a primitive cœlom. These spaces correspond with the narrow slits and limitations met with in the freshly extruded larvæ of

Agaricia and *Isophyllia*. In the later larvæ of *Lebrunia* the central part of the vacuolated tissue had become broken down, and cell débris and zooxanthellæ were seen to escape through the oral aperture; and thus the adult cœlenteron was produced, though for a long time the parietal and mesenterial endoderm remained greatly thickened.

Appellöf, toward the close of his paper, "Studien über Actinen-Entwicklung," discusses my conception that the endoderm of the larva of *Lebrunia* is for a time multilaminar, and concludes that I am mistaken in my interpretation of the appearances. He surmises that *Lebrunia* is exceptional in that its larval endoderm cells are greatly elongated and highly vacuolated, not that they represent a parenchymatous mass, as my observations imply. The various coral larvæ here investigated show that the more or less solid condition is by no means exceptional in the Zoantharia, but is rather the rule. The question at issue is whether the appearances presented by sections are due to the vacuolization of a comparatively few elongated cells, or whether the endodermal tissue at this stage is composed of numerous rounded or polygonal cells forming an embryonic parenchymatous mass.

In whatever direction sections are taken the appearances are the same, the tissue seeming constituted of rounded or polygonal elements; there is never a radiating appearance, such as would be expected did the cells represent a columnar epithelium. The absence of this can not be set down to the disappearance of cell limitations, for such are everywhere very obvious. Moreover, so far as can be judged, each vacuolated element is provided with a well-defined nucleus, adherent to the wall.

It is manifest, from all the stages available, that the central portion of the tissue becomes disorganized shortly after the larva's extrusion, when functional activity of the stomodæum has been established. As seen in sections, the middle of the larva at this stage is filled with granules of various kinds, some staining deeply and others colorless; zooxanthellæ and fragments of what seem to be cell walls are also plentiful. Were all the cells fixed to the mesoglœa by their base, we should then have to assume that their centripetal ends become disintegrated and the débris extruded, a proceeding which would hardly be expected to occur.

LARVA OF AGARICIA AGARICITES.

(Pl. XXV, figs. 165–167.)

A colony of *Agaricia*, freshly collected, extruded numbers of larvæ within a few hours, all of which were directly preserved. The specimens were opaque and about 3 mm. in length; some were strongly pear-shaped, and others nearly spherical, and all swam about from the beginning. So far as could be made out by examination of the living specimens under the microscope, no oral aperture was yet established; a few zooxanthellæ were present in the ectoderm around the oral extremity. Most of the larvæ partly collapsed on preservation, whether in formalin or corrosive acetic.

Sections reveal that the larvæ are all at the same stage of development. The interior is filled with a compact vacuolar tissue, leaving practically no free cavity, and six pairs of mesenteries are developed, all of which extend nearly the full length of the inner cavity; four pairs of the mesenteries are united with the stomodæum throughout its length, but the other two pairs nowhere reach it. Mesenterial filaments are already borne by all the six pairs of mesenteries, and become strongly developed toward the aboral extremity of the larva. Both transverse and longitudinal sections indicate that the oral aperture is not yet formed, though evidently just about to be so; the stomodæal tube already shows a definite lumen, but at its outer extremity the ectoderm cells still close over it, and would prevent any communication between the interior and the exterior. No ciliation of the stomodæal ectoderm can be made out, though this character is always very manifest in well-preserved examples of the adult polyps. That the cilia in this instance have not disappeared, owing to imperfect preservation, may be inferred from the fact that the external ciliation of the ectoderm is still clearly shown.

The outer ectoderm of the larva is a very broad layer, and the usual histological elements of the adult are already present, comprising supporting cells, gland cells, and nematocysts, with the addition toward the aboral extremity of a well-developed nerve layer. Zooxanthellæ

are very limited in number and distribution. Only a few occur around the position at which the oral aperture will be formed, as noticed among the external characters. The cellular constituents of the ectoderm are distinctly shown in larvæ doubly stained with borax carmine and methyl blue, and the enlarged bases of the cilia are clearly distinguishable. Apparently on preservation none of the gland cells extruded their contents, and these are now stained with the carmine, while the supporting cells and nematocysts are stained blue. Most of the gland cells have finely granular contents, but others are clear, and they may extend nearly the whole width of the layer. The nematocysts are small and not very numerous. In the deeper parts of the layer are numerous clear, elongated bodies, staining blue, with the nucleus red, which in all probability represent developing nematocysts. The nuclear zone is very sharply limited on its outer margin, and the peripheral zone, wholly devoid of nuclei, occupies nearly one-half the thickness of the whole ectodermal layer, made up for the most part of the swollen gland cells.

About midway down the column wall an ectodermal nerve layer begins to appear. At first very feeble, it becomes better developed as the aboral extremity is approached, until at the actual pole it is very prominent. What seem to be delicate nerve fibrils extend vertically from the mesoglœa, and then unite in a broad meshwork; under high magnification the mesh exhibits the cut ends of very delicate fibrils, especially well seen in transverse sections. At the actual extremity the gland cells are less plentiful and nematocysts are more numerous.

Throughout the larva the mesoglœa scarcely attains any appreciable thickness, but appears as a mere dividing lamella between the ectoderm and endoderm; even in the mesenteries it is barely seen as a definite layer. Associated with its endodermal surface are nuclear bodies which stain deeply in methyl blue, and exhibit somewhat of a punctate character, as if nuclei in some mitotic phase, but, owing to their minuteness, no further details can be made out. Similar appearances occur also in connection with the mesoglœa of the mesenteries, and may perhaps be concerned in the formation of the middle layer.

The endodermal cells are spheroidal or polygonal, and almost completely vacuolated. Zooxanthellæ crowd the endoderm cells toward the oral end of the larva, and are sparsely distributed throughout; they show a slight tendency toward a restriction around the periphery of the endoderm. Although compact, the endodermal tissue presents a definite series of internal boundaries associated with the mesenteries, which indicate the lines along which cavities or passages will be formed when the larva becomes distended and the cœlenteric cavity is ultimately established.

The freshly extruded larvæ of *Agaricia* are somewhat exceptional in the degree to which the mesenterial development has already proceeded. In all the specimens examined the Edwardsian mesenteries are complete, and though the fifth and sixth pairs are yet free from the stomodæum they extend vertically nearly the whole length of the larva. The dorsal directives cease aborally a little in advance of the remaining three pairs of complete mesenteries.

Mesenterial filaments are strongly developed on the Edwardsian mesenteries, and less so on the two incomplete pairs; in the former they are in direct continuity with the stomodæal ectoderm, but it is obvious that this can not be the case with the latter. The filamental tissue on the incomplete pairs only makes its appearance some little distance below the stomodæum, and is never so strongly developed as on the other mesenteries. On these the filaments are often weak for some distance, but toward their lower termination they become greatly developed, at least on the mesenteries of the first and second developmental pairs. Here they are very conspicuous objects in sections, and developing nematocysts and gland cells in various stages can be found. The filaments have already very definite boundaries distinguishing them from the rest of the endodermal tissue.

LARVA OF ISOPHYLLIA DIPSACEA.

(Pls. XVII, XVIII, figs. 125–128.)

A colony of *Isophyllia* was collected from which larvæ were freely extruded from the beginning. On their first appearance most of the larvæ were rod-shaped, but others were pear-shaped; at first the former would crawl along the floor of the vessel in a worm-like manner, while the others would swim freely throughout the water. The larvæ were larger than

those usually met with in corals, measuring fully 3 mm. in length. When first extruded they were densely opaque, and the posterior end (oral) was deeply pigmented. An hour or two after being set free some became greatly distended at the aboral pole, and as a consequence were more nearly transparent; others, again, became swollen at the oral extremity, the opposite end remaining narrow.

In the inflated larva represented in fig. 125 three pairs of mesenteries were already indicated, all extending downward from the minute, circular, oral aperture. The members of one pair of mesenteries extended nearly the whole length of the larva, and along their line of attachment were much darker and broader than the others. On one side of the pair were two other faint mesenterial attachments, which continued but a short way down the polyp, while on the other side was a third pair only just apparent, and having a still shorter vertical course. All three pairs, however, start from the uppermost extremity of the polyp.

Some of the larvæ immediately on extrusion were preserved in formol, and others in corrosive acetic, when they threw out a quantity of mucus, which resulted in the adherence of minute foreign particles. The distended larvæ nearly always collapsed during the process of preservation.

Transverse sections of the freshly extruded specimens reveal that the larvæ are practically solid bodies, the interior being filled with a compact vacuolated tissue, bearing numerous nuclei and zooxanthellæ. Boundaries in the vacuolar endoderm are indicated toward the middle, in association with the mesenteries, and in the middle of some of the larvæ there is a faint indication that the endodermal tissue is beginning to break down, but as yet they are practically solid.

Toward the oral extremity the endoderm is crowded with zooxanthellæ, which are only sparingly distributed elsewhere. An examination of the outer ectoderm reveals comparatively few algæ, and these are scattered somewhat uniformly throughout the layer. The strong pigmentation of the oral extremity, noticed among the external characters, is manifestly due to the accumulation of zooxanthellæ within the oral endoderm, not, as is more usually the case, to their presence in large numbers in the ectoderm.

Both longitudinal and transverse sections through the stomodæum indicate the absence of any actual lumen in the tube, and the compact character of the interior of the larva, above described, is not such as to suggest that the circulation of any internal nutrient fluid had been established up to the moment of liberation.

The uppermost sections through the oral extremity reveal the presence of three pairs of mesenteries, all extending from the outer wall to the stomodæum. The ventral pair, however, is represented only by the merest rudiments, and the dorsal pair extends but a short distance; neither pair stretches downward the full length of the stomodæum. The middle of the three pairs is by far the most important: its members are inserted on the stomodæum throughout its extent, and when they become free the edge is tipped with a mesenterial filament which appears as a deeply-staining tissue, wholly resembling that of the stomodæal ectoderm: the two are in absolute continuity with one another, and in every way seem one and the same tissue. The mesenterial filament extends nearly two-thirds the length of the polyp, and is very conspicuous in sections on account of the deeply-staining character of its constituent cells. The other mesenterial pairs present no indications of filaments.

I. dipsacea is of interest as showing the early stage at which the second and third pairs of mesenteries are united with the stomodæum: indeed, they seem to originate at the angle between the wall and stomodæal invagination, and thence grow down the column and the stomodæum.

The ectoderm is characterized by numerous large clear gland cells, which give out their mucus when the larvæ are preserved. Many large nematocysts are also present, and the aboral extremity displays a strongly developed nerve layer.

LARVA AND YOUNG POLYPS OF FAVIA FRAGUM.

(Pls. XIII–XV, figs. 96–116.)

The polyps of several colonies of this species collected around Port Henderson, early in April, were charged with larvæ, which were extruded singly from time to time. Occasionally, an unfertilized egg would also appear. The larvæ could be seen through the transparent walls

of the expanded polyp as opaque white bodies, moving freely about in the gastro-celomic and tentacular cavities; upon retraction individual larvæ often remained within the tentacular cavity, distending it and forming small protuberances on the surface of the colony. The usual occurrence of the larvæ within the tentacles would indicate that they made their exit through the tips of these organs, but although large numbers escaped while the colonies were under observation the actual point of extrusion was never determined. They were either shot out suddenly, with force enough to send them some distance, or merely escaped and fell on the general surface of the parent colony.

Some of the larvæ were able to swim about immediately on extrusion; others remained motionless for a few moments either on the surface of the water or the bottom of the vessel, and then commenced vigorous gyratory movements. The rotation was clock-wise when the larvæ were viewed with the narrow oral extremity upward. When first liberated, the larvæ show considerable power of adhesion at any part of their surface; on transferring them from one vessel to another they would often fix themselves within the pipette, and require a considerable force of water to dislodge them. Specimens might adhere either by their anterior or posterior extremity for a time, and then commence moving again.

When first expelled some of the larvæ were rod-shaped bodies, about 2 mm. in length, and rounded at each end; others were pear-shaped, the broader pole being directed forward and the narrow end backward in translation; others again were oval or spherodial. The individuals, however, were able to change from one form to another. Seen with the naked eye, or by means of a lens, the larvæ were strongly opaque, an internal yellowish mass being distinguished from a colorless or slightly green external layer. The narrow, posterior, oral pole was for a long time more darkly colored than the rest of the larva.

Under the microscope also the larvæ were perfectly opaque, the ciliation was uniform, and when first extruded no oral aperture nor mesenterial divisions could be discerned. The surface appeared minutely granular, white dots being irregularly distributed over the ectoderm. The denser coloration at the narrow oral extremity was seen to be produced by an accumulation of yellow cells within the ectoderm, which gradually diminished in number away from the extremity. It was possible to determine that the coloration of the internal endoderm was also due to the presence of zooxanthellæ. Soon after liberation, extrusions of yolk granules and zooxanthellæ from the oral extremity took place, and continued from time to time (fig. 96).

Many of the larvæ underwent much alteration in shape. The oral extremity became swollen, and the aboral narrow, a reversal of the primary condition (fig. 100); but when first extruded the larvæ sometimes exhibited the swollen oral extremity and narrow aboral.

Within a day or two certain of the larvæ had settled to the sides of the vessel, becoming flattened both orally and aborally; a few zooxanthellæ were still present around the oral aperture, which had now become functional. Some specimens would again detach themselves and move slowly around. After fixation the larvæ were more transparent, and at first four pairs of mesenterial divisions were visible from the outside, and later six pairs. The settled larvæ were soon able to extend themselves, and assume the columnar form, appearing greenish in color.

The various stages of mesenterial development were quickly passed through, until all the protocnemes were present, the Edwardsian mesenteries complete and the fifth and sixth pairs incomplete. Beyond this no increase in the number of mesenteries took place during a period of three weeks. Within four days six tentacular prominences were apparent, the larvæ at this stage usually appearing flask-shaped, with a broad base (fig. 107). During the early stages the tentacles often became involved in the expanded discal tissues of which they were outgrowths, and as a consequence were indistinguishable as separate organs. In a young polyp from another batch of larvæ, the six members of the inner entocœlic cycle also appeared in advance of the members of the outer exocœlic cycle (fig. 106).

One larva was secured attached to a fragment of glass, and could thus be examined as a transparent object, and its later development observed. In seven or eight days the mesenterial filaments were visible on the first and second pairs of mesenteries as darker internal organs, and in about fourteen days six small, clear, oval areas were recognizable within the entocœle of the

six pairs of protocnemes, their occurrence suggesting some connection with the first stages in the formation of the skeleton (fig. 108). They clearly correspond in position with the six septa of *Manicina* (fig. 135), and it is conceivable that they represent invaginations of the basal wall preceding the formation of the septa. No calcareous deposition however was observed to take place within them: probably the unfavorable conditions under which the larva was kept interfered with its normal development.

Small polyps are sometimes found around the larger colonies of *Furia*, and represent larvæ which have fixed themselves immediately or shortly after extrusion. From these several further stages of development have been secured, one of which is represented in fig. 109. The polyp is in a partly expanded state, and only the discal region is indicated, as seen under a low power of the microscope. The six pairs of primary mesenteries are present, the fifth and sixth pairs still free from the stomodæum; in addition to these a pair of mesenteries has appeared in each dorsal exocœle, and a small pair in each of the middle exocœles. At present the metacnemic pairs extend but a short distance over the margin of the disk, but are continued farther down the column wall. No mesenteries have yet appeared within the ventral exocœles. The significance of the stages in the mesenterial development here represented has been already noticed in discussing the appearance of the metacnemes in the Madreporaria generally.

Of the tentacles six entocœlic and six exocœlic members are already present, forming two cycles, the inner tentacles a little larger than the outer, and both slightly knobbed. In addition to these a tentacle has arisen in association with each pair of metacnemes, making sixteen in all. At this stage it was impossible from their position to say whether the new tentacles were entocœlic or exocœlic in relation to the pairs of metacnemes, but it is significant that they follow closely upon the development of the mesenteries. Most probably they are the entocœlic outgrowths which have appeared somewhat in advance of the exocœlic, following the sequence of the prototentacles.

The different stages secured in the development of *Furia fragum* afford a complete series illustrating the order of appearance of the mesenteries in corals, and it is desirable that they should be presented in their regular sequence. The series extends from larvæ with only one pair of complete mesenteries to young polyps in which fission is instituted. The earliest stage occurs in non-extruded larvæ obtained from a colony after decalcification (fig. 112). Three pairs of mesenteries are present, but only one pair is complete, and this divides the cœlenteric cavity into two unequal chambers. In the larger of these is a second pair of mesenteries, not complete as yet, but bearing rudimentary mesenterial filaments; in the smaller chamber is a third pair of mesenteries, which are very rudimentary. The first pair extends almost the whole length of the larva, the filaments strongly developed all the way; the second terminates some distance in advance of the aboral end; while the third has only a very limited course.

Larvæ which had been extruded a few hours when preserved reveal the next stage, represented in fig. 113. Two pairs of mesenteries are united with the stomodæum, and, by comparison with the previous figure, the new complete pair is evidently the dorsal pair, the second of the mesenterial sequence. The ventral pair (III, III) is no better developed than in the former figure, but in sections below the termination of the stomodæum a new pair has appeared between the dorso-lateral pair (fig. 114). This is manifestly the fourth pair in the mesenterial sequence, and it is inserted dorsal to the second pair. Also between the first and second developmental pairs are found the merest rudiments of another pair (V, V).

Sections of larvæ a little older, and in one case of a young polyp already settled, present the next stage, where three pairs of mesenteries are inserted on the stomodæum (fig. 115). Comparison with fig. 113 indicates that it is the third pair in the mesenterial sequence which has now reached completion. The fourth pair extends more upward, and the fifth pair has reached the level of the stomodæum; the sixth pair has not yet reached the stomodæal region, but is present below (fig. 116). Finally, in larvæ which have just settled (figs. 105, 106), four mesenterial pairs have become complete, and the fifth and sixth pairs are well developed in the upper part of the column, but remain free from the stomodæum.

The sequence for the protocnemic pairs is thus complete. The first and second pairs to arise become the ventro-lateral and dorso-lateral of the Edwardsian mesenteries, the third pair

constitutes the ventral directives, and the fourth the dorsal directives, while the fifth and sixth pairs, incomplete as yet, arise on the ventral aspect of the second and first pairs, respectively, the fifth a little in advance of the sixth. (See diagrammatic figures on p. 508.)

A young polyp, settled on the same block of dead coral as a mature colony, affords the next stages required in the sequence the manner of appearance of the first metacnemes. The living characters are shown in fig. 109, and a section through the decalcified polyp is diagrammatically represented on p. 509. The protocnemes are in the same stage as in the previous figure—the first four pairs are complete, but the fifth and sixth are still incomplete. Within the dorsal and middle exocoeles on each side a pair of mesenteries has appeared, the dorsal pairs being better developed than the middle. In fig. 15*f*, showing the arrangement in another decalcified young polyp, six pairs of metacnemes have appeared, completing the second cycle, and all the members of the first cycle are united with the stomodæum. The six metacnemic pairs thus follow a dorso-ventral, or antero-posterior, order in their appearance, but are now practically equal and constitute the second cycle of mesenteries.

Fig. 15*g*, p. 510, shows the manner of appearance of the first pairs of mesenteries which will constitute the third cycle of twelve mesenteries, or second cycle of metacnemes, and it is at this stage that fission is introduced (p. 511).

A tangential vertical section through one of the larvæ which had settled, but in which no septal formation had yet taken place, is represented by fig. 110, and the right half of the same section, more highly magnified, is represented by fig. 111. The four complete mesenteries extend from the base to the upper wall, and present a muscular development on each face, the fibers being cut obliquely. The endoderm is still greatly thickened, especially basally, while the superficial ectoderm has undergone but little change; zooxanthellæ are altogether absent, though present in abundance in the larvæ.

A great alteration has taken place in the basal ectoderm. It is no longer a broad columnar layer, but is represented by little more than fragments, which include a few nuclei and granular matter which stains deeply. The mesoglœa is likewise extremely narrow except mesenterially, where it is much broadened. In these regions can be seen structures similar to the wedge-shaped, striated, desmoidal processes characteristic of adult polyps, so that evidently these arise at a very early stage in the fixation of the larva: hints of the same processes also appear intermesenterially, where the mesoglœa is extremely narrow. The larva from which the sections were taken had been adherent to a fragment of glass for over a week, and, though no septa were formed, it is very probable that the basal plate had already been laid down, as this is one of the first parts of the skeleton to appear. The skeletogenic ectoderm is in much the same condition as in adult polyps, in regions where growth is not proceeding rapidly.

The passage from the narrow basal ectoderm to the broad ectoderm of the column at the margin of the section is abrupt. The cells around the indented vertical part at the right extremity of fig. 111 are somewhat modified compared with those beyond, and are probably concerned in the formation of the epitheca. This is certainly the case in the slightly older polyp of *Manicina* represented in fig. 137.

YOUNG POLYPS OF MANICINA AREOLATA.

(Pl. XIX, figs. 133–137.)

To the very complete description of the early stages in the development of this species given by Dr. H. V. Wilson, in 1888, I have nothing to add, and will therefore proceed to the point at which Wilson's researches terminated, namely, the formation of the skeleton. The latest stage reached in the growth of the Bahama specimens was one in which the twelve protocnemes were present, only two pairs of which were connected with the stomodæum. The stage is comparable with that represented in fig. 134, Pl. XIX (*cf.* Wilson's fig. 39), taken from a fixed larva four days after extrusion from the parent colony.

Out of many batches of larvæ extruded from a small Jamaican colony only a few individuals became fixed, and after several days these were reduced to two, which continued to live for nearly three weeks, though under somewhat unfavorable conditions. The larvæ were attached to frag-

ments of glass, and could be transferred from one jar to another, or submitted to microscopic examination. Usually they were kept in vessels in which living colonies of other corals, such as *Cladocora* and *Oculina*, were already established.

Shortly after fixation the first four pairs of mesenteries reached the stomodæum, but the fifth and sixth pairs remained incomplete for the whole period, and no trace of any metacnemes appeared. The tentacles protruded toward the beginning of the second week, and, at the time they could be definitely recognized, were already twelve in number.

One of the specimens, viewed as a transparent object, is represented in fig. 135. The mesogloeal portion of the mesenteries appears as a clear, colorless line; the Edwardsian mesenteries are united with the circular stomodæum, while the fifth and sixth bilateral pairs are incomplete. The knobs of the retracted tentacles stand out as darker circular patches, arranged in two alternating cycles of six each: the members of the inner cycle are entocœlic and those of the outer are exocœlic in position, varying but little in size. Within the entocœles of each of the six pairs of mesenteries is seen the first indication of the skeleton, represented by narrow, septum-like deposits, situated some distance from the periphery, and radiating toward the center. A basal granular deposit, the first formation of the basal plate, could also be distinguished, but was not studied in detail.

The second polyp is represented in fig. 136, but the corallum has not developed to the same degree as in the first polyp. In the dorsal or sulcular entocœle the calcareous deposit forms two small oval areas; in the sulcar entocœle the deposit is also oval and small; while in the lateral entocœles it bears more resemblance to a septum. The differences in extent of development suggest that the six septa may not arise with complete uniformity, but under the unfavorable conditions to which the polyps were subjected not much importance can be attached to the result. Through the oral aperture two other skeletal deposits can be distinguished, the first indications of the columella.

Fig. 135 should be compared with that given by von Koch (1897, p. 760) of the fully expanded young polyp of *Caryophyllia cyathus*. Here, also, the corallum appeared at the Edwardsian stage of mesenterial development; the tentacles are in two alternating cycles of six each, and the six primary septa have appeared, but are more peripheral in their distribution and are already united with the circular theca. In *Manicina* no thecal formation occurred during the short period the development was followed, but indications of an epitheca were observable.

Both of the young polyps of *Manicina* were decalcified, with the object of ascertaining the early stages in the modification of the polypal layers, consequent upon the formation of the skeleton.

A radial vertical section through one of the polyps, including two septal invaginations, is represented in fig. 137. It was from such sections that von Koch (1882) established the external character of the skeleton in corals. The actual outlines of the polyp are from a camera lucida drawing, while the diagrammatic outline of the skeleton has been added.

The polyp is flattened in retraction, resting upon the skeletal upgrowths, and the mouth is widely open. The right half of the section comprises a portion of a mesentery connected with the stomodæum, and bearing a mesenterial filament; the left half includes the section of a tentacle, which is only distinguishable from the rest of the ectoderm by its greater thickness and the presence of large nematocysts. The columnar and discal endoderm is narrow and contains many zooxanthellæ, while the basal, skeletotrophic endoderm is greatly thickened, except over the upper part of the septa. It is devoid of zooxanthellæ, and in its other characters closely recalls the layer as it occurs in the lower part of the skeletotrophic tissues in adult polyps (fig. 129). The mesogloea is extremely narrow throughout.

Greatest interest attaches to the basal skeletogenic ectoderm. In the actual sections scarcely any indications of the layer remain; it has either been removed by decalcification, or, more probably, has become greatly reduced as a result of the formation of the skeleton, a condition which has been found to characterize the older regions of most coral polyps. A few nuclei occur here and there, and in places a detached mesogloea-like membrane, representing the skeletal membrane of Bourne.

Where at each extremity the polyp turns upward the ectoderm for a short distance has

undergone a similar modification, though not quite to the same degree; more of the cellular character is retained than at the base, but the passage into the broad ectoderm of the column is abrupt. It is here that the epitheca is formed, and manifestly it is nothing more than the upturned continuation of the basal plate. The epitheca and basal plate are covered only on their inner surface by the polypal tissues, while the septal upgrowths from the basal disk are clothed on both sides. The first two parts of the skeleton can therefore increase in thickness and extent only on one face; but the septa are added to on both faces. The epitheca as yet is unconnected with the peripheral septal edges, but in older polyps it rests upon their free exposed margins.

POSTLARVAL DEVELOPMENT OF SIDERASTRÆA RADIANS.

In both its free and incrusting condition *Siderastræa radians* is a very abundant coral around Jamaica, and fertile colonies have been obtained, and the development of the larvæ and young polyps followed throughout a period of seventeen weeks.

In the earliest extruded larvæ the oral aperture is already established, and the interior is nearly filled with a vacuolated, parenchymatous tissue, containing numbers of zooxanthellæ uniformly distributed throughout. Four pairs of mesenteries are present; two lateral pairs are complete, but the dorsal and ventral directives are yet free. In later larvæ the ventral directives are inserted on the stomodæum, and the fifth and sixth pairs of mesenteries have appeared. The dorsal mesenteries were complete by the time the larvæ settled, the Edwardsian stage being thus reached, but mesenterial filaments were found only on the first and second bilateral pairs of mesenteries. The ectoderm is crowded with zooxanthellæ at the oral pole, and a few occur over all the layer, but become very sparse in the older larvæ. At the aboral pole the nerve layer undergoes a strong development, and nematocysts are more plentiful than elsewhere.

Wide slits and spaces, both intermesenterially and below the stomodæum, began to appear in the larvæ shortly after extrusion, and represent the permanent gastro-cœlomic cavity. Soon the whole of the central part of the vacuolated tissue breaks down, and the middle of the cavity is occupied by a mass of organic débris, among which are zooxanthellæ and granules of various kinds. Extrusions of such débris were often observed from the free swimming larvæ. Many of the larvæ became attached to pieces of glass, and the young polyps could thus be examined under the microscope in their living condition as transparent objects, and the development of the various organs and skeleton followed step by step. The full account of the postlarval development will be published shortly, but the salient results may be here briefly summarized.

Most of the larvæ were pear-shaped, the swollen extremity as a rule being the oral or posterior end in swimming. On fixation many grouped themselves together, and thus from primarily free and independent organisms young colonies were derived. Six pairs of mesenteries—the Edwardsian members complete, and the fifth and sixth pairs incomplete—were present in the newly settled larva.

Tentacles.—Six equal tentacles, representing a primary cycle, appeared a few days after fixation; but are exceptional among all corals whose development has yet been studied in that they arise from the exocœlic chambers, not the entocœlic, as is usually the case. Two or three weeks elapsed before the entocœlic cycle began to appear, when the members developed either simultaneously or in a successive manner. They were situated central to the first cycle to arise, and for a long period remained smaller than the others. The development of the two primary cycles of tentacles was thus centripetal, the outer exotentacles appearing first and the inner entotentacles next.

The entotentacles of the adult *Siderastræa* are bifurcated toward their extremity, and in the course of their development in the larval polyps the two halves were found to appear independently, and with a period of several weeks intervening. The common peduncle was developed later, and raised the two moieties above the disk. The exotentacles remained simple throughout.

The second cycle of mesenteries having appeared, another series of tentacles protruded from the six additional exocœlic chambers, and with the primary exotentacles formed an outer

cycle of twelve. Later, situated between the exocœlic cycle and the primary entotentacles, the members of the second cycle of entotentacles begin to appear, as outgrowths from the entocœles of the second cycle of mesenteries.

Thus the exotentacles, whether belonging to the primary or secondary order, appeared before the entotentacles, and from the beginning they constituted the outer cycle, at first with six and later with twelve members.

Mesenteries.—For about four weeks no increase beyond the six primary pairs of mesenteries took place, and the fifth and sixth pairs remained free from the stomodæum. Then a pair of mesenteries appeared within the dorsal exocœle on each side of the polyp. Their first indication was as two narrow lines along the column wall toward its aboral termination. These were followed by a pair in the right and left middle exocœles, and later by a pair in each ventral exocœle. For several weeks the pairs remained of different magnitudes, corresponding with the order of their appearance from the dorsal to the ventral aspect (fig. 6, p. 456). After the third month they began to extend across the disk, but, like the fifth and sixth pairs of protocnemes, never reached the stomodæum.

Corallum.—Three or four days after fixation, the skeleton was first observed in the form of six radiating septal upgrowths, practically equal in size, and situated within the six primary entocœles, about midway between the outer boundary and middle of the polyp. At the same time a narrow peripheral calcareous ring was formed, its outer surface uncovered by polypal tissues, and undoubtedly to be regarded as the *epitheca*. Macerations made later show the ring to be continuous with the *basal plate*, which very early made its appearance. A day or two after the formation of the first cycle of entosepta, the six exocœlic members began to appear, in some cases simultaneously, but in others in successive bilateral pairs from the dorsal to the ventral aspects (fig. 12, p. 492).

During the course of the third week other calcareous deposits took place, some appearing as angulated continuations of the primary septa, and others arising wholly independent. For two or three months the further development consisted mainly in the increase in size and complexity of the parts mentioned, the general impression being that of two cycles of septa, a larger and a smaller, having their peripheral extremity enlarged in a Y-shaped manner, but free from the epitheca. The columella was formed partly from independent upgrowths from the basal plate, and partly by centripetal extensions of the entosepta.

On the establishment of the second cycle of mesenteries, which naturally corresponded in position with the primary exosepta, new calcareous formations appeared independently at the periphery of the entocœles, and later fused with the primary exosepta already in the same radius. The peripheral angulations of the primary exosepta became new and independent exosepta, situated within the twelve exocœles. The skeletal changes now going on were somewhat obscure and complicated, but according to my interpretation they afford clear evidence that the members of the second cycle of entosepta must be regarded as new formations, even though later they fuse with the remnants of the primary exosepta. The continuations of the primary exosepta remain exosepta, and for the time being constituted the third cycle of septa. A distinct dorso-ventrality was manifest in the development of the septa.

PART II.

SYSTEMATIC.

CLASSIFICATION OF THE MADREPORARIA.

The absence of any extensive knowledge of the morphology of the polyps of the Madreporaria accounts, in some measure, for the anomaly that the classifications of the group proposed from time to time have been founded upon skeletal characters alone. The best known, and until recently most widely accepted arrangement, is that presented by Milne Edwards and Haime, in their Histoire Naturelle des Coralliaires (1857–1860). These writers divide the Sclerodermic Zoantharia, upon skeletal considerations only, into five sections: *Madreporaria aporosa*, *M. perforata*, *M. tubulosa*, *M. tabulata*, and *M. rugosa*. According to Professor Duncan, in Revision of the Families and Genera of the Madreporaria (1885), the Tubulosa no longer exists, and the section Tabulata has been eliminated by H. N. Moseley.[a] Duncan, however, accepts the Madreporaria Aporosa, Perforata, and the Rugosa. J. J. Quelch, in the report on the "Challenger" reef corals (1886), altogether rejects the ancient group of the Rugosa, and mingles its families with those of the more modern Aporosa.[b]

Mainly upon considerations of the presence or absence of a Randplatte or Edge-zone, von Heider (1886) has suggested the possibility of subdividing the Madreporaria into *Euthecalia* and *Pseudothecalia*; A. Ortmann (1890), from his studies of the thecal characters and methods of asexual growth, recognizes the two orders *Athecalia* and *Euthecalia*, and subdivides the first into three suborders: *Incepta*, *Synapticulata*, and *Pseudothecalia*. The latest important attempt at founding a taxonomic system, based entirely upon skeletal characters, is the arrangement proposed by Miss Ogilvie (1897), as a result of her elaborate investigations on the microscopic structure of the corallum.

While acknowledging the value of many of Miss Ogilvie's suggestions, the classification advanced has everywhere been received with hesitation. In his recent paper on the corals of the Gulf of Lyons, Professor Lacaze-Duthiers (1897) contends for the retention of the classification of Milne Edwards and Haime as entirely adequate for all practical purposes.

In the present connection it is not proposed to discuss all these suggested schemes. It is generally admitted that the skeleton alone is inadequate as a basis upon which to establish a natural classification. It is only needful here to refer to whatever attempts have been made to utilize the anatomical characters of the polyp. In general, the skeleton of corals so very closely reproduces the fundamental characteristics of the polyps themselves, that an approximate knowledge of the essential features of the latter can often be surmised from it, much more than in the case of the skeleton and soft parts of the more complex groups of animals. Thus, the

[a] See also Verrill, 1869, p. 518.

[b] Bourne, in the article "Anthozoa", in Lankester's Treatise on Zoology, adopts the classification of Duncan, with the modifications introduced by Quelch. In doing so, he writes (p. 70): "It cannot be pretended that it is a natural or a satisfactory classification, yet it is the best which can be offered in the present state of our knowledge. Other systems have been proposed, but they have not stood the test of criticism, and have been ephemeral."

relationships of the septa to the mesenteries and tentacles being established, Professor Haeckel's classification of the Anthozoa into Tetracoralla, Hexacoralla, and Octocoralla, applies with equal force to the polyps as to the corallum.

It was early recognized that externally the polyps of corals very closely resemble Actinian polyps, and subsequent investigations along anatomical and histological lines have but served to emphasize the unity of structure. The question therefore naturally suggests itself as to how far the principles of classification adopted in the latter can be applied to the former. The earlier subdivisions of the Actiniaria, as for example those adopted in Gosse's Actinologia Britannica (1860), and in Andres' Le Attinie (1883), rested wholly upon external characters. Mainly as a result of the Actinological researches of the brothers O. and R. Hertwig (1879), the great value of the arrangement of the mesenteries as an aid in classification was first realized. The report by Prof. R. Hertwig (1882) on the "Challenger" Actiniaria, as well as subsequent contributions by numerous workers, show how very widely and successfully anatomical characters may be employed in determining phylogenetic relationships in the group. The main subdivisions of the Actiniaria—Hexactineæ, Zoantheæ, Cerianthеæ—now rest most firmly upon the one character of mesenterial development and adult arrangement, while other distinctive features found to be associated with them prove that the selection has by no means an arbitrary significance.[a] The mode of development and adult arrangement of the mesenteries enable forms to be associated which agree in more fundamental details than is possible by any other selection, thus proving that the mesenteries most nearly afford a basis for a true natural classification.

In addition to the aid from the mesenteries, systematic characters of greater or less value among the Actiniaria are afforded by the arrangement and form of the tentacles; the distribution and extent of development of the musculature, especially the presence or absence of columnar ectodermal muscle fibers, and the nature of the sphincter muscle; the presence of vesicular or other outgrowths of the column wall; free, fixed, colonial, or simple habit; presence or absence of acontia, etc.

We may now see how far these structural characters, so helpful among the Actiniaria, have been or can be applied to the classification of the Madreporaria, or what others may be forthcoming within the group itself. G. C. Bourne, in 1887, discussed the subject of the arrangement of the Madreporaria in connection with his studies of the anatomy of the soft parts of certain species, and remarks (p. 12):

"It has long been felt that a classification of Madreporarian polyps based on a study of the corallum alone is unsatisfactory, and that any attempt to remodel the old classifications should depend on a systematic study of the relations between the corallum and the polyp. Owing to the difficulty of obtaining material, and of dealing with it when obtained, the number of forms examined is as yet small, and the results of recent researches have not advanced us very far towards an improved classification."

Later (p. 24), he writes:

"I have treated the questions relating to the corallum at length, because every fresh form that is examined convinces me that the expectations formed of founding a new classification of the Madreporaria on the anatomy of the polyp are to meet with disappointment. There is singularly little variation in the forms hitherto examined."

However, the same author (p. 29), regarding the presence or absence of radial symmetry and of a "Randplatte" as of taxonomic importance, suggests the following arrangement as warranted by the facts known at that time:

1. Madreporaria with no directive mesenteries and a perfectly radial symmetry, *Lophohelia*, *Mussa*, *Euphyllia*.

2. Madreporaria with directive mesenteries and a combined radial and bilateral symmetry, *Tubinaria*, *Rhodopsammia*, *Fungia*, and many others.

3. Madreporaria with reduced radial symmetry and marked bilateral arrangement of parts, *Madrepora*, *Pocillopora*, *Seriatopora*.

[a] The tendency in Actinological writings is now to regard each of these three divisions as ranking in importance with the principal divisions of the Anthozoa—Alcyonaria, Antipatharia, etc.

4. Madreporaria with a basal pseudotheca and no "Randplatte." *Flabellum*.

None of these characters, however, can be regarded as of importance in the foundation of the principal subdivisions of the group. Investigations on the Actiniaria, as well as those here given on the Madreporaria, indicate the exact value to be assigned such details as the presence or absence of directive mesenteries, while questions of symmetry, unaccompanied by developmental history, have very little significance. For example, the apical polyps of *Madrepora* exhibit externally the most perfect radial symmetry, while the radial polyps from which they are derived are markedly bilateral. The presence or absence of directives is a secondary, not primary, character, already shown to be dependent upon the mode of asexual reproduction of the species, and has therefore no fundamental significance. The marked bilateral arrangement of the parts in *Madrepora*, *Pocillopora*, and *Seriatopora* are a retention of larval characteristics.

The quotations from Bourne accurately represent the opinion of zoophytologists with regard to the classificatory value of the Madreporarian polyp, and little progress along such lines has since been made, while much attention has been concentrated on the skeleton.

Undoubtedly the mesenteries are the organs of greatest taxonomic importance among the Anthozoa; for the tentacles and most other outgrowths which may occur are arranged in strict accordance with them, and in the Madreporaria the arrangement of the septa follows most directly upon that of the mesenteries. From a truly morphological standpoint all other polypal structures are of subordinate value. It may, therefore, be safely accepted that so far as any classification among the Madreporaria can be founded upon differences in the mesenteric system it will be fundamental, and of course the same remark applies to the septal system, as this is determined by the former.

Reviewing the arrangement of the mesenteries so far disclosed within the Madreporaria a perfect uniformity occurs as far as the protocnemic stage, or stage with only six pairs of mesenteries. It seems doubtful, however, whether any species of living coral invariably retains this primary condition in all its mature polyps. No such group of Actinians is now known since Faurot (1895) discovered four or six pairs of rudimentary metacnemes in *Edwardsia*. By far the majority of the adult polyps of *Porites* and *Madrepora* never get beyond the protocnemic stage, but occasionally such examples occur. According to Moseley and Fowler, the adult polyps of *Pocillopora* and *Seriatopora* have only six pairs of mesenteries, but Verrill and Quelch mention that occasionally twenty-four septa are present, which would imply the occurrence of twelve pairs of mesenteries in the polyp.

The protocnemic stage being probably alike in all modern corals, it is clear that any divergences in the mesenterial plan must be looked for in the subsequent development, that is, in the metacnemic succession.

Two altogether different types of metacnemic sequence and adult arrangement are now known—the one in which the metacnemes appear in unilateral (isocnemic) pairs all round the polyp, and in the adult present a cyclic disposition, represented by the majority of corals; and the other with a bilateral origin and arrangement of the mesenteries throughout, as yet definitely ascertained only for the genera *Porites* and *Madrepora*. The two types have been shown to be somewhat comparable with the metacnemic sequence and resulting arrangement in the Hexactiniæ and Cerianthea among the Actiniaria, and I propose to make of them two Madreporarian groups of nearly equivalent value as follows:

Entocnemaria.—Madreporaria in which the mesenteries always arise in bilateral pairs, and beyond the protocnemic stage the increase takes place within one or both of the directive entocoeles.

Cyclocnemaria.—Madreporaria in which the mesenteries beyond the protocnemic stage arise in isocnemic unilateral pairs within the primary exocoeles. The mesenteries in the adult are usually arranged in two or more alternating cycles.

So far as our knowledge of the anatomy and development of coral polyps goes, the second group will include the majority of recent forms, and fossil genera in which a regular multicyclic disposition of the septa can be established, while the first will comprise *Porites*, *Madrepora*, and probably certain fossil corals exhibiting a bilateral arrangement of the septa. The Entocnemaria

were the earliest in the phylogenetic history of the Madreporaria, the Cyclocnemaria appearing comparatively late.

It is, of course, uncertain as to how far later researches on similar lines will reveal other systems of mesenterial and septal development. Any other distinct type which may be discovered will, however, merit recognition of equal value. Seeing that in the Zoantheæ, among the Actiniaria, another wholly distinct type actually exists, the possibility should be borne in mind. Among the bilateral Palæozoic corals growth occurred in a bilateral manner at other than the dorsal or ventral axial regions; the septal growth in Zaphrentoid corals like *Streptelasma* and *Zaphrentis* was undoubtedly unlike that in any of the forms here described. In many respects it suggests such a development as would be followed in polyps with a mesenterial sequence like that characteristic of the Zoantheæ."

One very suggestive result of the recent study of corals is the demonstration that very often an alteration of the septal arrangement takes place between its primary plan and that in the mature calice. Thus von Koch (1889), by a complete series of transverse sections, has proved that the octameral *Cyathophyllia rugosa* is hexameral so far as the two primary cycles of septa are concerned, and that it is only with the appearance of the third cycle that irregularities are introduced which lead to the octameral plan characteristic of the mature corallum.

In this connection the remarks of Count Pourtalès, in Deep Sea Corals (1871), are also particularly instructive. Discussing the order Rugosa he states:

"Mr. R. Ludwig has shown (H. von Meyer's Palæontographica, Vols. X and XIV) that the tetameral arrangement claimed for the Rugosa is only apparent, there being originally six primary septa; but that further development in each system is asymmetrical, and that two of the systems remain generally undeveloped. I had, before having knowledge of Ludwig's researches, come substantially to the same conclusions by the examination of *Lophophyllum proliferum* Edw. and H., from the carboniferous formation, a form very suitable for that study. When the youngest stage of the coral is examined by cutting through the tip of the conical *Lophophyllum proliferum*, six primary septa and six interseptal chambers are found, placed symmetrically on two sides of a vertical plane, and unequally developed."

This reference of the septa of the Rugosa or Tetracoralla to a primary hexameral system receives additional support from what is shown to be characteristic of the early polyps of the Actiniaria and Madreporaria. The protocnemic stage of recent corals is hexameral, whatever be the subsequent arrangement, and the evidence given above would seem to prove a like protocnemic stage for the ancient corals; in which case all the mesenterial and septal divergences characteristic of the fossil corals took place from this stage, as in living corals and anemones, and the adult tetrameral symmetry is only secondary.

The fact that in *Porites* and *Madrepora* only eight of the twelve protocnemes ever become complete, and that in other polyps the union of the remaining pairs with the stomodæum is always long delayed, may perhaps be taken as suggestive of an ancestry in which the unilateral pairs throughout consisted of a complete and incomplete moiety (anisocnemic), as in the Zoanthids of to-day.

The adult hexameral plan is by no means invariable among recent Madreporaria. Duncan (1885, p. 7), discussing the definition of the Madreporaria Aporosa by Milne Edwards and Haime, states: "Moreover the hexameral arrangement of the septa is not constant; it may be pentameral, heptameral, octameral, or decameral." The recent deep-sea genera *Haplophyllum* Pourtalès, and *Cuynia* Duncan, have been assigned tetameral septa, as is also the case with the Cretaceous *Holocystis* M.-E. and H. It will be necessary in these cases to ascertain the developmental history of the corals before the exact value can be accorded their adult symmetry.

Whether the primary plan of the mesenteries and septa of the Palæozoic corals were tetameral or hexameral, it has been clearly shown that the mesenteries and septa increased in a bilateral manner from two or more restricted regions. This was first emphasized by Ludwig (1862,

"Relationships of the Rugosa (Tetracoralla) to the living Zoantheæ." Johns Hopkins Univ. Circ., vol. xxi, no. 155; also, Ann. Mag. Nat. Hist., ser. 7, vol. x, May, 1902.

1865) and Kunth (1869–70), and is regarded by Neumayr (1889) as a characteristic of the highest morphological significance. The bilaterality in many forms is only clearly developed in the early stages, but the external surface of corallites often exhibits pinnate streaks or ridges which correspond with the internal septa, and these demonstrate conclusively the bilateral manner in which the septa have arisen, e. g., *Streptolasma*, *Zaphrentis*.

In the Cyclocnemaria the mesenteries are as a rule arranged in two or more regular cycles, while in the Entocnemaria they are in one cycle only, with merely alternately large and small members. In the absence of any knowledge of the soft parts of a coral we may assume that in general the septa of the former group will be polycyclic, while those of the latter will be monocyclic or at most dicyclic. Where asexual reproduction by incomplete discal fission prevails, there is a tendency toward the dicyclic condition, but these forms can be readily distinguished from the Palæozoic types with merely large and small alternating septa.

With regard to the further employment of the mesenteries and septa of Madreporaria for taxonomic purposes, the wide differences in the arrangement and nature of these organs in gemmiferous and fissiparous genera may now be considered. In mature polyps of the former it has been found that a cyclical regularity prevails, and two pairs of directives are always present, but in the latter the introduction and continuance of fission carries with it marked changes, not only in the mesenteries, but also in the septa and tentacles. No other polypal characteristic seems to exert such a profound influence upon the nature of the compound coral as a whole. But by no means can the results of fission be regarded as of such fundamental significance as those distinguishing the Entocnemaria and Cyclocnemaria. The young polyps of both gemmiferous and fissiparous genera are built upon exactly the same plan, and it is only with the advent of vegetative reproduction that they become divergent.

Fissiparity would appear to be a condition which may arise in any group of corals, and its occurrence does not necessarily indicate any natural relationship among the forms in which it prevails. In any classificatory scheme it can probably be regarded as only of subfamily importance, which is practically the position assigned it by Duncan.[a] In this case the divisions, in whatever families they occur, may be defined as follows:

Gemmantes. Asexual reproduction takes place by gemmation, and each polyp represents a distinct individual. The tentacles, mesenteries, and septa are arranged in alternating cycles, and two pairs of directive mesenteries are present in each polyp.

Fissiparantes.—Asexual reproduction takes place by stomodæal fission, without the production of morphologically complete polyps. The tentacles, mesenteries, and septa, after fission is established, are not arranged in regular alternating cycles, and no new directive mesenteries arise.

The arrangement and form of the tentacles in the Madreporaria can not attain that systematic value which they possess in the Actiniaria. In the latter the origin of one or more tentacles from a single mesenteric chamber is a character of much importance, and affords a means of dividing the Hexactiniæ into the two suborders Actininæ and Stichodactylinæ. In the corals no instance of the stichodactylinous condition has been met with, and any other tentacular characteristic so far disclosed seems worthy of only generic, rarely of family, recognition. With the exception of the bifurcated entocœlic tentacles in the single genus *Siderastræa*, the organs are invariably simple in corals. As a rule they are arranged in close, alternating, entacmæous cycles, but in the Fungidæ the cycles are distant and tend to lose their regularity of disposition. The prevalence of the knobbed or swollen tentacular apex in corals is noteworthy, considering how rarely it occurs in the Actiniaria (e. g., *Corynactis*, *Ricordea*, *Corallimorphus*). Tentacular introversion is probably very general throughout the Madreporaria, but rare among the Actiniaria.

The sphincter muscle is another structure which the Herwigs first brought into prominence as an aid in the classification of Actinian polyps. It occurs toward the apex of the column wall in nearly all anemones, and, next to the arrangement of the mesenteries and tentacles, occupies an important place in all Actinological studies. Various types of sphincter are recognized, such as

[a] For later results, see foot-note, p. 541.

"diffuse endodermal," "restricted endodermal," "constricted endodermal," "aggregated," "single or double mesogloeal," and one or another is usually found to be characteristic of Actiniarian families.

When the polyps of the Madreporaria are taken into account, this structural feature is found to be almost entirely wanting. In most corals a circular endodermal muscle is present, but it rarely undergoes any increased development toward the apex of the column, such as can be regarded as constituting a special sphincter. In the larger polyps, like those of *Orbicella* and *Isophyllia*, a slight concentration of muscle fibers takes place, but only deserving of the title of "diffuse endodermal muscle," which represents the simplest form of sphincter development (Pl. VIII, fig. 65). In *Isophyllia* (Pl. XI, fig. 124) the mesogloeal processes supporting the musculature become a little more thickened and branched, and the whole structure may perhaps be regarded as having attained the next type of muscular complexity, that known as the "restricted endodermal."

The mesenterial musculature, likewise, presents no important differentiations in the coral species studied. Different degrees of development of the longitudinal retractor muscle are indicated by more or less deeply folded or branched mesogloeal plaitings, but present none of the variety of form met with in the Actiniæ. The basilar muscle is absent, and the parieto-basilar appears to be the same.

The nature of the column wall and disk in Madreporarian polyps, likewise, affords few distinguishing features. It is in all cases devoid of the simple or complex outgrowths, such as acorhagi, adhesive or spheroidal verrucæ, which characterize many genera and even families of Actiniæ. In the more or less retracted condition, under which coral polyps generally will be studied, one can merely distinguish forms with a smooth surface, as contrasted with exteriors which are verrucose, the latter condition a result of the costal or septal denticulations upon which the tissues come to rest.

Among the Actiniaria, Carlgren (1893) has employed the presence or absence of ciliated bands to the mesenterial filaments, and the presence or absence of an ectodermal musculature and ganglion layer on the column wall, as features of diagnostic and phylogenetic importance. As already shown, the mesenterial filaments of all the Madreporaria are alike in the absence of true independent ciliated bands, and any muscular or nervous elements with which the ectoderm of the column wall may be provided do not form distinct layers.

On the other hand, certain polypal characteristics occur within the Madreporaria which are either wanting or do not assume much importance within the Actiniaria. Among these may be mentioned the resulting form of the colony due to the method of vegetative growth, the canal system of perforate corals, the presence of synapticular perforations, the septal and other invaginations of the basal disk, and the extrusion of mesenterial filaments along with the mesenteries to which they are attached. All these will be found to be of systematic importance in polypal studies, though not attaining the value assigned them in works concerned only with the skeleton.

The canal system of the Porose corals, representing as it does merely complicated outgrowths of the basal wall, has but little morphological significance, though modifying the corallum and polypal tissues profoundly. The importance assigned the presence or absence of the canal systems in the classificatory scheme of Milne Edwards and Haime has been of great utility, but the character has not that fundamental value which one would desire for a primary division, and can not take precedence of the mesenterial and septal arrangement in any natural system. The same must be said also of the synapticula, which are the chief characteristics of the Fungacea. They are merely skeletal growths connecting adjacent septa, but in the genera *Siderastræa*, *Agaricia*, and *Fungia* they are certainly associated with peculiarities in the form of the tentacles and their wide distance apart, hence their presence may be indicative of some deeper natural relationship.

I have thus briefly indicated the anatomical and histological features in the species of Madreporaria here studied which are available for purposes of founding a more natural classification than those yet proposed. It must be admitted that twenty-six species, distributed among twenty

genera, is but a mere fragment of the group for this purpose, even when combined with the knowledge available from the labors of others. It should, however, be taken as a contribution around which other researches may accumulate.[a]

The only fundamental distinction which the facts as yet seem to warrant is the recognition of the two great groups, Entocnemaria and Cyclocnemaria. The material studied is insufficient to determine the exact taxonomic value of the canalicular system and the formation of synapticula. Their small morphological value has been noticed, but it is not certain as to how far other important structural features may be associated with their presence. From the conditions already described in *Siderastrea* and *Agaricia*, there would seem to be some connection between the occurrence of synapticula and peculiarities in the tentacular system. I have therefore for the present retained the divisions of Perforata and Aporosa, and Fungacea, until further results can be obtained which will enable their precise significance to be understood.

From the few generic representatives studied, it would be premature to attempt a diagnosis of the polypal characteristics of the families included, and I have therefore omitted such entirely. No doubt some of the generic characters given should rank as of family importance. I have attempted to define the genera in terms of the polyp, at the same time giving the species from which alone the characters have been drawn. To the definition of each genus I have added the diagnosis given by Duncan (1885) in the "Revision," so that in each case the skeletal and polypal descriptions can be compared side by side. It will be understood that the latter definitions are founded entirely upon the types studied, and consequently may require modification as the soft parts of other representatives become known. Before any genus or species of coral can be fully known, it is necessary, of course, to possess descriptions of both the skeleton and the polyp, but the scope of the present work is wholly confined to the latter, and does not presume a complete systematic account of the species.

I have fully described only a single representative of each genus, though in many cases other species have been investigated. In the interests of systematic studies upon the West Indian Madreporaria, it is highly desirable that a comparative description should be made of the polyps of as many representatives of each genus as possible, in order to determine the range of variation, and material for such is now in hand.

[a] Certain results, bearing upon the morphological classification of the Madreporaria, have presented themselves since the above was written, and are given in a series of four papers, "The Morphology of the Madreporaria," appearing in the Annals and Magazine of Natural History, 1902–3. The distinctions already found between corals reproducing by gemmation and by fissiparity obtain a greater phylogenetic significance from the fact that apparently the one or the other method of growth is altogether characteristic of any particular species. There seems to be no intermingling in a species as regards the two methods of asexual growth; it is shown that the few instances of simple fission hitherto considered to occur in corals which are usually gemmiferous, are really examples of a peculiar method of budding, which I have termed "fissiparous gemmation." The distinction between fissiparous and gemmiferous corals must be regarded as of greater taxonomic importance than is accorded it above. Further, the mesenterial increase beyond the protocnemic stage, occurring in *Porites* and *Madrepora*, is shown to be associated with fissiparous gemmation, hence the process can not be compared with the metacnemic growth in corals generally. Studies upon other than West Indian representatives of the genera are necessary before the full morphological value can be assigned the great differences between the mesenterial plan of *Porites* and *Madrepora* and that of other corals.

MADREPORARIA.

Anthozoa of which the polyps are either simple or colonial; the basal ectoderm gives rise to a continuous external calcareous skeleton, usually consisting of basal, peripheral, and radial elements. Colonial polyps are in communication around the proximal termination of the column, and sometimes by basal canals perforating the skeleton. Tentacles in alternating cycles, often with a knobbed or swollen apex. Stomodæum smooth or ridged, without gonidial grooves or siphonoglyphs. The mesenteries include a primary cycle of six pairs, appearing successively in bilateral pairs, two pairs of which are directives, and usually a second series which arise antero-posteriorly, as isocnemic exocœlic pairs all round the polyp and become arranged in cycles, or as bilateral pairs at one or more restricted regions of the polyp. Mesenterial filaments simple, without lateral ciliated bands. Lower region of gastro-cœlomic cavity subdivided by septal invaginations, alternating with the mesenteries, sometimes perforated by skeletal growths. Reproduction sexual and asexual; asexual reproduction frequent, by gemmation and fissiparity.

I.—ENTOCNEMARIA.

MADREPORARIA IN WHICH THE MESENTERIES ALWAYS ARISE IN BILATERAL PAIRS, AND BEYOND THE PROTOCNEMIC STAGE THE INCREASE TAKES PLACE WITHIN ONE OR BOTH OF THE DIRECTIVE ENTOCŒLES.

A.—SECTION PERFORATA.

MADREPORARIA IN WHICH THE BASAL DISK FORMS CANAL-LIKE OUTGROWTHS PERFORATING THE SKELETON, WHICH IN COLONIES PLACE THE DIFFERENT POLYPAL CAVITIES IN COMMUNICATION.

Family MADREPORIDÆ.

Genus MADREPORA Linnæus.[a]

Polyps small, often dimorphic (axial and radial), forming ramose, foliaceous, or incrusting fixed colonies, united one with another superficially by continuations of the column wall (cœnosarc) without lines of demarcation; pericalicular continuation of gastro-cœlomic cavity by canals without mesenterial prolongations. Free portion of column only slightly protrusible, more so in apical polyps; incapable of overfolding; no sphincter. Tentacles of radial polyps six in number, equal, acute; tentacles of radial polyps strongly bilateral in axial-abaxial plane, larval in extent of development, twelve in number, rarely more; unicyclic, smooth, not knobbed at apex, introvertible. Stomodæal walls smooth.

Mesenteries unicyclic, in *Edwardsia*-stage, rarely more than six pairs, when increase takes place by the addition of bilateral pairs within the two axial entocœles; all filamentiferous. Septal invaginations usually twelve, dicyclic, entocœlic and exocœlic, axial and abaxial often largest, interrupted below, unite centrally (columella), forming six distinct mesenterial loculi which terminate gradually or are truncated. Gastro-cœlomic cavities in communication throughout colony by a basal canal system, as well as by pericalicular canals.

Asexual reproduction by columnar gemmation, rarely by fissiparous gemmation.

EXAMPLES.—*Madrepora muricata* Linn.; *forma prolifera* (Lam.), *cervicornis* (Lam.), *palmata* (Lam.).

[a] "Colony very variable in shape, branching, bush-shaped, expanding, flat, corymbiform, or foliaceous, pedunculate or incrusting. Gemmation around the parent corallite and from the side of the other calices. Cœnenchyma abundant, spongy, reticulate, spinulose, growing exogenously from the porous walls of the corallites. Calices variable in shape, projecting or immersed, but never all so; terminal calices, or some among the mass, longest or largest (parents). Septa distinct, variable in solidity, two opposite primaries largest and nearly meeting. Twelve tentacles, and one larger than the others. No columella. An endotheca may exist, which occasionally becomes tabulate." (Duncan, 1885, p. 183.)

MADREPORA MURICATA Linnæus.

(Pls. I–III, figs. 1–27.)

External characters.—Madrepores are everywhere abundant on the reefs around Jamaica, and in other places on the sea floor, where conditions are favorable. The three forms, or rather groups of forms, recognized by Brook (1893), and by practically all writers, are always readily distinguishable, and are often found living together. Broadly speaking, they are as follows:

1. The flabellate or palmate colonies, with large, flat or concave fronds, usually several radiating from an incrusting base: *Forma palmata.*

2. Much-branched colonies, several branches radiating obliquely from a common center, main branches about 1.7 cm. thick at the base: *Forma prolifera.*

3. Large, more erect colonies than the last, less branched except toward the periphery, stem and branches much stouter, from 2 to 4 cm. thick: *Forma cervicornis.*

In Jamaican waters the three typical forms are distributed as follows: Thin flabellate colonies occur in the shallowest regions, beginning at a depth sufficient to permit of their extremities being exposed during the lowest tides, and extending downward to several fathoms. Beyond a fathom or two these are for the most part replaced by the palmate variety, in which the proximal part of each division becomes very thick and may be nearly rounded, the distal region only being thin and flattened. Associated with the flabellate and palmate colonies may be the *prolifera* form, but this rarely reaches so near the surface as *palmata*. At depths of from two to three fathoms the true *cervicornis* commences, and often forms dense thickets.

Where a properly equipped laboratory is not established, some difficulty is experienced in securing the polyps in a fully expanded state under conditions suitable for observation. *In situ* they may sometimes be seen fully expanded, but, upon breaking off a fragment for closer examination, the shock causes the polyps throughout the branch to retract. The axial polyps are then retracted to such a degree that no trace of them is distinguishable, and the radial polyps display only the tips of a few tentacles just within the calice. Brought into the laboratory in this condition, and placed in the shade, they usually expand a little farther, so that the tentacles of the radial polyps can be counted and their general arrangement made out. At night they expand to their full degree.

The whole of the living surface of a colony is covered with a smooth delicate tissue, which adheres closely to the skeleton over the costæ and echinulations, but is free over the intervening canal spaces. Microscopic examination reveals that the superficial covering of the skeleton is for the most part double: an inner wall adheres directly to the skeleton, while the outer is more or less free from it (Pl. I, figs. 2–6). On full expansion of the polyps the outer fleshy covering becomes slightly distended, and on retraction or preservation is partly depressed within the intercostal grooves. The superficial tissues are continuous throughout, without any grooves limiting one polyp from another. Over the greater part of a colony the polyps are closely arranged, separated by a very limited cœnosareal area; in the older regions the polyps are more distant than in growing parts. When the polyps are expanded the superficial covering of the colony passes uninterruptedly into the column wall of the polyp, and the two are seen to be direct continuations of one another (fig. 1*a*).

The polyps found at the apex of branches differ so markedly from the lateral or radial polyps that it will be necessary to describe the two separately. The apical polyps are difficult to obtain in a fully expanded condition for observation; usually they are retracted within the calice to such a degree that no trace of the tentacles is presented. On favorable occasions, however, the polyps extend beyond the corallum for a distance of 3 mm., when they are seen to be perfectly radial in their outward symmetry, and of the same diameter as the aperture of the corallite beyond which they protrude. The column wall is cylindrical, smooth, colorless, and so transparent as to permit of the internal mesenteries and short stomodæum being seen. At the inner margin of the apex of the corallite the column wall of the polyp is in continuity with the cœnosarc, and distally it passes uninterruptedly into the tentacles and disk.

In their typical, fully developed condition, the tentacles of the apical polyps are only six in number (fig. 1*b*). They arise at the margin of the disk from the alternate entocœlic spaces, and may terminate either acutely or in a rounded manner; they are broadest at their origin, and a wide interspace occurs between any two adjacent members. The surface is smooth throughout, no urticating spots being visible. During full expansion the tentacles may be overhanging and digitiform; when only partly retracted they are seen as six short vertical processes, protruding beyond the mouth of the corallite. The marginal spaces between the tentacles correspond with the exocœlic chambers, and are sometimes rounded, while in other cases small processes, like rudimentary tentacles, are present.

The disk is circular, the central naked area being very small, and either flattened or slightly convex, according to the state of distension. The twelve internal mesenteries, and their relations to the other parts of the polyps, are easily seen through the transparent walls. The mouth is extremely small, circular, and without prominent lips and gonidial grooves; sometimes the lips are a little protruding. The diameter across the disk and tentacles is 6 mm., and the length of a tentacle 2.5 mm.

All stages, from the twelve tentacles present in radial polyps to the six characteristic of typical axial polyps, can be observed toward the margins of growing colonies; and a study of this region of a colony, especially in the palmate forms, indicates that almost any of the radial polyps by excessive growth may become axial polyps. In doing this the polyp increases in size, and at the same time its tentacles undergo modification. The six entocœlic tentacles become still larger and all equal, while the six exocœlic become less important and in time wholly disappear, but for a long time one or more of the exocœlic tentacles may be represented by mere processes. Thus a true external dimorphism exists between the typical radial and axial polyps, though the one may pass into the other.

On several occasions the tentacles of an axial polyp were introverted, even while the column wall and disk were still extruded; only six slight opacities remained to indicate the former position of the outgrowths, and the margin of the column and disk as a whole was merely rounded. The infolding of the tentacles was occasionally observed in the radial polyps; later, the tentacles were slowly protruded, in the same way as described for the genus *Porites*, where introversion is more frequent and may be better observed.

The radial polyps, even when expanded to their full degree, never protrude far beyond the aperture of the calice, and, owing to the oblique, usually nariform aperture of the latter, the amount varies in different parts of the same polyp. At the sides, where the wall of the corallite is lowest, the column wall is free for 1 to 2 mm., but is not seen anteriorly. As the aperture of the corallites is rarely directed upward, the plane of the disk of the expanded polyps is oblique to the axis of the colony, or may be directed inward to the sides, or in almost any direction. Wherever exposed, the column wall is smooth, thin walled, and partly transparent.

The tentacles of the radial polyps are, as a rule, twelve in number, but of different dimensions: six larger alternate with six smaller, the former communicating with the entocœles and the latter with the exocœles. The members of both series also vary in size among themselves. The larger tentacles are situated at the same distance from the center of the disk as the smaller, so that practically the twelve constitute a single cycle, not differentiated into an inner and outer cycle, as is most usual in coral polyps. All the tentacles are broadest at their origin, but they narrow beyond, and may terminate bluntly or acutely. The relative sizes of the different tentacles in each series have been already described, and are best understood from figs. 1*a*–1*a*.

The distinctly bilateral character which the tentacles give to the lateral polyps is most marked toward the ends of the branches, where growth is rapid and the polyps larger. In partial retraction the anterior tentacle usually protrudes beyond the margin of the corallite, and considerably beyond the other members. In the more proximal regions of a colony, where the polyps are somewhat smaller, the tentacles tend to become approximately equal, but even here the anterior tentacle can generally be recognized by its being slightly more swollen, and lighter in

color than the others. The polyps on the sides of galls are also very diminutive, apparently undergoing retrogression (fig. 1*f*).

The form assumed by the tentacles is somewhat dependent upon the degree of expansion of the polyp. When enlarged to their utmost they are digitiform and overhanging, occasionally distinctly swollen at the apex; at other times, when not fully extruded, they are erect and more subulate.

The disk is very small and flat, and, as just mentioned, may look in almost any direction with regard to the axis of the branch, according to the plane in which the aperture of the corallite is placed. The mouth is circular or oval, without thickened lips and gonidial grooves; looked at from above, the aperture often appears excentric, being situated nearer the axis of the branch, the axial tentacle overhanging (fig. 1*d*).

The movements of the polyps are rather slow, and the tentacles rarely ever wave about like those of anemones; in a colony one polyp may retract independently of another. White mesenterial filaments may be extruded through the wall of any part of the polyp, but the phenomenon does not readily take place.

The full complement of twelve tentacles is reached at a very early stage in the development of new polyps; even in the second or third bud visible below the axial polyp they can all be recognized. In some cases, however, developing polyps occur with only eight tentacles; the two abaxial lateral and middle lateral of the smaller series, on each side, are the last to be developed.

Slight variations may be noted as regards the polyps of the different forms of colonies. In general the polyps of *palmata* are somewhat smaller than those of *prolifera* or *cervicornis*, but they exhibit exactly the same relations in regard to the size of the tentacles. In the older parts of all colonies the anterior tentacle is scarcely larger than the others, the polyps attaining a more approximate radial symmetry. Usually the tentacles seem more pointed in *palmata*, digitiform examples not often occurring, but they may assume this form when fully extended.

The corallites are often larger and more tubular in *palmata* than in the other two *forma*, and the disk of the polyps is directed toward the free growing edge. When fully expanded only the disk and tentacles extend beyond the corallum, but practically no free portion of the column wall can be seen except in the apical polyps. The disk is circular or slightly oval; the mouth very small and circular or oval.

Immersed polyps are usually very numerous on palmate colonies, especially on the upper surface of a colony, and away from the free growing regions. They are somewhat smaller than the others, but all gradations can be traced toward the fully developed individuals. When alive the immersed polyps very rarely extend beyond the corallum, and the tips of the tentacles only are visible. Their smallness did not allow of any differences in the size of the tentacles being determined; in some examples less than twelve were present, while in others a greater number were found. The scattered polyps on the under surface of palmate colonies are usually smaller than those on the upper surface. Double polyps with two oral apertures sometimes occur (fig. 1*f*).

The color varies but little in all the Jamaican Madrepores. Colonies as a whole are lighter or darker shades of brown, sometimes becoming green, yellow, or orange. Different regions, however, vary in intensity, some being quite colorless and others darker than the general surface. The coloration is wholly due to the presence in the endoderm of symbiotic yellow cells or zooxanthellæ; where these are few in number the coloration is faint, while where they are entirely absent the area is altogether colorless, the white corallum showing through the thin, transparent tissues. The tissues directly along the edge of the striæ and apex of the echinulations are devoid of color, there being over these, as shown in fig. 7, only a very thin endoderm without zooxanthellæ. In the intervening spaces the yellow cells are abundant. The tissues at the apical region of the corallites are usually colorless, and microscopic examination reveals that, though the endoderm is well developed, zooxanthellæ are absent (fig. 8); also, as a rule, the axial polyps in palmate colonies are colorless. The distal region of the polyps on the upper surface may be colorless, while the under polyps are uniformly brown.

In the same way the large anterior tentacle of radial polyps is nearly colorless, as is also the case with the small tentacle on each side of it, and less so the next tentacle. In a partly retracted condition the tentacles are often darker than any other region of the polyp, the endoderm being thickened and its zooxanthellæ crowded; when fully inflated the color of the polyps as a whole becomes paler. The absence of color toward the margins of the colonies probably indicates that these are regions of rapid growth, the polypal growth being in advance of that of the multiplication of zooxanthellæ.

In no case have any traces of ectodermal coloration been found. This uniformity of color of the West Indian *Madrepora* is in marked contrast with the vivid and varied tints described by Saville Kent for most of the species of the genus occurring on the Australian Barrier Reef (1893).

Anatomy and histology.—The column wall is everywhere very narrow, in sections measuring 0.08 mm. across. The ectoderm is constituted largely of unicellular oval gland cells with clear contents. Sometimes the contents of the gland cells stain slightly, and in sections the mucus can often be seen extruded, forming an irregular outer covering to the ectodermal cells. Small nematocysts of two kinds occur somewhat sparsely—a long, thin-walled form in which the spiral thread is distinctly visible, and a smaller thick-walled oval variety in which the internal thread is scarcely recognizable. At the apex of growing branches the ectoderm cells are often much longer than elsewhere, measuring 0.07 mm. (figs. 7–9).

The mesoglœa is throughout a very thin supporting lamella, but wherever it attains much thickness it is found to be clear, transparent, and homogeneous, without connective-tissue cells.

The endoderm varies somewhat in character, according as zooxanthellæ are present or absent. At the tips of branches, which in the living condition are colorless, the endoderm of the column wall is a very narrow layer, the cells but little vacuolated, and the nuclei comparatively large and somewhat regularly arranged (fig. 8); but where the symbiotic algæ occur the layer is broader and the cells more vacuolated. All gradations can be traced between the total absence of the algæ and their presence to such an extent as to constitute nearly the whole layer. In radial sections of the column wall are seen the cut ends of delicate endodermal muscle fibrils, arranged in a circular manner, and forming a very thin muscular layer, which extends the whole length of the wall, and is continuous with the circular endodermal musculature of the tentacles. This diffuse endodermal musculature probably acts as a sphincter during the retraction of the polyps: there is, however, no concentration of the muscle fibrils on mesoglœal plaitings, such as can be regarded as forming a special sphincter muscle; the mesoglœal surface remains smooth throughout.

Histologically the outer covering of the skeleton differs in no essential respects from that of the column wall proper, the two being merely continuations of one another. Where the wall rests upon the echinulations, continuity with the skeletotrophic tissues is established, and the endoderm and mesoglœa of the two pass into one another. The figures show that the actual apex of the echinulation is covered by its own skeletogenic ectoderm, the mesoglœa, and the outer ectoderm. No muscle fibers are determinable in the cœnosareal endoderm, such as occur in the free portion of the column wall.

In sections toward the apex of axial polyps, the corallar ridges are often unprotected by soft tissues. This is probably due to the very thin walls having broken down during decalcification, but in most carefully prepared material no remains can be found, and the very broad ectoderm overlying the canals passes inwardly as the calicoblast layer.

The tentacles in strongly retracted radial polyps often appear as mere longitudinal ridges of the wall of the polyps, and neither in longitudinal nor transverse sections is any part free from the disk. In other cases, however, isolated circular sections of the tentacles are obtained, showing that during retraction the organs may retain their distinctness as outgrowths of the disk. Longitudinal sections present no sharp line of separation between the upper region of the column wall and the tentacles. The transverse section through the tentacular region, represented in fig. 3, exhibits the six larger and six smaller tentacles all at the same level, and nearly filling the calicinal cavity; they are outgrowths of both the entocœlic and exocœlic chambers, the larger tentacles

arising from the former. No intervening discal tissue occurs between the origin of one tentacle and that of the next, as is the case in the axial polyps. In the particular section represented the larger tentacles are practically all of the same size, but in other sections the anterior tentacle predominates over the others, or at some levels may even be the only one represented; the smaller tentacles, in their varying dimensions, correspond with their proportions in the living polyps.

The tentacular ectoderm (fig. 10) is a uniformly broad layer, and in sections is roughly divisible into three zones: (1) An outer, nearly colorless zone, with numerous nematocysts, and very few gland cells; (2) a middle, deeply-staining nuclear zone; and (3) an inner, less defined fibrillar zone, terminating in a layer of delicate muscle fibrils, longitudinally arranged. Conical enidocils occur, seen especially in the living tentacle. The nematocysts are of the same form as in the cœnosarc, but the long variety with a thin wall and strongly marked spiral thread is most abundant. The nematocysts are distributed nearly uniformly throughout the length of the tentacular wall, not restricted to special batteries as in most corals; proximally they are somewhat less numerous than above. In some sections a distinct nerve layer is manifest, situated a little distance from the mesoglœa.

The mesoglœa is a thin supporting lamella, slightly thickened proximally. It may be partly folded in retracted specimens, but nowhere becomes plaited for the purpose of affording additional support to the musculature.

The endoderm exhibits marked variations, as in the case of the column wall. Where zooxanthellæ are not present in the cells the layer is very regular, and much thinner than the ectoderm; the cells are filled with protoplasm which stains slightly, and the nuclei are comparatively large and arranged in a very regular row. Where symbiotic algæ occur the layer as a whole becomes much broader, the cells are more vacuolated, and the internal limitations are very irregular. The endodermal circular musculature is comparatively well developed.

Sometimes the endoderm of one tentacle will be entirely without zooxanthellæ, while another of the same polyp will be crowded with them along the whole of its length; in other cases they may be absent from the distal region of a tentacle and occur proximally. Corresponding variations have been noted in the coloration of the tentacles in the living polyp.

Below the tentacular region of retracted polyps the disk extends vertically for a short distance, and then nearly horizontally, passing into the vertical stomodæum (fig. 11). The peripheral discal area presents histological details similar to those of the tentacles, but the more central region becomes narrower and nematocysts are rare in the ectoderm, while granular gland cells occur here and there. Zooxanthellæ are usually sparsely distributed, or altogether absent from the discal endoderm.

The six tentacles in the axial polyps are entocœlic in position, and therefore correspond with the larger members of the radial polyps. They are larger than in radial polyps, and in transverse sections appear as triangular ridges of the disk; the longitudinal and circular musculatures are somewhat better developed than in the radial polyps, and the mesoglœa is slightly plaited to afford additional support for the endodermal fibers. The disk also shows the ectodermal musculature very clearly; zooxanthellæ are entirely absent from the endoderm, otherwise the histological details of both the ectoderm and endoderm are the same as those of the radial polyps.

The stomodæum is narrow and approximately circular in transverse sections, and the walls hang vertically for some distance within the cœlenteron (fig. 2). They are of equal thickness throughout, and present no indications of a gonidial groove. In the figure the wall narrows a little toward its free extremity on the left side and terminates abruptly; on the right side of the section the wall is seen to be in continuity with the filament of a mesentery, and the tissues of the two pass insensibly into one another.

The surface of the stomodæum is strongly and uniformly ciliated; nematocysts and granular gland cells are numerous, some of the latter staining very deeply. An extremely weak ectodermal musculature and nerve layer can be detected in transverse sections, and circular endodermal muscle fibers in radial sections. Isolated typical cells are represented in fig. 13.

Transverse sections through the stomodæal region of both radial and axial polyps reveal

eight complete mesenteries and four incomplete members, arranged in bilateral pairs, as represented in fig. 4. The retractor muscles on the mesogloeal plaitings are clearly distinguishable, and indicate that the two axial pairs of mesenteries are the directives; the complete mesenteries remain attached to the stomodæum at about equal distances apart throughout its length. In serial transverse sections the incomplete mesenteries usually extend below the stomodæal area, but occasionally they cease before its lower extremity is reached; their vertical extent is greatest in the axial polyps. As the complete mesenteries become free they all bear mesenterial filaments. The four pairs, equally developed, continue after the incomplete mesenteries have disappeared (fig. 5); then the dorsal directives are lost, and shortly afterwards the ventral directives, and the four lateral mesenteries continue together for some distance (fig. 6); soon the dorsal of the lateral pairs disappears, and finally the last pair. Thus a definite order of disappearance is followed by the six mesenterial pairs in passing a series of transverse sections in review, the pair considered to be the first to appear in coral larvæ extending farthest, and the most recent pairs to arise extending least. Sometimes the two moities of a pair die out together, but more often the mesentery on one side will continue a little below the corresponding member on the other side.

In the lower part of their course certain of the mesenteries, usually the first three developmental pairs, become convoluted at their free edge; and as the septal invaginations here meet in the middle of the polypal cavity, and give rise to distinct interseptal loculi, each mesentery is frequently in a chamber by itself.

No indication of any perithecal continuation of the mesenteries occurs; in living expanded polyps the partitions can be seen to pass uninterruptedly from the column wall down to the calicular cavity, and serial transverse sections confirm this.

On each face of a mesentery the endoderm immediately behind the filament becomes considerably swollen, and contains zooxanthellæ and numerous granular gland cells; a few nematocysts also are found. The endodermal enlargement extends nearly as far as the termination of the mesentery (fig. 14).

In axial polyps the portion of the mesentery peripheral to the swollen region remains long and very narrow, retaining its musculature and plaited mesogloea, and zooxanthellæ occur here and there. The first three developmental pairs of mesenteries in radial polyps may become convoluted in the lower region, each bearing a mesenterial filament of the usual type, with swollen endoderm immediately behind (fig. 6). The filaments are here often crowded with long nematocysts, somewhat recalling the acontia of Actiniæ, and may persist as far as the termination of the mesentery. At their origin in the polypal wall the mesenteries are very narrow, and are situated at about equal distances apart all round. The endodermal epithelium is a narrow layer and without zooxanthellæ.

In the tentacular region of retracted polyps the mesenteries are very short transversely, and the musculature is somewhat strongly developed, especially in axial polyps. The mesogloea is here deeply plaited, but is smooth on the opposite face, where weak oblique muscle fibers are indicated (fig. 12). In axial polyps the musculature of the four incomplete mesenteries is developed almost as strongly as that of the eight complete mesenteries.

The gastro-cœlomic cavity proper, independent of its canal outgrowths, originates in the buds in one of the ordinary superficial canals (figs. 22–27), but later becomes much larger and provided with its own system of canals, and terminates proximally either abruptly or in canalicular prolongations.

For some distance downward the cœlenteron is approximately circular in outline, or oval in many radial polyps; the continuity of the walls is interrupted here and there by the canal outgrowths, but otherwise each polypal cavity is distinct.

The septal invaginations, which are mostly entocœlic, vary in extent; usually only one, the axial, is very pronounced, and may almost completely subdivide the gastric cavity. Toward the lowermost region, where only two or four mesenteries remain, the polypal cavity is nearly always completely divided into two by the union of the axial and abaxial septa; in other cases, as in fig. 6, the central portion is almost obliterated by six broad triangular septal

invaginations; the contorted mesenteries may then be pressed into the various canals, and the individuality of the polypal cavity is largely lost.

In its simplest condition, as in the free portion of individual polyps, the canal system consists of the following: (1) A series of longitudinal and transverse peripheral canals within the grooves between the contiguous ridges of the skeleton, and more proximally in the depressions between the echinulations. Their uninterrupted vertical extent is not great (fig. 2), and they become very irregular in the echinulate region; even in the more distal areas the canals are connected laterally, and by this means are placed in communication with one another. Below the costate region of a corallite, both the vertical and lateral canals are so interrelated as to produce a more or less regular peripheral reticulum. (2) As shown in figs. 3 to 6, the peripheral canal system communicates by short radial canals with the coelenteric cavity of the polyps, several such canals usually occurring in each transverse section. The broader skeletal region of fig. 4 reveals, however, that internal enlargements and lateral communications between one radial canal and another make their appearance within the wall of the corallite, so that the thicker regions of the corallum are penetrated throughout by a canal reticulum.

At the apex of the corallite, the peripheral system of canals also communicates with the central polypal cavity over the edge of the theca (fig. 2).

The peripheral canals are somewhat flattened on their outer aspect, and often triangular in transverse sections, but the internal are more circular; so close, however, is the reticulum in the more apical region of the polyps that the canals are rarely seen in circular sections, but as elongated, irregular communicating spaces. In the older parts of the colony, where the space occupied by the skeleton and by the canals is more equal, the latter are in more regular concentric series.

The lining of all the canals is a very thin unilaminar layer of ciliated endodermal cells, the deeply-staining nuclei of which are arranged with considerable regularity; zooxanthellæ are usually absent, but are sometimes found in the skeletal layer of the superficial canals, and even in the older and deeper regions of the corallum. The mesoglœa is everywhere a thin supporting lamella. The skeletogenic layer is represented in the growing regions by a broad columnar layer (fig. 8), but is scarcely determinable in the more terminal regions. Desmoidal processes are numerous in places, and in the actual growing regions the skeletal matrix may remain after decalcification (figs. 7, 18).

Ripe polyps seem very rare; ova only have been met with on one occasion.

Family PORITIDÆ.

Genus PORITES Milne Edwards and Haime.[a]

Polyps small, distinct, forming incrusting, massive, foliaceous, or dendroid colonies, fixed or free; united closely with one another along a common thecal edge, without perithecal continuation of the mesenteries. Column wall smooth and cylindrical, may partly fold over the disk on retraction, no sphincter. Tentacles small, twelve in number, rarely more, unicyclic, sometimes in bilateral larval stage, digitiform, smooth or tuberculated, introvertible. Stomodæal walls smooth.

Mesenteries unicyclic, rarely more than six pairs, when increase takes place by the addition of bilateral pairs within the sulcar or sulcular entocœle, only three or four pairs complete and filamentiferous. Septal invaginations usually twelve, entocœlic and exocœlic, interrupted, unite centrally (columella) below, forming six distinct loculi, which are abruptly truncated. Gastro-cœlomic cavity of polyps in communication throughout colony by a basal canal system, and also by marginal apertures.

Asexual reproduction by intercalary columnar gemmation, rarely by fissiparous gemmation. Viviparous.

Examples.—*Porites astræoides* Lam., *P. divaricata* Les., *P. furcata* Lam., *P. clavaria* Lam.

[a] "Colony ramifying, or in tufts, or foliaceous, often massive, and lobed or low, incrusting or not. A basal epitheca invariable in the last instance, frequent in all. Corallites with trabeculate and perforate walls, not distinct from those of their neighbors, and therefore without intermediate coenenchyma. Calices small, pentagonal. Septa twelve or less, feebly developed, trabecular or spinulose. A small columella, forming at its free edge a knob or a trabecular point or a style. Pali five or six, and not very distinct from the septal ends, in a circle around the columella. Endotheca exists sparingly, and may be dissepimental or tabulate, or may be mere stereoplasm." (Duncan, 1885, p. 187.)

PORITES ASTRÆOIDES Lamarck.

(Pls. III–V, figs. 28-42.)

External characters.—The species is met with in abundance in all the regions of coral growth, from a depth of 3 or 4 feet downward; sometimes many colonies occur closely associated, at other times they are widely scattered. The colonies form large, incrusting, hemispheroidal, or nearly spheroidal masses, the surface usually sub-botroidal or with gibbosities.

The polyps are small and closely arranged, completely hiding the surface of the corallum when fully expanded. In this condition each appears to arise from a pentagonal thecal margin, common to the surrounding polyps, without any division into calicular and perithecal regions. On retraction of the polyps, the column rests upon the septal edges, and the tentacular ring is more central (fig. 34).

During full expansion the column is smooth, erect, and cylindrical, and so thin-walled as to allow the internal mesenteries to be seen through. The diameter is 2 mm., and the height above the corallum 3 mm.; as a rule the proximal and distal diameters are slightly larger than the middle. Distally the column wall passes uninterruptedly into the tentacles, and is rarely folded over the disk; usually, on full retraction, it is merely drawn within the calice, the tips of the tentacles and disk being still visible (fig. 35).

The tentacles are extremely small, digitiform or acute, smooth, and arranged in a single cycle. They are practically equal in size, but sometimes one of the axial members is slightly larger than the others. In nearly all cases they are twelve in number, but on most colonies a few larger polyps occur in which the tentacles vary from sixteen to twenty-four. Usually they are about 2 mm. in length. When the polyps are fully expanded the tentacles are overhanging, and those of adjacent polyps intermingle. The organs are freely introverted, and in some instances they actually disappear, becoming part of the marginal tissues of the column wall and disk; sometimes the column wall of a polyp may be extended to its full degree, but the tentacles are indicated only by twelve, lighter colored, circular or oval areas at the margin of the disk, each with a minute aperture in the middle (fig. 35).

The disk is circular, smooth, and very thin walled; the internal mesenteries can be seen through, and their actual arrangement around the stomodæum determined (fig. 32). The mouth is either circular or slightly oval.

The colors of the colonies as a whole are very variable, and often brilliant; indeed, the species is one of the most gaily colored of all the West Indian corals, and, occurring in large masses, often becomes an important constituent in determining the general coloration of the reefs. As a rule the colonies are a bright blue, pale yellow, or yellowish green. Various colors occur side by side, and sometimes one portion of a colony will be blue and another yellowish green. The pale yellow colonies frequently exhibit restricted patches more brilliant than others, some even becoming brownish; other colonies may be a dull yellowish-brown, or even a blackish-brown.

New polyps arise among the others mainly by intercalary gemmation. In all colonies many young examples with less than twelve tentacles occur. Fissiparous gemmation has been observed on one or two occasions (p. 513).

Certain colonies have been found which at first sight appeared in the normal healthy condition, but on careful examination no actual polyps could be discerned; tentacles were indistinguishable, and the whole polypal tissues, though pigmented, seemed in a state of decay.

Examined in the laboratory, the living polyps are seen to be constantly and quickly retracting to a limited degree, and then slowly expanding again. When fully expanded, agitation of the water moves them to and fro. They may retract below the edge of the calice, the tips of the tentacles still showing or wholly covered (fig. 35).

Numerous parasitic Cirripedes are usually found associated with the colonies, inextricably inclosed by the overgrowth of the corallum. Around these the polyps are smaller and more closely arranged.

Anatomy and histology.—The column wall is thin and delicate throughout, the mesoglœa appearing as a mere separating lamella. In addition to the usual supporting cells and clear gland cells, the ectoderm contains numbers of cells with yellow granular contents (fig. 36). The

color-bearing cells are much shorter than the height of the ectoderm layer, and occur at all levels within it, from the free surface to the mesoglœa. They readily separate in macerations, and are very irregular in outline; the various stains have little effect upon them, except that the nucleus comes out distinctly (fig. 37). The superficial ciliation of the column is preserved in most places. The endoderm is narrower than the ectoderm, and also contains numerous yellow granular cells, while zooxanthellæ are very abundant. There is no evidence in sections of any ectodermal or endodermal musculature, though in all probability weak endodermal fibers are present, and bring about the overfolding of the column wall on retraction.

The stomodæum exhibits the usual histological structure as regards its ectoderm. Toward the lower termination the latter becomes slightly thinner intermesenterially, and passes backward for a short distance up the endodermal surface. Where the mesenteries are attached it extends outwardly along both faces, and then appears to be continued downward as the mesenterial filament. In retracted polyps the ectodermal layer is often folded vertically in a very regular manner (fig. 28).

In practically all the polyps examined only six pairs of mesenteries occur, and of these four pairs are usually complete in the upper region, while the two remaining pairs never reach the stomodæum, and extend for only a short distance below the stomodæal region. The sulcular or dorsal directives are sometimes free throughout, and in other cases generally cease their connection with the stomodæum in advance of the other three pairs (fig. 30), which always remain attached as far as the aboral termination. The three pairs of complete mesenteries alone bear mesenterial filaments, and continue their course some distance below the others. Toward their lower extremity the first pair of mesenteries may become slightly convoluted, but the mesenteries as a whole have a comparatively short vertical extent, being practically limited to the upper half or third of the polyp.

The retractor muscles of the mesenteries are moderately well developed on small mesoglœal plaitings, and readily permit of the paired arrangement being established. The form of the plaitings varies in different mesenteries, and even in different parts of the same transverse section, as shown in fig. 38. The mesenterial epithelium is distinguished by the predominence of large, clear, gland cells; these constitute in places nearly the whole thickness of the endoderm, while toward the free margin accumulations of protoplasm, nuclei, and zooxanthellæ are to be found. In a portion of one colony the contents of the glands had evidently been discharged into the gastro-cœlomic cavity just before the death of the polyp, for, on being stained with hæmatoxylin and sectionized, the whole of the upper region of the polyps appeared as if embedded in a gelatinous mass, the secretion itself staining feebly. On preservation the polyps exude a large amount of mucus. Zooxanthellæ and yellow pigment cells, and an occasional large oval nematocyst, also occur in the mesenterial endoderm. The mesoglœa is very narrow and homogeneous, but forms slender outgrowths for the support of the musculature.

The mesenteries in transverse sections are sometimes observed to be free at their peripheral end for a short distance vertically, and rounded off (fig. 38). This is found opposite a radial canal, so that where these outgrowths are formed mesenterially, the mesentery is without of any peripheral support.

Immediately below the stomodæal region, the mesenterial filaments on the first three developmental pairs are merely incipient (fig. 29), and never get beyond this stage except in the first and second pairs of mesenteries. In these the filament becomes more or less definitely rounded off from the mesentery for a very short distance, and the mesoglœa bifurcates within it (fig 39). Comparatively few nematocysts occur in the filaments, and are all of a medium size.

The skeletotrophic tissues comprise by far the greater proportion of the soft parts of a colony, lining the walls of the corallite and the whole of the canal system, while the mesenterial tissues scarcely extend beyond the upper half of the polyps (Pl. V, fig. 40). The endoderm is a comparatively broad layer, and below undergoes certain modifications; no cellular distinctions can be made out, but the whole layer, with the exception of the free margin, exhibits a vacuolated condition. Fine granules along the walls of the meshwork stain with aniline blue, but not readily with carmine; occasionally a yellow pigment cell or a zooxanthella may also occur. Along a narrow zone, at the margin of the layer, nuclei, zooxanthellæ, pigment granules, and

protoplasm are accumulated, the first mentioned often forming a very regular row. The layer is thinner in the upper region of the polyp, and the vacuolisation is not so complete; but even here the cellular distinction is almost lost, except as regards the clear gland cells (figs. 38, 39).

The mesoglœa is very thin throughout, and the skeletogenic ectoderm is distinguishable only at the growing points, as a deeply-staining layer without distinct cell limitations (*cal*, fig. 38). The desmoidal processes are everywhere feebly developed.

The individuality of the polyps is usually retained throughout their length, both under low magnification of merely decalcified material and throughout microscopic sections. Each polyp is, however, seen to be connected with the others, at different points along the whole of its length, by the complicated system of very short canals which penetrate the skeleton; in transverse sections at any level five or six canals are nearly always connected with each polyp (figs. 29, 42). The polyps are truncated below, as in the case of the imperforate corals; the canals are thus practically restricted to the lateral regions, not prolonging the polyp basally.

The gastro-cœlomic cavity of each polyp is most distinct in the upper region, as here the septal invaginations are either wanting (figs. 28, 30), or proceed but a short distance centrally, and rarely with any constancy all round. Both entocœlic and exocœlic invaginations may occur, and at nearly any level one or other, or both, may be wanting. The septa in *Porites* are perforate, and in the polyp this is represented by interruptions in the invaginations. As the lower regions are approached, the septal invaginations become more pronounced, and meet the spine-like, columellar invaginations in the middle, thus cutting off one portion of the cavity from another (fig. 39). In transverse sections the septal invaginations are nowhere as regular as in nonperforate corals (*cf.* figs. 42, 49).

To such a degree may the subdivision of the cœlenteron proceed toward the terminal region that, in sections, the individual polyps seem constituted only of a series of canals, some containing mesenteries, but mostly empty.

In addition to the basal canalicular connections, the cœlentera of the polyps communicate with one another over the edge of the theca, as in the case of other corals (figs. 31, 40).

Gonads have not been found in any of the polyps examined. In the outer polypal wall appear many spheroidal bodies, which, at first sight, may be taken for spermaria. They never occur, however, in the mesenteries, but usually in the endoderm of the column wall or disk (fig. 36). They may be the sporogonia of the parasitic algæ which are so prevalent within the corallum, but the connection has not been traced.

II.—CYCLOCNEMARIA.

MADREPORARIA IN WHICH THE MESENTERIES BEYOND THE PROTOCNEMIC STAGE ARISE IN ISOCNEMIC PAIRS WITHIN THE PRIMARY EXOCŒLES. THE MESENTERIES IN THE ADULT ARE USUALLY ARRANGED IN TWO OR MORE ALTERNATING CYCLES.

B.—SECTION APOROSA.

MADREPORARIA IN WHICH THE BASAL DISK IS IMPERFORATE, AND THE GASTRO-CŒLOMIC CAVITIES OF COLONIAL POLYPS ARE IN COMMUNICATION ONLY AROUND THE PROXIMAL TERMINATION OF THE COLUMN.

Family ASTRÆIDÆ.

A.—GEMMANTES.

ASTRÆIDÆ IN WHICH ASEXUAL REPRODUCTION TAKES PLACE BY GEMMATION, AND EACH POLYP REPRESENTS A DISTINCT INDIVIDUAL. THE TENTACLES, MESENTERIES, AND SEPTA ARE ARRANGED IN ALTERNATING CYCLES, AND TWO PAIRS OF DIRECTIVE MESENTERIES ARE PRESENT IN EACH POLYP.

Genus ASTRANGIA Milne Edwards and Haime.[a]

Polyps smooth, either isolated or connected by a thin narrow basal continuation of the column wall; tissues appearing delicate; perithecal continuation of gastro-cœlomic cavity and mesenteries; form

[a] "Colony incrusting. Corallites short, arising from calcareous basal expansions, close, more or less turbinate or cylindrical. Calice circular, deep, and large. Columella papillary, and formed of a network of trabeculæ with

incrusting colonies, or groups of more or less isolated corallites. Column wall cylindrical, elongated, on retraction may almost completely cover the disk; no sphincter. Tentacles entocœlic and exocœlic, incompletely tetracyclic, long and narrow, entacmæous, tubercular, with knobbed apex. Stomodæal wall smooth.

Mesenteries regularly hexamerous, incompletely tricyclic, six pairs complete, two pairs directives, all filamentiferous. Septal invaginations hexamerous, entocœlic and exocœlic, incompletely tetracyclic, below nearly all united centrally, forming almost distinct mesenterial loculi.

Asexual reproduction by gemmation from the lower part of the column wall or the basal expansion.

EXAMPLE—*Astrangia solitaria* Lesueur.

ASTRANGIA SOLITARIA Lesueur.

(Pls. V and VI, figs. 43, 44, 45, 47.)

External characters.—The species is met with all round the Jamaica coast, mainly in regions of coral growth. Polyps of various sizes occur in groups of from three or four to a dozen or so, incrusting blocks of dead coral or other objects, often on their under surface. The individuals of a group are either connected with one another by basal columnar expansions or stolons, or are entirely free and separated for a greater or less distance. The corallites rise but little above the surface of attachment, and the proximal region is frequently hidden by Nullipores. The incrustations may continue their growth until they cover practically the whole of the external skeletal surface, or even pass beyond, the column wall retreating accordingly. Where Nullipores are absent the column wall may extend downward over the external surface of the corallite for two or three millimeters, and continue for some distance as a basal expansion.

The column wall is smooth, delicate, transparent, and usually circular in outline, rarely oval; the diameter varies from 3 to 6 millimeters. On full expansion it exhibits longitudinal ridges and furrows, and on partial retraction the wall is withdrawn a little within the calice; but during full retraction it may be greatly depressed, extending centrally so as to almost completely hide the tentacles and disk. The upper portions of the septa are very distinctly seen through the polypal tissues, and can be readily counted and their arrangement in cycles followed.

The tentacles are long and narrow on full expansion of the polyps, narrowing slightly from their origin to the free extremity, and terminating in a white, opaque, spheroidal swelling, very distinct on full or partial expansion. The tentacular walls appear unusually thin and transparent, and are provided with close-set batteries of nematocysts, which stand out prominently. Sometimes these are white, but are often a delicate iridescent green, more rarely brown. During full extension the tentacles remain overhanging. The arrangement in cycles is not readily followed, but it is easily seen that one tentacle arises over each septum, and the plan can be determined from these. Six prominent septa form a first cycle, six smaller alternating septa form a second cycle, while the third and fourth cycles rarely show hexamerous completion, and the tentacles correspond (fig. 43). The innermost tentacles are the largest, measuring about 3 mm. in length.

The disk is circular, thin-walled, and transparent, allowing the six pairs of complete mesenteries to be seen through. A few minute green spots are arranged in radiating rows. The mouth is very long transversely, slit-like when closed, oval when open; the lips are white laterally, while the two extremities may be green. Four ridges can sometimes be made out on each side of the stomodæum; oftentimes the lips are drawn together in the middle, leaving only two distinct apertures, one at each end. The mouth was triangular in one example, and seven pairs of complete mesenteries could be seen through the disk, instead of the usual six, indicating some structural irregularity.

Polyps living on the under surface of blocks of coral are often colorless throughout, or display only very delicate tints within restricted areas. In other cases the polyps are brightly colored, brown and green predominating. The column wall may be purplish or brown, green

additions from the septal ends; outer papillæ resembling those of the septa, or differing in consequence of a large paliform tooth being on some septa. Septa unequal, not exsert, some united, granular at the sides, denticulate, and often with a paliform tooth. Costæ visible on the wall near the calice especially. Epitheca absent. Dissepiments few and distant." (Duncan, 1885, p. 66.)

toward its free edge, the color often disposed in lines. The general surface of the tentacles is colorless, but green, white, or brown tubercles, and an opaque white or green knob, are often exhibited. The transparency and delicacy of the living tissues, as compared with other corals, are due to the absence of zooxanthellæ.

On irritation the mouth opens suddenly, the polyps as a whole retract, and the column wall becomes partly drawn over the disk and tentacles.

Anatomy and histology.—In the retracted condition nearly the whole of the column wall is withdrawn within the calice; at most only a very narrow zone extends down the exterior of the corallite. In sections the column wall is very narrow, becoming a little thicker at its proximal termination. The ectoderm is seen to be ciliated, and clear mucous glands are abundant, surrounded by supporting cells. The mesoglœa appears only as a thin supporting lamella. A feeble endodermal musculature can be made out, and zooxanthellæ are absent from the endoderm.

The tentacles are both entocœlic and exocœlic in position. The ectodermal layer is broad, especially at the tip, and contains long, narrow nematocysts, both terminally and in restricted regions laterally. In retracted tentacles the nematocyst areas overlap the rest of the ectoderm; nervous elements are clearly displayed at the tip of the tentacle, and gland cells with clear contents are numerous proximally. The mesoglœa is broader than in the column wall, and a weak musculature is developed on either side. In the columnar endoderm, as elsewhere throughout the polyp, occur numerous spheroidal bodies, usually with perfectly clear contents and without a nucleus, and staining in carmine much more deeply than the other histological elements of the tissues. In a few cases the spheroids are found with granular contents, or a single nucleus may be detected; rarely others present what seem to be stages of reproduction by simple fission. The bodies are of about the same dimensions and form as ordinary zooxanthellæ, but their uniform structure, usually without any nucleus or vacuole, at once distinguishes them from the symbiotic algæ. They present all the characters of nutritive unicellular organisms, and similar bodies are not infrequent in other species of corals, and also in anemones. Though occurring throughout the endodermal layer, they are most numerous in the swollen mesenterial epithelium, generally considered to be the principal seat of intracellular digestion (fig. 45). Their strong power of taking up coloring matter makes them very distinctive objects, and in any polyp their distribution is somewhat irregular.

In vertical sections of retracted polyps the central part of the disk is partly inturned, so that it appears nearly in the same vertical line as the stomodæal wall; but histologically the line of separation is very marked and sudden. The ectoderm of the disk resembles that of the column wall in the abundance of mucous cells, and displays a very weak ectodermal as well as an endodermal musculature. The stomodæum is very short and partly reflected at the lower termination. Its ectoderm is constituted almost wholly of ciliated supporting cells, the aggregated nuclei forming a distinct, deeply-staining zone. The layer is uniform all round, no distinct ridges and grooves being determinable as in the next species.

Six pairs of complete mesenteries constitute the first cycle, and of these two pairs are directives. In most cases two incomplete pairs occur within the primary exocœles, instead of one or three pairs, as the laws of Actinian symmetry require (fig. 47). Of the two pairs in each system, one belongs to the second mesenterial cycle and the other to the third cycle, though both are nearly of the same size. In one polyp sectionized transversely only six pairs of complete and six pairs of incomplete mesenteries were present; but usually some of the tertiaries occur in addition, though very rarely the complete cycle of twelve is represented. The order of mesenterial increase, as revealed by the many polyps of a single group, has already been described (p. 459, *et seq.*).

In the more distal region of the polyp the mesenterial musculature is well developed, especially toward the insertion of the mesentery. The mesoglœa on the face bearing the retractor muscle is thrown into complicated folds, varying greatly in degree in different members. The opposite face of the mesoglœa may be also slightly folded, and the muscle fibrils in places are strongly developed and appear vertical in direction. The musculature is nearly as strongly developed on the secondary and tertiary mesenteries as on the primary. In the lower

regions the mesoglœa of all the mesenteries becomes extremely thin, and the musculature is then scarcely determinable (fig. 45). Where the mesoglœa of the mesenteries is united with that of the column wall it forms the usual desmoidal processes for attachment to the corallum.

Mesenterial filaments may occur on the mesenteries of all the three cycles, though as a rule they are incipient on the smallest members. The filaments on the imperfect mesenteries commence as high as the stomodæal region, while on the primary mesenteries they are developed in continuity with the stomodæal ectoderm as the mesenteries become free. The terminal edge of the stomodæal wall is continued along the twelve primary mesenteries for some distance, and the filament is there cordate in transverse section, and histologically resembles the stomodæal ectoderm (fig. 44); later, the filament becomes rounded like that on the incomplete mesenteries, and nematocysts and gland cells are more numerous than above (fig. 45). As a rule the mesenterial epithelium is swollen and rounded immediately behind the filament. The mesenteries are but slightly convoluted in the proximal region, and the filaments there become crowded with large oval nematocysts, which show the spiral thread very distinctly.

The cells of the mesenterial endoderm are crowded with fine granules; and in the lower regions all the cell outlines are lost, and the contents include somewhat coarse granules, which stain feebly (fig. 45). The endoderm cells of the column wall and of the septal invaginations are also densely granular, and contain in addition numbers of the brightly-staining, spheroidal bodies referred to above.

As the proximal region of the polyps is approached, the interseptal loculi become more and more distinct from one another, and the middle is almost entirely occupied by the columellar invaginations. The mesenteries disappear before the aboral region is reached, or only mere rudiments remain. The skeletotrophic endoderm is very narrow above (fig. 44), but becomes very broad below, and is crowded with densely granular material, all the cell outlines being lost (fig. 45). The mesoglœa is indistinguishable as a distinct layer, and few traces of the skeletogenic ectoderm remain.

The corallum is penetrated throughout by a very delicate boring alga, which occupies the corallar space after decalcification. It is most abundant in the superficial layers of the skeleton. Spicules of boring sponges are also frequent.

Genus PHYLLANGIA Milne Edwards and Haime.[a]

Polyps smooth, distinct, isolated or in close or distant groups, tissues appearing delicate and transparent; perithecal continuation of gastro-cœlomic cavity and mesenteries; form short incrusting corallites of various sizes. Column wall cylindrical, often prolonged basally, on retraction may nearly or completely cover the disk; feeble sphincter muscle. Tentacles hexamerous, tetracyclic or incompletely pentacyclic, entocœlic and exocœlic, long and narrow, entacmæous, tubercular, apex knobbed. Stomodæal wall strongly ridged.

Mesenteries hexamerous, largest polyps incompletely tetracyclic, six to twelve pairs complete; two pairs of directives; all filamentiferous. Septal invaginations hexamerous, entocœlic and exocœlic, largest polyps incompletely pentacyclic, radially short in upper region and below incompletly united centrally.

Asexual reproduction by gemmation from the base or basal expansion of the column wall.

EXAMPLE. —*Phyllangia americana* Edw. & Haime.

PHYLLANGIA AMERICANA Milne Edwards and Haime.

(Pl. V, fig. 46.)

External characters. —The polyps occur in small groups of a dozen or so attached to blocks of coral, stones, etc., often to their under surface. In any group the polyps vary much in size. Some are still connected by the pericalicular continuation of the column wall, others only by a

[a] "Colony incrusting, forming clusters of moderately large turbinate corallites, close or rather distant. Corallites rather short. Calices circular, except where crowded, deep. Columella small or well developed, trabeculate from the septal ends; with from one to three or four pillars rising from the base and uniting and joining the trabeculæ; upper surface ragged or papillose. Septa well developed, numerous, unequal, some exsert, entire or minutely denticulated, granular, with or without paliform lobe. Costæ usually well developed. Epitheca wanting. Endotheca moderate. Basal expansion spreading, calcareous." (Duncan, 1885, p. 67.)

thin broad, basal extension of the corallum, while others are wholly isolated. In a series of eight polyps, none was distant more than 15 mm. from what might be regarded as the central polyp; three were still connected by a delicately ridged, band-like skeletal deposit, and of these one polyp was much larger than the other two. The column wall of one appeared to have just rounded itself off, but the other was still united basally with the larger polyp.

The column is usually circular, but sometimes is slightly oval, and often oblique to the surface of attachment, so that one side of the polyp is longer than the other. The column wall is smooth, subcylindrical, and short, extending but a short distance over the outer edge of the corallum, the remainder of the skeleton being hidden by various kinds of Nullipores and other foreign growths. The column can be overdrawn within the calice, so as to leave no central aperture, and completely hide the disk. The lower terminal margin of the edge-zone in isolated polyps is circular. Structurally the wall is very thin and transparent, and during full expansion is situated some distance from the corallum; the internal mesenteries and the skeleton are seen very distinctly through it.

The tentacles in the partly expanded condition are short and stout, with a broad base; they become long and narrow when fully extended, terminating in a small opaque swelling or knob. The surface is tuberculated, owing to the presence of minute nematocyst batteries; otherwise the walls are very delicate and perfectly transparent. The tentacles are about 8 mm. long on full expansion, and different cycles exhibit but slight variations in length. Thirty were counted on one polyp, thirty-six on another, and fifty-four on a third. Owing to their closeness, and small difference in size, it is practically impossible to determine from the tentacles themselves their cyclic arrangement, but it is readily seen that one occurs over each septum, and these follow the hexameral plan.

The disk is smooth, generally oval, very thin walled, and so transparent as to allow of the internal mesenteries being clearly seen. The peristome is usually much elevated; the mouth is slit-like, and extends nearly across the naked part of the disk. The stomodæal walls are sharply marked off from the disk, and present very deep ridges and furrows; in four polyps the ridges were twelve in number, and in two other polyps eighteen ridges occurred. At each angle of the mouth the disk is deeply rose-colored, thus affording a strong contrast with the whiteness of the stomodæal wall.

The tissues of the polyps as a whole seem very delicate, and on expansion are perfectly transparent, mainly owing to the absence of zooxanthellæ. The proximal region may be slightly brown, while the upper part of the column on partial extension is a rich dark brown. The discal area is a delicate rose color. The angle at each end of the mouth is a much deeper rose, while the tips and the lateral nematocyst batteries on the tentacles may be a delicate green, and the general surface perfectly colorless and transparent. The ridges on the stomodæal walls are a dense white, and the intervening grooves darker. In fully retracted specimens the coloration is much deeper, mostly a rich dark olive, except over the septal edges, which always stand out as very distinct white ridges.

At night, in the laboratory, the polyps are seen distended to their utmost, raised a few millimeters beyond the corallum, and the tentacles extended vertically upwards, horizontally, or overhanging. In the ordinary day condition the polyps are partly expanded, raised but little above the corallum; the tentacles may then be erect or mingle with one another centrally, and the mouth is open or closed. Sometimes the mouth will close quite suddenly, and then slowly open; or it may open to such an extent as to permit of the walls of the stomodæum being visible for the whole of their length, and even allow the actual interior of the polyp to be seen. On irritation the mouth opens suddenly, and afterwards closes slowly.

Anatomy and histology.—The column wall as a whole is very thin, becoming a little thicker toward the tentacular region. The ectoderm comprises mainly clear glandular cells and supporting cells, with a few small nematocysts in the upper region. The mesoglœa appears as a clear homogeneous layer. The endoderm is very narrow, and its free surface is even; zooxanthellæ were wholly absent from the specimens examined.

Such a histological structure at once explains the clear transparent delicacy of the living

tissues already noticed among the external characters. The coloration of the living polyp is apparently superficial, for in no part of the ectoderm or endoderm can any elements, such as pigment granules, be discovered, which may be considered as giving rise to the bright delicate colors.

The ectoderm of the column wall is somewhat thickened at its lower termination, and passes abruptly into the skeletogenic (basal) ectoderm lining the outside of the theca. Throughout the polyp the mesoglœa is a perfectly clear, homogeneous layer, in most cases indistinguishable from the field of the microscope; an included cell occurs but rarely. In the distal region of the column the mesoglœa becomes broader, and immediately below the tentacular region is slightly folded on its endodermal surface to afford additional support to the endodermal sphincter muscle. The latter is but feebly developed, and is continuous with the circular musculature of the tentacles.

The tentacles are both exocœlic and entocœlic in position. In sections through distended specimens the ectoderm presents alternate swollen and narrow areas. The former correspond with the tubercles noticed among the external features, and are constituted mainly of long, narrow, thin-walled nematocysts with a close spiral thread, while the intermediate areas are formed of a narrow epithelium resembling that of the column wall. In addition to the long narrow nematocysts, the apical knob contains a few oval nematocysts with a loose spiral thread; a few large granular gland cells also occur in the deeper regions of the apical and lateral thickenings. In longitudinal sections through retracted tentacles the ectoderm appears as a very thick, irregular layer, the nematocyst batteries overlying one another, as in the *Solenastræa* (Pl. X, fig. 75). The tentacular musculature is well developed, and immediately beyond is a layer of very close, deeply-staining fibrils, with nuclei sparsely scattered among them. These extend from the muscular layer for some distance, and end in a more or less distinct narrow zone. The structure evidently corresponds with the nerve layer so frequently met with in the larger polyps of the Actiniaria.

In retracted tentacles the mesoglœa is folded on its endodermal border, and supports a comparatively well-developed circular musculature. The endoderm is extremely narrow, the cells are charged with protoplasmic contents, and show little or no vacuolization. Zooxanthellæ, such as occur in most Zoantharia, are absent, but here and there throughout the polyp are the spheroidal, homogeneous, deeply-staining bodies, already described as occurring in *Astrangia*. These are distributed more or less irregularly throughout the endoderm of the polyp, but are not so numerous as in the species just mentioned.

The radial ectodermal musculature of the disk is arranged on fine mesogloeal plaitings, a little stronger near the tentacular region; here also small nematocyst batteries are present. The more central part of the discal wall is very delicate in all its three layers.

The stomodæal tube is very short in retracted specimens, and its lower extremity is folded backward and outward, and narrows intermesenterially. The ectoderm is strongly ridged vertically, the ridges corresponding in number and position with the insertion of the mesenteries; the mesoglœa and endoderm remain uniform all round. The ridges are practically equidistant in transverse sections, and here the ectoderm bears large oval nematocysts and granular gland cells; in the intervening grooves the layer is narrower, and constituted mainly of supporting cells. The ciliation is uniform all round, and very delicate ectodermal and endodermal muscular fibrils can be seen in sections. The ectoderm of the ridges terminates in direct continuity with the filaments of the complete mesenteries.

The mesenteries are hexamerous, but the arrangement in alternating cycles is rarely completed all the way round. In one polyp sectionized transversely (p. 464), ten pairs of mesenteries were united with the stomodæum, and of these two pairs were directives. The ten pairs consist of six primary pairs and of four secondary pairs, the two remaining pairs of this latter order being imperfect; in the uppermost stomodæal region, however, one of the pairs becomes complete. An alternating tertiary order of twelve incomplete pairs may occur, but as a rule some pairs are rudimentary or absent. Thus there may be from six to twelve complete pairs, according to the size of the polyp, and from two to twelve pairs of

tertiary mesenteries. The sequence of the mesenteries in this species has been already noticed (p. 464.)

The individual mesenteries are characterized by the thickness of the mesoglœa, and by the intricacy and depth of the plaitings for the support of the longitudinal musculature. The foldings are nearly as complicated on the incomplete mesenteries as on the members of the first and second cycles, and continue thus throughout the length of the mesentery; slight variations in details occur in different mesenteries. The cut ends of the fibrils of the retractor muscle are very minute. The oblique musculature on the opposite face is strongly developed, and the fibrils appear to be nearly vertical in direction; in the case of the complete mesenteries a very distinct plaiting of the mesoglœa takes place in the stomodæal region, thus increasing the effectual surface. The cells of the mesenterial epithelium in the upper regions are mostly filled with deeply-staining, protoplasmic contents, and only a few clear gland cells occur. In the lower regions the layer thickens, and the contents become finely granular, the cell outlines disappearing.

Filaments may occur on all the mesenteries, and closely recall those of *Astrangia*. The first part of the filament on the complete mesentaries is cordate in transverse sections, and histologically resembles the stomodæal ectoderm, the tissue being of a similar character all round. Soon, however, the filament becomes circular, and nematocysts and gland cells are more numerous on the anterior part of the filament; the mesenterial mesoglœa on each side also becomes swollen immediately behind the filament. Still lower the filament is strongly charged with large, oval, thin-walled nematocysts. The organs are slightly convoluted below, and by no means crowd the cœlomic cavity.

The septal invaginations extend centrally but a short distance, and only toward the proximal region are both entocœlic and exocœlic invaginations represented. The skeletotrophic endoderm is much thickened below, and is densely granular, the granules of different sizes being somewhat uniformly distributed throughout the layer. The lateral walls of the invaginations are deeply indented, corresponding with the granules on the septal faces.

Within the edge-zone the mesenteries are mostly incomplete on the inner side, so that the perithecal chambers are but imperfectly divided.

Genus CLADOCORA Milne Edwards and Haime.[a]

Polyps smooth, distant, forming bush-shaped or fasciculate colonies, free or fixed, and often separated into subcolonies of from two to five polyps; perithecal continuation of the gastro-cœlomic cavity and mesenteries. Column wall smooth, cylindrical, elongated, on retraction may close over nearly the whole of the disk. Tentacles hexamerous, entocœlic and exocœlic, tricyclic, or incompletely tetracyclic, entacmæous, finely tuberculated, knobbed or rounded at end. Stomodæal walls ridged.

Mesenteries regularly hexamerous, dicyclic or incompletely tricyclic, six pairs complete, two pairs of directives, all filamentiferous, extrusible. Septal invaginations entocœlic and exocœlic, tricyclic or incompletely tetracyclic, below unite centrally (columella), giving rise to twelve separate mesenterial loculi.

Asexual reproduction by lateral columnar gemmation, rarely by fissiparous gemmation.

EXAMPLE. —*Cladocora arbuscula* (Lesueur).

CLADOCORA ARBUSCULA (Lesueur).

(Pls. VI–VIII, figs. 48–63.)

External characters.—Small bush-like colonies of this species occur in numbers in the shallow waters of Kingston Harbor, and at other points around the coast, either free or attached to loose pebbles or shells. Larger colonies are found in water of from three to six feet, and thickly incrust the wooden piles of wharfs and buoys, or even the bottoms of boats plying in the harbors.

[a] "Colony bush-shaped or branched or fasciculate. Corallites variable in length, erect, often flexuous, cylindrical, and free laterally. Calices circular and shallow. Columella well developed. Septa exsert, subequal, rounded, and finely dentated and granulated laterally. Pali exist before all the cycles except the last. Wall compact, moderately thick. Costæ simple, granular, or finely echinulate, straight. An incomplete epitheca, which often gives rise to horizontal collarettes, may extend from one corallite to another. Endotheca scanty. Gemmation lateral and often in pairs from the same height on the stem." Duncan, 1885, p. 70.)

Each colony is usually divisible into smaller subcolonies, in which a certain number of the polyps are still united one with another by the column wall. In any distinct subcolony rarely more than four or five polyps are united, branching at an angle varying from nearly a right angle to about 45°. Sometimes a single polyp may be disconnected from all the others, or only two or three may be in union. All stages in the formation of subcolonies, by the disappearance of the intervening portion of the soft tissues, are presented. During the process the proximal part of the column wall of two united polyps becomes constricted more and more, and finally the last connecting strand breaks down, and the polyps are completely isolated. The separation of individual polyps is more frequent in some of the humbler, bushy colonies, while other colonies are met with in which all the polyps are still united, no subcolonies being formed, or very sparsely.

The part of the skeleton exposed by the withdrawal of the lower perithecal portion of the column wall and skeletotrophic tissues is at first clean and white, and covered with a very thin epitheca; but worm tubes, algæ, etc., from the older, dead parts of the colony soon encroach upon it.

The column wall is cylindrical, and extends downward over the outside of the skeleton for a varying distance in different polyps, but rarely exceeding 5 mm. from the thecal edge. The surface is smooth and semitransparent, and is very distinctly ridged and grooved throughout its extent, the ridges corresponding with the costæ and the grooves with the internal attachment of the mesenterial continuations. The mesenteries seem to extend the full length of the column, but sections reveal that toward the lower extremity some become free from their inner attachment, or may disappear altogether (figs. 51, 54). When the polyps are expanded to their full extent, the column, tentacles, and disk become removed some distance from the underlying skeleton, and the columnar ridges and grooves are not very pronounced. The column may extend upward as much as 4 mm. beyond the theca, and the disk, becoming conical, may add another 4 mm. On full retraction the tissues adhere very closely to the corallum, following its elevations and depressions; above, the column wall is overfolded, so as to cover the tentacles and greater part of the disk. On partial retraction the column wall is sometimes constricted in a circular manner, just below the tentacular zone. The lower, terminal edge of the column of the lowest polyp in a subcolony is very sharply defined, and the upper passes directly into the tentacles.

The tentacles are in three or four cycles, but beyond the first cycle of six the arrangement is difficult to determine, as but small variations in size are exhibited, and the cycles are closely arranged. The general appearance is that of two alternating cycles of nearly equal size. The total number of tentacles varies from twenty-four to thirty-six; thirty and thirty-four are most frequently counted.

All the tentacles are rather broad at the base, and narrow towards the apex, which is slightly swollen or knobbed. In the expanded condition the organs are usually overhanging, often one cycle to a greater extent than the other. Sometimes the members of the outer cycle may be reflected to such a degree as to be opposed to the column wall, while those of the inner cycle remain erect. Occasionally the tentacles may be shorter and more swollen proximally, as in the figure given by von Heider of *C. cespitosa* (1881), but generally they are long and narrow. In one or two instances a tentacle with a bifurcated apex has occurred, each half provided with a swollen tip.

The tentacular walls are very delicate and transparent on full distention, bearing minute white tubercles over the whole surface. Like the apical swelling, these are only thickenings of the ectoderm, and on microscopic examination are seen to be batteries of stinging cells. The tentacles correspond in position with the septa and costæ, which are easily seen through the semitransparent tissues; the inner tentacles are placed over the larger septa, and the outer cycle over the alternating smaller septa. The tentacular apex has considerable adhesive power, holding on to any body brought in contact with it; the distal part of the stem also tends to fold round any object. The length of the innermost tentacles during full extension may be as much as 6 mm.

The disk is smooth, circular, 2 or 3 mm. in diameter, and radiately grooved in correspondence with the internal complete mesenteries. In retraction it is depressed for some distance within the calice, assuming a cup shape; but sometimes the peristomial region is elevated. The

peripheral part is usually more vertical, and bears the tentacles at its rim. During full expansion the disk may be raised centrally to the extent of 4 mm. beyond the tentacular zone, and in this condition it is conical in shape, and swollen a little at the stomodæal region; the walls are very thin and transparent, and permit of the arrangement of the mesenteries being followed.

The stomodæum often protrudes a little, in which condition vertical ridges and furrows can be clearly seen, six on each side. In polyps partially exposed at the surface of the water, the mouth becomes enlarged and circular in outline, to such an extent that the interior of the polyp below the short stomodæum is visible.

The color of the polyps throughout is a lighter or darker shade of brown, due to the color of the chromoplastids in the endodermal zooxanthellæ. The ectoderm itself is colorless and transparent, as can easily be seen when living tentacles are examined under the microscope; hence the whiteness of the tip and tubercles on the tentacles, and of the lining of the stomodæal wall. When the tentacles are contracted they become very dark brown, except at the tips, the density in coloration resulting from the more closely aggregated unicellular algæ. The margin of the peristome is at times a bright iridescent green. Where colonies occur on the underside of some rock, or in such a position that little light reaches them, they may be colorless throughout, or show all gradations from the normal intensity toward a bleached condition.

The species is very favorable for the study of lateral columnar gemmation, and different stages have been already described (p. 501). A single polyp, or maybe two, arises from the upper portion of the column wall of another polyp, and in turn gives origin to other buds. The perithecal portions of the mesenteries of the parent seem altogether independent of the mesenteries of the bud, but four or five costæ of the parent corallite are continuous with the same number of the bud. Very rarely a bud may arise on the disk of a large polyp in such a way that the two are surrounded by a common tentacular system and a single column.

The buds develop to a certain extent before any septal formation can be recognized; in one case twelve mesenteries could be made out through the semitransparent tissues of the distended bud, without any evidence of septa or even of tentacles. The lower side of the bud grows in advance of the upper, hence the angle which the axis of the bud makes with that of the parent polyp; the lower tentacles likewise arise in advance of the upper. The manner of growth of the mesenteries has already been described (p. 458).

The colonies live well in aquaria, the numerous symbiotic algæ in the endoderm serving to keep the water aërated, without any artificial means or constant exchange. All the members of a subcolony respond when one is irritated, but slightly later. On retraction, the disk is lowered, and its peripheral portion and the tentacles are ranged along the inside wall of the calice, resting on the septa (fig. 48), so that the mouth and middle region of the peristome are alone visible; the column wall is then drawn horizontally over the margin of the calice, the circular edge nearly closing in the middle.

The most usual living condition appears to be one of moderate expansion, with the tentacles erect or overhanging. Mesenterial filaments may be extruded, though very rarely, through the mouth or other part of the disk, and have been observed displaced to such a degree as to enter the tentacular cavities. They can be again indrawn. On narcotization with menthol the tissues shrink somewhat, and the mouth becomes widely open and circular.

Anatomy and histology.—Throughout the whole of its length, extending from the outer row of tentacles to its terminal proximal margin, the column wall presents a uniform structure (figs. 52*a*, 59). The ectoderm is the best developed of the three layers, and comprises numerous unicellular gland cells with the contents clear or feebly granular. They constitute almost the entire layer, and are mostly ovoid in shape, and may extend the whole thickness of the layer. The interstices between the cells are filled by ciliated supporting cells with rounded or oval nuclei. Seen in surface view the ectoderm gives the appearance of a mosaic, the large polygonal gland cells forming clear areas, limited by the supporting cells as a kind of matrix. A few granular gland cells and small nematocysts are also present.

At its proximal termination the ectoderm thickens somewhat, and histologically is very sharply marked off from the skeletotrophic ectoderm. The mesoglœa is usually very narrow, but becomes thicker in the region of the mesenteries, appearing triangular in transverse sections;

at its lower termination it also thickens, then immediately thins out as it passes into the skeletotrophic tissues. The endoderm is a narrow, somewhat uniform layer, the cells of which contain numerous zooxanthellæ; clear gland cells are scarcely represented.

In all the tentacles a battery of nematocysts occupies the apex, and smaller batteries occur in different areas along the whole length of the stem. The former gives rise to the white apex noticed among the external characters, and the latter correspond with the smaller elevations along the stem of the tentacles. In sections of extended tentacles the ectoderm is swollen in the region of the batteries, and narrow in the intervening spaces (fig. 50). The nematocysts of the batteries are long and narrow, the internal spiral thread being so fine as to be determined with difficulty. Two kinds occur, one about half as long as the other; they are practically limited to a peripheral zone in the ectodermal layer, and this they crowd to the exclusion of nearly all other elements.

In the living condition the cnidocils are seen very distinctly as delicate triangular processes from the surface of the ectoderm, and cilia occupy the areas between. The larger nematocysts when shot out present an elongated oval cyst, and a long thread strongly barbed and thicker proximally, but very fine and smooth distally. Of the smaller nematocysts the thread is simple, and only partly extruded in most cases. Elongated, deeply-staining, homogeneous bodies are to be seen in the deeper parts of the ectoderm, and are no doubt developing nematocysts. Their internal end borders almost directly on the mesoglœa, so that in attaining maturity they must migrate toward the periphery.

The rounded nuclei of the ectodermal cells stain deeply, and stand out very distinctly from the other parts of the layer. In sections they are arranged just within the nematocyst zone, and a clear zone intervenes between the musculature and the nuclear region. Large, ovoid, gland cells, with coarsely granular contents, occur throughout the ectoderm, and occupy the greater proportion of the layer in sections, but are not so numerous in the region of the batteries. The ectodermal longitudinal musculature, though weak, is clearly distinguishable throughout the tentacles, the mesoglœa supporting it being slightly sinuous in some examples. Compared with its condition in most other regions of the polyp the mesoglœa of the tentacles is well developed. The internal limitations of the endoderm are irregular, some portions extending more within the lumen than others; zooxanthellæ are numerous, and the endodermal musculature is very weak.

The ectoderm of the disk contains numbers of clear glandular cells, and an occasional nematocyst; the endoderm is a broad layer, and zooxanthellæ are abundant within its cells. A circular endodermal musculature can be readily distinguished, but no radiating ectodermal muscle fibers have been detected.

In retracted polyps the central part of the disk is drawn somewhat internally, so that the actual lips are formed by it, and here the endodermal musculature is most obvious; but a little within the apparent mouth the ectoderm undergoes great histological modification, and assumes the usual characters of the stomodæal epithelium. The stomodæum is oval in transverse sections, so that the median axis of the polyp is easily determined. The walls are very short in vertical sections, and folded vertically and transversely (fig. 56), and in some polyps the ridges opposite the insertion of the mesenteries are well developed. At its lower termination the stomodæal ectoderm is strongly reflected, and passes for some distance along the two faces of the complete mesenteries, becoming continuous with the mesenterial filaments (figs. 51, 60).

The structure of the stomodæal wall is the same all the way round in any transverse section, there being no histological differentiation distinguishing the ridges and furrows. Its ectodermal layer begins to narrow below, and mesenterially is in continuity with the tissue of the filaments. The ectoderm consists mostly of ciliated supporting cells, but long unicellular granular gland cells, the contents of which stain deeply, are also present. Many of the narrow gland cells extend outwardly as far as the margin of the layer, that is, a little beyond the nuclear zone, and are thus very distinct for this part of their length (fig. 52*b*). Long narrow nematocysts, and also a large oval form, occur in the lower regions, and a great number of granular cells, especially toward the mesogloeal limits of the layer. No trace of an ectodermal musculature or nerve layer can be seen.

Six pairs of mesenteries, constituting the first order, are perfect, and of these, two pairs, situated one at each end of the longer axis of the stomodæum, are directives (fig. 49); in serial transverse sections these are the first to cease their connection with the stomodæum (fig. 51). The second cycle of mesenteries also consists of six alternating pairs, which are of moderate length in transverse sections, but never reach the stomodæum. For some distance below the stomodæum little difference exists in the radial length of the mesenteries of the two cycles, but toward the lower region the second-cycle members lose their filaments, and disappear in advance of the others (figs. 54, 55).

Members of a third cycle of mesenteries usually occur, but instead of consisting of twelve pairs, that is, a pair in the exocœle between each pair of mesenteries of the first and second order, only two to six pairs are developed, all situated on the sulcular or sulcar aspect, as the case may be, in regard to the members of the first order (fig. 49). Often the two mesenteries forming a pair are not of equal length in transverse sections, nor do they extend for the same distance along the length of the polyp. All the members of the third order extend but a very short distance below the stomodæal region. The mesenteries of the two first cycles bear filaments of exactly similar structure, but they are rarely fully developed on the members of the incomplete third cycle.

The mesenterial plan of an irregular polyp, having three pairs of directives, is represented in fig. 53; probably it represents a stage toward fissiparous gemmation.

When free the mesenteries are somewhat clavate in form in transverse section, very narrow at their origin in the body wall, and broadening a little until they terminate in the enlargement of the filaments. The mesoglœa is narrow at its origin, and widens beyond, narrowing somewhat again toward its free end, and then enlarging at the base of the filament. It is a clear, homogeneous layer without cellular contents, and the face bearing the retractor muscle is thrown into deep, simple or slightly complicated folds, nearly alike throughout its radial length, but a little more pronounced in the middle. The opposite face bearing the oblique musculature is smooth (fig. 59).

The retractor muscle extends as a simple layer of vertical muscular fibers over the whole surface of one mesenterial face, and the musculature on the opposite face can be readily distinguished in slightly oblique sections. Below the stomodæum the musculature is equally developed on each face of the mesentery for some little distance from the origin, and the fibers on both faces are nearly vertical in direction. The muscle fibers can be traced for a short distance along the body wall, continuous with those from the mesentery, recalling the parieto-basilar muscles of the Actiniaria. As the mesenteries become shorter transversely, and lose their filaments, the musculature is of the same character all the way round.

As shown in fig. 51, the terminal portion of the stomodæal wall becomes reflected outwardly, so that in transverse sections it is cut through twice. The ectoderm narrows somewhat, and passes for some distance along the two faces of a mesentery, swelling a little and then terminating rather abruptly. Traced section by section each mesentery ultimately severs its connection with the stomodæum, but is still capped by the same deeply-staining tissue; thus absolute continuity is made between the stomodæal ectoderm and the mesenterial filaments, and for some distance the histological elements are much the same in both. In the section through the terminal stomodæal region, represented in fig. 51, all the stages in the separation of the six pairs of mesenteries can be observed, the directives being the first to become free.

A transverse section through a filament, just after the mesentery becomes free from the stomodæum, is represented in fig. 57*b*. The outline for a short distance is cordate, and histologically the filament is constituted of ciliated supporting cells, which are somewhat longer toward the apex than laterally. Long narrow nematocysts occur in this region of the polyp, mostly aggregated about the apex, as well as granular gland cells, especially noticeable toward the internal limits. The mesoglœa from the mesentery passes toward the middle of the filaments, enlarges somewhat, and then sends a branch to each side. The musculature can in most cases be distinguished on both faces of the mesoglœa of the mesentery, thence passing to the concave surface of the filamental portion. A punctate appearance is also presented around the convex border, indicating

nervous elements; the posterior margins of the filament inclose a tissue exactly resembling that of the mesenterial epithelium.

Traced below, the filament undergoes some change in outline, and two lateral lobes of endoderm are developed to a greater or less extent. This is shown in fig. 57*c*. The lateral lobes differ but slightly from the ordinary mesenterial epithelium, except that the cells are longer and the nuclei are aggregated toward the free surface. As shown in the particular example figured, the lobes on the two sides are not always symmetrical.

Still lower in the polyp, where a certain degree of convolution takes place, large oval nematocysts predominate in the filament, and gland cells are more numerous (fig. 58). All stages in the development of the large nematocysts can be traced, from one in which the contents are perfectly homogeneous and deeply-staining, with no trace of any thread, to the more mature forms where the spiral thread is fully developed.

The skeletotrophic tissue is narrow throughout, and the three layers—endoderm, mesoglœa, and ectoderm—can usually be distinguished, though not always the last. The endoderm in the upper region differs only slightly from its character in other regions of the polyp, being a simple compact columnar layer, the cells of which contain zooxanthellæ and much granular matter. The mesoglœa is extremely thin, and rarely distinguishable as more than a dividing lamella between the two cellular layers. The appearance of the ectoderm in the upper, rapidly growing parts of the polyp is represented in figs. 59, 63. The free border is jagged and irregular in outline, as if torn from some other surface with which it was in structural continuity, and the cells form a simple columnar epithelium. Away from the upper edges of the septa, etc., the calicoblast layer becomes much reduced in thickness, and loses its columnar character; generally a few desmoidal processes occur in sections near the insertion of a mesentery.

Toward the floor of the calice the calicoblastic layer is often found in an active condition, and the endoderm over it is much thicker and crowded with coarse granules; in such cases dissepiments are probably in course of formation.

The gastro-cœlomic cavity above is only partly subdivided by the mesenterial and septal invaginations (figs. 49, 53), and is continued over the edge of the calice as a narrow space, again subdivided by mesenterial partitions and costal outgrowths (fig. 54). In the lower regions the central part of the cavity becomes more encroached upon by the ingrowth of the septa, and by the great increase in thickness of the endodermal layer covering them (figs. 54, 55). Ultimately the twelve entocœlic septa meet in the middle, and twelve interseptal chambers are formed, wholly cut off from one another, and each partly subdivided by the exocœlic septa which never meet in the middle.

Genus ORBICELLA Dana.[a]

Polyps verrucose, distinct, closely united one with another along a polygonal base, and forming massive colonies of various shapes, fixed, incrusting, or free, with perithecal continuation of the gastro-cœlomic cavity and mesenteries. Column cylindrical, polygonal at the base, on retraction may almost completely fold over the disk; diffuse endodermal sphincter muscle usually present. Tentacles hexamerous, entocœlic and exocœlic, tricyclic or tetracyclic, tuberculated, sometimes swollen toward the origin, rounded at apex, introvertible, cycles close or widely apart. Stomodæal wall ridged.

Mesenteries hexamerous, usually di- or tri- cyclic, one or two cycles complete and filamentiferous, two pairs of directives present. Septal invaginations entocœlic and exocœlic, tri- or tetra-cyclic, dividing the gastro-cœlomic cavity into partly distinct chambers.

Asexual reproduction by marginal and intercalary gemmation.

EXAMPLES. *Orbicella annularis* (Ell. & Sol.), *O. radiata* (Ell. & Sol.), *O. cavernosa* (Linn.).

[a] "Colony of various shapes, convex, subspherical, subplane, short or tall, adherent, incrusting, or free. Corallites united by continuation of the exotheca, which exists between and beyond the costæ beneath the surface, rarely by the costæ themselves. Walls usually, but not invariably, stout. Calices with free circular margins, more or less crateriform and elevated. Columella well developed, spongy, and not projecting, with a plain free surface. Septa exsert or not, with well-developed lamina, thicker near the margins than near the columella, where there is often a paliform tooth, dentate. Costæ well developed, passing over the surface for some distance; where seen on the wall of a corallite they are lamellar and well developed, often spiny. Endotheca well developed. Exotheca between and usually beyond the costæ, well developed. Epitheca may or may not exist. Gemmation intramarginal, and from the area between the calices." —*Helioseræ*, Duncan, 1885, p. 104.

ORBICELLA ANNULARIS (Ellis & Solander).

(Pls. VIII-X figs. 64–73.)

External characters.—The species occurs on coral areas in small or large, fixed, nearly spheroidal masses; also as an incrustation occupying areas several feet across. Small isolated colonies are sometimes conical. In places it is an important constituent of the reefs. During partial expansion the distal parts of the polyps are 2 or 3 millimeters apart, and on full expansion the column becomes raised above the surface of the corallum for about 3 mm., in which condition the individual polyps become so much enlarged that the columns may press against one another. The column wall is smooth and cylindrical, and the proximal boundary of each polyp is indicated by a polygonal shallow groove. When retracted, strong external ridges and deep grooves correspond with the septa and mesenteries respectively. The costal ridges are alternately large and small. The column can be partly drawn, iris-like, over the disk, but never so as completely to hide it; on very strong retraction of the polyps the exsert edges of the costæ project greatly, as if perforating the tissues.

The tentacles are very short, appearing in two alternating cycles, usually of twelve each; the inner and larger correspond with the primary and secondary septa, and the outer and smaller with the tertiary septa. They vary very much in character under different conditions of expansion of the polyp. Normally the tentacles are digitiform outgrowths, with a swollen apex, but during full expansion the walls of the polyps may be swollen to such a degree that the tentacular walls become involved in the disk, and practically disappear, their position being indicated only by slightly raised, light-colored, triangular areas, small and large alternating. In some polyps the organs are imperfectly developed, so that no definite protuberances are represented; at other times mere pyramidal processes appear at the apex of the costal ridges, a larger and inner cycle alternating with a smaller and outer. During retraction the tentacles are hidden under the overfolding column wall. The organs thus differ much from those in *O. radiata* (p. 423).

The naked portion of the disk is about 5 mm. across. It is deeply depressed when the polyps are expanded, and almost completely hidden on retraction. The peristome may be much or only slighted elevated, but there are no true lips, the boundary of the disk and stomodæum being sharply defined by differences in pigmentation. The mouth is generally open and oval shaped, and stomodæal ridges are not distinguishable.

The color of the colonies as a whole is usually a steel gray or dark brown, and the tissues generally appear dense and nontransparent. In some the tentacles and disk are a bright emerald green, and an iridescent appearance is often produced by the presence of minute, white granules all over the column wall and middle region of the disk. The stomodæal wall is colorless.

White, coiled mesenterial filaments may be extruded through temporary apertures in any part of the superficial tissues, and may be again indrawn.

Asexual reproduction takes place by intercalary and marginal gemmation. Buds with only eight tentacles have been observed.

Anatomy and histology.—The proximal region of the column wall is sinuous in transverse sections, consisting of alternating larger and smaller ridges, separated by more or less acute grooves; the former correspond with the costal evaginations, and the latter with the line of attachment of the perithecal portion of the mesenteries. The wall consists of a broad ectoderm and endoderm, but the mesoglœa is thin, except at the line of attachment of the mesenteries. The outermost layer is provided with scattered nematocysts throughout its extent, and finely granular, pigment matter occurs in its deeper regions, sometimes extending to the surface. The granules appear as if irregularly distributed in patches among the various cellular constituents, and in all probability they function as pigment matter, and give rise to the dense opaque appearance of the living tissues; many clear gland cells occur in addition (figs. 64, 65).

Zooxanthellæ are very numerous in the endoderm cells, and a layer of delicate muscle fibrils can be made out in vertical sections, especially in the distal region of the column wall. The layer is sufficiently well developed to warrant its being regarded as a special sphincter muscle of the diffuse endodermal type (fig. 65).

The ectoderm of the tentacles is somewhat broader than that of the column wall, and the apical region is crowded with narrow nematocysts, showing distinctly the internal spiral thread. Among these are a few larger cysts, which stand out very prominently on account of the highly refractive character of the wall, axis, and spiral thread; usually one or more lateral batteries are also seen in sections. The longitudinal ectodermal and circular endodermal musculatures are both clearly determinable, and outside the former a nerve layer is sometimes displayed.

Pigment granules occur very sparingly in the ectoderm of the disk, and in the living polyps this area is usually more transparent than the column wall; clear mucous gland cells are numerous, and nematocysts are developed here and there. A very delicate ectodermal and endodermal musculature is present, and the external ciliation is sometimes persistent in preserved material. The mesoglœa is a rather broad layer, and numerous zooxanthellæ are present in the endoderm. In strongly retracted specimens the discal ectoderm is inturned for a short distance within the stomodæal cavity (fig. 67).

The stomodæum extends but a short distance vertically, and at its lower termination is folded outwardly and upwardly, so that in transverse sections it may appear twice, the two being a wide distance apart. Its ectoderm comprises at least two kinds of narrow nematocysts, as well as a few examples of a large, oval, thin-walled variety. Different stages in the development of the latter are easily recognized by the deeply-staining character of both the cyst wall and the contents. Large, oval or spheroidal, unicellular gland cells occur, charged with large, colorless or slightly yellow, spheroidal granules, which do not stain in hæmatoxylin or borax carmine; they are prominent features in all the internal tissues, both mesenterial and skeletotrophic. In addition to these are numerous gland cells with finer granular contents which stain intensely.

Owing to the shortness of the stomodæum, the backwardly folded condition of its walls in retracted polyps, and the great number of mesenterial prolongations and septal invaginations, the arrangement of the mesenteries can be determined only with difficulty. Two polyps sectionized transversely contained twelve pairs of mesenteries, of which six pairs are complete and six incomplete; among the former, two pairs, situated at opposite extremities, are directives. In retracted polyps, where the column wall becomes overdrawn within the calice, transverse sections pass through the latter twice, and all the mesenteries extend from one wall to the other. The imperfect mesenteries stretch for some distance centrally, but are never convoluted like the complete members. Fully developed filaments are borne only by the mesenteries of the first order, but at the free edge of the others a small number of cells with deeply-staining nuclei occur, very readily distinguished from the undifferentiated mesenterial epithelium, though passing gradually into it. From its close resemblance to the mesenterial filaments in the early larval stages the tissue manifestly represents as an incipient filament.

The mesenterial epithelium is a broad layer, characterized by an abundance of gland cells with large granules (fig. 72); many clear gland cells also occur, and nematocysts rather sparsely. The mesoglœa is thickly developed in retracted polyps, and the face on which the retractor muscle occurs exhibits rounded folds or narrow plaits for giving additional surface to the musculature. The foldings are somewhat irregularly disposed, and scarcely alike on any two mesenteries, and are more strongly developed in some regions than in others (fig. 68). The oblique musculature on the opposite face of the mesentery is distinct in the upper regions of the polyp, and where the mesenteries shorten below, the fibers are nearly the same in direction all the way round.

The perfect mesenteries are larger and become much convoluted in the middle region of the polyp, nearly filling the gastro-cœlomic cavity, but the proximal region of the polyp is altogether devoid of mesenteries. In vertical sections the organs are seen to be restricted to the upper half or two-thirds of the polyp (fig. 67).

In the upper region the perithecal portion of the mesenteries extends wholly across the space from the column wall to the skeletotrophic tissue; but toward the lower termination some become free from the column wall, remaining attached only to the skeletal lining. The musculature is about equally developed on each face in the lower regions, and each set of fibrils extends in the same direction, the mesoglœa remaining nearly smooth; above, the face bearing the retractor muscle is slightly plaited. The endoderm as a rule is much swollen toward the insertion of the mesentery on the column wall.

The mesenterial filaments exhibit the usual histological details. Two or three kinds of nematocysts and gland cells occur (fig. 72a), and the mesenterial epithelium immediately behind is not always swollen to the degree usual in the Madreporaria. In the lower regions large oval nematocysts predominate.

The filaments on certain of the mesenteries undergo a glandular differentiation within a limited portion of their extent, and all stages in the process, from the normal filament to the wholly glandular, can be followed. The general characteristics of these organs have already been given (p. 473). Where best developed the filamental cells, with the exception of the supporting cells, are all modified, and are filled with a finely granular substance (figs. 69–71).

Septal invaginations occur within all the entocœles and exocœles, but the entocœlic extend by far the most centrally; the exocœlic never appear as more than shallow internal depressions of the skeletotrophic tissues. The entocœlic invaginations are usually twelve in number, and are approximately equal in their radial extent; six correspond with the mesenteries of the first order, and six with the mesenteries of the second order. Although practically equal in size, the twelve entocœlic septa will therefore represent the first and second orders, corresponding with the primary and secondary orders of mesenteries, while the twelve septa, corresponding with the exocœles, will constitute a third order. An examination of the skeleton reveals that a slight distinction in thickness and in radial extent can often be made between the septa of the first and second order, while the members of the third never project far from the thecal wall. The interseptal loculi are not completely separated from one another, that is, they remain in communication centrally, indicating that the columella does not wholly occupy the center of the calice. Adjacent septa do not as a rule fuse within the central region, and the center of the calice is occupied for the most part by the large vertical teeth, one of which arises from each septum of the first and second orders. Outwardly, the costal evaginations are strongly developed, and are on the same radii as the septal invaginations.

The endoderm of the skeletotrophic tissues is a narrow layer in the upper region of the polyps (fig. 68), and contains zooxanthellæ and conspicuous granular gland cells. As the more internal regions are approached, the layer becomes much broader, and its cells undergo the usual vacuolization, most of the contents being aggregated toward the free surface. Zooxanthellæ and gland cells occur, however, as far as the basal extremity (fig. 73).

The skeletotrophic mesogloea is everywhere very thin, except at the insertion of the mesenteries on the corallum, where it is broadened and bears numerous desmocytes. Corresponding with the smoothness of the theca, and of the faces of the septa, there is an absence of indentations on the skeletal tissues, such as occur where echinulations are present.

The skeletogenic ectoderm has almost wholly disappeared, except at certain places, such as the edges of the costæ and septa. At these the layer retains a considerable thickness (fig. 66); longitudinal sections also reveal that the layer may be in an active condition along the extreme basal area, and the mesogloea here becomes a little broader (fig. 73). It is manifest that the activity of the skeletotrophic layer in this region is associated with the formation of dissepiments.

Zooxanthellæ occur everywhere in the endoderm, and algal filaments penetrate the skeleton throughout.

Genus SOLENASTRÆA Milne Edwards and Haime.[a]

Polyps smooth, very close or more distant, united along a polygonal base, perithecal continuation of the gastro-cœlomic cavity and mesenteries very restricted, sometimes none at all; form light, massive, incrusting or free colonies. Column cylindrical, polygonal at the base, on retraction upper part folds over the disk: no sphincter muscle. Tentacles tricyclic and hexamerous, tuberculated, swollen at apex. Stomodæal wall ridged.

Mesenteries dicyclic, hexamerous, both cycles filamentiferous, two pairs of directives. Septal invaginations entocœlic and exocœlic, tricyclic, united centrally (columella), thus forming a separate chamber below for each mesentery, transversely truncated below.

Asexual reproduction by intercalary, marginal, and fissiparous gemmation.

Example. *Solenastræa hyades* (Dana).

[a] "Colony massive but light, convex above, incrusting or tall, often gibbous, rarely plane. Corallites long or short, united by a well-developed exotheca, which extends beyond the small costæ. Calices with free margins, which are usually circular, but sometimes unsymmetrical in outline. Columella spongy or feebly developed. Septa thin or stout, imperforate, dentate. Endotheca fairly developed. Gemmation extracalicinal." (Duncan, 1885, p. 107.)

SOLENASTREA HYADES (Dana).

(Pls. X–XIII, figs. 74–91.)

External characters.—Free colonies of this species are to be found lying on the sea floor at the eastern end of Kingston Harbor, often incrusting or inclosing some pebble, shell, or other foreign body. I have not met with it elsewhere around Jamaica.

The polyps in any colony may be either very close together or wide apart, the polygonal divisions between one polyp and another being strongly marked. When the polyps are distended to their full extent, the column wall reaches 2 or 3 mm. beyond the corallum, and is cylindrical, or it may be slightly constricted at the middle and enlarge again distally. The wall is adherent to the skeleton only at the polygonal line of union of adjacent polyps.

During partial expansion the column wall is somewhat infolded within the calice, and the tentacles protrude from beneath, leaving the middle region of the disk and mouth exposed. On complete retraction the calicular portion of the column wall is further depressed and overfolded, almost completely hiding the disk and leaving but a small central aperture (fig. 74). The extent of the perithecal part of the column during retraction varies much in different regions of a colony, according as the polyps are close together or widely apart.

The column wall is smooth, thin walled, and ridged and grooved in correspondence with the internal costæ and mesenteries. The costal areas are practically equal, not divided into alternately small and large divisions, as is more usually the case. The corallum shows very distinctly through the thin, extracalicular portion of the column wall.

The tentacles are in three cycles, arranged according to the formula 6, 6, 12, and correspond in position with the septa. The total, 24, is occasionally departed from; in young polyps it is less, and very rarely it is more. The tentacles of the innermost cycle are 2.5 mm. in length, and differ but little from those of the second cycle, while they are nearly double in size the members of the last cycle. On the living polyp they appear as two alternating cycles of larger and smaller tentacles, the inner and larger communicating with the entocœles, the outer and smaller with the exocœles. Their lateral walls are provided with small urticating areas, white upon a transparent background; the apex is white and rounded, or distinctly knobbed. On full expansion of the polyps the tentacles are overhanging, and when all are extended they practically cover the colony, giving to it a delicate, pale brown, fleecy appearance.

The disk is smooth, circular, and radiately ridged and grooved, with rounded elevations along the ridges, corresponding with the denticulations along the edges of the septa. The discal diameter during full expansion is about 3.5 mm.

The peristome is often much elevated, ending sharply in the narrow, slit-like mouth. Under some conditions the peristome and mouth are both rounded, and at other times the lips may approximate in the middle, the two ends remaining open and serving as a means of communication between the exterior and interior. The approximation may be so pronounced as to give rise to the appearance of two quite distinct oral apertures. The stomodæal walls display six white longitudinal ridges with alternating grooves on each side, and are capable of almost complete eversion.

Colonies as a whole are lighter and darker shades of brown, the tissues being delicate and partly transparent. The basal region of the column wall is often light brown, and the white skeleton shows through; on partial retraction the intracalicular portion of the column wall and the disk are dark brown, as well as the tentacles. The swollen tips of the tentacles and the stinging areas are colorless, and iridescent green radiations are occasionally present on the disk and on the inner face of the tentacles. In some instances the polypal tissues on the under surface of a colony were perfectly colorless and transparent, and examination revealed an absence of zooxanthellæ from the endoderm.

The polyps do not expand during the day with the same readiness as some species, but at night are seen opened to their full degree. Irritation of one polyp is slowly responded to by those immediately surrounding. Mesenterial filaments can be emitted through the mouth on

irritation, and are again withdrawn. New individuals arise amongst the others at any spot along the line of union of contiguous polyps, and also around the margin."

Anatomy and histology.—The column wall is very thin in microscopic sections, the mesoglœa being scarcely determinable as a distinct layer. The ectoderm is constituted almost wholly of clear gland cells, and in vertical sections these are regularly arranged and lie closely together; nuclei occur in the intervals between one gland cell and another, and give rise to a discontinuous zone about the middle of the layer. In the more internal parts occur smaller gland cells with granular contents, and also a number of nuclei closely apposed to the mesoglœa. The endoderm is very thin, often not more than the diameter of a single zooxanthellæ across. No muscle fibrils are seen on either side of the mesoglœa, not even in the capitular region of retracted polyps (figs. 76–78).

The tentacular ectoderm is a broad layer, especially at the tip, where it is constituted largely of supporting and nematocyst-bearing cells; fewer clear gland cells, and more of the granular variety, occur than in the column wall. In retracted specimens the lateral nematocyst batteries stand out prominently, while the intervening areas are very narrow (fig. 75). The nematocysts are mostly of the long, narrow, thin-walled form, and an occasional large oval specimen may be present, especially at the tip. A distinct longitudinal ectodermal muscle layer occurs, while the endodermal musculature is weak, becoming a little stronger proximally. The endoderm is richly supplied with zooxanthellæ.

The disk presents no important histological differences from the column wall. The stomodæum is very short in fully retracted polyps, its walls being greatly folded transversely, but in the examples studied the ectoderm presents no special vertical folds with mesoglœal thickening, although strong ridges are noted among the external characters.

The mesenteries are in two cycles of six pairs each, the first only reaching the stomodæum (fig. 81). Two pairs of directives occur in all cases. Beyond the primary and secondary cycles new mesenteries are added in double unilateral pairs, of which one pair becomes complete and the other remains incomplete, in such a manner that no additional third cycle is formed. Such enlarged polyps ultimately undergo tissiparous gemmation. A septal invagination of the skeletotrophic tissue occurs within each entocœle and exocœle.

The mesenterial endoderm bears numerous clear mucous cells and zooxanthellæ. The mesoglœa is a broad, clear, homogeneous layer above, but narrows below. For some distance from the line of origin of the mesentery one face of the mesoglœa is thrown into numerous close folds for giving increased support to the retractor muscle, but the opposite face remains smooth.

Mesenterial filaments occur on all the mesenteries, and are somewhat exceptional both in form and structure. The filament is nowhere sharply distinguished from the mesenterial epithelium, but the two tissues pass insensibly into one another. The free end of the mesentery is simply clavate, the thickened region, whether filament or mesenterial endoderm, consisting mostly of ciliated supporting cells (fig. 85). At the actual tip one or two nematocysts may occur, and in the lower convoluted region numerous large oval nematocysts are found as usual. With such a form and structure the mesenterial filaments bear very close comparison with the incipient stages of the filaments on the incomplete mesenteries of most other corals.

The skeletotrophic endoderm is narrow in the upper region of the polyp, but becomes very broad below (figs. 75, 79). Zooxanthellæ are present throughout, and in the lower region gland cells with exceptionally large granules begin to be numerous; the individual granules are nearly as large as the zooxanthellæ and are highly refractive. As the lower regions are approached the endoderm undergoes an increase in thickness; the zooxanthellæ and granular gland cells are still plentiful, and along with the nuclei are nearly all aggregated toward the periphery of the layer.

The supporting lamella of the skeletotrophic tissues is very thin throughout, only clearly determinable as a distinct layer at the place of origin of the mesenteries, and in these regions desmoidal processes can be distinguished. The skeletogenic ectoderm remains as a somewhat distinct layer, even in the most proximal regions, though in some places more than others

[a] Fissiparous gemmation has since been found to occur.

(fig. 79, 85). It nowhere becomes a typical columnar epithelium, but remains highly granular, with indistinct cellular divisions, and nuclei here and there. The skeletogenic ectoderm, and less so the mesoglœa and endoderm, are much indented, corresponding with the granules on the septal face (fig. 84).

The gastro-cœlomic cavities of the different polyps communicate with one another by means of the perithecal continuations of the mesenterial chambers. In retracted polyps the perithecal chambers are deeply concave outwardly, the mesenteries being very short, but the inner wall against the theca is nearly flat.

In the upper sections of retracted polyps the twelve mesenterial chambers, separated from one another by the septal invaginations, and each containing two mesenteries, are in communication with the middle of the gastro-cœlomic cavity. But below, each chamber becomes divided into two by an exocœlic septal invagination, so that twenty-four mesenterial chambers are formed, each containing only one mesentery. These chambers are wholly distinct from one another in sections, separated by the septa and columella; the exoseptal invaginations do not reach the columella, but unite laterally with the entoseptal invaginations of the second order (fig. 84).

B.—FISSIPARANTES.

ASEXUAL REPRODUCTION TAKES PLACE BY STOMODŒAL FISSION, WITHOUT THE PRODUCTION OF MORPHOLOGICALLY COMPLETE POLYPS. THE TENTACLES, MESENTERIES, AND SEPTA, AFTER FISSION IS ESTABLISHED, ARE NOT ARRANGED IN REGULAR HEXAMERAL CYCLES, AND NO NEW DIRECTIVE MESENTERIES ARISE.

Genus FAVIA Oken[a].

Polyps verrucose, usually distinct, slightly distant; occasionally two or more oral apertures are inclosed within a single tentacular system; gastro-cœlomic cavity and mesenteries prolonged perithecally; form convex, hemispherical, free, or incrusting colonies. Column cylindrical, oval, or irregular in outline, on retraction almost completely folded over the disk; no sphincter. Tentacles irregularly multicyclic, entocœlic and exocœlic, stem tuberculated, knobbed or rounded terminally. Stomodæal ridges well developed, variable in number.

Mesenteries irregularly multicyclic, all filamentiferous, directives present only in larval polyps. Septal invaginations entocœlic and exocœlic, irregularly multicyclic, not wholly uniting centrally; mesenterial loculi only partly distinct, obliquely truncated basally.

Asexual reproduction by partial or complete fission. Polyps monœcious, viviparous.

EXAMPLE.—*Favia fragum* (Esper).

FAVIA FRAGUM (Esper).

(Pls. XIII–XV, figs. 92–116.)

External characters.—The colonies are usually small, 5 to 10 cm. in diameter, subhemispherical or irregularly shaped, attached by a narrow base to dead coral masses or other foreign objects, and inhabit the shallow waters on the reefs. They are easily detached from their basal support. The surface of the colony is approximately regular when the polyps are retracted, but becomes uneven during full expansion, as some polyps extend higher than others, and otherwise vary much in size. The polyps may be either round, oval, or triangular in outline, and on full expansion are separated 6 or 7 mm. from one another. In the majority of cases only one oral aperture is surrounded by a tentacular system, but sometimes there may be two or even three apertures on a single disk, and all stages toward complete fission by the ingrowth of the lateral wall of the calice are to be met with on a colony.

The polygonal lines of union of the column wall of contiguous polyps are not clearly indicated by any smooth groove, but perithecal mesenterial attachments, alternating with the costæ, are

[a] "Colony hemispherical, convex, lobed, rarely subplane, fixed, free or incrusting. Corallites united by their costæ and by a cellular exotheca. Calices variable in distance, with free margins, subcircular, oval, deformed in outline. The columella is spongy. The septa are exsert, cross the wall, and the septo-costæ unite with those of other calices, or are separated by a groove. The septa are dentate, and the inner teeth simulate pali. Endotheca well developed. Epitheca often exists. Increase by fissiparity, the resulting corallites soon becoming separate." (Duncan, 1885, p. 100.)

distinct. Corresponding with the denticulations of the costæ, the surface of the column wall is strongly verrucose over its entire length, a larger series of verrucæ alternating with a smaller, the latter not always extending as far upward as the tentacular zone. On full expansion the verrucæ are oval shaped, and arranged in single rows over each mesenterial interspace. During full retraction the column wall is overdrawn within the calice, so as to completely hide the tentacles, leaving only the middle region of the disk exposed.

The tentacles are arranged in several series, but appear approximately dicyclic, an inner, larger cycle corresponding with the larger costæ and septa, and an outer, smaller with the small costæ and septa. When fully expanded, the tentacles of the inner cycle are seen to be situated at slightly different distances from the center of the disk, indicating separate orders, but no hexameral or any other regularity can be established. In preserved colonies the tentacles appear as two rows of short processes around the margin of the column. The total number may vary from about thirty to sixty, according to the size of the polyp; thirty-six were present on a medium-sized polyp.

The tentacular stem is finely tuberculated, bearing white urticating spots, and a rounded, thickened area occurs at the apex, rarely appearing knob-like; otherwise the walls are very delicate and transparent on expansion. Sometimes the tentacles, even during full expansion of the polyp, are shrunk so that they appear darker in color, and the apex is broader than the rest. On partial expansion the tentacles are elongated, and the members of contiguous polyps may intermingle; usually they are short, stumpy, and rounded at the apex.

The surface of the disk is finely verrucose, the verrucæ being oval and arranged along the radiating areas, alternating with the internal attachment of the mesenteries. They exhibit an approximate cyclical arrangement. In the more circular polyps six radial areas can be made out, extending as far as the stomodæum, and alternating with these may be one, three, or five shorter radial areas, the number being inconstant even in individual polyps. In larger polyps more than six pairs of radii are seen to reach the stomodæum. During partial expansion the disk is deeply depressed, but on full expansion becomes strongly convex, extending above the tentacular zone in some cases as much as 5 mm. The diameter of the disk of an average, simple polyp is about 5 mm. The peristome may be much elevated, and the mouth at the apex is elongated. The stomodæum is colorless, and during full expansion is seen distinctly through the transparent tissues of the disk; slight ridges and furrows are present, usually four to six on each side.

The color of the colonies varies from a light, clear, yellowish green to almost black, the lower portion of the column being somewhat lighter, owing to the white corallum showing through. A dark pigment is sometimes arranged in small oval patches, corresponding with the verrucæ, but the more general coloration is due to the presence of zooxanthellæ in the endoderm; sometimes the disk shows a light green iridescence. In some instances a thin white opacity occurs around the upper margin of the column, opposite the large tentacles.

Asexual reproduction takes place by fission. Two or more oral apertures on an elongated disk are the first indications of the formation of new polyps; later the tentacular zone and a septum from each side grow inward and complete the separation into two polyps, which remain united only peripherally. In some cases fissiparity results in two practically equal polyps, but in most instances one is larger than the other. During the early stages two oral apertures are found close together, each smaller than usual.

Stages in the separation of the fissiparous polyps can be best made out in decalcified portions of colonies. The polyps first divide superficially, and as growth continues they separate further and further below; the skeletal tissues also grow inward from above downward, until the mesenterial loculi of each polyp become separated all the way. Instances occur in decalcified colonies in which the polyps are wholly separated above, each with its oral aperture, system of tentacles, and column, but below they apper as a simple polyp. In a portion of a colony decalcified twenty-two oral disks were counted, but only sixteen distinct aboral disks. The process of fission in this species has been more fully described on p. 508.

The polyps are often expanded during the day, but like most other corals are seen at their best at night time. The superficial tissues are then raised for several millimeters above the skeleton, and appear thinner walled and slightly more transparent, allowing the white skeleton to be seen through, and the various stages of fission to be more readily followed. White mesenterial filaments can be extruded through any part of the polypal wall.

Colonies have been found at various times of the year bearing free larvæ. Occasionally simple young polyps are met with attached to older colonies, evidently derived from larvæ which settled directly in the neighborhood of the parent. The hexameral cyclic plan prevails throughout the simple polyps, but is lost when fissiparity commences.

Anatomy and histology.—The ectoderm of the column wall is a narrow layer with numerous clear gland cells, but no granular gland cells, nematocysts, nor muscle fibrils are distinguishable. The mesogloea is nearly as broad as the ectoderm, and connective tissue cells are present here and there. The endoderm is crowded with zooxanthellæ, and delicate circular muscle fibrils can be made out.

The tentacles are very short in sections of partly retracted polyps. The ectoderm of the swollen apex is a broad layer, its peripheral half crowded with long narrow nematocysts, bearing a closely spiral thread. In the deeper regions occur numerous, strongly stained examples in different stages of development; a larger nematocyst, showing the central axis very distinctly, may occasionally be seen. The urticating spots noticed amongst the external characters appear in sections as lateral rounded elevations of the ectodermal layer, and bear nematocysts similar to those of the knob. The merest trace of an ectodermal musculature occurs. In preserved specimens the tentacular endoderm practically leaves no lumen above, its cells being largely vacuolated and crowded with zooxanthellæ; the muscular fibrils are also slightly better developed than in the ectoderm. The discal endoderm consists mainly of clear gland cells, and the ectodermal and endodermal musculatures are of the weakest character.

The stomodæum is very short in vertical sections, terminating below in a rounded edge internesenterially, while mesenterially it is continued into the mesenterial filament. Where the stomodæum is widely open the surface is even, but where it is closed strong vertical ridges and furrows occur. The ectoderm is a very uniform layer of strongly ciliated supporting cells, with interspersed large oval nematocysts, and the endoderm is nearly devoid of zooxanthellæ.

The number and arrangement of the mesenteries are very variable, depending upon the size of the polyp and the rate of growth at any particular region. Three orders can usually be made out, though rarely presenting a cyclic regularity (fig. 93); no directives have been found in the many polyps sectionized, though they occur in the larval polyps. The last cycle of mesenteries extends but a short distance vertically, and all the mesenteries may bear filaments. The mesogloea is usually strongly developed, and one face is much plaited for affording support to the retractor muscle. Toward their lower termination many of the mesenteries are convoluted at their filamental edge, but the foldings are not so numerous as to crowd the gastro-cœlomic cavity.

The mesenterial filaments are of the usual type, with the swollen mesenterial epithelium behind highly vacuolated. Some of the filaments become greatly enlarged proximally, and charged with large oval nematocysts with the thread arranged in a wide spiral; transverse sections through these are not infrequent in sections, and present a very characteristic appearance (fig. 94). Two or three of the filaments in each polyp undergo a special glandular modification (p. 474); for a short distance vertically all the cells, with the exception of a few supporting cells, become enlarged and charged with a bright yellow, finely granular substance.

Only entocœlic septal invaginations occur throughout the greater part of the polyp, alternately large and small, corresponding with the similar pairs of mesenteries (fig. 93). In the uppermost region, however, exocœlic invaginations extend a very short distance inwardly and vertically.

Proximally, the interseptal loculi are never wholly cut off from one another, there being no solid columella in the corallum.

The skeletotrophic tissues present no exceptional character; the endoderm is a delicate layer throughout, increasing in thickness and vacuolization in the proximal regions; the gland cells are practically all of the clear variety, and zooxanthellæ appear but sparingly. The layer is sharply indented in places, corresponding with the echinulations on the face of the septa.

The polyps are hermaphrodite; ova and spermaria may be borne in close contiguity by the same mesentery, though more often they are on separate mesenteries. Occasionally a mesentery, in section, will contain only a single large ovum.

Gonads, along with far advanced larvæ, were present in all the polyps of several colonies at Bluefields, during the month of November. Larvæ were also liberated from colonies collected in April, while other colonies contained nearly ripe eggs.

Genus DICHOCŒNIA Milne Edwards and Haime.[a]

Polyps verrucose, close or more distant, the line of separation distinct or absent, very variable in size and outline, one, two, or many oral apertures on a single disk; gastro-cœlomic cavity and mesenteries prolonged perithecally; form massive, pedunculate, hemispherical, or plane colonies. Column cylindrical, oval or irregular, on retraction folding over the tentacles and periphery of the disk, no sphincter muscle. Tentacles irregularly multicyclic, entocœlic and exocœlic, stem knobbed or rounded terminally. Stomodæal ridges well developed, very variable in number.

Mesenteries irregularly multicyclic, all filamentiferous, directives absent. Septal invaginations mainly entocœlic, but in places exocœlic, not wholly uniting centrally.

Asexual reproduction by stomodæal fission, which may be complete or incomplete.

EXAMPLE. — *Dichocœnia stokesi* Edw. and Haime.

DICHOCŒNIA STOKESI Milne Edwards and Haime.

(Pl. XVI, figs. 117–120.)

External characters. Colonies of this species have been obtained at a depth of 10 or 12 fathoms in attempts to trawl over the Pedro Banks. It is not met with in shallower water, so that its habitat differs somewhat from that of the other species here described, which have all been obtained at wading depths.

The polyps have been examined only in the retracted condition, when they scarcely project above the general surface of the colony. The individual polyps or polypal systems vary considerably in magnitude and form. The largest are oval, or narrow and elongated, the smallest circular or subtriangular; the long diameter may vary from 1 cm. to several centimeters, and the short diameter is usually only 3 mm. Sometimes only one oral aperture occurs on a disk, but often two or more are present. The two or three small colonies available for study do not exhibit the meandering disal systems such as are figured in "Florida Reefs", Pl. X. The external lines of division between the individual polyps are mostly well marked, and usually subpentagonal in outline; in some instances, however, they are indistinguishable.

The column wall is strongly ridged and grooved in the retracted state, the ridges exhibiting small mammiform verrucæ, corresponding with the echinulations along the costal edges. In retracted polyps the upper part of the column is partly overdrawn, and the greater portion of the disk remains visible.

The tentacles appear as if arranged in two alternating cycles, and are both entocœlic and exocœlic.

The disk shows feeble radiating ridges and furrows, and upon retraction is much depressed within the calice. The mouth is elongated and remains partly open; the lips are thickened and protrude slightly. The stomodæal wall is thrown into deep ridges and furrows, the number varying much in different polyps, according to the size of the oral aperture.

Asexual reproduction takes place by fissiparity, and appears to be in most rapid progress

[a] "The colony is massive, pedunculate, hemispherical, lobed, or plane, and the large upper surface presents numerous low calices, some circular in outline, others united in short series. Columella small, sublamellar, or subpapillary. Septa well developed, entire, usually exsert. Pali before most of the septa. Costæ rather large, spinulose, and merging into the granular, dense, and highly developed intercalicular cœnenchyma, and they are seen to the base. Epitheca rudimentary. Endotheca exists. Increase by fissiparity and upward growth, accompanied by cœnenchymal development." (Duncan, 1885, p. 99.)

around the margin of the colonies. The polyps are here more closely arranged than toward the middle of the colony, and different stages in the separation of the daughter polyps can be followed.

The height of decalcified polyps is about 5 mm., and in fresh material the lower one-third of the embedded tissues is of a dark-green color, contrasting strongly with the upper, pale colored tissues. The number of septal indentations is very irregular; all numbers from six or eight to twenty may occur, and exhibit different degrees of radial intrusion from above downward. An indentation may be double in the upper region and single below.

Anatomy and histology.—The ectoderm of the column wall is constituted of long columnar cells, among which are few mucous cells and no nematocysts. Small, highly refractive pigment granules occur, distributed throughout the layer with an approximate uniformity. There is no evidence of the granules being restricted within limited groups, or of concentration toward the the inner portions of the layer. The granules are colorless in preserved material, but green in living polyps, and are no doubt the chief cause of the green coloration of the polyp, and the general opacity presented by the external tissues. The mesoglea is very thin, but thickens a little along the line of attachment of the mesenteries. The endoderm is a broad layer with an abundance of small zooxanthellæ, as well as a few cells with colored granules.

The ectoderm of the tentacles is a greatly thickened layer, and, except proximally, is crowded peripherally with nematocysts of two kinds—the long narrow form, and a short, stout, highly refractive variety; pigment granules are sparsely distributed throughout. The ectodermal musculature is well developed, and the nerve layer is sometimes seen at some little distance from the mesogloeal surface. The endoderm fills the lumen in retracted tentacles, and is crowded with zooxanthellæ; a weak endodermal muscle is also distinguishable. The ectodermal and endodermal musculatures of the disk are clearly recognizable, and nematocysts are found in the peripheral region. The stomodæum is short in vertical sections, and deeply folded transversely; large nematocysts occur in the outer zone of the ectoderm, and gland cells with granular contents are scattered about. The stomodæal ectoderm terminates in continuity with the mesenterial filaments.

A small polyp sectionized transversely contained only four pairs of complete mesenteries, and four pairs of incomplete mesenteries alternating with these (fig. 119). In the upper region eight corresponding entocœlic septal invaginations occur, practically equal in size; below, however, a slight invagination is found within the exocœles, thus constituting a third order of septa. In some instances a member of a third cycle of mesenteries is developed. Another polyp contained eighteen pairs of mesenteries, but no pairs of directives were found. The mesenteries are long in transverse sections, narrow above and broad below, where they branch considerably. The mesenterial epithelium is greatly swollen on the side bearing the retractor muscle; the mesoglœa is perfectly homogeneous, and is much and deeply folded to give an increased surface for the retractor muscle (fig. 120). The oblique musculature is also strongly developed, and toward the insertion of the mesenteries the mesoglœa becomes folded for its support. Sections of the muscle fibers indicate that they are practically vertical on each side of the mesentery.

The mesenterial filaments are simple and rounded above, in places sharply marked off from the endodermal enlargements behind; in many, however, there is no sharp line of distinction between the filament and the mesenterial endoderm. Proximally, where the mesenteries branch greatly, the filaments are likewise much developed, and here they bear large nematocysts and gland cells with coarsely granular green contents. The lower skeletotrophic tissues are characterized by an abundance of chlorophyll-like granules within the swollen endodermal layer. Even to the naked eye these give a strong green appearance to the lower third of the polypal tissues upon decalcification, and in sections the granules are seen to be thickly distributed throughout the layer. The granules vary a little in size and are more refractive than the surrounding cellular constituents. They appear to be of a similar nature to the granules occurring within some of the glandular cells of the mesenterial filaments, and are found only sparingly in the upper polypal endoderm; zooxanthellæ here appear to take their place.

Genus ISOPHYLLIA Milne Edwards and Haime.[a]

Polyps large, coarsely and irregularly verrucose, tissues dense and strongly pigmented; one or many oral apertures on a single disk, which is often prolonged linearly; give rise to massive fixed colonies, convex or subplanate above. Gastro-cœlomic cavity and mesenteries prolonged perithecally around the margin of the colony. Column wall occasionally distinct, generally united with that of the contiguous rows along a common narrow or broad thecal edge; on retraction may fold over the tentacles and lateral portions of the disk. Sphincter muscle well developed. Tentacles approximately dicyclic, entocœlic and exocœlic, introvertible, short, stem with circularly arranged urticating areas, rounded or knobbed terminally. Stomodæal walls deeply ridged.

Mesenteries irregularly dicyclic, in irregular stomodæal systems; all filamentiferous; directives absent; mesenteries and filaments partly protrusible. Septal invaginations mainly entocœlic; interseptal chambers not wholly distinct below.

Asexual reproduction by partial or complete fission.

EXAMPLE.—*Isophyllia dipsacea* Dana.

ISOPHYLLIA DIPSACEA Dana.

(Pls. XVII, XVIII, figs. 121–128.)

External characters.—The colonies are convex or flat, massive, non-incrusting, attached by a narrow base, and subcircular or irregular in outline. The specimens met with often attain a diameter of 5 or 6 inches, and occur on the reefs from a depth of 3 or 4 feet downward. The discal areas are mostly continuous, but in places the column wall extends across, and completely separates one discal system from another. The systems are arranged in a somewhat radiating manner, especially in young colonies, but the disposition becomes more irregular in older specimens. The separate discal systems vary much in their extent; sometimes a simple polyp occurs with only a single oral aperture, but in most cases the disks become meandering as a result of imperfect fission. Under ordinary conditions of retraction, the distal thickened margin of the columnar areas extends more than half-way down the calice, and becomes overfolded so as to cover the tentacles and peripheral portions of the disk. The column wall extends over the margin of the colony for nearly a centimeter, inclosing continuations of the gastro-cœlomic cavity and mesenteries.

The superficial tissues as a whole appear very coarse, and are dark and non-transparent, causing the colonies to stand out prominently against the white coral sand of the sea floor, or against other lighter corals. Examined closely, the surface of both the column and disk presents a finely granular appearance, which on microscopic investigation is shown to be due to aggregations of granules within the ectodermal cells.

The line of union of contiguous columnar areas is clearly indicated by a shallow groove, which is smoother and less densely pigmented. The surface of the column generally is very irregular under ordinary retraction, and the septal spines and teeth give rise to rows of protuberances, varying in size and height, and only approximately representing larger and smaller alternating rows. They appear as verrucæ on the retracted polyps, and are scarcely noticeable on full distention. Owing to the thickness and opacity of the tissues, the lines of attachment of the internal mesenteries are ordinarily not visible externally.

On retraction the tentacles are hidden under the partly overhanging columnar areas, and on expansion they appear in two alternating rows, the outer a little smaller than the inner. They are short, either narrow and columnar, or swollen and tapering, with an opaque white apex, either in the form of a distinct knob or as a mere lighter area. The surface of the stem bears oval or irregularly shaped nematocyst thickenings, with the long axis arranged circularly; otherwise the walls are nearly colorless and transparent.

[a] "The colony is massive, convex above or subplanate. The corallites are in short or long linear series, which are united by their walls completely, or having a slight groove between them, or united below by the walls and close to the surface by costæ and exotheca. Calicular centres distinct in the series. Columella spongy. Septa numerous, much spined. Collines stout, tall, may be furrowed on the top. Endotheca abundant." (*Symphyllia*, Duncan, 1885, p. 91.)

Under ordinary conditions the discal areas are deeply depressed, and flat or slightly concave; on full expansion they are raised a great height above the coralhum. The surface appears very coarse, owing to the presence of much granular matter and the verrucæ over the septal spines; near the periphery, in the area more or less hidden by the overhanging column wall, the disk seems thinner, and the dense pigmentation is almost wanting.

Usually the oral apertures appear as narrow slits, about 3 mm. in length, with the long axis along the length of the disk; at other times they are situated at the apex of a conical peristome. When open the mouth is oval or nearly circular in shape, displaying the intense white stomodæal walls. The latter are strongly ridged and furrowed, the number of ridges varying in different polyps from twelve to twenty-four; when the mouth is partly opened a sharp line of demarcation exists between the disk and stomodæum. The mouths are about 7 mm. apart in the living condition, and about 5 mm. in preserved colonies.

The prevailing colors are dark green, brown, and yellow, with minute, opaque white, superficial granules, distributed practically all over. These latter interfere somewhat with the distinctive characters of the other colors. The yellow color predominates along the thecal ridges, and the green along the valleys. Irregular, opaque white, cream, or green patches are sometimes present on the disk, ending in streaks toward the periphery – that is, in the region covered by the overfolding column wall.[a]

On irritation numerous prolongations of the mesenteries and filaments are extruded through various regions of the body wall; sometimes the greater part of the colony will be thus covered, presenting a very beraggled appearance. On withdrawal, the apertures through which the mesenteries protruded may be so large as to be visible with the aid of a lens, and remain open for some time; afterwards they close and leave no external evidence of their former presence. The thin transparent mesentery can be easily distinguished from the dense white filament in any protruded portion, and the former is often greenish in color.

Anatomy and histology.—The ectoderm of the superficial body wall is remarkable for the abundance of a finely granular pigment substance within the cells, and for the comparative fewness of the clear gland cells. This condition is no doubt the principal cause of the dense opacity of the outer tissues already described. The pigment matter is unaffected by carmine stains and hæmatoxylin, and appears yellowish brown or greenish in sections, and in macerated tissues. It is mainly restricted to the deeper regions of the layer, where it is either continuous or distributed in more or less isolated irregular patches (fig. 122). Toward the tentacular region of the column wall clear gland cells are more numerous than elsewhere.

The mesoglœa is of moderate thickness, and contains numerous connective tissue cells distributed throughout. Sometimes their processes are seen in connection with the endoderm, sometimes with the ectoderm, or may even stretch across from one layer to the other. A slight difference in consistency in the mesoglœa is also apparent in preparations stained with aniline blue; lighter, tube-like portions extend across the whole layer, or in other sections appear as so many circular disks staining less deeply than the surrounding mesoglœa.

Zooxanthellæ occur in large numbers in the endoderm of the column, while the musculature is strongly developed in the upper region, more so than in any other species here described. The inner surface of the mesoglœa, for some distance, forms pointed, rounded, or dendriform plaits for its support, and the muscular fibrils themselves are somewhat large in transverse section, constituting what must be regarded as a definite endodermal sphincter muscle (fig. 121). The whole form resembles what has been described in certain Actiniaria as a "restricted" sphincter muscle.

The tentacles in retracted polyps are crowded under the overhanging thickened edge of the column wall, and may or may not be introverted. Histologically they differ much from the column wall. The ectoderm is a deep layer, containing numerous gland cells and a marginal zone of very narrow nematocysts; the granular pigment matter is absent from the more

[a] Prof. A. E. Verrill (1901) alludes to the very varied colors of the *Isophyllia* at Bermuda. He notes that some specimens were phosphorescent at night, and that this property seemed to be related to the white pigment.

proximal region, but occurs more distally, and an ectodermal musculature is strongly developed. The endoderm contains few zooxanthellæ.

The peripheral ectoderm of the disk presents a wide contrast from that of the more central area. The latter very closely resembles the outer layer of the column wall, being opaque throughout, with the granular matter strongly developed; at the periphery, however, the ectodermal cells are longer, a larger number of clear gland cells are present, and little granular matter occurs. A few nematocysts may also be present, but apparently no ectodermal musculature is developed. The mesoglœa is a little thinner than in the column wall, and its endodermal aspect is plaited for the support of the musculature, most marked in the peripheral region.

Transverse sections of the stomodæum display strong vertical ridges opposite the insertion of the mesenteries, while the intervening areas are much thinner; large oval nematocysts occur in the ectoderm of the ridges, but are absent from the grooves, which in their turn are more strongly ciliated. The ridges and furrows thus present somewhat the same histological differences which exist between the general ectoderm and the gonidial grooves in Actinians. The granular pigmentation characteristic of the ectoderm of the column wall is absent from the stomodæal ectoderm: the mesoglœa is everywhere thin, and only a weak endodermal musculature is developed.

The mesenteries are without any regular cyclic arrangement, and no directives occur. The greater number of the pairs are complete, but alternating incomplete pairs are also present in places, the different pairs varying in size. The incomplete members are evidently recently developed pairs which in time will become complete.

The mesoglœa on the mesenterial face bearing the retractor muscles is wavy in transverse sections, or forms numerous plaits, which, however, vary greatly in the extent of their development, both in different mesenteries and in different regions of the same mesentery. In the middle region of some of the mesenteries both mesoglœal faces are sinuous for some distance, and the oblique musculature on the opposite face is strongly developed. The mesenterial epithelium is narrow above, but becomes very broad below, and consists mainly of clear gland cells; zooxanthellæ are also present. In the lower region most of the mesenteries become much convoluted, and nearly fill the septal loculi. Mesenterial filaments are borne on all the mesenteries, whether complete or incomplete; the mesenterial endoderm behind is swollen in some instances and not in others. Clear gland cells are somewhat numerous in the upper course, and in the lower are many large oval nematocysts. In some cases the filament has undergone complete glandular modification, and the areas stand out very prominently in sections, as the contents of the gland cells are a deep yellow. The modification is limited to the filament, without involving the endoderm behind.

The skeletotrophic tissues are characterized by the great thickness of the endoderm in the lower regions, and by its almost complete vacuolization. Actual cell outlines have altogether disappeared, and the few protoplasmic contents are aggregated in a narrow marginal zone. The calicoblast layer is broad in some regions; numerous desmoidal processes occur along the course of the insertion of the mesenteries, and here the mesoglœa is much broadened.

The septal invaginations are only entocœlic, and do not encroach much upon the gastrocœlomic cavity until near the aboral end of the polyp, but even here the interseptal chambers are not distinct from one another.

Female gonads were present on some of the mesenteries, restricted in their distribution toward the insertion of the mesentery in the body wall. Generally only three or four ova are seen in a transverse section of any mesentery, and may occur on either the complete or incomplete mesenteries.

Genus MANICINA Ehrenberg.[a]

Polyps verrucose, incompletely separated, forming broad, continuous and sinuous discal and columnar systems, and giving rise to small, massive, elongated or subhemispherical colonies; attached when young by a conical pedicle, but afterwards free with a subconical or nearly flat base. Column wall distinct throughout in young, later partly united along the apex of broad inturned collines; in retraction may fold over the tentacles and cover the marginal area of the disk; no sphincter. Perithecal continuation of the gastro-cœlomic cavity and mesenteries; proportionately more in young. Tentacles in three or four irregular, alternating, entacmæous cycles, entocœlic and exocœlic, short, introvertible, rounded or knobbed terminally, surface of stem with oval urticating areas. Oral apertures numerous, variable in size. Stomodæal walls deeply ridged.

Mesenteries hexamerous and regularly multicyclic in young, with two pairs of directives; later, in irregular, multicyclic, stomodæal systems without additional directives; all filamentiferous; increase in regular hexamerous cycles in young, but irregularly by unilateral pairs later.

Mesenteries and filaments protrusible. Septal invaginations mainly entocœlic, regularly multicyclic in young, more irregular later.

Asexual reproduction by continuous stomodæal fission. Polyps monœcious, viviparous.

EXAMPLE.—*Manicina areolata* (Linn.).

MANICINA AREOLATA (Linnæus).

(Pls. XVIII, XIX, figs. 129–137.)

External characters.—Isolated colonies of all sizes, from 2 to 9 or 10 cm. in length, are met with in shallow water all round the coast of Jamaica; while from somewhat deeper regions examples have been obtained as much as 20 cm. across. Young specimens are attached by a small base to some pebble, coral, or shell, but older specimens are free. In their early condition the colonies are somewhat crateriform, but soon become elongated and strongly sinuous, very deep bays and convexities being formed along what might be regarded as the primary axis. Circular forms are sometimes found. When young the axial line joining all the oral apertures may be nearly straight, but later is strongly indented. The discal areas are nearly always continuous, rarely separated by a transverse division, and are often arranged in parallel rows.

The column wall extends over the thecal edge as far as the base in young polyps, but less so as the colony enlarges. In older specimens it may extend for about 5 mm. down the theca, the remaining naked portion of the corallum being coated with a thin epitheca, to which small molluscs, worm tubes, etc., adhere. In the retracted, or even partly retracted, condition, the column wall extends within the calice for some distance. It is incapable of completely closing over the disk on full retraction, but folds over the tentacles. During full distension the polyp may extend upward for a centimeter or more beyond the corallum.

The column wall is strongly ridged, in alternate broad and narrow areas, the former only corresponding with septa. The ridges bear closely arranged verrucæ, slightly thicker and differently colored from the rest of the wall. The apex of the broader areas is often prolonged a little, almost recalling the acrorhagi of certain anemones.

During retraction the edge-zone adheres closely to the skeleton, the echinulations of the costæ showing through; but on full expansion the wall becomes raised some distance above the corallum, and is then practically smooth, the verrucæ being represented by small opaque spots.

The tentacular zone constitutes a distinct boundary between the column wall and disk, and is comparatively broad on full expansion of the polyp. Three or four alternating cycles of short, stout tentacles occur in young polyps, the members of the innermost cycle being about 5 mm. in length. The alternations, however, are rarely regular; smaller tentacles may mingle with

[a] "Colony massive, free or pedunculate, broad-based, subhemispherical, tall, and convex or subconical or short. Corallites with their walls fused with those of their neighbors, except in young forms. Calicinal valleys long, broad and deep, united by simple or broad and furrowed collines. Calices with indistinct centres. Columella spongy, essential. Septa close, thin, strongly granulated laterally, the principal with a paliform lobe, and with the free edge divided by fine teeth, which are regular, close, and largest near the columella. The common plateau is furnished with costæ, which are delicate and dentate, and are partly covered by an epitheca, which is readily detached. Endotheca abundant, unequal." (Duncan, 1885, p. 88.)

the larger. In fully established colonies the tentacles appear practically dicyclic, and are both entocoelic and exocoelic in position; the former are the more internal, and correspond with the septa below, while the exotentacles have no corresponding septum beneath. Usually the tentacles are shortly conical, with a white opaque apical swelling, not forming a distinct knob; at other times they are narrower, and more elongated, and the apex appears as a spheroidal knob. White, oval or irregular nematocyst batteries, varying in size and arranged circularly, occur all over the surface. On full expansion the tentacular walls may become involved in the discal tissues, to such an extent that they appear as mere circular patches, barely distinguishable except for the presence of the denser apical region. Under certain conditions some of the tentacles have been found completely introverted, oval apertures indicating their position externally; under these circumstances the disk appears as a smooth, naked, flattened expansion, not sharply marked off from the column.

The disk is verrucose, usually depressed, and ridged and grooved radiately, the grooves corresponding with the mesenteries. The radiating areas are larger and smaller, but the alternation is not always regular; where the discal system is elongated the areas become more transverse. Numerous oral apertures occur along the discal depressions, and vary much in size. Some may have a longer diameter of 2.5 mm.; the smaller are circular, but others are oval, the greater diameter being always along the larger discal axis. The mouths are usually open, allowing the stomodæal wall to be seen, and often occur on a distinct raised peristome; when closed they appear as mere slits in the disk. In the condition of partial expansion the apertures occur at intervals of about half a centimeter, the number varying, of course, with the size of the colony.

The stomodæum is sharply marked off from the disk, no rounded lips intervening; under certain conditions it may be partly extruded. The walls are very deeply ridged, as many as seven or eight, or even ten, ridges occurring on each side. They can be seen to correspond with the line of attachment of the mesenteries on the internal side, and thus represent the number of complete mesenteries associated with each stomodæum.

During full expansion the polypal tissues are semi-transparent, and the internal mesenteries can be seen through. In one case seven pairs were found to reach the stomodæum, and in another ten pairs; in one colony the numbers of perfect mesenteries around four oral apertures were 12, 15, 17, and 20, respectively. The course of the mesenteries from the periphery towards the stomodæum, as seen through the disk, is mostly at right angles to the calice wall. In some pairs the course is curved, while in those most distant from the oral aperture it may form an obtuse angle. The mesenteries are also seen extending the whole way down the edge-zone, as in the column wall of an Actinian.

The color is very variable, even in colonies living within the same area. Yellowish brown, as in so many other corals, is the fundamental color, and upon this may be superposed an ectodermal opaque white or green. The column wall generally exhibits only lighter and darker shades of brown, due to the internal zooxanthellæ; and sometimes the whole colony may be of this character. The disk in most cases is lighter than the rest of the colony, often an opaque pale green; the color here appears quite superficial, as if produced by some dense, opaque white or pale green ectodermal deposit. The rows of verrucæ also may be opaque white, while the ground color is green. A similar appearance, though somewhat less dense in character, may occur on the upper region of the column wall. In numerous colonies at Bluefields the coloration was distributed in darker and lighter irregular patches. When the polyps are fully distended, the distinctive colors largely disappear, the tissues becoming a pale brown, and more or less transparent. The tentacles are always colorless and transparent, but more opaque over the lateral urticating areas, and entirely so at the apical swelling. A dull, white ring may surround the oral cone.

Colonies have been collected of which the gastro-colonic cavity contained numerous free swimming larvæ, readily seen through the partly transparent tissues. Many also circulated freely within the tentacular cavities. Most of the larvæ were elongated, with a light broader pole, directed forward in progression, and a dark brown, narrow, posterior pole. At times they

moved about very rapidly within the interior of the parent, and numbers would be shot out together on irritation.

In the increase in size of the colony by partial discal fission, pairs of small oral apertures are frequently observed very close to one another, each exhibiting but a few stomodæal ridges (eight to ten), in such a way as to leave little doubt that the two have resulted from the division of a single large aperture.

The polyps do not readily respond to irritation, but retract and expand slowly. White mesenterial filaments, with parts of the mesenteries to which they are attached, are extruded through the mouth upon slight disturbance, and can be again withdrawn. On irritation the filaments may protrude in great profusion through any part of the disk, but no apertures are ordinarily distinguishable. Large quantities of mucus were emitted on preservation of the colonies. The action of the superficial ciliation can be readily observed by placing some light particles on the middle of the disk; the particles are carried slowly outward, and for some distance down the edge-zone.

Anatomy and histology.—The column wall is a thin layer throughout. In the ectoderm unicellular mucous glands, with clear contents, are very abundant, and less so small narrow nematocysts. No pigmented granular cells are seen, the tissues, as noted amongst the external characteristics, being nearly transparent. The mesoglœa is thin, except where united with the mesenteries, and the endoderm is much narrower than the ectoderm, and its cells contain zooxanthellæ. Very delicate endodermal muscle fibers can also be detected, but in the upper region no concentration of the fibrils occurs in any way suggestive of a sphincter muscle.

In sections of retracted polyps the tentacles are frequently found introverted within the entocœlic and exocœlic chambers. The ectoderm is a much thickened layer, crowded with long narrow nematocysts, with a very distinct spiral thread. They are more numerous apically, and at places corresponding with the lateral thickenings; a few gland cells with deeply-staining contents occur, and also developing nematocysts in the deeper situations. An extremely weak ectodermal and endodermal musculature can be distinguished, and the endoderm is a comparatively thin layer without zooxanthellæ.

The disk differs but little from the column wall, except that all the layers are somewhat thicker, and both the ectodermal and endodermal musculatures are better developed; small nematocysts also occur peripherally.

The stomodæal ectoderm is thrown into very deep vertical folds, each ridge corresponding with the point of attachment of a mesentery, and supported by a long, narrow, mesoglœal axis. The layer is very broad, and the well-defined nuclear zone is situated a little below the free surface; very large nematocysts, showing the internal thread, occur here and there, and in the deeper regions others can be traced in various stages of development (figs. 129, 131).

Two principal orders of mesenteries are present—complete and incomplete, each pair embracing, as it were, a septum. At irregular intervals are pairs of much shorter mesenteries, which appear to be in process of development, but not representing a distinct order or cycle. The order of appearance of the mesenteries for this species has been already described; larval polyps are regularly hexameral (fig. 132), but this is lost after fission is instituted (p. 502, *et seq.*).

The mesoglœa on the face bearing the retractor muscle is usually folded, but, as shown by figs. 129 and 130, no regularity is maintained, and the opposite face may also be deeply sinuous. The mesenterial filaments as a rule are present on all the mesenteries, but on the youngest members they may be only incipient.

Septal invaginations are found within all the entocœlic chambers, and occasionally one is seen within an exocœlic chamber; but in these latter instances higher sections usually reveal a pair of small mesenteries, so that it may be doubted whether exosepta ever really occur.

As shown in fig. 129, the skeletotrophic endoderm varies greatly in character in the different regions, being greatly thickened and vacuolated in the lower and peripheral areas, and narrow over the septal invaginations.

Genus COLPOPHYLLIA Milne Edwards and Haime.[a]

Polyps verrucose, incompletely separated, giving rise to broad, continuous, flexuous, discal and columnar systems, and producing massive, light, flattened or slightly convex colonies, fixed by a broad or pedunculate base. Column wall united with that of contiguous rows along a broad common plateau, having a restricted, perithecal continuation of the gastro-cœlomic cavity and mesenteries, better developed at the periphery of the colony; in retraction the column wall folds over the tentacular zone and covers the margin of the disk; no sphincter. Tentacles in two, alternating, slightly entacmæous rows, entocœlic and exocœlic. Disk with numerous oral apertures, variable in size; stomodæal walls deeply ridged.

Mesenteries acyclic and mainly complete, with occasional incomplete developing pairs; arranged in irregular stomodæal systems; all filamentiferous; directives absent, except in larval polyps; increase by irregular addition of unilateral pairs; partly extrusible. Septal invaginations mainly entocœlic, uniform when fully developed, not all meeting in the middle.

Asexual reproduction by incomplete fission.

EXAMPLE.—*Colpophyllia gyrosa* (Ell. & Sol.).

COLPOPHYLLIA GYROSA (Ellis & Solander).

(Pl. XXII, fig. 148.)

External characters.—The species occurs somewhat sparingly in Kingston Harbor and on the reefs outside, the colonies forming massive, hemispherical or irregular blocks on the sea floor, which are usually easily detached. The broad discal valleys, thick thecal ridges, and strongly developed septa give the species a coarse appearance *in situ* compared with most other corals. The distance from the apex of one thecal ridge to another is variable, but is usually between 2 and 3 cm. The valleys are sinuous, never extending for more than a short distance in a straight line, and usually sloping toward the periphery; a very shallow depression also occurs along the middle of the thecal ridges. A broad edge-zone is found around the margin of the colony, and also a narrow extracalicular continuation of the cœlomic cavity and mesenteries along the contiguous thecal rows.

The polyps are very rarely seen in their expanded condition. During the ordinary condition of retraction the upper margin of the column wall is withdrawn within the calice for about half the height of the thecal ridges, and appears almost in continuity with the disk, the tentacles being completely hidden by it. The wall is divided into longitudinal ridges and furrows, in correspondence with the internal septa and mesenteries, and the marginal teeth on the septa give an external verrucose appearance to the walls. In some places the longitudinal ridges are all equal, but in most a much smaller verrucose ridge alternates with the larger, though never for more than three or four consecutive pairs.

In the retracted condition of the polyps the tentacles are entirely hidden under the overfolding column wall, and have not been seen fully extended. Microscopic examination indicates the presence of lateral nematocyst areas and of a large terminal battery, so that in all probability they closely resemble the tentacles of *Manicina*.

The disk is radiately divided around the oral apertures by the internal mesenteries and septa, or, where the valleys are long and straight, the divisions become more parallel; verrucæ occur over the areas corresponding with the septa, but not all the rows extend as far as the stomodæum.

The oral apertures are oval or round when open, slit-like when closed, the longer diameter being along the length of the disk. The apertures are from 1 to 2 cm. apart. The stomodæal walls are provided with strongly marked vertical ridges, five to ten on each side, and in the living condition they appear intensely white against the darker valleys.

The general coloration of the polyps *in situ* is light or dark brown. Examined more closely, the column wall is brown with grayish verrucal rows. The disk may exhibit a bright, iridescent

[a] "Colony massive, light and fragile, with a broad base, or pedunculate. Corallites united by their costæ, the walls never fusing at the calicular surface, where they are very slender. Calicinal valleys moderately long, flexuous, large, deep, with the calicinal centers more or less distinct. Columella rudimentary or none. Septa excessively thin, long, slightly exsert, and striated laterally; their free margin is delicately toothed and slightly excised near the middle. The common plateau has small lamellar costæ, broken up by dentations which are horizontal." (Duncan, 1885, p. 94.)

green, arranged in parallel or radiating rows, while the verrucæ along the septal ridges are gray. The green may predominate to such an extent as to give a decided tinge to the colony as a whole.

White mesenterial filaments can be extruded through any part of the superficial tissues, and quantities of mucus are given out on rough handling or preservation.

Anatomy and histology.—The column wall is delicate and deeply folded in preserved material. The ectoderm is a broad layer in which large, clear gland cells are by far the main constituents; in many places extruded mucus can be seen adhering. Supporting cells appear to merely serve as lines of separation between the closely arranged gland cells. In the lower region of the ectoderm the cells contain finely granular matter, very irregularly distributed. In some spots the granular matter may be wholly absent, and the clear contents extend the whole thickness of the layer; in others it is deposited but a short distance from the mesogloeal boundary, and gives the appearance of interstitial cells, each with its own rounded nucleus; again, in restricted areas, the cells may be wholly granular as far as the outer surface of the ectoderm. Long, narrow nematocysts occur here and there. In tangential sections toward the periphery of the ectoderm a very regular polygonal arrangement is presented by the gland cells, the supporting cells occupying the interstices. The outer ciliation is obvious in most preparations.

The mesogloea of the column wall is thin and nearly homogeneous; included cells occur but rarely. The endoderm is, like the ectoderm, highly glandular, and in addition contains many zooxanthellæ. A delicate circular musculature is developed, but presents no indication of forming a special sphincter in the terminal region.

The tentacles exhibit a broad ectoderm, and at intervals along the sides and at the apex are peripheral zones of nematocysts, all of the long, narrow variety, with a close spiral thread. A distinct zone of nerve fibrils is present toward the discal termination, and the ectodermal and endodermal musculatures are both well represented.

Histologically the disk differs in no important respect from the column wall: the endodermal musculature is of the weakest character, while the presence of an ectodermal muscle layer is not determinable with certainty. The stomodæum is oval, and of considerable vertical length; in retracted polyps it is deeply folded both longitudinally and transversely, so much so that in some transverse sections it appears for half a dozen times. The very pronounced vertical ridges noted amongst the external characters are not so marked a feature in transverse sections, especially when the stomodæum is open. The ectoderm exhibits the same histological structure all the way round; the mesogloea is usually thicker at the positions corresponding with the insertion of the mesenteries, and in some places regular ridges are formed. Very few nematocysts occur in the stomodæal ectoderm; the cells are nearly all ciliated supporting cells, while granular gland cells are distributed at intervals.

The mesenteries are only divisible into complete and incomplete pairs, there being no regular cyclical arrangement; further, the alternation of complete and incomplete pairs is by no means uniform; sometimes two or three successive alternations may occur, and at other times all the pairs will be complete for some distance. There is little doubt that the incomplete pairs are but new pairs in process of growth which will ultimately become complete, and can not, therefore, be regarded as representing a distinct order. No directives occurred among a large number of mesenteries examined.

The mesogloeal lamina of the mesenteries is very variable in character, being in some places broad and in others narrow. The foldings for the longitudinal musculature, as a rule, are only feebly developed, but on one member of a pair they may be very pronounced, while scarcely distinguishable on the other. The oblique musculature is weak above, but stronger below. The mesenterial epithelium is broad, and comprises mainly clear gland cells; very often the clear secretion is preserved in the act of extrusion.

The mesenterial filaments are of the usual type, but certain of the mesenteries become greatly convoluted below, the filament following the convolutions all the way; in such cases the convolutions in section constitute a very close, irregular mass (fig. 148).

The septal invaginations are in nearly all cases entocœlic, but occasionally a short invagination may occur without any associated mesenteries being discoverable, so that probably the septa may appear somewhat in advance of their corresponding mesenteries and thus be exocœlic.

Genus MÆANDRINA Lamarck.[a]

Polyps verrucose, incompletely separated, forming mainly continuous, meandriform discal and columnar systems, and giving rise to massive, convex, gibbose, subplane or subspheroidal colonies, fixed by a comparatively narrow or broad base; perithecal continuation of the gastro-cœlomic cavity and mesenteries at the margin of the colony. Contiguous column walls united along a narrow, common, thecal ridge; on retraction capable of folding over the tentacles and covering the lateral margins of the disk; no sphincter. Tentacles in two, alternating, slightly entacmæous rows, entocœlic and exocœlic, introvertible, short, rounded terminally, stem with irregular urticating areas. Disk with numerous, closely arranged, small oral apertures. Stomodæal walls deeply ridged.

Mesenteries all complete, with occasional incomplete developing pairs, arranged in irregular stomodæal systems; all filamentiferous; directives absent; increase irregularly by addition of single unilateral pairs. Mesenteries and filaments protrusible. Septal invaginations entocœlic and exocœlic, dicyclic, interseptal loculi incompletely separated below.

Asexual reproduction by continuous incomplete fission. Polyps monœcious.

Example.—*Meandrina labyrinthica* (Ell. & Sol.).

MEANDRINA LABYRINTHICA (Ellis & Solander).

(Pls. XX–XXII, figs. 138–147.)

External characters.—The colonies are massive, subspheroidal, the upper surface uniformly rounded, not thrown into gibbosities. The species occurs in abundance on the reefs around Jamaica, often forming blocks several feet across, and fixed by a narrow, irregular base; even large colonies are free or are readily detached when collecting.

The external appearance of the living colonies varies greatly according to the condition of expansion or retraction of the superficial soft tissues. The general relations during partial retraction are best conceived of as a double system of meandriform depressions, separated by a fringe of short tentacles. One series of grooves is formed by the continuous, narrow, discal areas, the other by the united column walls of two contiguous polypal systems. The discal troughs are much deeper than the columnar, and occur within the united calices; the slight columnar depressions run along the common thecal edges or collines, and the line of union of the two adjacent column walls is clearly indicated at the bottom.

On full expansion the superficial tissues become distended to such a degree that they are raised for several millimeters above the skeleton, the discal region increasing from 2 to 8 mm. across. Along the line of union the two contiguous column walls remain affixed to the skeleton, so that the walls on each side rise almost vertically from the line of attachment, and may actually apply themselves to one another by their outer surface, or remain separated only by very steep valleys. In the former case the two contiguous fringes of tentacles intermingle in such a way that the whole surface of the colony presents to view little more than the enormously enlarged, convex discal areas. During maximum expansion the tentacles and the verrucæ may almost entirely disappear, the walls of the former becoming part of the flat discal tissues. In the fully retracted state the appearances are reversed; the deeper valleys are now formed by the discal areas, and the ridges by the columnar expansions resting on the septa. The column may become partly overfolded, and under some conditions the two overfolding walls connected with each discal system may extend horizontally, and almost come into actual contact, so as to completely hide the tentacles and disk.

The column wall appears thick and opaque when the polyps are retracted, but more delicate and transparent when fully expanded. The surface exhibits verrucose ridges and smooth furrows, corresponding respectively with the internal septal and mesenterial divisions. The

[a] "Colony massive, dense, convex, gibbose, subplane or subspheroidal, largely fixed by its base. The series of corallites unite by their walls, which are compact, and produce long, simple ridged collines. The valleys are sinuous, long, but vary in length, depth, breadth, and meandroid nature. Calices mostly indistinct, some may be circumscribed. Columella formed by masses of spongy tissue well developed. The septa are close, parallel, their inner edge thickened and enlarged transversely; upper margin denticulate, moderately granular laterally. Union of the transverse enlargements of neighbouring septa near the columella often occurs, and gives a paliform appearance. Endotheca and epitheca exist." (Duncan, 1885, p. 88.)

verrucæ form alternating larger and smaller rows, corresponding with the larger and smaller septa below, and are round, lighter in color, and closely arranged; they may appear contiguous in the larger rows, but are more distant on the shorter. A narrow, smooth area at the base of the walls indicates the line of union between one column wall and another, while distally it passes uninterruptedly into the tentacles. When the body wall is lying upon the skeleton the discal valleys are about 4 mm. across.

The tentacles form a narrow fringe along the two margins of each discal area. They are short and dicyclic, the members of the inner row slightly larger than those of the outer; the former correspond with the larger entosepta, and the latter with the small exosepta (fig. 139). During ordinary extension the inner tentacles are 2 mm. long; they are broad at their origin, and either terminate bluntly or are slightly knobbed. On full expansion the knob is displayed as a thickened, lighter, opaque area, the tentacles as a whole being shortened but more swollen. The surface of the stem is almost covered with small, oval or irregularly shaped, white, urticating spots, none, however, so large as that at the apex.

The naked portion of the disk is very narrow, about 2 mm. across in the retracted condition, and is usually depressed. Its surface is verrucose in parallel or slightly radiating rows, the rows corresponding with the septa below, while the grooves between correspond with the mesenteries.

The oral apertures are very small, oval, or slit-like, or may be circular when opened to their full extent. The larger axis is along the length of the discal areas, and is about a millimeter long; during retraction the apertures are separated from one another by a distance of 2 or 3 mm. The stomodæal wall is thrown into deep vertical ridges and furrows, varying in number from three or four to eight on each side (fig. 147).

The color of the colonies in general is dark or grayish brown when the polyps are retracted, or green may predominate. The discal areas often show a superficial, opaque green, or may be dark brown; the column walls for some distance on each side of the line of union may also be bright green. The tentacles are a transparent dark brown. All the external tissues become more translucent and lighter in color when the polyps are fully expanded, appearing then as a pale brown. Small grayish spots usually occur over the verrucæ along the middle of the ridges.

On irritation, or under unfavorable conditions, white mesenterial filaments can be emitted through the mouth, disk, and column wall, sometimes in such profusion as to almost cover the whole of the colony.

The usual method of reproduction consists in the formation of additional oral apertures on the discal areas, each aperture having a distinct stomodæum and mesenterial system associated with it. No further polypal separation as a rule takes place, the tentacles and column wall being part of the general system. Occasionally the column wall may grow transversely, and thus cut off a portion of the disk bearing one or more apertures.

Anatomy and histology.—The ectoderm of the column wall is characterized in places by an abundance of cells containing finely granular pigment, which gives a relative opacity to the sections wherever it occurs. The granules are situated mostly in the deeper portions of the layer, but are sometimes continued as far as the surface. They no doubt influence the external coloration, and give rise to the comparative opacity of the tissues already noticed in the living retracted polyps. In addition to the granuliferous cells, numbers of clear, unicellular, mucous glands occur, extending across the whole thickness of the layer, and rendered very conspicuous by reason of the perfect transparency of their contents. The long supporting cells constitute, as it were, a matrix in which these broader, granular, and mucous cells are embedded, and the nuclei form an interrupted zone just within the margin; small, narrow nematocysts also occur.

The mesoglœa is a comparatively well-developed layer in some polyps, but thin in others, varying with the state of expansion or retraction of the polyps. Included connective tissue cells are somewhat numerous, and a delicate fibrous and vacuolated appearance is presented by sections stained in picro-carmine.

The endoderm is of about the same thickness as the ectoderm, and its cells contain zooxanthellæ. These are mostly restricted to the inner (mesoglœal) two-thirds of the layer, while the nuclei and

protoplasm of the endodermal cells are more obvious peripherally. Only the faintest indication of an endodermal musculature occurs, even in the most distal region of the column.

The tentacles are seen in transverse and vertical sections as simple outgrowths of the margin of the disk, and a wide lumen remains in the partly expanded condition (fig. 139). The cells containing pigment granules are here much less numerous than in the column wall, and are mainly restricted to the proximal region. The ectoderm is broad; and long, narrow nematocysts occur in patches along the walls and at the apex, rendered very obvious by the internal spiral thread. The tentacular ectodermal and endodermal musculatures are moderately developed, and toward the apex a very distinct ectodermal nerve layer occurs.

The disk presents no histological features distinguishing it from the column wall, except that the endodermal musculature is somewhat better developed, and pigment granules are more numerous in the middle regions than toward the periphery.

The stomodæum is remarkable for the prominence of the vertical ridges. In transverse sections they stand out as very definite rounded projections of the wall, opposite the insertion of the mesenteries, and histologically they differ somewhat from the intervening intermesenterial depressions (fig. 147). The mesoglœa at the base of the ridges is a little swollen, and sends processes among the ectodermal cells. The latter are mainly long, ciliated, supporting cells, the nuclei of which form a deeply-staining zone. In the deeper parts of the ridges are found numbers of pigmented granular cells; large oval nematocysts with a spiral thread, along with a second much smaller form, occur peripherally, along with granular gland cells. The ectoderm and mesoglœa of the grooves are narrow, the former containing but few granular cells and nematocysts; the ciliation is uniform all round the stomodæum, or may be somewhat stronger in the grooves than in the ridges. A muscular layer of the weakest character can be distinguished on the endodermal surface of the mesoglœa. In partly retracted specimens the lower portion of the stomodæum extends horizontally for some distance between the mesenteries, while as these latter cease their connection they become tipped with a tissue resembling the ectoderm of the stomodæal ridges, and directly continuous with the mesenterial filaments.

The mesenteries are arranged in unilateral pairs throughout, but vary much in size. By far the majority of the pairs reach the stomodæum, but incomplete pairs occur here and there, some large and some small; these will evidently in time also become complete. In the several stomodæal systems represented in fig. 141 all the pairs were complete, the number of mesenterial pairs inserted on each mesentery being variable. The separation between one polypal system and another is always in the entocœlic plane on each side, as already described in the section on fission (p. 513).

In transverse sections through the soft tissues covering the most distal part of the calicular ridges the mesenteries on opposite sides of adjacent polypal systems may or may not correspond with each other (fig. 138). They are arranged at practically equal distances apart, so that the entocœlic and exocœlic chambers are about equal. In the upper region the septal invaginations are both entocœlic and exocœlic, but occasionally the latter invaginations are wanting; in the lower part of the polyp only entocœlic ingrowths occur (fig. 142). In the corallum it is seen that the small exosepta have a corresponding short vertical range. As shown in fig. 138, the edge of the mesenteries after leaving the column wall has a free course before becoming adherent to the skeleton; some of the mesenteries, as toward the right end of the section, are becoming attached to the skeletotrophic tissues while others are yet free. The boundary groove of two column walls is therefore not attached directly to the skeletotrophic tissues, but through the intermediation of the mesenteries. In fig. 139 all the mesenteries are connected with the skeleton.

The mesenterial mesoglœa is comparatively well developed, and on the entocœlic face is finely plaited to afford additional support to the musculature, while the exocœlic surface is smooth; here, as elsewhere in the mesoglœa, included connective tissue cells are common. The muscular fibrils are very delicate, and in the upper region extend nearly in the same direction on each face. Among the many mesenterial pairs passed in review no directives have been observed.

The mesenterial epithelium is crowded with clear gland cells, and zooxanthellæ are plentiful. In the lower region of the polyps certain of the mesenteries become greatly convoluted; the

mesoglœa also becomes very thin, and the epithelium in some cases undergoes a glandular modification.

The filaments are of the usual Madreporarian type, with the mesenterial endoderm swollen behind (fig. 143). Numerous long, narrow, nematocysts occur, and more rarely one of the large oval form; supporting cells almost surround the hinder region, and diminish in length towards the mesoglœal axis. Granular cells, somewhat similar to those in the column wall and stomodæum, are found in the anterior portion of the filament.

The swollen mesenterial endoderm immediately behind the filament is remarkable for the abundance of large, pyriform, clear or almost clear, gland cells. Zooxanthellæ are here absent, except in the lower regions, and very few granular gland cells are seen. In most instances the expanded region terminates gradually, passing into the ordinary endodermal lining (figs. 143–145).

Certain of the filaments become glandular in character throughout a part of their course, having their cells either wholly or in part charged with a bright yellow, granular substance. A similar glandular character may be assumed also by the swollen mesenterial endoderm immediately behind the filament, no sharp line of separation distinguishing the two series (figs. 144, 145).

The endoderm of the skeletotrophic tissue is a narrow epithelial layer in the upper region of the polyps, and contains zooxanthellæ and clear gland cells, but in the lower region it undergoes a great alteration. It gradually increases in thickness until it is enormously broad, and loses at the same time most of the zooxanthellæ and granular cells; the nuclei diminish in size and are accumulated toward the free surface, and the whole tissue stains but little. The supporting lamella is clearly distinguishable, and desmoidal processes occur practically throughout its skeletal surface, though more pronounced along the line of attachment of the mesenteries. The ectoderm or calicoblast layer is a uniform, thin epithelium in the regions of active growth, as at the edges of the septa. The region around the insertion of the septa in the polypal wall also appears to be one of active growth, the cytoplasm and large nuclei of the calicoblasts staining deeply.

The polyps are hermaphrodite: male and female elements may occur on the same mesentery (fig. 140), or on separate mesenteries (fig. 146).

Family OCULINIDÆ.

Genus OCULINA Milne Edwards and Haime.[a]

Polyps smooth, usually spirally arranged, raised obliquely from the surface of the colony, distant, except toward the apex of the branches, form fixed arborescent colonies or tufts. Perithecal portion of the gastro-cœlomic cavity and mesenteries (edge-zone) greatly prolonged, may pass into "cœnosarc." Free portion of column cylindrical or somewhat conical, overfolding on retraction; no sphincter. Tentacles hexamerous, tricyclic, entocœlic and exocœlic, minutely tuberculated and knobbed. Disk circular, often prolonged in a conical manner. Stomodæal walls feebly ridged.

Mesenteries hexamerous, dicyclic, six pairs complete, all filamentiferous, two pairs of directives. Septal invaginations hexamerous, tricyclic, entocœlic and exocœlic, unite centrally (columella) in lower region, and divide the gastro-cœlomic cavity into twelve distinct loculi, each with two unpaired mesenteries.

Asexual reproduction by columnar gemmation at the apex of the branches; rarely by fissiparous gemmation.

EXAMPLE.—*Oculina diffusa* Lamarck.

[a] "Colony arborescent or in tufts. Corallites arranged more or less distinctly in ascending spiral series, or scattered irregularly, prominent or sunken, often arising from an incrusting base. Cœnenchyma solid and smooth or finely papillose. Calices circular, oval, prominent or depressed. The columella either well developed and papillary at the surface, compact at the base, or rudimentary. The septa are well developed, entire or slightly spinulose where free, some exsert. Pali exist before all the septa except those of the last cycle. Costæ as striations, or decided projections extending a short distance from the calicular margin. In rapidly growing forms there is no cœnenchyma independent of the buds. Endotheca may exist." (Duncan, 1885, p. 41.)

OCULINA DIFFUSA Lamarck

(Pl. XXII, fig. 149.)

External characters.—Small colonies of this species are met with in abundance in the shallow waters of Kingston Harbor, attached to loose objects on the sea floor; also in similar positions at Bluefields Bay. Large arborescent colonies, 10 to 12 cm. across, occur among the coral growth within the Harbor a little beyond Port Royal, and also on the piles of the Port Royal Dockyard. In these latter places they are associated with large colonies of *Cladocora arbuscula*, both species appearing as light or dark brown arborescent masses.

The column wall is much prolonged perithecally, a wide interval separating one polyp from another, except in the neighborhood of the apex of the branches, where the individuals are closely arranged. The polyps are usually raised some distance above the general surface of the colony in an oblique manner, and are either circular or oval in section. They are subspirally disposed, and the actual line of union of contiguous column walls is not always determinable. The external grooves corresponding with the internal attachment of the extracalicular mesenteries are at first very pronounced, but tend to disappear toward the proximal termination of the polyp; this actually takes place only in the older parts of a colony. On full expansion the column wall becomes raised above the edge of the theca, and is cylindrical, smooth, thin-walled, and transparent.

The tentacles are in three cycles, and usually number 24, arranged in the formula 6, 6, 12. The members of the first and second cycles are practically equal in length, and measure 5 mm.; they narrow but slightly from the proximal to the distal extremity, and the tips are colorless and slightly swollen. The surface is minutely tubercular, owing to the presence of clusters of nematocysts. The tentacles may be erect, spreading, or overhanging, according to the state of expansion of the polyp; on full retraction they appear as mere processes of the disk.

The disk is circular in polyps situated some distance from the apex of the branches, and about 4 mm. across on full expansion. During ordinary conditions it is depressed or flat, but the peristomial region may become conical on full expansion, extending beyond the tentacular zone for some distance (fig. 149). Radiating ridges and grooves are presented, and the internal mesenteries can be seen through; of these latter six pairs reach the stomodæum, and six pairs extend about half way across the disk. Polyps occasionally bear two oral apertures on a large oral disk, surrounded by a single system of tentacles (fissiparous gemmation).

The mouth is slit-like, and the stomodæum shows six white longitudinal lines on each side, corresponding with the attachment of the perfect mesenteries.

The column wall is light or dark brown in color, the grooves being always darker than the ridges. The tentacles and disk on full extension are a light brown, becoming much darker in retracted examples. The lips and stomodæum are white. The white edges of the septa and costæ show through very distinctly, especially on full expansion, when the colonies as a whole assume a lighter appearance. Examples obtained from shady places, as under the wharfs at Port Royal, may be perfectly colorless from an absence of zooxanthellæ.

Asexual reproduction takes place by columnar budding at the apex of the branches; fissiparous gemmation also takes place occasionally. In the laboratory the polyps remain partly expanded during the day, and are greatly distended at night. On retraction the column wall is drawn, iris-like, within the calice, so as to cover and conceal the tentacles and most of the peristome. Irritation of one polyp is responded to by others immediately around, and retraction proceeds after a short interval.

Anatomy and histology. The elongated column wall and perithecal skeletotrophic tissues inclose between them a large cœlomic space, partitioned longitudinally by the perithecal portion of the mesenteries. The superficial longitudinal chambers thus formed differ from those of most corals in that they are not again partly subdivided by costal ingrowths or echinulations, the outer surface of the corallum being nearly smooth; very shallow striæ above indicate the former position of the perithecal mesenteries, but the intervening space is not raised into strong costæ or echinulations. In retracted polyps the distal region of the column is drawn deeply within the

calice, so that transverse sections show an outer and an inner columnar wall before the tentacular zone is reached. The inner chambers are here partly subdivided by the septal intrusions.

The ectoderm of the outer wall is made up almost entirely of unicellular mucous glands, the contents of which are perfectly clear; supporting cells surround each gland cell, their aggregated nuclei giving rise to a distinct middle zone. Gland cells with granular contents occur in the deeper parts of the layer, and small deeply-staining nuclei. Both the mesoglœa and endoderm are extremely thin, and the latter contains zooxanthellæ. Nematocysts are apparently absent from the ectoderm, and only the weakest endodermal musculature can be detected in the upper region. Where the mesenteries are united to the outer walls of the corallum the usual striated mesogloeal processes are produced for attachment along the skeletal grooves, but are weak in character, and continue to be observable for some distance away from the mesenteries; in fact, they occur somewhat freely throughout the skeletal tissues. Perhaps the increased distribution is in some way determined by the unusual smoothness of the corallum, rendering increased attachment for the soft parts necessary. The skeletogenic ectoderm is extremely narrow, even in the growing parts of the corallum.

The tentacles are very short in retracted specimens; the ectoderm is deeply folded, and much swollen at the stinging areas. The apex is the broadest part of the layer, and the nematocysts there are of two kinds: a small, narrow, thin-walled form, which also occurs in the lateral areas, and a large, oval, thick-walled form restricted to this region of the tentacle. The layer also contains numerous clear and granular gland cells, similar to those in the column wall. An ectodermal musculature is clearly distinguishable on slight sinuations of the mesoglœa, and from it delicate fibrils pass to a nerve layer. The endoderm cells contain numerous zooxanthellæ, and also give rise to a weak endodermal musculature.

The stomodæum is oval shaped in transverse sections, and the ectoderm is thrown into five or six folds on each side, which, however, bear no constant relationship with the attachment of the mesenteries. Owing to the obliquity of the polyps, one end of the stomodæum generally terminates in advance of the other in a series of transverse sections. The ectoderm passes for some little distance along the two faces of each of the complete mesenteries, and the mesenterial filaments of all the perfect mesenteries appear as if continuations of the stomodæal ectoderm. The stomodæal ectoderm is constituted of ciliated supporting cells, among which are long, narrow, gland cells, with fine granular contents; in contrast with the gland cells of the column wall, these stain deeply and extend beyond the nuclear zone to the free surface of the ectoderm. A few large nematocysts are also scattered about, but apparently none of the smaller forms. The mesoglœa is extremely thin, and no musculature is determinable on either side of it; the endoderm contains many zooxanthellæ.

Six pairs of mesenteries reach the stomodæum, while other six alternating pairs remain incomplete throughout. The musculature is extremely weak in the upper region, so that it is difficult to distinguish whether directives are present or not. In the proximal regions the musculature becomes better developed, and is supported on delicate mesogloeal folds, and here it is possible to make out the two pairs of directives.

The mesenterial filaments on the complete mesenteries are in continuity with the stomodæal ectoderm, and histologically the two are much alike, being constituted of ciliated supporting cells, gland cells, and narrow nematocysts. At first the filaments are cordate in section; later they are nearly circular, and the mesenterial epithelium behind is swollen, so that a trilobed character is given to the free extremity of the mesentery as a whole. In the lower regions the mesenteries become convoluted, and the filament is not sharply marked off from the endodermal epithelium. Large and small nematocysts, similar to those in the ectoderm of the stomodæum, are numerous in some of the filaments, but not in all. The filaments on the imperfect mesenteries, which never reach the stomodæum, are first indicated in the distal region by a small group of deeply-staining nuclei at the free extremity; soon, however, they develop so as to exactly resemble those of the complete mesenteries, and in the lower region it is impossible to distinguish between the filaments of the two cycles. The mesenterial endoderm throughout contains numerous zooxanthellæ.

For some distance below the stomodæum the cœlenteron is imperfectly partitioned by the septal invaginations, but toward the base it becomes divided into twelve distinct loculi, each of which contains two unpaired mesenteries. Central to the loculi are sections through the invaginations which covered the pali and columella; they are at first free, but below are continuous with the septal invaginations. At first each loculus is partly divided along its peripheral border by the exocœlic septal invaginations, but these disappear in the lower regions, and each loculus is then a simple chamber. The convoluted mesenteries at first crowd the loculi, but afterwards wholly disappear.

C.—SECTION FUNGACEA.

MADREPORARIA IN WHICH THE MESENTERIES AND THE BASAL WALL LINING THE INTERSEPTAL LOCULI ARE PERFORATED BY SKELETAL BARS. TENTACLES OFTEN SMALL, SIMPLE OR DIMORPHIC, WIDELY SEPARATED.

Family PLESIOFUNGIDÆ.

Genus SIDERASTRÆA Blainville.[a]

Polyps smooth, distinct, form compact, massive, convex or plane, incrusting colonies; united with one another along a common polygonal edge, without perithecal continuation of the mesenteries. Column wall smooth, short, not overfolding on retraction. Tentacles small, knobbed, in somewhat irregular cycles, distant from one another; sessile and exposed on retraction; dimorphic—an inner (entocœlic) series bifurcated, an outer (exocœlic) series simple. Stomodæal walls smooth.

Mesenteries completely or incompletely tricyclic; six pairs complete, two pairs of directives, all filamentiferous, perforated by synapticula. Septal invaginations entocœlic and exocœlic, completely or incompletely tricyclic; incompletely separated for the greater part of their length, and perforated by several longitudinal rows of circular skeletal ingrowths (synapticula).

Asexual reproduction by intercalary and marginal gemmation. Viviparous.

Examples.—*Siderastræa siderea* (Ell. & Sol.), *Siderastræa radians* (Pallas).

SIDERASTRÆA SIDEREA (Ellis & Solander).

(Pls. XXII–XXIV, figs. 150–160.)

External characters.—Colonies of this species often form large, massive, compact, subspheroidal or incrusting masses on the sea floor about the reefs. The polyps are closely arranged and polygonal in outline at the base; adjacent polyps are united along a narrow, common calicinal wall, so that no pericalicular continuation of the column wall and gastro-cœlomic cavity is possible. The polyps in a colony are not disposed in any regular plan; a slight tendency to a linear or circular arrangement is apparent in places, but the intercalation of new individuals at any spot introduces irregularities.

The polyps do not readily expand, and even when this does take place the superficial tissues are raised only a little above the corallum, and the column is somewhat dome shaped, not assuming the regular cylindrical form characteristic of coral polyps generally. Outside the tentacular zone, but not sharply marked off from it, is a very limited, smooth, polygonal area, which is all that represents the column wall during partial or complete retraction. In the latter condition the superficial tissues are deeply depressed, and lie closely over the septa, being thrown into corresponding ridges and furrows (fig. 156).

The tentacles in partly retracted polyps appear as short, stumpy processes of the disk, widely separated from one another, the tentacular zone occupying nearly the whole of the superficial area of the polyp (fig. 150). They are broad at the base, but narrow a little terminally, becoming swollen at the apex. The inner entocœlic members are bifurcated distally, and during retraction one moiety is disposed on each side of the underlying septum; the outermost exocœlic

[a] "Colony massive, convex or plane, dense, incrusting. Corallites united by thin and often indistinct walls. Calices subpolygonal, deep, margins rounded. Columella small, papillary, made up of ascending trabeculæ, which often fuse, here and there, into a mass. Septa solid, rather close, thin, denticulate where free, often uniting. Two rows of synapticula close to the wall unite the opposed septal lamellæ, and tend to fill up the interseptal loculi near the wall. Septa imperforate. Endothecal dissepiments few. Gemmation submarginal." (Duncan, 1885, p. 134.)

tentacles on the other hand are simple, and the apical swelling lies over the apparent inner termination of the septum below (figs. 151, 154, 155). The organs remain exposed, the column wall being incapable of closing over them, but so minute are they that in completely retracted preserved material it is often impossible to distinguish them, even with the aid of a lens. When fully expanded the tentacles are short; the common stem of the bifurcated form extends but a short distance, and the apex of the bifurcations is rather pointed, and bears a white nematoblast area. The simple tentacles have a short, thick stem, and the apex is rounded, tipped with a battery of nematocysts.

The hexameral cyclic arrangement of the tentacles can be determined with a little care. No difference in size can be determined among the bifurcated examples, and these are disposed so as to form two or three alternating cycles; but the twelve members which should constitute the third cycle are not always present. The simple, outermost tentacles represent a fourth cycle, more or less polygonal in form, and equaling in number the sum of the three inner cycles, a multiple of six being rarely present.

In rare cases one or more entotentacles of a fourth cycle may be developed, as in the polyp from which fig. 150 was taken, even though the third cycle is not completed in all the other systems. In such cases the exotentacles would be considered as the fifth cycle.

The naked portion of the disk is smooth, and very limited in extent in comparison with the broad tentacular zone. During partial retraction the peristome is elevated, the mouth is long and oval, and the white lips contrast strongly with the dark-brown disk. The stomodæum is smooth, without permanent ridges and furrows.

On the sea floor the colonies as a whole appear a characteristic reddish-brown color. On closer examination the disk is found to be somewhat darker than the rest of the polyp; the areas along the lines of union of adjacent polyps and also over the septa are lighter, the corallum partly showing through. The tentacles are a little paler; but, on the whole, the polyps are remarkably uniform in color. The young polyps on a colony are for some time much lighter colored than the rest. When a living colony is broken across, the superficial part of the skeleton for about a centimeter in depth is frequently of a pink color, contrasting strongly with the corallum below, which is a dense white.

New polyps arise along the line of union of adjacent polyps, and for some time they usually project slightly above the general surface of the colony. The extrusion of mesenterial filaments through the mouth or polypal wall has not been observed.

Anatomy and histology.—The ectoderm of the column wall contains numerous clear gland cells, and here and there a small oval nematocyst in which the axis is clearly distinguishable. The mesoglœa is everywhere extremely thin except along the line of attachment of the mesenteries. The endoderm contains numerous zooxanthellæ, and only the merest trace of any circular musculature can be detected.

The tentacles have a very characteristic relation in conformity with what has been noted amongst the external characters. In transverse sections through the uppermost region of retracted polyps, passing through the sloping disk, the outermost series of tentacles are first come upon, appearing as simple, nematocyst-bearing swellings of the ectodermal layer, directly overlying the septal ridge (fig. 154). A little below these the bifurcated tentacles appear in section, but in this case each knob of the tentacle is situated laterally, one along each side of the septal invagination, and the intermediate connecting tissue, which passes over the septal edge, resembles that of the disk (fig. 155). Each half of the apical portion of the tentacles stands out as a wing-like thickening of the superficial wall, and outwardly is crowded with long, narrow, stinging cysts; but the peduncle, as such, wholly disappears, becoming involved in the discal tissues. No ectodermal or endodermal muscle fibers have been recognized on the walls of the tentacles.

The disk presents no histological characters distinguishing it from the column wall, except that a slight musculature is developed in connection with both the ectoderm and endoderm.

The stomodæum is folded both vertically and horizontally in retracted polyps, and the aboral termination is directed outwardly and backwardly. Twelve complete mesenteries are attached

internally at about equal distances apart, and the backwardly directed, free edge of the stomodæum passes outwardly for some distance along their faces, and is continuous with the mesenterial filaments. A few nematocysts are found in the stomodæal ectoderm, and long narrow gland cells toward the outer part of the layer. The mesoglœa is extremely delicate, while the endoderm is slightly broader than that of the column wall.

Three orders of mesenteries occur. The members of the first order reach the stomodæum; the secondary pairs may extend centrally nearly as far as the stomodæum; while those of the third cycle are some distance away, but are nevertheless well developed (fig. 153). Apparently the complete condition should be six pairs of perfect mesenteries, two pairs of which are directives; six alternating pairs constituting the second cycle; and twelve alternating pairs making up the third cycle—twenty-four pairs in all. This regularity, however, is not attained in any of the polyps sectionized transversely. In two examples only one pair of directives occurs, the corresponding axial pair having the retractor muscles on the faces turned toward one another. Eleven mesenteries extended as far as the stomodæum in one polyp, while the twelfth never reached so far; in another specimen the two pairs of directives were normally developed. Usually one or more of the pairs necessary to complete the twelve pairs of the outermost, third cycle are wanting; rarely one or more pairs of a fourth cycle are present.

Except in the uppermost region, each interseptal loculus appears broken up into separate chambers, as a result of the presence of synapticula. The mesenteries extend as far as the peripheral boundary of the polyp only within the uppermost stomodæal region; below this region the interseptal loculi are devoid of any contents in their peripheral chambers, the mesenteries having wholly disappeared. In some cases the mesenteries may extend across two chambers, as seen in transverse sections, but rarely more; in vertical peripheral sections traces can sometimes be found extending through three or four rows of synapticula (fig. 156). The manner of disintegration and resorption of the peripheral and aboral areas of the mesenteries, as they become perforated by the synapticular growths, has been already described (p. 487). Centrally some of the mesenteries extend more than halfway down the length of the polyps, but none reach the aboral termination, and all are much shorter peripherally; in the middle part of their course they become somewhat convoluted.

In the upper region the retractor muscles of the mesenteries are comparatively well developed, arranged on slight foldings of the mesoglœa which extend nearly across the face (fig. 158); in favorable sections the oblique musculature on the smooth face of the mesentery is also distinguished. The mesenterial epithelium contains numbers of zooxanthellæ and irregular, highly refractive granules. Sometimes these latter occur singly, at other times in groups, or even in rounded masses; they seem to be inclosed in vacuoles, and are perhaps products of digestion. The granules seem more numerous where the disorganization of the mesenteries is taking place, so that probably the products of this activity are absorbed by the more centripetal mesenterial epithelium, as well as by the endoderm of the skeletotrophic tissues.

Fully developed mesenterial filaments occur on all the mesenteries, including those of the second and third cycles, which never reach the stomodæum. In the stomodæal region the incomplete mesenteries exhibit only the earliest stages in filamental development; the tissue at the free end stains more deeply than the rest of the epithelium, but is not swollen (fig. 158). Lower, however, the filaments become rounded, nematocysts and deeply-staining gland cells occur, and the mesenterial epithelium immediately behind is usually swollen and rounded off; in some cases, as in fig. 159, no endodermal swelling occurs. In the aboral region the filament disappears some distance in advance of the mesentery.

In retracted polyps the gastro-cœlomic cavity above is divided centrally only by the mesenterial partitions, but in the peripheral portion it is subdivided in addition by the septal invaginations (fig. 153). The interseptal loculi are very narrow, and where the larger septa meet in the middle some of the interseptal chambers are wholly cut off from one another, each partly subdivided peripherally by the shorter exocœlic invaginations. Owing to the presence of synapticula, and the union of the septa with one another centrally, the polypal cavity in sections appears greatly subdivided and intruded upon. The individual interseptal chambers never

become wholly distinct centrally; groups of two, three, or four chambers, as the case may be, communicate and feebly hang together after decalcification.

The skeletotrophic tissues are strongly developed, and both the ectoderm and endoderm remain broad layers throughout; the mesoglœa, on the other hand, is only determinable as a dividing line between the two. The endoderm is constituted largely of clear gland cells, the nuclei and zooxanthellæ arranged in a more or less distinct marginal zone. Peripherally in the upper region, and throughout the lower region, very deeply-staining, finely granular protoplasmic differentiations occur (fig. 160); in the avidity with which they take up stains such as hæmatoxylin, carmine, etc., and on account of their finely granular structure, they recall nuclei in the early stages of mitosis. They are distributed in the deeper parts of the layer, usually close to the mesoglœa, and sometimes are present in large numbers.

In the peripheral and lower regions the calicoblast layer remains very broad; in fact, as broad or even broader than the endoderm (fig. 157). It has lost all the ordinary characters of a columnar epithelium; cell divisions are not determinable, and the contents are mainly protoplasmic, with numerous very large vacuoles, and small, rounded granules, which stain readily. The granules are often arranged in irregular rows, stretching from the mesoglœa to the free surface, in which latter region they are most crowded. Now and again very small ovoid bodies are met with, which readily stain; they appear to be the same as those described by Bourne as modified nematoblasts.

In the more central parts of the polyps the calicoblast layer is somewhat thinner, and nuclei are more numerous, and here it is found assuming a more columnar character. Deeply-staining desmoidal processes occur, most usually connected with the synapticula (fig. 157), though not limited to this position. The skeletotrophic tissues in both species of *Siderastræa* are exceptional in the slight increase in thickness which the endoderm undergoes from above downward, as well as in the persistence of the calicoblast ectoderm as a broad layer.

Female gonads were found in many of the polyps sectionized from one colony. The ova occur singly, or two or three together, near the attached end of the mesentery, and are elongated and rather irregular in shape, having to adapt themselves to the very narrow interseptal loculi within which the mesenteries occur. The length of an ovum is often three or four times the breadth. They may occur on any of the mesenteries of the three orders.

Family LOPHOSERIDÆ.

Genus AGARICIA Lamarck.[a]

Polyps smooth, discal and tentacular systems distinct, but columnar boundary indeterminate; arranged in subconcentric groups which are more or less radiately separated; united with one another along a common thecal edge, which is strongly marked concentrically, but usually less so radially; the gastro-cœlomic cavity and mesenteries are continued at the margin (edge-zone); form a frondiform or horizontally flattened foliaceous skeleton, with polyps on both sides or only on upper side, fixed by a broad incrusting base. Column wall not overloding on retraction; no sphincter. Tentacles rudimentary or small, tubercular or digitiform, distant from one another, subcyclical, exocœlic wanting.

Mesenteries irregularly multicyclic, directives wanting; all filamentiferous; increase by irregular intercalation of single unilateral pairs. Septal invaginations entocœlic and exocœlic; irregularly multicyclic. Interseptal loculi perforated above by circular skeletal ingrowths (synapticula).

Asexual reproduction by complete discal fission?

Examples.—*Agaricia fragilis* Dana, *A. agaricites* (Linn.).

Vaughan (1901, p. 63) agrees with Gregory in combining the genera *Agaricia* and *Myeadium*, and recognizes only the two West Indian species, *A. fragilis* and *A. agaricites*. The specific distinctions are, however, very slight, but among living colonies, as with the coralla also, coarser and more delicate forms can always be separated. Structurally I have been unable to detect any important differences between the two species. Only *A. fragilis* will be here described.

[a] "Colony foliaceous and irregular in shape. Calices on one or both surfaces, circumscribed or limited at least on two sides, in transverse or concentric series, which are separated by unequal ridges (collines), over which the confluent septo-costæ pass. Columella tuberculous, papillose, or compressed. Septa confluent, not numerous. Common plateau striated and naked. Synapticula exist." (Duncan, 1885, p. 161.)

AGARICIA FRAGILIS Dana.

(Pls. XXIV, XXV, figs. 161–164.)

External characters.—Colonies form delicate, flattened, subcircular or irregular expansions, attached to some coral block by a broad, irregular base. Young colonies may be wholly incrusting, but later the thin peripheral regions become free. Typical examples are very regular in form, the polyps arranged in incomplete concentric series. Where freedom of growth is not permitted, the colony may be irregular in outline, and vertical expansions may then arise from its general surface, bearing polyps on both sides. The thickness of the central region varies greatly, and a gradual thinning takes place toward the periphery, which is very delicate. In an actively growing colony the periphery is a broad marginal zone without actual polyps, and the polypal tissues are continued on the under surface.

The thecal ridges are arranged concentrically and radiately, but the regularity is often departed from; the concentric ridges are more pronounced than the radial, and some project higher than others. Similarly with the radial ridges, some are nearly of the same height as the concentric ridges, and may inclose two or more polyps of which the radial ridges remain lower. In the retracted condition the central region of each polyp is deeply depressed within the calice, so that each polypal area is distinctly separated from the others. The usual distance from one concentric ridge to another is 3 mm. and from one radial ridge to another 2 mm.

As shown in the transverse section represented in fig. 164, the side of the polyp toward the periphery of the colony is more spreading than that toward the center, and thus the stomodæum is not always in the middle of the disk. Owing to the arrangement of the thecal ridges in a roughly concentric and radial manner the form of the individual polyp becomes somewhat quadrangular.

The edge-zone at the margin of the colony is very delicate, and closely adherent to the corallum; sometimes it covers only a very limited peripheral portion of the under surface, the remainder being hidden by various foreign growths; in other cases it may spread for some distance over the surface of the foreign body to which the colony is adherent.

The column wall of the individual polyp is very limited in extent, but is a little broader along the concentric borders than on the lateral borders. The boundary between the column wall of one polyp and that of another is only approximately determinable along the apex of the thecal ridges; there is no dividing groove in the soft tissues limiting the individual polyps, such as is found in most corals.

The superficial polypal tissues are smooth, and so thin as to allow the septo-costæ to be seen through. In retraction these give rise to somewhat prominent ridges on the column wall, those of adjacent polyps corresponding and being continuous. The septal ridges are visible from the outside, and different orders are represented. In most places only alternately large and small elevations are indicated, but elsewhere members less completely developed may denote later cycles, or perhaps new septa in process of growth, which in time will attain the dimensions of the others. The complete number of septal ridges on seven polyps was found to be as follows: 18, 20, 22, 24, 26, 28, 30, numbers which possess no hexameral constancy.

The boundary between the column wall and disk also is not well defined, owing to the irregular arrangement, and, in some cases, apparent absence of the tentacles. During retraction no overfolding of the wall takes place, so that the tentacles, disk, and mouth are always exposed. On expansion of the polyps the superficial walls are raised but a short distance above the corallum, and the column wall becomes only approximately cylindrical in form, remaining attached along the thecal edges.

The tentacles are very rudimentary; indeed, in some living colonies they were indistinguishable even with the aid of lens, and such is often the case in preserved colonies. In other instances the merest tubercular elevations over the larger septo-costæ were the only indications; none ever occur over the alternating small septo-costæ, which on subsequent examination are found to be exocœlic in position. The tentacles usually vary in number from ten to eighteen, and are comparatively widely separated from one another. Where no tentacles are apparent there is clearly no line of demarcation to be established between the disk and the column wall of

the polyp. The organs occur over the apparent centripetal termination of the septa, and no cyclic regularity can be established (p. 429).

The disk is small, subcircular, smooth, thin-walled, and very limited in extent. The mouth is small, circular or oval in shape, sometimes with a prominent peristome.

The general color of the colonies as a whole is a bright reddish brown, and minute, emerald green circles indicate the positions of the numerous mouths. Observed with a lens the bright green, peristomial color fades gradually toward the middle of the disk. Sometimes a faint iridescent green extends over the whole surface of the colony. The septo-costæ show through the tissues as lighter lines. Occasionally the green oral coloration may be absent, or replaced by a bright orange color.

New polyps arise near the margin of the colony, but from the external indications it is impossible to say whether by gemmation or fissiparity. The mesenterial arrangement, however, agrees with that of other forms in which fissiparity is undoubted; Ortmann (1890, p. 288) places the species under the division of "Cœnenchymknospung."

The species occurs somewhat sparingly in shady places on the coral reefs around the Port Royal Cays, from a depth of 3 to 4 feet downward. The bright, reddish brown color of the colonies as a whole renders them very conspicuous against the white dead coral blocks to which they are usually attached.

Anatomy and histology.—The outer superficial covering of the colony is very delicate, and the same remark may be made of the tissues as a whole; the column wall in sections is only 0.023 mm. in thickness. It forms very deep ridges and furrows, and in preserved material usually rests directly upon the skeletotrophic tissues of the septal ridges (fig. 162). Mesenteries are attached along the lines of depressions, but their vertical extent is very limited as they approach the thecal wall, increasing toward the more central part of the polyp. Little or no histological distinction separates the column wall, the tentacular zone, and the more central part of the disk, while in sections the tentacles themselves are only determinable by the occurrence of a few closely arranged large nematocysts in certain swollen regions (fig. 163).

The ectoderm of the column wall contains numerous clear gland cells, and small nematocysts occur here and there, and in some places accumulations of granular matter are found in the deeper portions of the layer. The mesoglœa appears as an extremely delicate supporting lamella; the endoderm is also a comparatively thin layer, and its cells contain only a few zooxanthellæ.

The tentacles are represented in sections as single, slightly swollen batteries of nematocysts, 0.05 mm. across, situated over a septal ridge, and disposed at different distances from the oral aperture. A weak ectodermal and endodermal musculature can be detected in connection with the tentacles, though not in any other region of the outer wall. The stomodæum is smooth all around and presents no distinctive features.

The mesenteries are delicate structures, the mesoglœa being thin and the epithelial layer very narrow. The retractor musculature is feeble, and is supported upon slight mesoglœal foldings; zooxanthellæ occur but sparsely in the endoderm. Peripherally the mesenteries have only a short vertical extent, but centrally they extend nearly the full vertical height of the polyp.

The mesenteries are irregular in number and arrangement, and, as in the case of polyps reproducing by fission, directives are always absent. A transverse section through a polyp immediately below the stomodæal region is represented in fig. 161, from which it is seen that little regularity obtains in the relative sizes of the mesenteries, and in the alternation of larger and smaller pairs; as shown in fig. 164, from a section through the stomodæal region of another polyp, a regular alternation of complete and incomplete pairs may occur. The incomplete pairs as a rule vary much in size, and in places a pair may be missing, while of the complete pairs some may cease their connection with the stomodæum in advance of the others, or even one moiety before the other. In one polyp all the mesenterial pairs, with one exception, were united with the stomodæum, and entocœlic and exocœlic septal invaginations occurred with perfect regularity. The number of complete pairs bears no suggestion of any hexameral symmetry; seven equal pairs are present in the polyp from which fig. 164 was taken, and eight pairs in another polyp.

In sections through the upper regions of the polyp the continuity of the mesenteries is often interrupted by the presence of synapticular perforations; further, some of the mesenteries are continuous from one polyp to another. The continuity of the mesenteries of contiguous polyps is without doubt to be associated with the absence of distinct polypal limitations noticed among the external characters, and also with the confluent septo-costæ characteristic of the genus; probably also it has some bearing upon the method of asexual growth of the colony, which calls for more detailed study.

Mesenterial filaments occur on all the mesenteries, but in the upper region are very rudimentary in character, and imperfectly separated from the mesenterial epithelium. In the lower region of the polyp many of the filaments undergo an enormous development in connection with the convolution of the mesenteries. They mostly fill the septal loculi, and bear numerous, closely arranged, large nematocysts, and many clear, brightly staining gland cells, and others with coarsely granular contents.

The skeletogenic ectoderm is rarely determinable in ordinary decalcified material, but desmoidal processes are numerous along the line of attachment of some of the mesenteries. The skeletotrophic endoderm remains a very narrow layer throughout, undergoing but little increase in thickness in the lower regions.

In the ordinary condition of retraction the gastro-cœlomic cavity is very limited in extent. The central cavity is prolonged upward and outward between the mesenteries and the septa as far as the edge of the theca, and is there placed in communication with that of adjacent polyps (fig. 162). Downward the cavity soon diminishes in peripheral extent, and centrally is broken up into distinct chambers by the inward growth of the septal invaginations which meet in the middle. For some distance the interseptal loculi are crowded with the enlarged and convoluted mesenterial filaments.

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EXPLANATION OF PLATES.

Wherever the skeleton is shown in relation to the soft parts it is represented by uniformly dotted areas. The ectoderm is usually indicated by the conventional columnar epithelium, the mesoglœa by a black line, and the endoderm as a tinted layer. In sections drawn under low magnification, as in Pl. I. figs. 2–6, the calicoblast layer is usually not indicated, the mesoglœa appearing to rest directly upon the skeleton. The retractor muscle on the mesenteries is conventionally represented by small processes from the face of the mesoglœa. The orders or cycles of mesenteries and septa are denoted by Roman numerals.

REFERENCE LETTERS ON THE FIGURES.

cal .....calicoblast layer.
cal. w.....calicinal wall.
col. w.....column wall.
d.....directives.
des. pr.....desmoidal processes.
disk .....disk.
ect .....ectoderm.
ect. m .....ectodermal muscle.
end.....endoderm.
end. m.....endodermal muscle
en. t.....entotentacle.
ex. t.....exotentacle.
gr. gl .....granular gland cells.
m .....mesentery.
m. fil .....mesenterial filament.
mes .....mesoglœa.
m. end .....mesenterial endoderm.
nem. bat.....nematocyst battery.
nr. l .....nerve layer.
ov.....ovum.
o. a.....oral aperture.
r. ect .....reflected ectoderm.
r. m .....retractor muscle.
sep. inv.....septal invagination.
sk .....skeletotrophic tissue.
sk. ect .....skeletotrophic ectoderm or calicoblast layer.
sk. end .....skeletotrophic endoderm.
sk. mx.....skeletal matrix.
sper .....spermarium.
sph. m.....sphincter muscle.
st .....stomodæum.
sup. can .....superficial canal.
syn.....synapticulum.
t .....tentacle.
zoox.....zooxanthella.

PLATE I.

MADREPORA MURICATA Linnæus.

FIG. 1.—*a*, Polyps at the apex of a branch of *M. corricornis*. The single apical polyp is larger than the five radial or lateral polyps, and bears only six equal tentacles. *b*, An apical polyp viewed from above. The comparative radial extension of the mesenteries can be seen through the transparent discal wall. *c*, A radial polyp, partly expanded, viewed from the side. *d*, *e*, Fully expanded radial polyps viewed from above. *g*, *f*, Reduced polyps growing on galls produced by the presence of algal growths. *h*–*o*, Different polyps of *M. palmata*; *j*, polyp with only ten tentacles; *l*, a double polyp with two oral apertures; *o*, two retracted intercalary polyps. Enlarged.

FIG. 2.—Longitudinal section through a retracted radial polyp. The polyp is withdrawn within the calice, the actual oral aperture (*o. a.*) being situated much below the apex of the corallite. The tentacles (*t.*) appear as thickenings of the inturned discal wall. On the right side the stomodæal ectoderm is in continuity with the filament at the free edge of a mesentery. The mesenteries and their filaments are convoluted below, and different portions are seen in section. On the left side the gastro-cœlomic cavity is in communication with the superficial canals over the edge of the theca. × 50.

FIG. 3.—Transverse section through a retracted radial polyp, at about the level *t.* in the previous figure. The upper part of the polyp is axial and the lower abaxial in relation to the branch on which it was growing. All the six pairs of mesenteries stretch from the skeletotrophic wall to the inturned disk. A tentacular protuberance arises from each mesenterial chamber, the entocœlic members being larger than the exocœlic. At this level the anterior tentacle (lower in the figure) is no larger than the other entotentacles, while the exocœlic member on each side of it is scarcely seen as a protuberance. The outer column wall (cœnosarc) rests upon twenty-four costal ridges, but no peritheeal prolongations of the mesenteries occur. × 50.

FIG. 4.—Transverse section through the same polyp, at the level of the stomodæum (about *m.* in fig. 2). The axial-abaxial relations are the reverse of those in fig. 3, that is, the lower side is axial and the upper is abaxial. × 50.

FIG. 5.—Transverse section through another polyp, some distance below the stomodæal region. Only three pairs of mesenteries now occur, the other three having disappeared. The black oval bodies in the endoderm of this and the next figure represent a parasitic Protozoon. × 50.

FIG. 6.—Transverse section through the same polyp at a still lower level. Only two pairs of mesenteries are present, but owing to their convoluted character each appears several times in the same section. The polypal cavity is greatly encroached upon by six septal ingrowths. × 50.

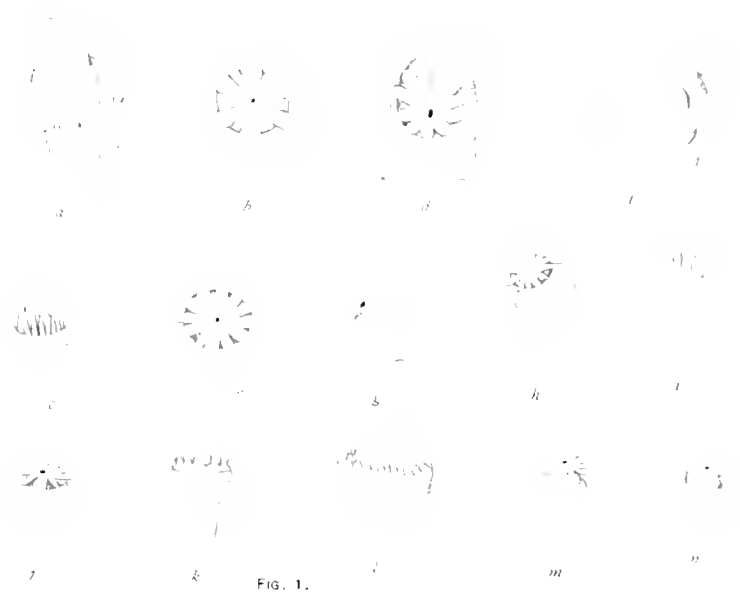

FIG. 1.

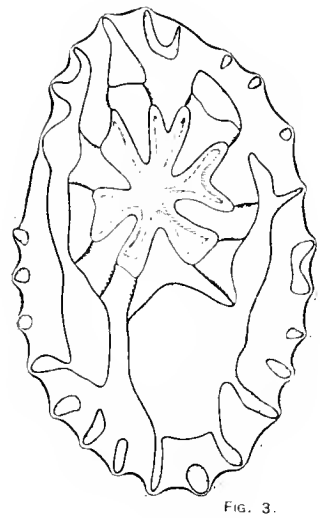

FIG. 3.

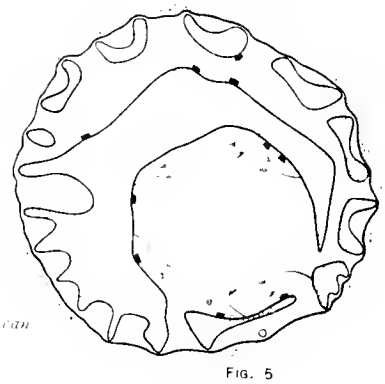

FIG. 5

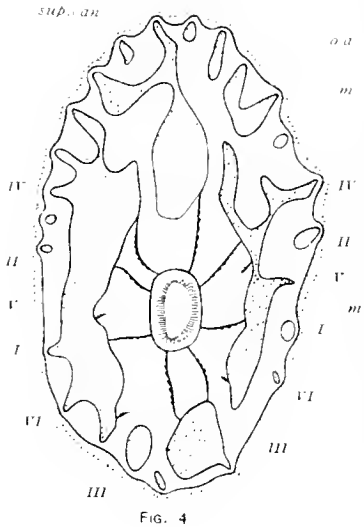

FIG. 4

FIG. 2.

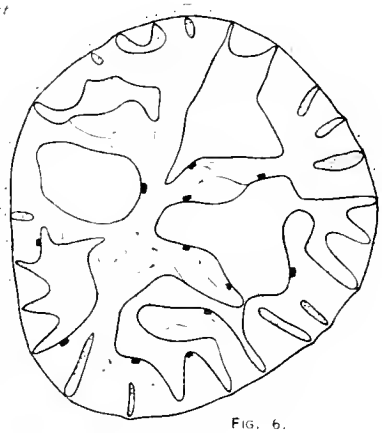

FIG. 6.

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PLATE II.

MADREPORA MURICATA Linnæus.

FIG. 7.—Transverse section through a portion of the external covering of the skeleton (cœnosarc) and the superficial longitudinal canals. The outer endoderm of the canals is crowded with zooxanthellæ, while they are more sparse internally, where the endoderm is narrow. The calicoblast layer has almost disappeared, but the denser part of the skeletal matrix remains, associated with desmoidal processes. × 320.

FIG. 8.—Transverse section through the tissues covering the uppermost part of the skeleton of an apical polyp, representing a superficial canal and part of one adjacent on the right side. The outer ectoderm is much broader than in the previous figure, and the calicoblast layer (*cal.*) is also better developed. The endoderm lining the canals is devoid of zooxanthellæ, and the mesoglœa is only a mere lamella. × 320.

FIG. 9.—Cells from the cœnosarc: *a*, Two varieties of nematoblasts; *b*, supporting cells; *c*, granular cell from endoderm, containing two zooxanthellæ. × 450.

FIG. 10.—Transverse section through a portion of a tentacle showing the well-developed nerve layer (*nr. l.*), the cnidocils, and cilia on the ectoderm and endoderm. × 320.

FIG. 11.—Longitudinal section through the disk and uppermost part of the stomodæal wall. × 320.

FIG. 12.—Transverse section through two mesenteries (directives), and the stomodæal wall and skeletotrophic tissues to which they are attached. × 300.

FIG. 13.—*a*, Two gland cells from the stomodæum; *b*, group of ciliated supporting cells from the stomodæum. × 450.

FIG. 14.—Transverse section through a mesentery, terminated by a mesenterial filament. × 320.

FIG. 15.—Cells from mesenterial filament: *a*, various gland cells; *b*, nematoblast; *c*, supporting cells from posterior region of filament; *d*, cell with zooxanthellæ from the mesenterial epithelium. × 450.

FIG. 16.—Transverse section through a canal near the apex of a branch, showing the deep calicoblast layer, and the narrow ciliated endodermal lining of the canal. × 320.

FIG. 17.—Section through a decalcified canal wall some distance from the apex. × 320.

FIG. 18.—Section through the wall of a canal, and a portion of the organic matrix remaining after slow decalcification. The section is taken from near the growing apex of a branch. Toward the upper part the matrix is still connected with the canal wall, but elsewhere has become shrunken from it. The matrix shows no cellular structure, but in appearance very closely resembles the actual skeleton as seen in surface view (*cf.* fig. 19). × 320.

FIG. 19.—Surface view of part of the macerated corallum near the growing apex. × 320.

FIG. 20.—Mesentery from a bud, showing the early development of the mesenterial filament; the latter is at first indistinguishable from the mesenterial epithelium. × 320.

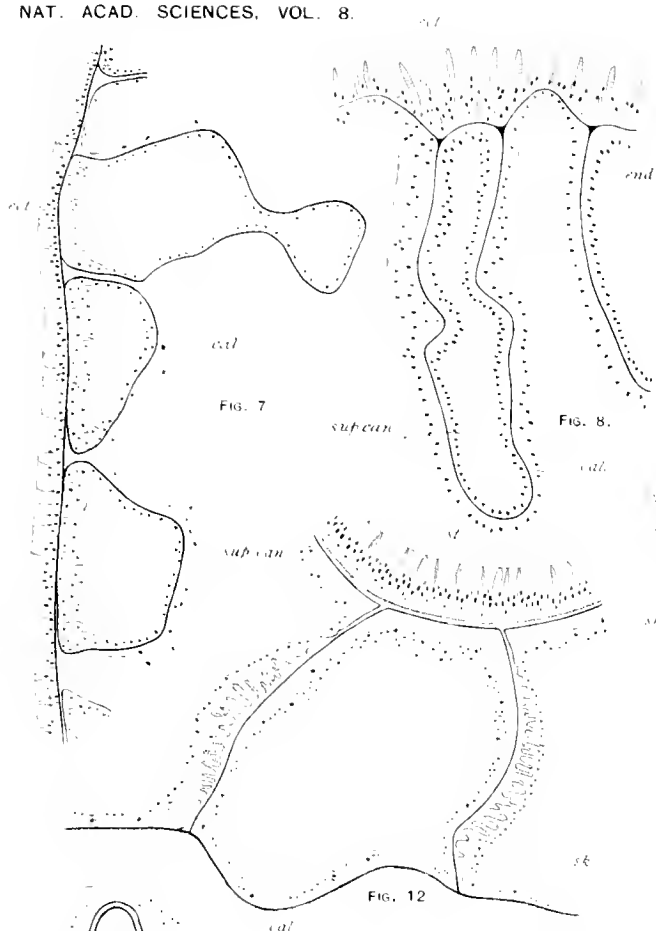

FIG. 7.

FIG. 8.

FIG. 12.

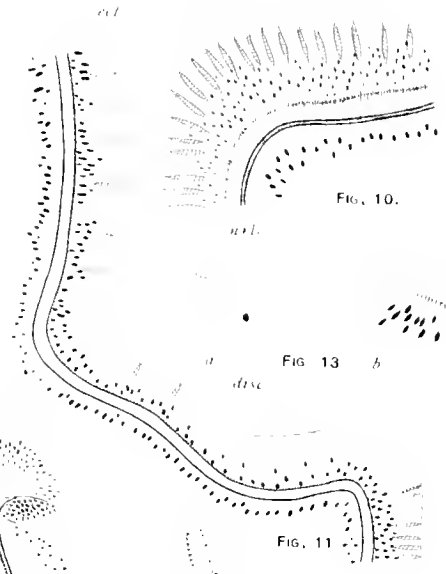

FIG. 11.

FIG. 10.

FIG. 13 b

FIG. 14.

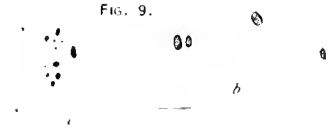

FIG. 9.

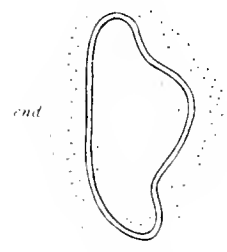

FIG. 16.

FIG. 15.

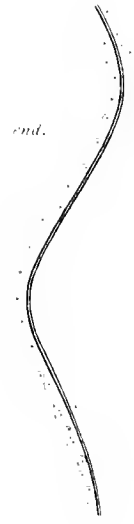

FIG. 18

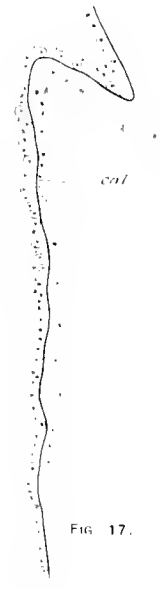

FIG. 17.

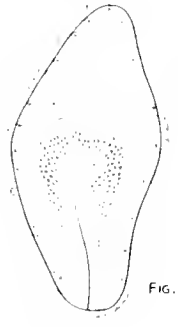

FIG. 20.

FIG. 19.

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PLATE III.

MADREPORA MURICATA Linnæus.

FIGS. 22-27.—Series of sections through the cœnosarc, illustrating the formation of a bud. For explanation, see p. 497. × 50.

PORITES ASTRÆOIDES Lamarck.

FIG. 28.—Transverse section through the upper stomodæal region of a partly expanded polyp. × 110.

FIG. 29.—Transverse section of the same polyp, immediately below the stomodæal region. Rudimentary mesenterial filaments occur on only the first three developmental pairs of mesenteries. × 110.

FIG. 30.—Transverse section through a partly expanded polyp. The polyp is somewhat depressed within the calice, so that the middle of the section includes the stomodæal region, and the periphery includes the greater part of the circular theca, the two wholly separated from one another except at a narrow region on the right side. Within seven of the twelve primary mesenterial chambers is a transverse section of an introverted tentacle (*t.*), the apex of the tentacle being represented in four of the sections by a specially thickened region. The ectoderm of the tentacles is now internal, and the endoderm external. Only three pairs of the primary mesenteries are complete, the dorsal directives having become free, their rudiments being seen still inserted on the stomodæal wall. The stomodæal ectoderm is regularly folded, but in a different manner from fig. 28. The double column wall ceases a few sections below, and the continuity of the mesenteries, from the thecal wall to the stomodæum, is then established. × 50.

FIG. 31.—Transverse section through the uppermost region of the calicinal edge common to four contiguous polyps. The partial limits of the four polyps are shown by four curved lines. Rudiments of eight exsert septa occur, and the first indications of two mesenteries. The gastro-cœlomic cavities of the four polyps are in superficial communication by means of the interseptal spaces. × 50.

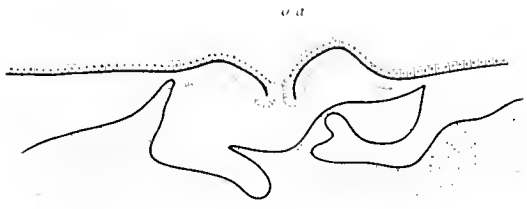

FIG. 22.

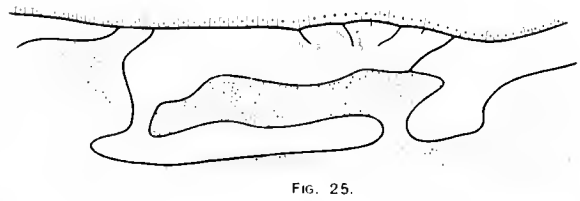

FIG. 25.

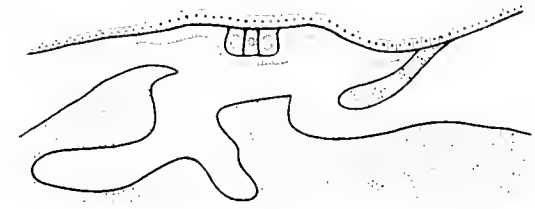

FIG. 23.

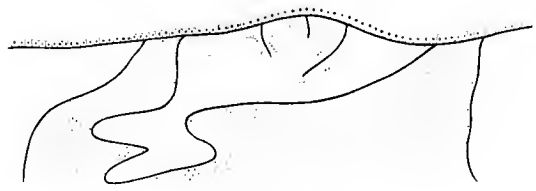

FIG. 26.

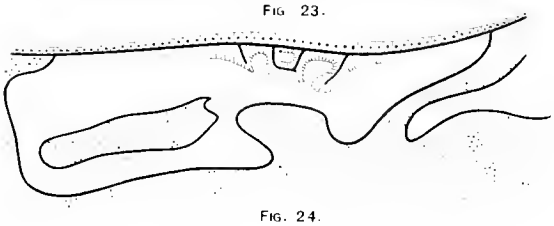

FIG. 24.

FIG. 27.

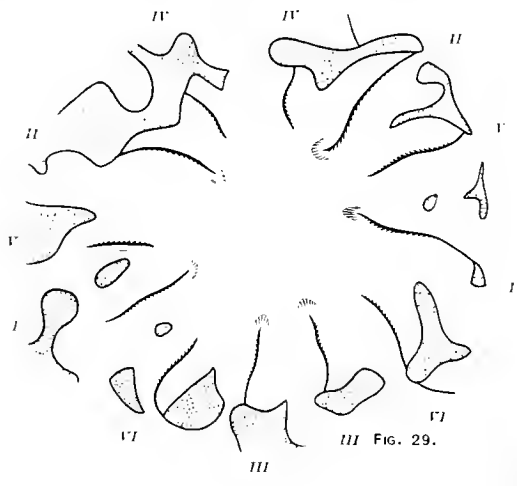

FIG. 29.

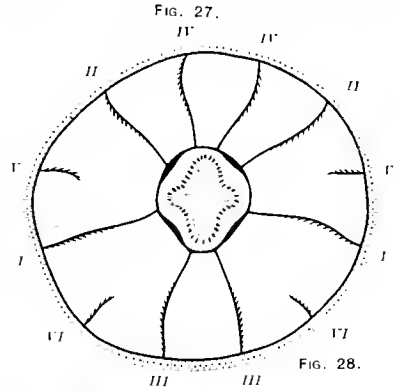

FIG. 28.

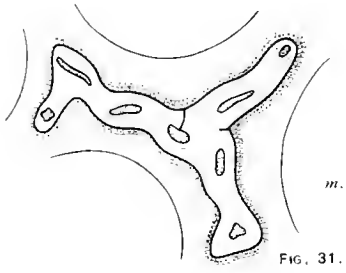

FIG. 31.

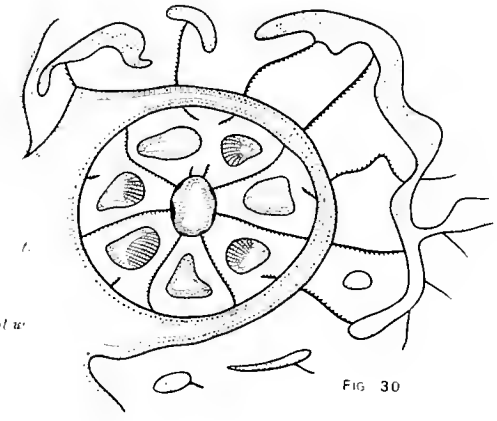

FIG. 30

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PLATE IV.

PORITES ASTRÆOIDES Lamarck.

Fig. 32.—Discal view of two enlarged polyps in which the tentacles are fully expanded; the radial extent of the mesenteries can be seen through the transparent discal wall: *a*, *P. divaricata*; *b*, *P. clavaria*.

Fig. 33.—An expanded polyp of *P. clavaria* in which most of the tentacles are introverted, two only being partly expanded.

Fig. 34.—Retracted polyp of *P. clavaria* with the tentacles and disk still exposed.

Fig. 35.—Retracted polyps of *P. clavaria*. In the two to the right the column wall is partly folded over the disk, but admits of the tips of the tentacles and middle of the peristome being seen; the tentacles are wholly hidden in the polyp to the left.

Fig. 36.—*P. astræoides*. Vertical section through a portion of the column wall with two mesenteries attached. The section was doubly stained with borax carmine and methyl blue; the yellow contents of the pigment cells were unaffected, the nucleus alone taking up the carmine. The nature of the nearly circular body in the middle is somewhat doubtful. Similar bodies occur in numbers within the tissues of some polyps, but are absent from others; perhaps they are the reproductive sporogonia of the perforating algæ, but the connection with the algal filaments has not been traced. Between the two mesenteries is the skeletotrophic covering of a septum, and in the space formerly occupied by the corallum are found certain bodies which seem to represent the early stages in the growth of the algal filaments. The endodermal epithelium of only one face of the mesentery to the right is represented. × 900.

Fig. 37.—Isolated pigment cells from the column wall, with a group of supporting cells. × 900.

Fig. 38.—Transverse section through a mesentery, a little below the point at which it becomes free from the stomodæum. The peripheral end at this level is opposite a canal, and therefore appears free from any connection with the polypal wall. The centripetal end is tipped with a deeply staining tissue, closely resembling the stomodæal ectoderm; as yet it can scarcely be regarded as a mesenterial filament. On some of the complete mesenteries the filament is never developed beyond this stage, but on others it becomes definitely rounded off from the mesenterial endoderm (*cf.* fig. 39). The endoderm is highly glandular, and bears yellow pigment cells, zooxanthellæ, and a few large nematocysts. The mesenterial plaitings supporting the retractor muscle are very feeble. To the right of the mesentery is a transverse section through the skeletotrophic tissue covering a palus. The endoderm is very glandular, like that of the mesentery, the mesoglœa is extremely thin, and the calicoblast ectoderm at this level is a deeply staining layer, with numerous nuclei and highly protoplasmic cells. × 400.

Fig. 39.—Transverse section through an interseptal loculus, some distance below the stomodæal region. The loculus contains a single, well-developed mesentery. The calicoblast layer at the periphery is represented only by granular matter, with small nuclei here and there. The skeletotrophic endoderm scarcely differs from its condition in the upper regions (*cf.* fig. 36). The mesenterial endoderm is much less vacuolated than above, and the filament is rounded off, and displays the usual histological details, except for the occurrence of the irregular yellow pigment cells. × 400.

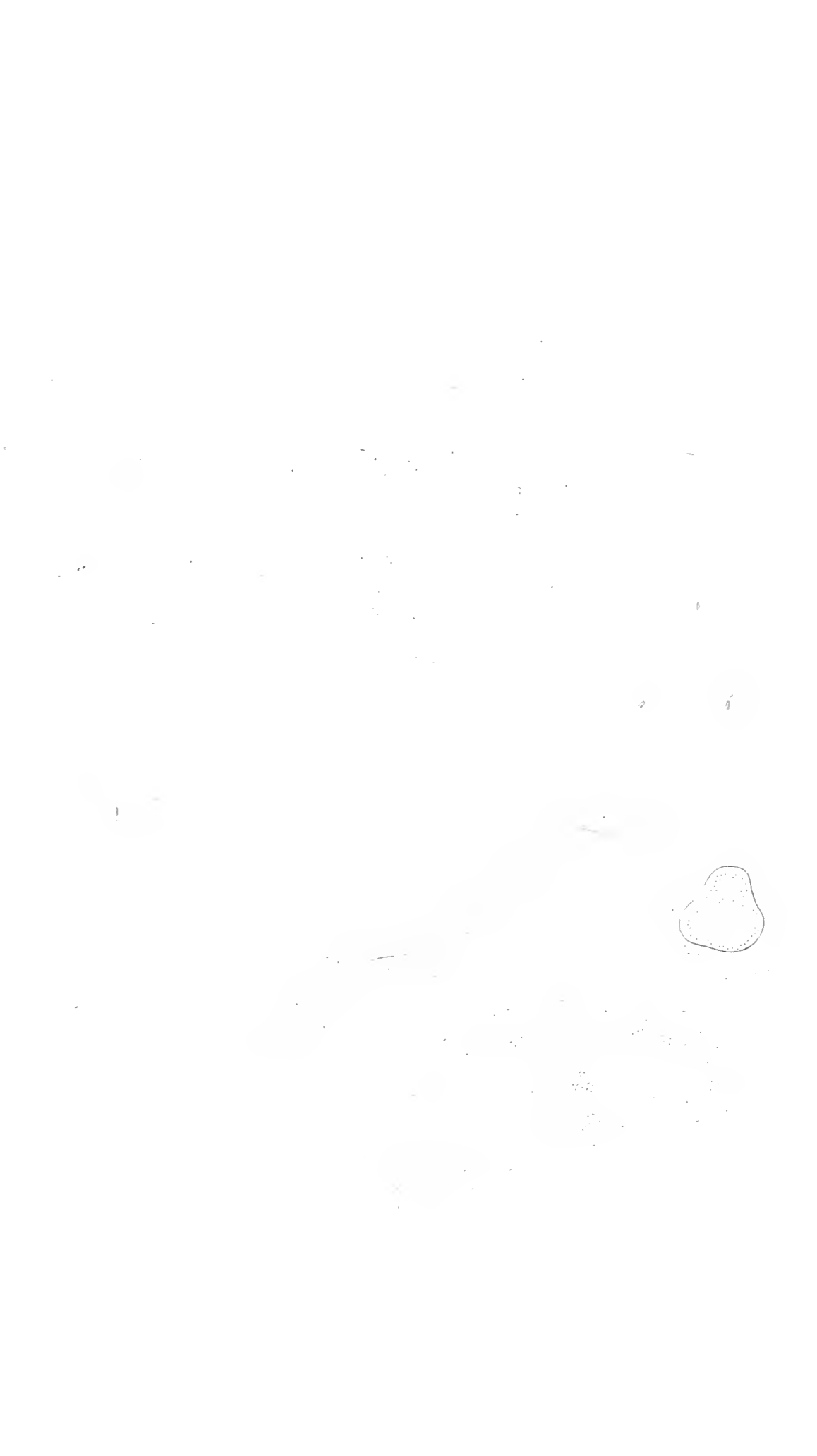

PLATE V.

PORITES ASTRÆOIDES Lamarck.

FIG. 40.—Vertical section through a polyp, a little to one side of the oral aperture. The laterally folded stomodæal wall (*st.*) is included in section, with three mesenteries attached. Portions of three introverted tentacles (*t.*) are also included, the one to the left showing the external opening and the thickened apex. The column wall to the left rests directly upon the thecal wall, while to the right a narrow canal permits of communication of the polypal cavity with the one adjacent. × 50.

FIG. 41.—Transverse section through the stomodæal region of a polyp with seven pairs of mesenteries—that is, one pair (A, A) more than usual—situated within the entocœle of the ventral directives (III, III). (The ventral surface is placed above and the dorsal is below, a reversal of the usual position throughout the drawings.) × 100.

FIG. 42.—Transverse section a little below the stomodæal region of a polyp having ten pairs of mesenteries—that is, four pairs (A—D) more than usual (*cf.*, fig. 11 b, p. 469). × 50.

ASTRANGIA SOLITARIA Lesueur.

FIG. 43.—Transverse section through the tentacular region of a retracted polyp, showing the relationship of the mesenteries, and the tentacular outgrowths from each mesenterial chamber (*cf.*, fig. 8g, p. 463). The exocœlic tentacles are the smallest, and the others vary in size according to the order of the entocœlic chamber from which each arises, the six largest communicating with the six primary entocœles (I). × 50.

FIG. 44.—Transverse section through a mesenterial filament, immediately below the stomodæal region, and part of the skeletotrophic tissue lining the wall of the septal loculus (*sk.*). At this level the filament does not differ histologically from the stomodæal ectoderm, and the skeletotrophic endoderm is very narrow. The calicoblast layer is practically absent, only a few nuclei occurring here and there. × 300.

FIG. 45.—Transverse section through a mesentery, and part of the lining of the septal loculus in which it is inclosed. The mesenterial filament is here more characteristic in form, and the endodermal epithelium immediately behind is much swollen on each side. The skeletotrophic endoderm is now greatly thickened and highly granular. The dark circular bodies are probably nutritive particles. × 300.

PHYLLANGIA AMERICANA Milne Edwards & Haime.

FIG. 46.—Two polyps, united only by a basal skeletal expansion. The column wall is so transparent as to allow the skeleton to be seen through. The polyp to the left is nearly fully expanded, the peristome protruding as high as the tentacles; the polyp to the right is partly retracted, the column wall nearly covering the tentacles. The tentacles are knobbed and tubercular.

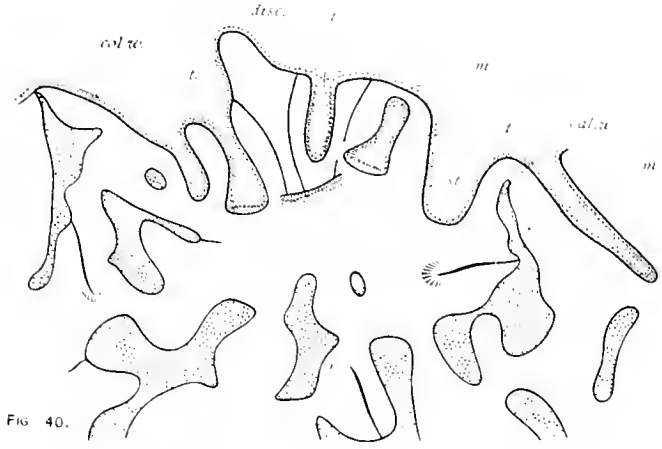

FIG. 40.

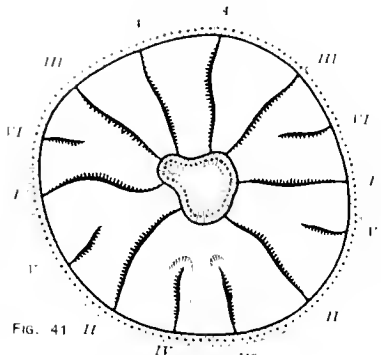

FIG. 41.

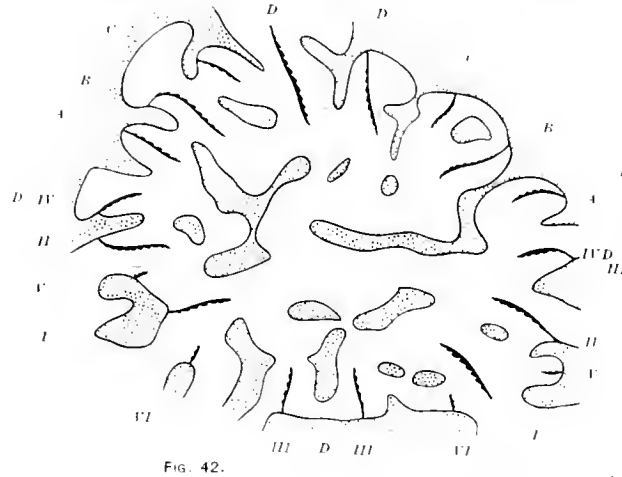

FIG. 42.

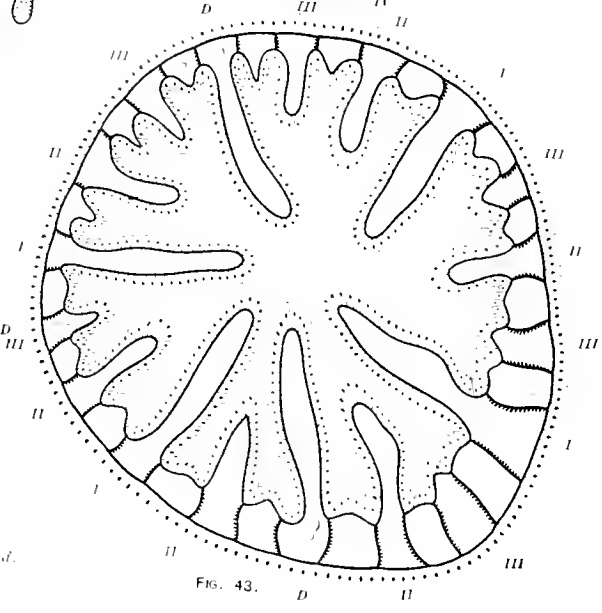

FIG. 43.

FIG. 45.

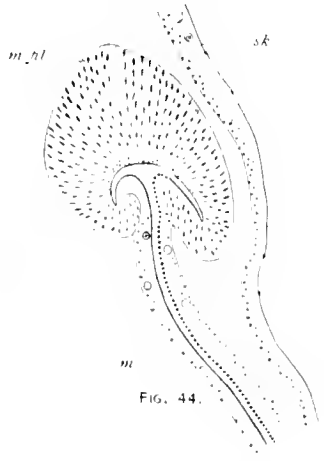

FIG. 44.

FIG. 46.

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PLATE VI.

ASTRANGIA SOLITARIA Lesueur.

FIG. 47.—Transverse section of a polyp through the stomodæal region. The mesenterial notation is given in fig. 8e, p. 462. At this level some of the mesenteries stretch in undivided continuity from the column wall to the stomodæum, only sections of the exsert septa being represented; others are already separated into calicular and pericalicular parts by the upgrowth of the thecal wall. × 50.

CLADOCORA ARBUSCULA (Lesueur).

FIG. 48.—Portion of a colony constituted of two subcolonies, one having three united polyps and the other two.

FIG. 49.—Transverse section through the stomodæal region of a polyp, presenting the relationships of the mesenteries and septal invaginations. The perithecal part of the polyp is not represented. (See also p. 458.) × 50.

FIG. 50.—Transverse section of a retracted tentacle, showing the distribution of the nematocysts in isolated projecting batteries. × 300.

FIG. 51.—Transverse section of a portion of a polyp through the lowermost part of the stomodæal region. The stomodæal ectoderm is reflected along each of the three mesenteries still connected with the stomodæum. The pair of directive mesenteries to the right are now altogether free, but each is capped by a tissue exactly like that lining the stomodæum. Mesenterial filaments are already developed on the incomplete mesenteries, which never reach the stomodæum. The perithecal parts of the mesenteries do not exactly correspond in number with the intercalicular mesenteries, those of the younger members not having yet reached so far. × 50.

FIG. 52.—*a*, Transverse section through a portion of the column wall. The ectoderm comprises mostly large gland cells, and the endoderm contains many zooxanthellæ. *b*, Transverse section through a part of the lower stomodæal region. The ectoderm is constituted mainly of ciliated supporting cells and granular gland cells, those in the deeper parts of the layer differing from the more peripheral. × 320.

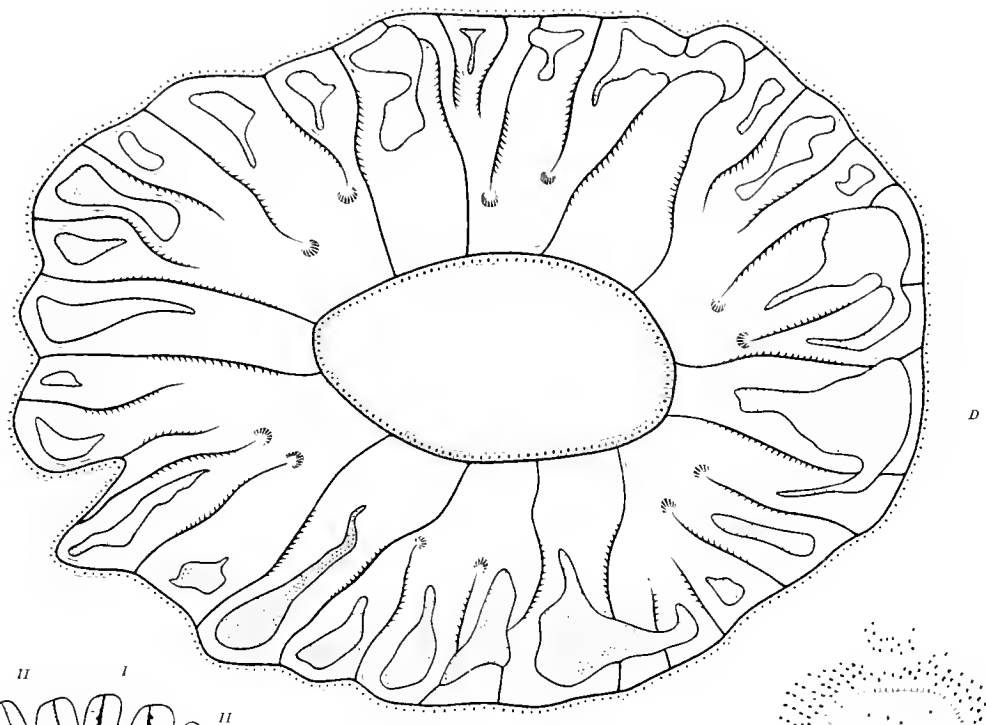

FIG. 47.

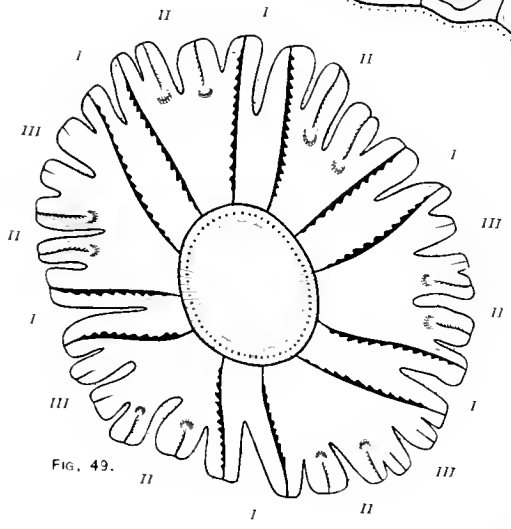

FIG. 49.

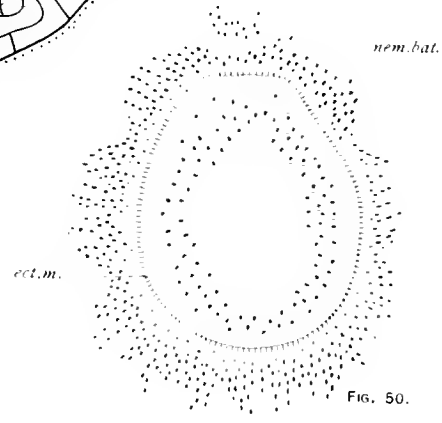

FIG. 50.

FIG. 48.

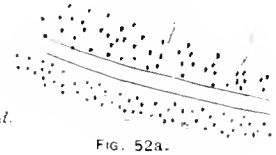

FIG. 52a.

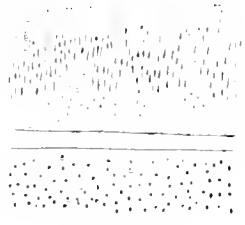

FIG. 52 b.

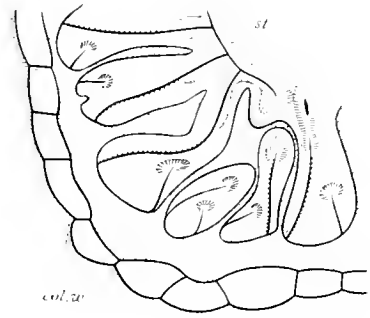

FIG. 51.

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PLATE VII.

CLADOCORA ARBUSCULA (Lesueur).

FIG. 53.—Transverse section of an enlarged polyp, with a triangular stomodæal tube and three pairs of directives (D). The alternation of complete and incomplete mesenteries is irregular. × 50.

FIG. 54.—Transverse section through the lower part of a polyp, showing how the polypal cavity is encroached upon and subdivided into more or less distinct chambers by the septal ingrowths. The skeletotrophic endoderm is somewhat thickened, compared with its condition in the upper region. The perithecal parts of the mesenteries are now beginning to cease their connection with the skeletotrophic wall. · 50.

FIG. 55.—Transverse section of the same polyp at a still lower level. The perithecal part of the polypal wall is here absent, and the polypal cavity is broken up into twelve distinct loculi by the middle union of the septa. A remnant of the polypal cavity yet persists in the center. The mesenteries have nearly disappeared. × 50.

FIG. 56.—Vertical section through the middle part of the disk and the stomodæum, showing the folded character of the latter in retracted polyps. On the left side the stomodæal wall is in connection with a mesentery, while on the right it is free and narrowed. · 120.

FIG. 57.—*a*, Transverse section of the free extremity of a mesentery of the second order, showing the earliest appearance of the mesenterial filament. *b*, Transverse section through a mesenterial filament immediately on becoming free from the stomodæal region. *c*, The same filament some distance below the stomodæal region. (See p. 472.) · 320.

FIG. 58.—Section of a part of a convoluted mesentery, with the filament at each end containing large oval nematocysts with a spiral thread. · 250.

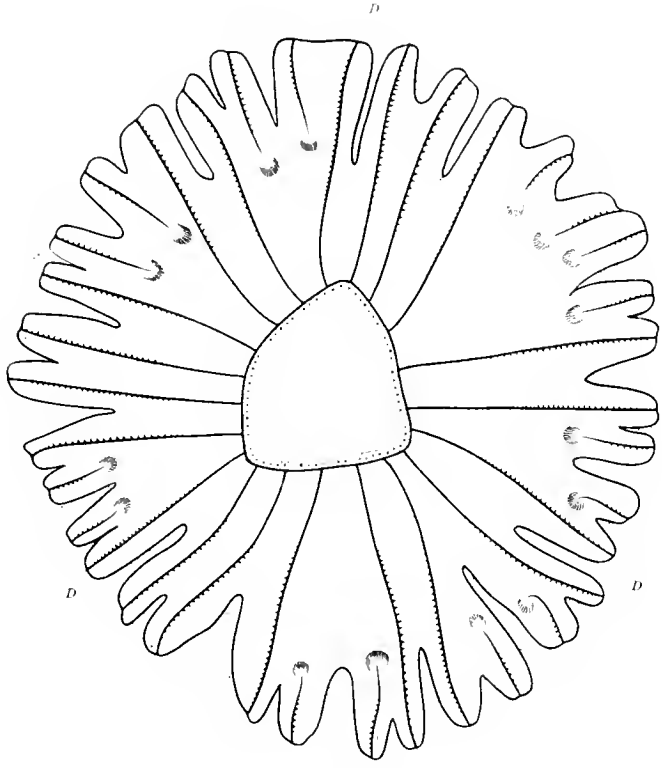

FIG. 53

FIG. 57a.

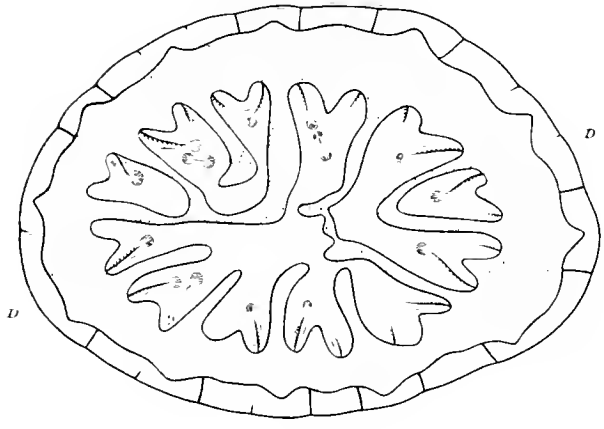

FIG. 54.

FIG. 57b.

FIG. 57c.

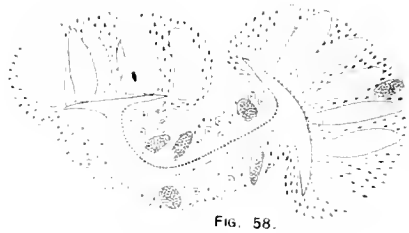

FIG. 58.

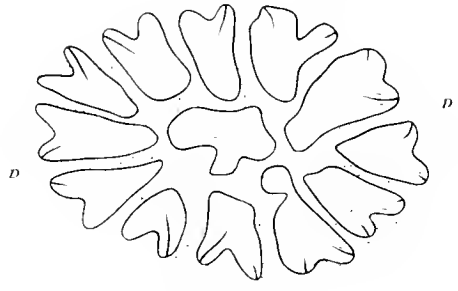

FIG. 55.

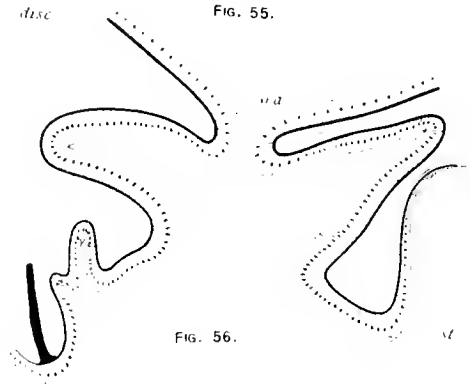

FIG. 56.

PLATE VIII.

CLADOCORA ARBUSCULA (Lesueur).

FIG. 59.—Transverse section through a part of the discal region of a retracted polyp, with two attached mesenteries (directives) and the entocoelic septal invagination (*sep. inv.*). The skeletogenic ectoderm (*cal.*) lining the inner calicinal wall is a very distinct layer at this level, and also along the innermost part of the invagination, but is absent from the lateral surfaces. × 320.

FIG. 60.—Transverse section through the elevated peristome of a bud polyp. Five pairs of complete protocnemes are present; the incomplete sixth pair is represented below, along with the six pairs of first-cycle metacnemes. The reflected stomodæal ectoderm (*r. ect.*) is seen on the left side (*cf.*, fig. 51). × 120.

FIG. 61.—Transverse section of a bud polyp with eight complete mesenteries, which at the level represented are filamentiferous. Two unilateral pairs of metacnemes (A,A) have appeared on the ventral, sulcar, or outer border. × 70.

FIG. 62.—Transverse section of a pentameral bud polyp, with the metacnemic pairs showing successive stages in development from the lower (abaxial) to the upper (axial) aspect. × 70.

FIG. 63.—Section of the upper skeletotrophic layer, where the calicoblast layer is well developed. Desmoidal processes are indicated by the striated bodies, but in the section are free from the mesoglœa. × 320.

ORBICELLA ANNULARIS (Ellis & Solander).

FIG. 64.—Radial section through the column wall, perforated for the passage of a mesenterial filament and the mesentery to which it is attached. (See p. 475.) × 300.

FIG. 65.—Radial section through the infolded edge of the column wall of a retracted polyp. The endodermal musculature forms a weakly diffuse endodermal sphincter muscle; pigment granules occur in groups in the ectoderm of the outer part of the wall. × 300.

FIG. 66.—Section through the skeletotrophic tissue lining the upper part of the theca. The edge of the broad calicoblast layer (*ect.*) is irregularly jagged. × 400.

FIG. 59

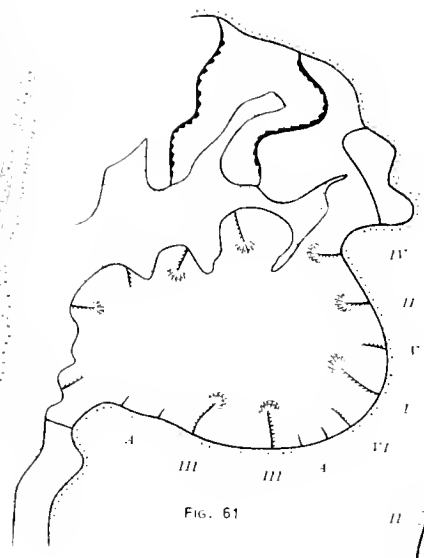

FIG. 61

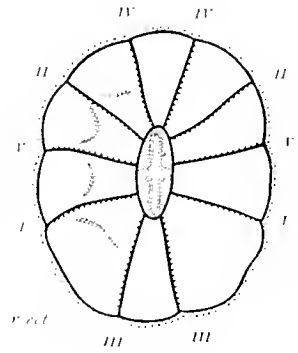

FIG. 60.

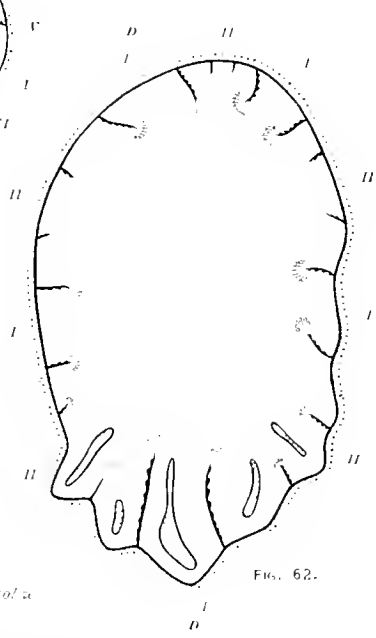

FIG. 62.

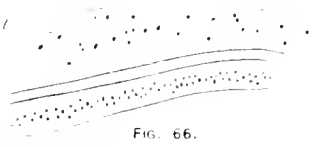

FIG. 66.

FIG. 63.

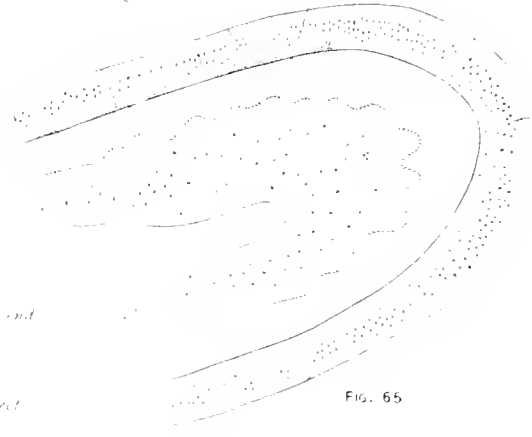

FIG. 65

FIG. 64.

PLATE IX.

ORBICELLA ANNULARIS (Ellis & Solander).

FIG. 67.—Radial vertical section of a decalcified, partly expanded, polyp. The column wall on each side passes uninterruptedly into a tentacle, bearing nematocysts at the apex; the disk is elevated around the mouth, and is partly indrawn, the actual stomodæal ectoderm commencing a little within the tube. The mesenteries are represented by sections in different directions, and are limited in their distribution to the upper half of the polyp. On the left side a mesentery is cut obliquely, stretching from the column wall to the disk, and on the right side one stretches from the disk to the skeletotrophic lining of a septum. The two oval bodies a little above the middle are sections of the modified glandular mesenterial filaments, found within this and other species. The lower half of the polypal cavity is practically empty, but is largely intruded upon by the thickened endoderm of the skeletotrophic tissues. On the left side the polypal cavity is continued over the thecal edge, but its communication with the adjacent polyp is interrupted, while on the right side the continuity is preserved. Desmoidal processes (*des. pr.*) are strongly developed at the point of separation of the polyp and the others adjacent. × 70.

FIG. 68.—Transverse section through a complete and incomplete mesentery and the entoseptal invaginations which inclose them. The larger mesentery stretches from the thecal wall to the inturned column wall, and about the middle its mesoglœa is deeply folded on both faces for the support of the retractor and oblique musculature. Toward its insertion on the skeletotrophic tissues the mesogloeal foldings are more normal, and occur only on the face bearing the retractor muscle. The small incomplete mesentery bears a single ovum. No exoseptal invagination are present at this level. × 110.

FIG. 69.—Transverse section through a portion of a mesenterial filament which has become wholly glandular and greatly enlarged. Drops of the secretion are represented oozing out in places. The glandular cells are supported behind upon the swollen mesenterial endoderm. × 320.

FIG. 70.—Tangential section of a similar glandular filament. The middle gland cells are cut transversely, and are polygonal in outline, while the marginal are cut obliquely. × 320.

FIG. 71.—Free glandular and supporting cells from a mesenterial filament. × 450.

FIG. 72.—Transverse section through a mesenterial filament, showing the more usual structure, for comparison with the glandular modification in fig. 69. × 320.

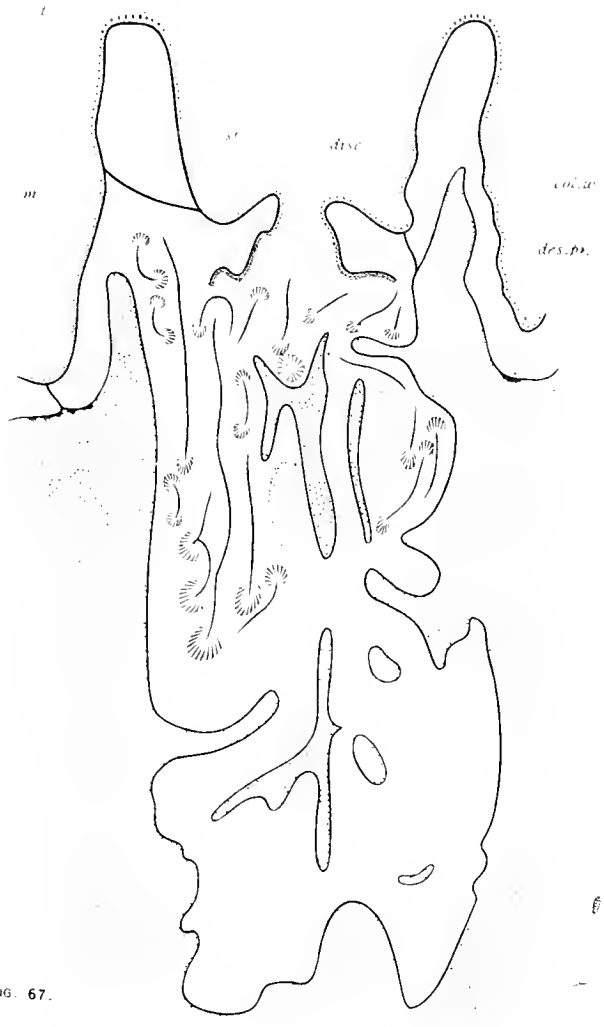

FIG. 67.

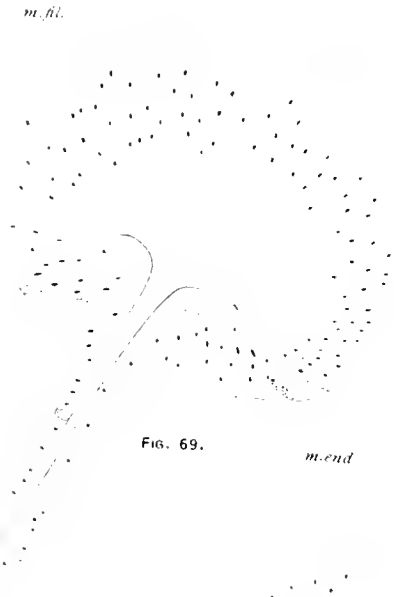

FIG. 69.

FIG. 70.

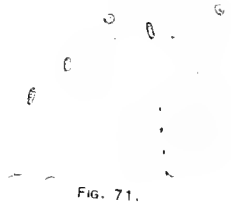

FIG. 71.

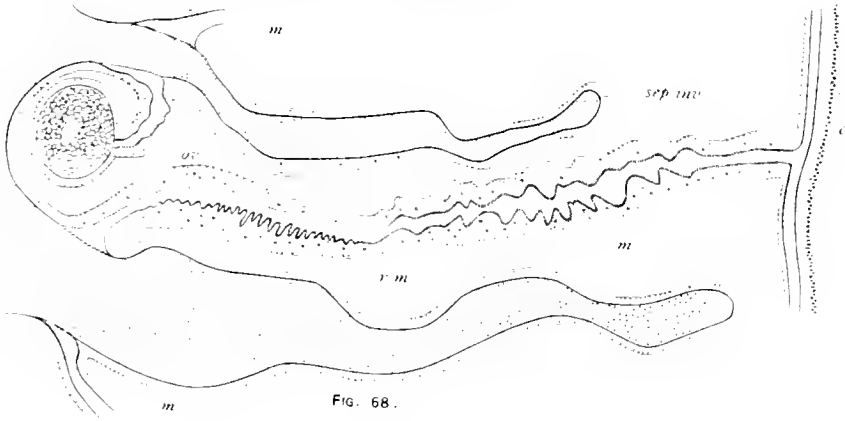

FIG. 68.

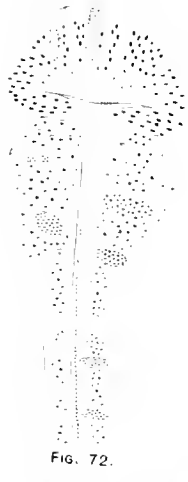

FIG. 72.

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PLATE X.

ORBICELLA ANNULARIS (Ellis & Solander).

Fig. 73.—Vertical section through the skeletotrophic tissue lining an interseptal chamber at its basal termination. *In situ* the basal part of the loculus would rest upon a skeletal dissepiment. The endoderm at the sides is greatly thickened, measuring 0.1 mm. in section, and is largely vacuolated with but few protoplasmic contents; the calicoblast layer of the lateral walls has nearly disappeared. The endoderm at the flattened termination of the loculus is much narrower, and closely resembles the layer in the upper parts of the polyps. The calicoblast ectoderm (*cal.*) is also a well-developed columnar epithelium, resting upon the skeletal membrane (*sk. m.*). The latter is well shown, and in some places is united with the ectoderm and in others free from it. At the left edge it is continued along the lateral wall. Desmoidal processes from the mesoglœa are developed, extending across the calicoblast layer to the skeletal membrane. The active condition of the calicoblast probably denotes that the formation of a dissepiment was in process when the polyp was preserved. × 300.

SOLENASTREA HYADES (Dana).

Fig. 74.—Group of five polyps. The uppermost is nearly fully expanded; the others are in different states of retraction. In some the tips of the tentacles are just visible, while in others they are completely covered by the overfolded column wall, only the middle of the peristome being visible. Enlarged.

Fig. 75.—Transverse section through a portion of the upper region of a retracted polyp. The section includes a knobbed tentacle, and shows the lateral nematocysts arranged in projecting groups. The nerve fibers are also clearly seen at the base of the knob. The ectodermal and endodermal musculatures of the tentacles are cut obliquely, and the latter is seen in continuity with the musculature of the mesenteries. The skeletotrophic endoderm is here a very narrow layer (*cf.* fig. 79), and the calicoblast layer has almost disappeared. × 300.

Fig. 76.—Vertical section through the column wall, showing the arrangement of the clear gland cells in the ectoderm. × 900.

Fig. 77.—Tangential section through the ectoderm of the column wall, to the outside of the nuclear zone. The interstitial supporting cells only partly separate the gland cells, which are polygonal in transverse section. × 900.

Fig. 78. Tangential section through the ectoderm of the column wall at the level of the middle nuclear zone. × 900.

Fig. 79.—Longitudinal section through the skeletotrophic layers toward the lower termination of the polyp. The endoderm is greatly thickened, and contains many large granules, either scattered or aggregated within distinct cells. The calicoblast layer is finely granular, and presents no cell outlines. × 300.

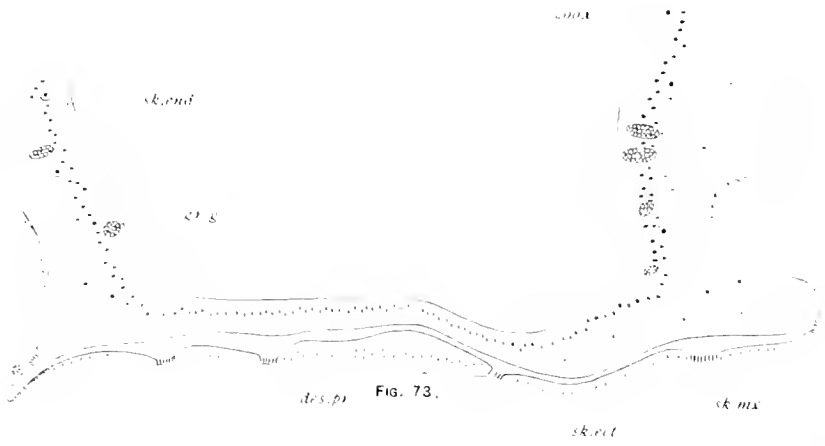


FIG. 73.

FIG. 74.

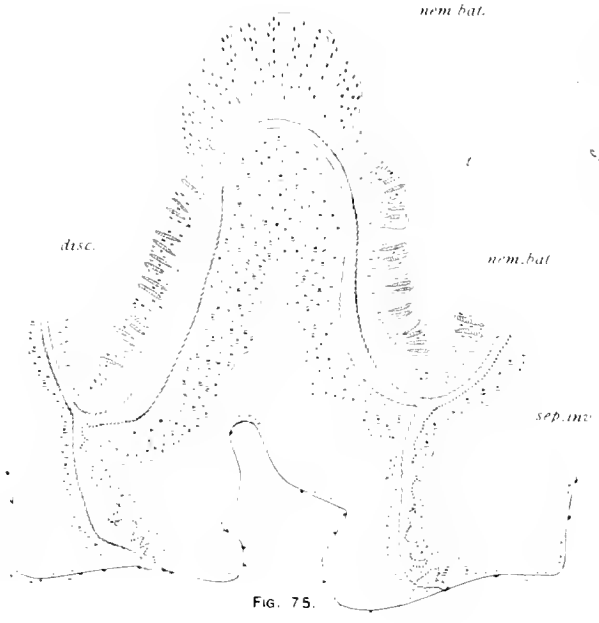


FIG. 75.

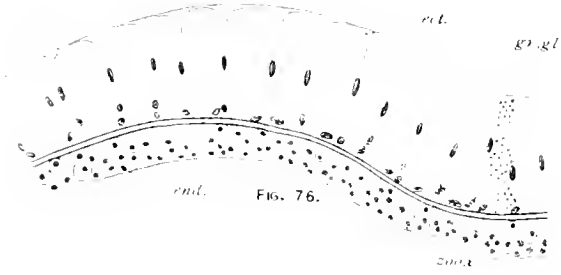


FIG. 76.

FIG. 77.

FIG. 78.

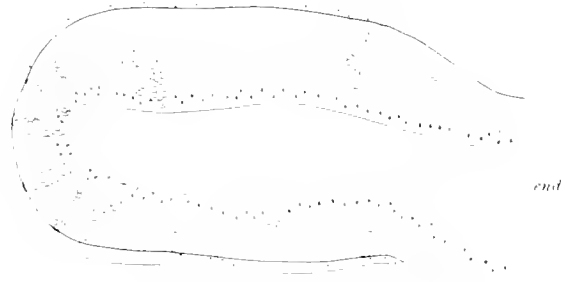


FIG. 79

PLATE XI.

SOLENASTREA HYADES (Dana).

FIG. 80.—Transverse section through the upper part of a retracted polyp. At this level all the mesenteries extend from the thecal wall to the inturned column wall. × 100.

FIG. 81.—Transverse section through the stomodæal region of the same polyp, showing the relationships of the two orders of mesenteries and the septal invaginations. × 100.

FIG. 82.—Transverse section through the stomodæal region of a bud polyp. The protocnemes are at the Edwardsian stage of development, and a pair of metacnemes (A, A) has appeared within each of the middle primary exocoeles. × 110.

FIG. 83.—Oblique section of the same bud polyp, including the central peristome and the outer zone of tentacles. On the right side a tentacular protuberance is already formed from the entocoele of the rudimentary pair of metacnemes (A). × 110.

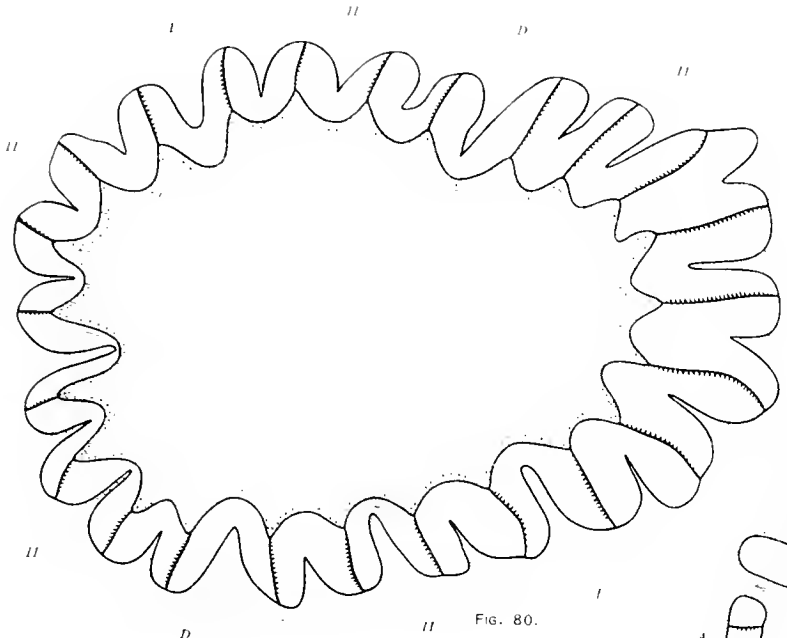


FIG. 80.

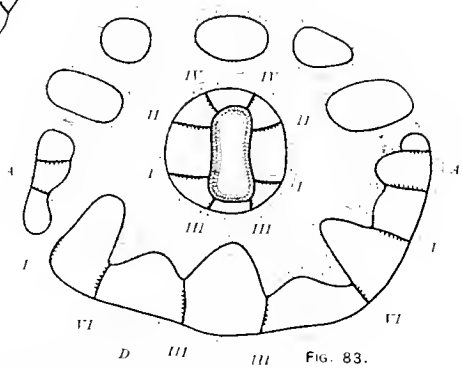


FIG. 83.

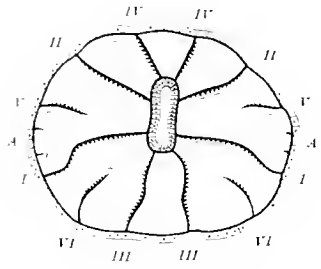


FIG. 82.

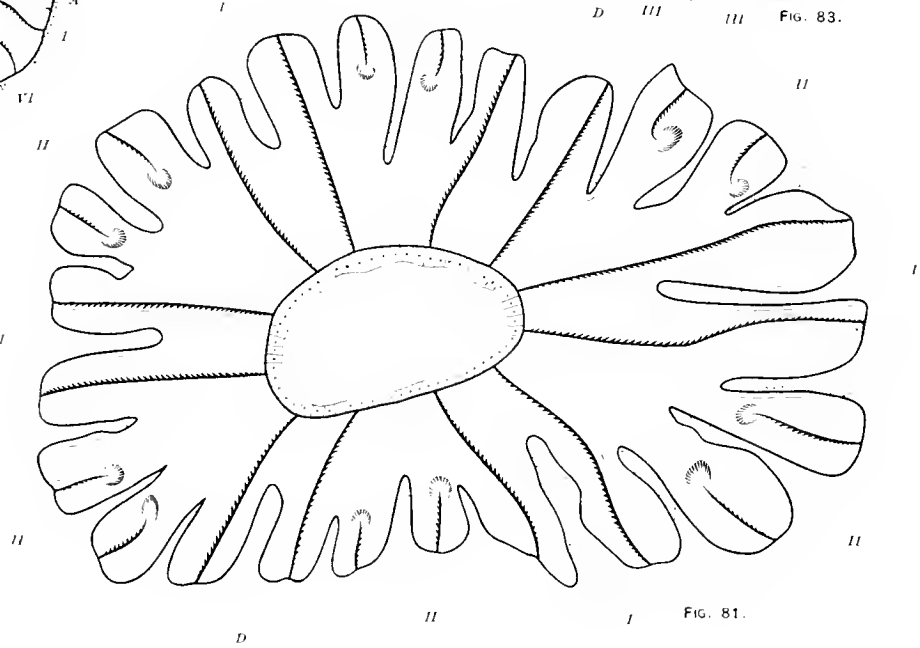


FIG. 81.

PLATE XII.

SOLENASTRÆA HYADES (Dana).

FIG. 84.—Transverse section through the lower region of the same polyp as that from which figs. 80 and 81 are taken. At this level the entocœlic and exocœlic septa are all fused in the middle to form the columella. Twenty-four distinct loculi occur, each containing a single mesentery. The outer indentations of the locular walls correspond with the strong granulations on the faces of the septa. × 100.

FIG. 85.—Transverse section through a septal loculus, about the middle of the length of the polyp. The filament of the included mesentery is somewhat incipient in character, not being sharply separated from the stomodæal endoderm. The skeletotrophic endoderm is comparatively narrow, and the calicoblast layer is well developed in places. × 300.

FIGS. 86–90.—Sections of a bud polyp taken at different levels, representing the order of appearance and relationships of the mesenteries and septa. In fig. 86 two metacnemic pairs (A, A) have appeared within the dorsal exocœles. For fuller description see pp. 456 and 499. × 100.

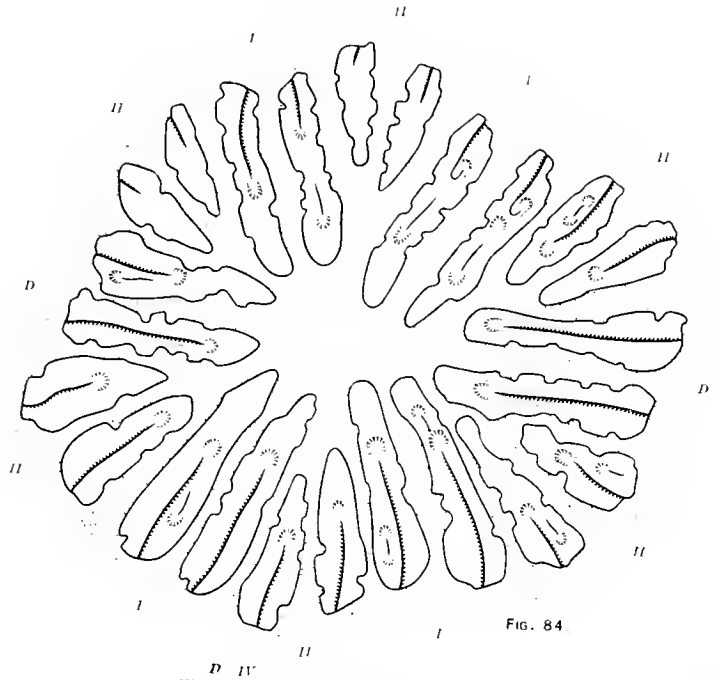


FIG. 84

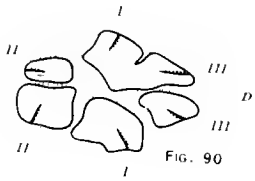


FIG. 90

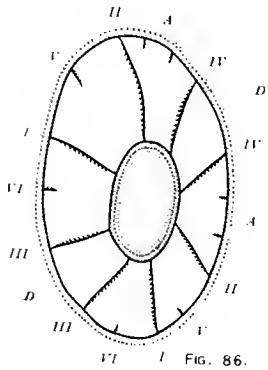


FIG. 86.

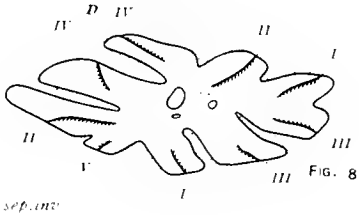


FIG. 89.

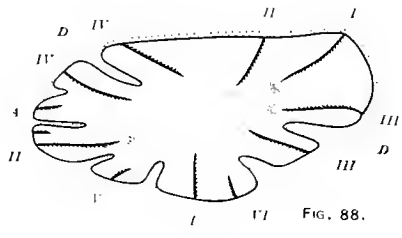


FIG. 88.

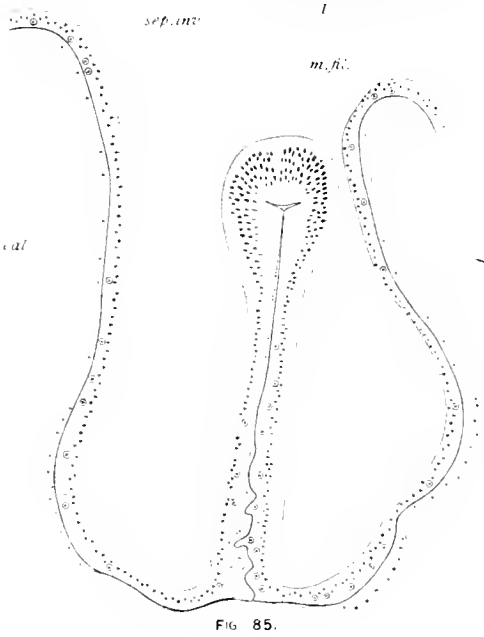


FIG 85.

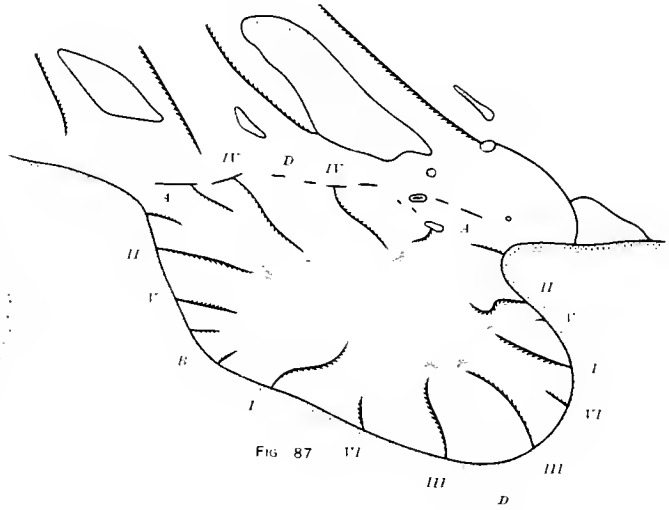


FIG 87

J. E. D. del.

PLATE XIII.

SOLENASTREA HYADES (Dana).

FIG. 91.—Transverse section through another bud polyp of *Solenastrea*, showing the proportional development of the mesenteries. (See p. 500.) × 100.

FAVIA FRAGUM (Esper).

FIG. 92.—Section of aboral surface of a decalcified polyp; the lateral invaginations correspond with the various septa, and the middle with the skeletal processes from the floor of the calice. No hexameral regularity can be established. 8.

FIG. 93.—Transverse section of a polyp through the stomodæal region, showing the irregular arrangement of the mesenteries and septal invaginations. The latter are mainly entocœlic. × 45.

FIG. 94.—Tangential section through a mesenterial filament in the lower region. The middle part is crowded with large nematocysts. × 320.

FIG. 95.—Section through a mesentery along the edge by which it is adherent to the corallum. Conical or wedge-shaped desmoidal processes (*des. pr.*) extend all the way, some of them being cut transversely toward the lower part of the section. × 320.

FIG. 95*a*.—Transverse section through a mesentery, just below the stomodæum. The mesentery is divided into two parts by a discal invagination which appears as a canal. (See p. 434.) × 70.

FIGS. 96–100.—Larvæ. Figs. 96–99 represent the various forms of the larva immediately after extrusion; fig. 100 with the oral pole swollen and the aboral narrow, the form often assumed a day or two after extrusion. Fig. 96 is viewed as a transparent object, the others by reflected light. Extrusion of cell débris is represented as taking place from the oral aperture in fig. 96. Enlarged.

FIG. 101.—Form assumed by larva which never attained fixation.

FIG. 102.—A free swimming larva, about 10 days old, in which twelve tentacular prominences occur.

FIG. 103.—A larva shortly after settling. The larva is now flattened, but non-transparent, and only four pairs of mesenteries are indicated on the outside.

FIG. 104.—Upper view of a distended, non-transparent larva, a few hours after settling. The twelve mesenterial chambers are already formed.

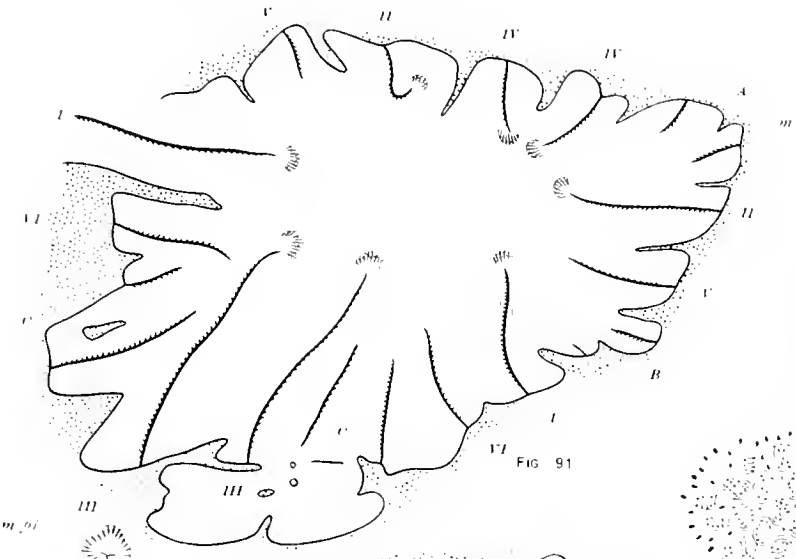


FIG. 91

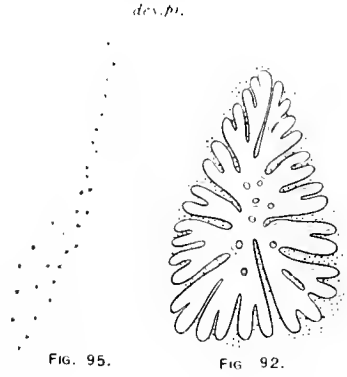


FIG. 95.

FIG. 92.

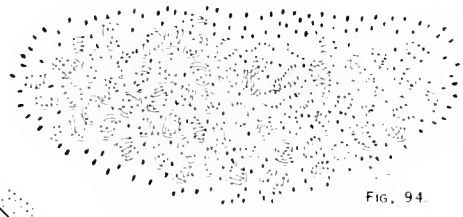


FIG. 94.

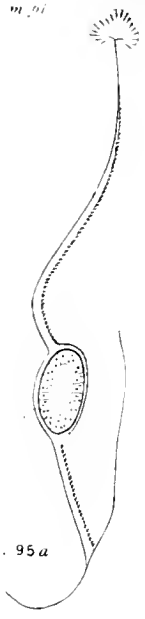


FIG. 95a

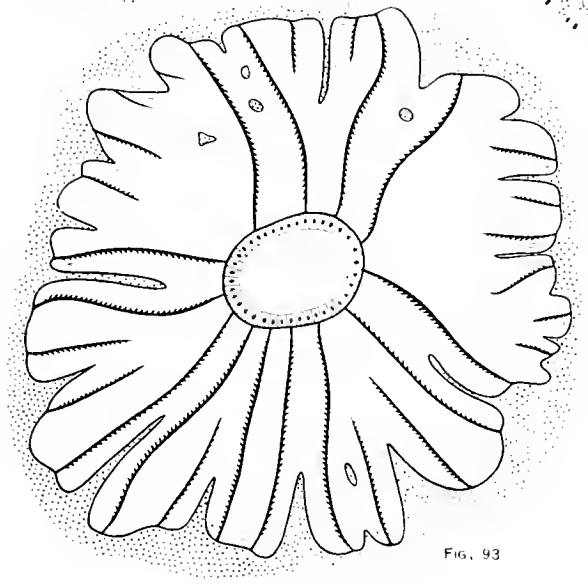


FIG. 93

FIG. 101.

FIG. 102.

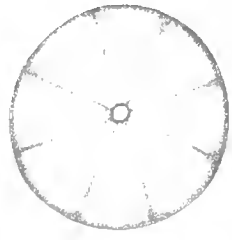


FIG. 103.

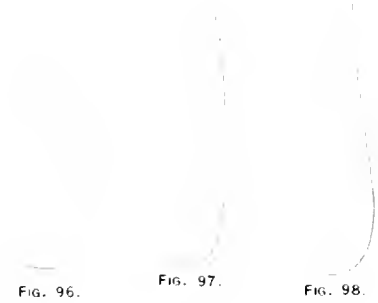


FIG. 96.

FIG. 97.

FIG. 98.

FIG. 99

FIG. 100.

FIG. 104

J. E. D. del.

PLATE XIV.

FAVIA FRAGUM (Esper).

FIG. 105.—A somewhat later larval stage than that represented on Pl. XIII, fig. 104. The Edwardsian mesenteries are complete, but the fifth and sixth pairs have not reached the stomodæum.

FIG. 106.—A young polyp, about a week after settling, with six equal entocœlic tentacular prominences; viewed from above.

FIG. 107.—Another young polyp, showing six tentacular prominences. About a week after settling.

FIG. 108.—A young polyp about three weeks after fixation. Tentacles were visible under certain conditions of expansion, but not in the preserved preparation from which the drawing was made, having evidently become part of the polypal wall. The four irregular dark patches associated with the two lateral complete mesenteries on each side represent the mesenterial filaments. The six oval lighter areas within the primary entocœles indicate the place of origin of the six primary septa.

FIG. 109.—A much later larval polyp, viewed from above. The twelve prototentacles are already established, and an additional tentacle has appeared within the dorsal and middle interspaces on each side. Transverse sections of the same polyp (p. 509) reveal that a pair of metacnemes has arisen on the column wall, within the dorsal and middle exocœle on each side, so that the additional tentacles are outgrowths of the entocœles of the new pairs of metacnemes. The entocœlic metatentacles, like the prototentacles, thus arise in advance of the exocœlic members (p. 432).

FIG. 110.—Vertical tangential section of the young decalcified polyp represented in fig. 108. The four complete mesenteries are seen in their vertical extent, and in such a section divide the polyp cavity into five chambers. The basal ectoderm (calicoblast layer) which produces the basal plate has almost disappeared. × 79.

FIG. 111.—The right half of the same section more highly magnified. Remnants of the calicoblast ectoderm are seen, along with feeble desmoidal processes, especially at the basal extremity of the mesenteries. × 300.

FIG. 112. Transverse section through the stomodæal region of a larva taken from a preserved fertile polyp: the dorsal surface is lower and the ventral is upper. Only three pairs of mesenteries are developed, one pair of which is complete; pair II, II is better developed than pair III, III. Cell débris and free zooxanthellæ are seen in the larval cavity, now well established. The "Reflected ectoderm" is well shown on the endodermal side of the stomodæum. × 250.

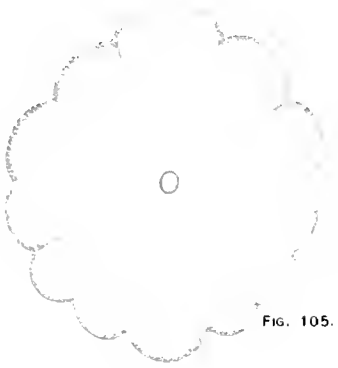


FIG. 105.

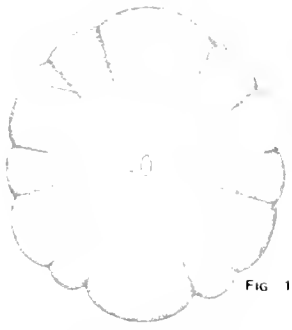


FIG. 106.

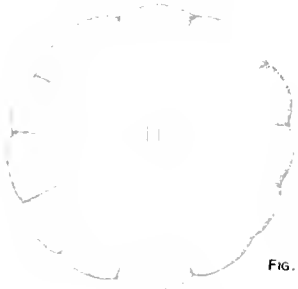


FIG. 108.

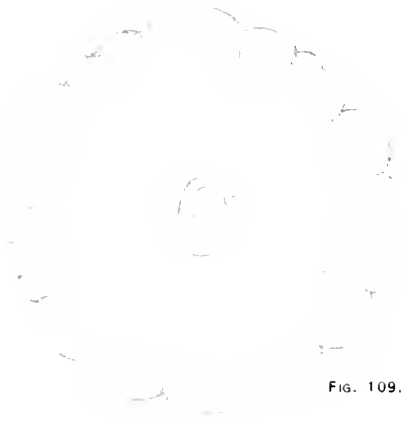


FIG. 109.

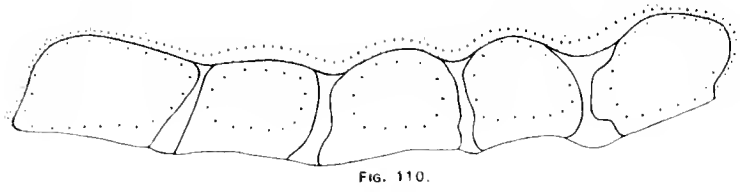
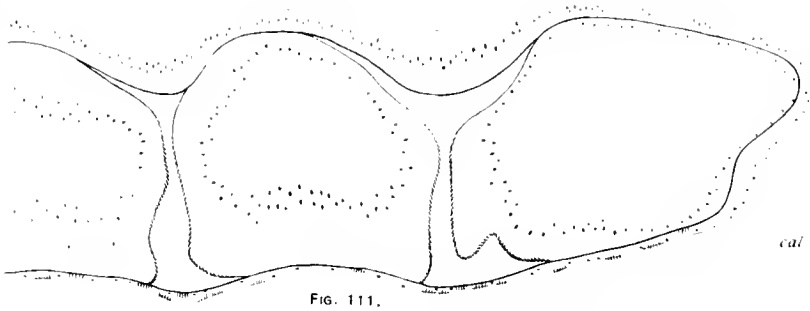


FIG. 110.

m



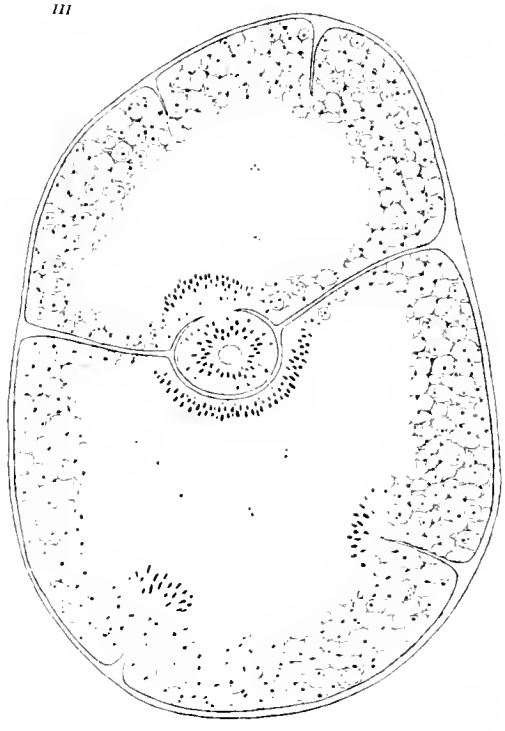
cal

FIG. 111.

III

III

FIG. 107.



I

II

I

II

FIG. 112.

J. E. D. del.

PLATE XV.

FAVIA FRAGUM (Esper).

FIG. 113.—Transverse section through the stomodæal region of a larva after six hours' extrusion. Two pairs of mesenteries are here complete. × 200.

FIG. 114.—Transverse section through the same larva, a little below the stomodæal region. Two additional pairs of mesenteries (IV, IV; V, V) are developed at this level, but no trace of a sixth pair. × 200.

FIG. 115.—Transverse section of a somewhat older larva. Three pairs of mesenteries are here complete, and the fourth and fifth pairs extend higher than in the last larva. × 200.

FIG. 116.—Transverse section of the same larva a little below the stomodæal region. Six pairs of mesenteries are now present, filaments occurring on the first three developmental pairs. × 200.

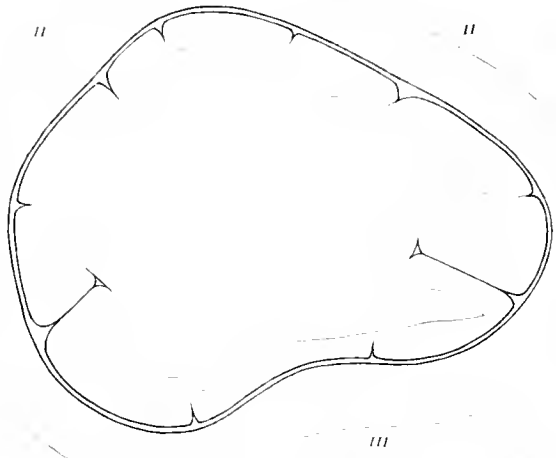


FIG. 114

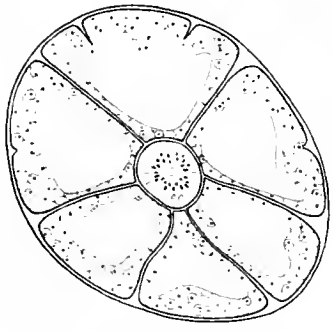


FIG. 115.

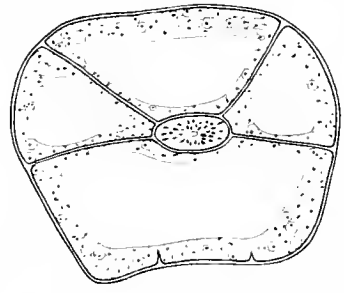


FIG. 113.

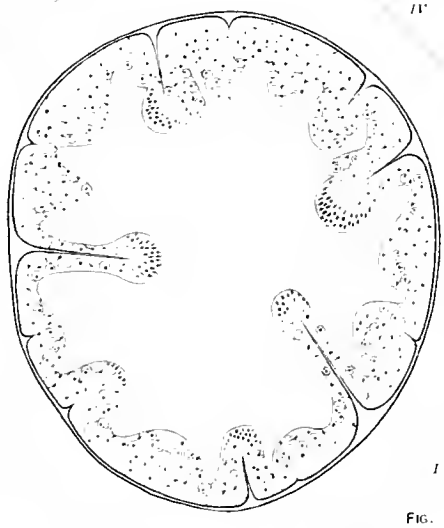


FIG. 116

J E D del.

PLATE XVI.

DICHOCŒNIA STOKESI Milne Edwards and Haime.

FIG. 117.—Transverse section through part of the upper region of a strongly retracted polyp, showing how the discal tissues may be drawn downward within the polypal cavity, so as to form the so-called mesenterial funnels (*cf.* fig. 95*a*). (See p. 434.) × 100.

FIG. 118.—Transverse section of the disk invaginated between two mesenteries. The section is much lower than that from which the former figure was taken. × 100.

FIG. 119.—Transverse section through a small separate polyp with four pairs of complete mesenteries, none of which are directives, and four incomplete pairs. The septal invaginations are mainly entocœlic. The stomodæal ridges and grooves are well shown. × 100.

FIG. 120.—Transverse section through a mesentery with complicated mesogloeal plaitings for the support of the retractor muscle. × 300.

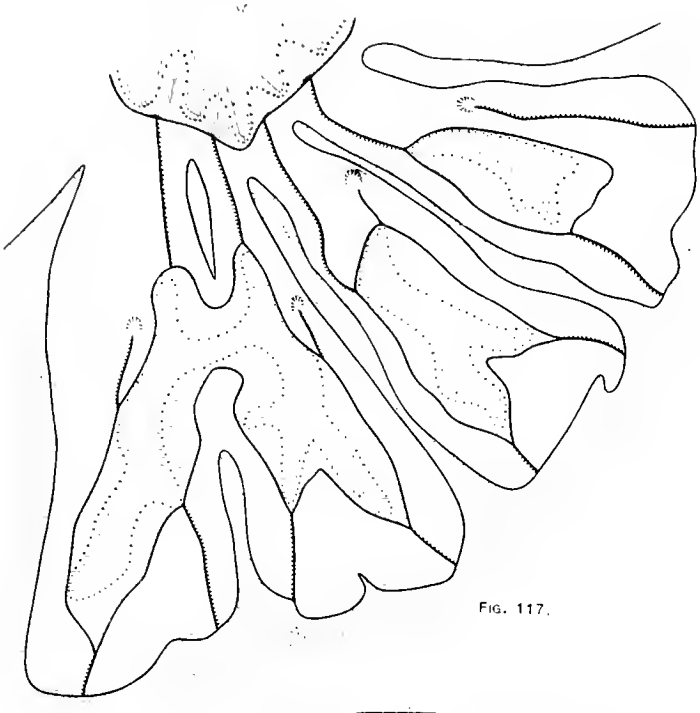


FIG. 117.

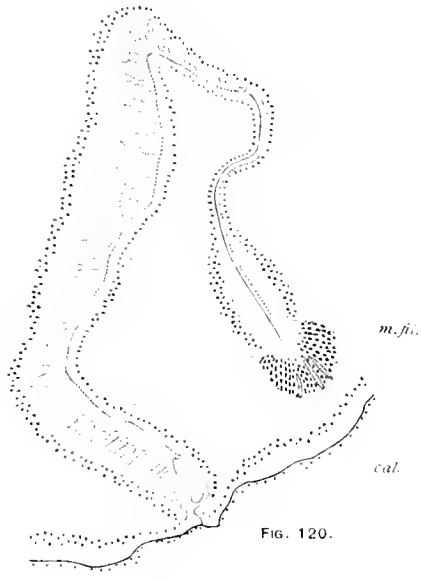


FIG. 120.

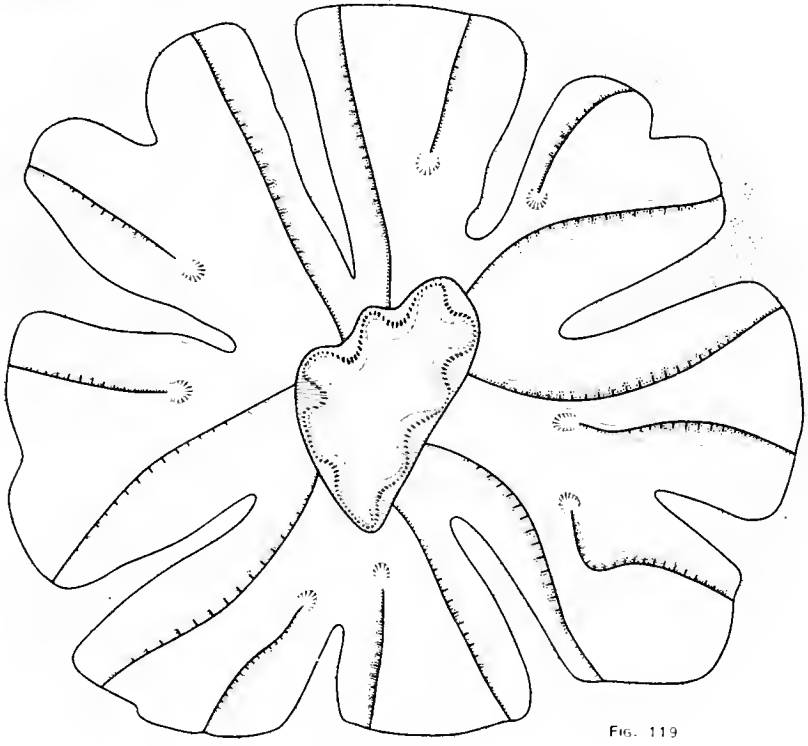


FIG. 119

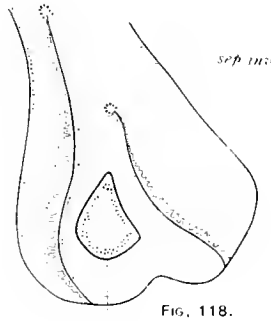


FIG. 118.

disc.

PLAT XVII.

ISOPHYLLIA DIPSACEA Dana.

FIG. 121.—Vertical section through the overfolded part of the column wall of a retracted polyp, showing the sphincter muscle supported on somewhat complicated mesogloeal foldings. × 200.

FIG. 122. Vertical section through a part of the column wall. Dark granular matter occurs in restricted patches within the ectoderm. × 220.

FIG. 123.—Free portion of a mesentery terminated by a mesenterial filament. The musculature is here very feeble, and the mesogloea is narrow and smooth on both faces. × 300.

FIG. 124.—Isolated nematocysts; *a*, from tentacular ectoderm; *b*, from mesenterial filaments. × 900.

FIG. 125.—Larva shortly after extrusion. The wall is partly transparent, and shows three pairs of mesenteries; one strongly developed pair extends practically the full length of the larva, while the two others extend but a short distance. Enlarged.

FIG. 126.—Transverse section through the uppermost stomodæal region of a freshly extruded larva. Two pairs of mesenteries with thickened mesogloea extend from the column wall to the stomodæum, but the ventral pair (III, III) is free. × 200.

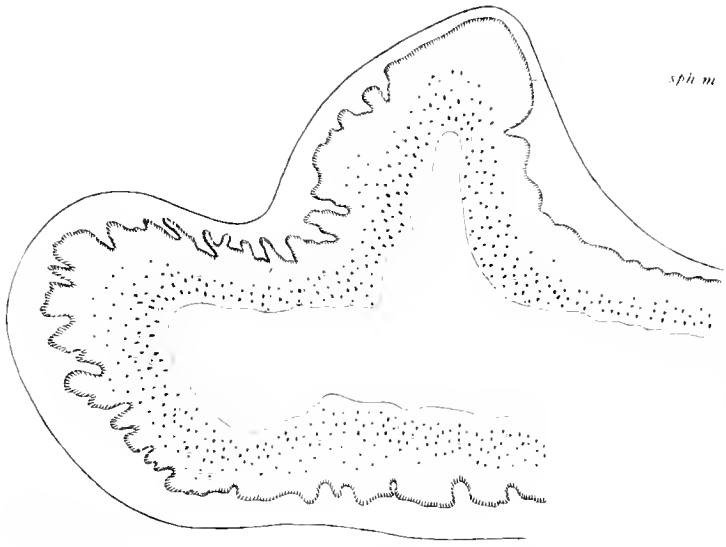


FIG. 121.

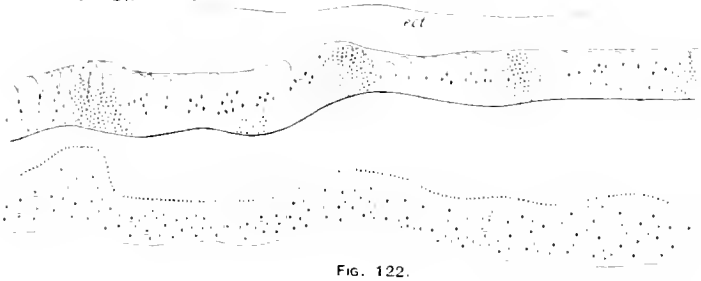


FIG. 122.

FIG. 123.

FIG. 124a.

FIG. 124b.

FIG. 125.

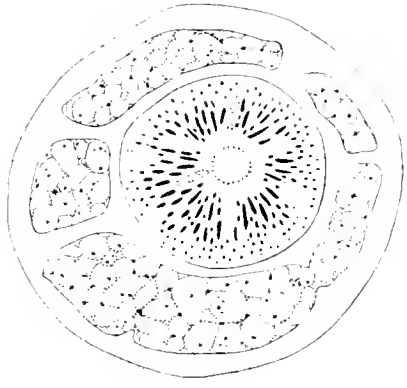


FIG. 126.

J. E. D. del.

PLATE XVIII.

ISOPHYLLIA DIPSACEA Dana.

FIG. 127.—Transverse section through the stomodæal region of the same larva as that from which the section represented on Pl. XVII, fig. 126, was taken. At this level the ventral pair of mesenteries has already disappeared, and the members of the dorsal pair are very rudimentary. "Reflected ectoderm" is seen on the upper and lower borders of the stomodæum. The larval cavity is occupied by a highly vacuolated tissue containing many zooxanthellæ. × 200.

FIG. 128.—Transverse section through the same larva below the stomodæal region. The members of one pair of mesenteries are very strongly developed and bear filaments. The polypal cavity is still filled with the vacuolar tissue, which shows divisions here and there, especially around the mesenterial filaments. An odd mesentery is strongly developed on the lower surface, and is probably to be regarded as an irregularity. × 200.

MANICINA AREOLATA Linnæus.

FIG. 129.—Transverse section through a complete mesentery toward the lower part of the stomodæal region, including the portion of the stomodæal wall and skeletotrophic tissue to which it is attached. The mesogloeal folds supporting the retractor muscle are simple, and mainly restricted toward the basal insertion of the mesentery. The muscular fibrils on the other face of the mesentary are well developed, especially toward the middle, where they are cut obliquely; elsewhere they are cut practically transversely. At this level the skeletotrophic endoderm lining the calicinal wall is greatly thickened and vacuolated, with very few protoplasmic contents, and the nuclei limited toward the margin; the skeletotrophic endoderm of the septal invagination is, however, very narrow. There are practically no remains of the calicoblast layer nor desmocytes, and the skeletotrophic mesogloea is a thin lamella. × 300.

FIG. 130.—Transverse section through an incomplete mesentery, terminated at its free extremity by a rudimentary mesenterial filament. The face of the mesogloea bearing the retractor muscle is very deeply plaited almost throughout its extent. A comparison with fig. 129 shows how greatly the mesogloeal folds may vary within the same species. × 300.

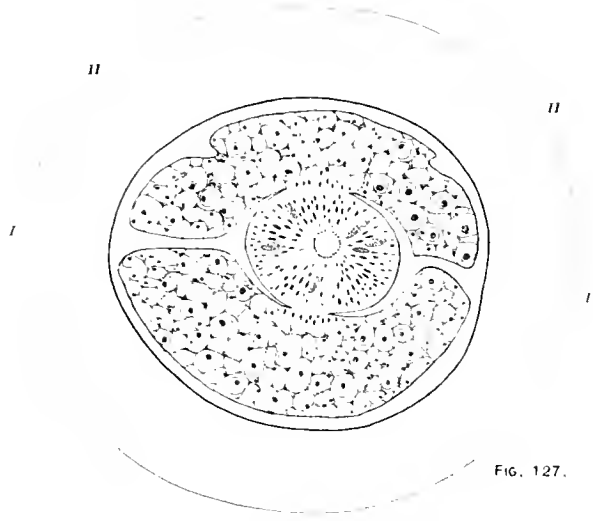


FIG. 127.

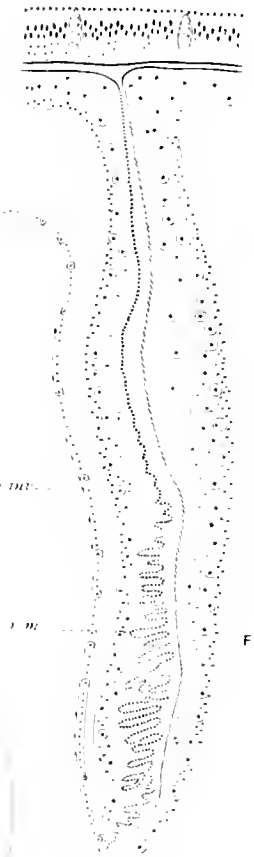


FIG. 129.

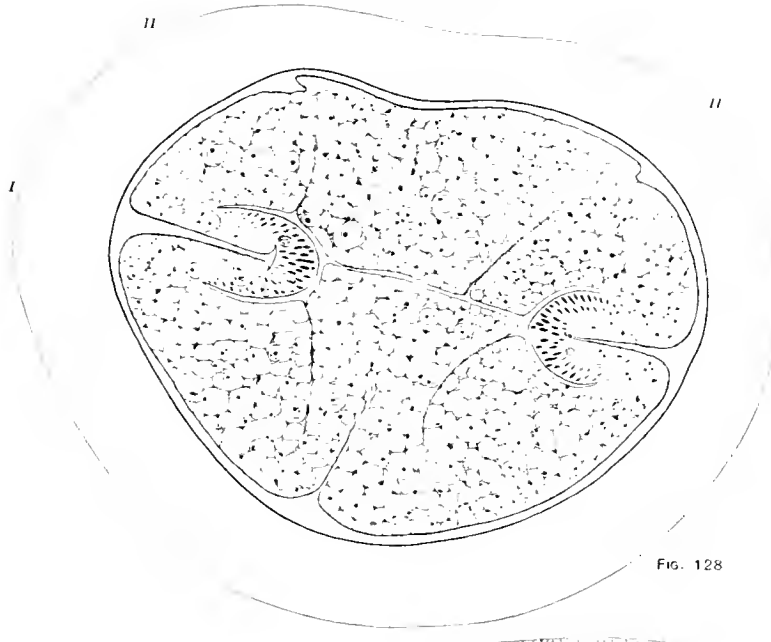
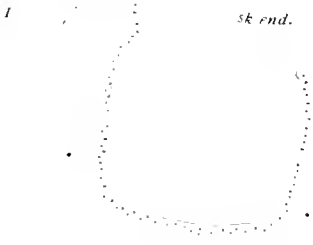


FIG. 128



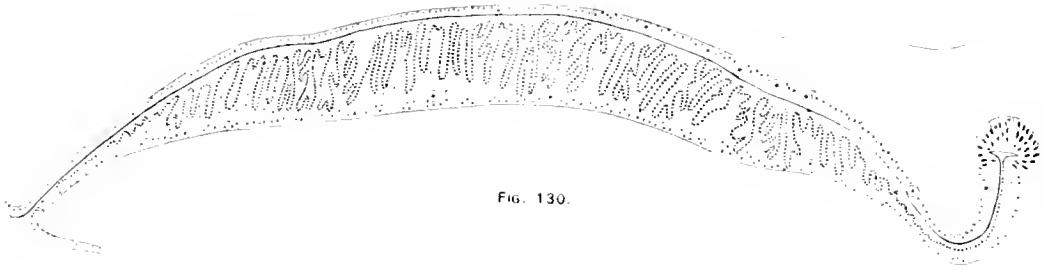


FIG. 130.

J. E. D. del.

PLATE XIX.

MANICINA AREOLATA Linnæus.

FIG. 131.—Transverse section through the stomodæum of a polyp, showing the relationship of the ridges and furrows to the internal attachment of the mesenteries. × 110.

FIG. 132.—Transverse section through a young polyp toward the inner termination of the stomodæum. The mesenterial plan is represented on p. 504, fig. 13*f*. At this level the edge-zone is already terminated at some places, but persists at others. Only certain of the perithecal continuations of the mesenteries extend thus far, and some have ceased their connection with the skeletotrophic wall, while retaining that with the column wall. The isolated portion of the column wall at the upper side of the figure is exceptionally distended, and only fragments of the mesenteries are included. × 70.

FIG. 133.—Freshly extruded larvæ. In the one viewed from above (*b*) three pairs of mesenteries are already united with the stomodæum, and three other pairs are free. Enlarged.

FIG. 134.—Another larva, about four days old, adherent to a plate of glass. The mesenteries are at almost the same stage as in the larva represented in fig. 133 (*b*), but pair III, III, has not yet reached the stomodæum. Enlarged.

FIG. 135.—Young polyp, twenty-one days after extrusion, fixed to glass and viewed as a transparent object. The tentacles are incapable of complete retraction, and appear as twelve spheroidal knobs arranged in two alternating cycles of six each. The eight Edwardsian mesenteries are complete, but the remaining four are incomplete. The skeleton is represented by six entocœlic radiating septa; the basal plate was also developed, but is not shown. × 70.

FIG. 136.—Another young polyp of the same age, in which the formation of the six septa has not proceeded regularly. The first trace of the columella appears in the middle. The tentacles are not distinctly seen, having become depressed in the discal wall. × 70.

FIG. 137.—Vertical section of the young polyp represented in fig. 136, after decalcification. The section passes through the wide oral aperture; the stomodæum terminates freely on the left side, but is in union with a mesentery on the right side. A tentacular thickening occurs on the left, and serves to delimit the oral disk and column wall. The basal disk is practically devoid of any ectodermal (calicoblast) layer, but toward the free column wall at each end it begins to appear. A septal invagination occurs on each side, the polypal wall resting upon them. Histologically the endoderm of the basal disk differs from that of the column and oral disk. × 200.

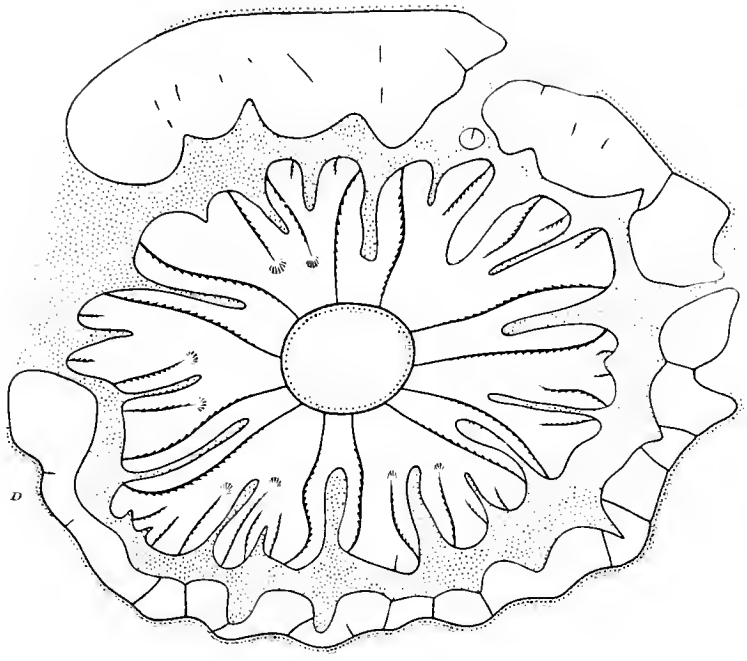


FIG. 132

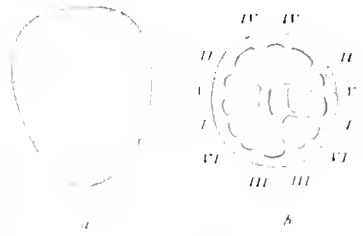


FIG. 133.

FIG. 136.

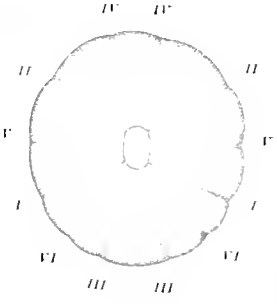


FIG. 134.

FIG. 135.

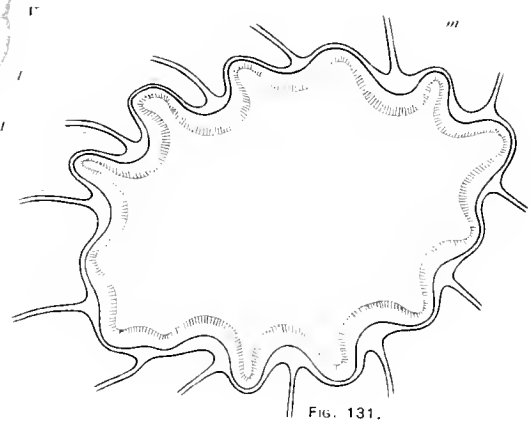


FIG. 131.

FIG. 137.

J. E. D. del.

PLATE XX.

MEANDRINA LABYRINTHICA (Ellis & Solander).

FIG. 138.—Transverse section through the upper part of the polypal tissues covering a collinal ridge; the column wall and mesenteries on one side belong to a different series of polyps from those on the other side. The irregular parts of the corallum included are the first traces of the exsert septa and thecal wall. The septa at this level are both entocoelic and exocoelic the former being much better developed. Certain of the mesenteries are free for some distance at their inner extremity, and others are already attached to the skeletotrophic tissues. The mesenteries are arranged at practically equal distances apart, and no directive pairs occur. The pairs of the two adjacent systems do not correspond. × 75.

FIG. 139.—Transverse section through the tentacular region of the same retracted colony. The middle skeletal area represents the thecal wall common to two polypal systems; small exoseptal invaginations occur in addition to the entoseptal. The rounded evaginations of the mesenterial spaces represent the tentacles; the entotentacles (*e.t.*) are larger than the exotentacles (*ex. t.*). × 75.

FIG. 140.—Section through an incomplete mesentery, and part of the wall of the septal loculus in which it is inclosed. Three ova and two spermaria occur within the mesentery. The skeletotrophic endoderm is highly vacuolated, the nuclei and protoplasmic contents aggregated mainly toward the margin. × 110.

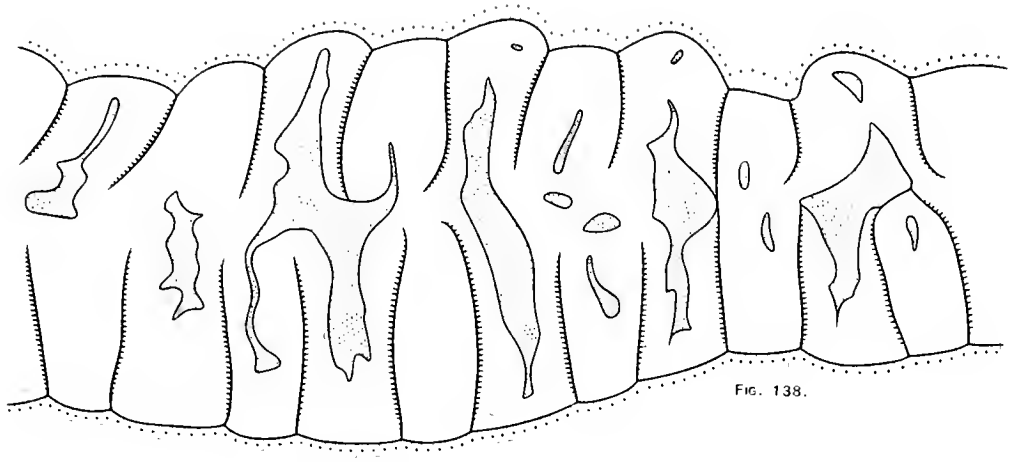


FIG. 138.

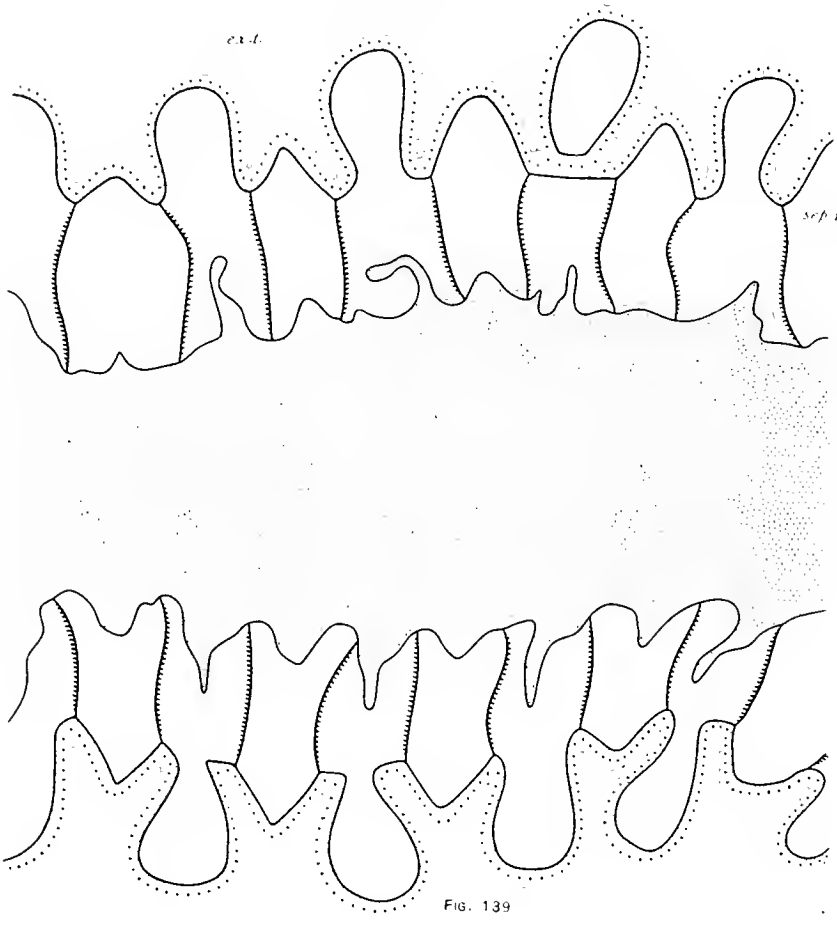


FIG. 139.

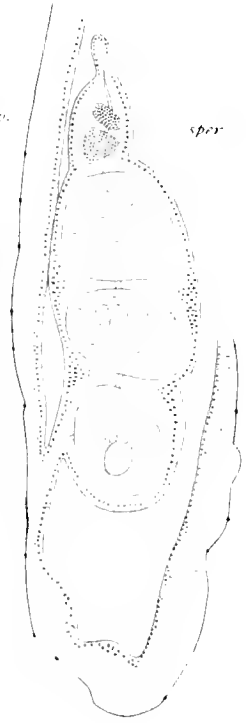


FIG. 140.

J. E. D. del.

PLATE XXI.

MEANDRINA LABYRINTHICA (Ellis & Solander).

FIG. 141.—Transverse section through the stomodæal region of part of a colony, including four stomodæa and their associated mesenteries. The number of mesenteries inserted on each stomodæum is variable, and in the portion represented no incomplete pairs occur. The septal invaginations at this level are mainly entocœlic. The line of separation between each stomodæal system passes through two entocœles, never through an exocœle. No pairs of directives ever occur. The endoderm is not represented. × 40.

FIG. 142. Transverse section at a still lower level, showing how the polypal cavity is encroached upon by the ingrowth of the entosepta and their fusion in the middle. In some cases the interseptal loculi thus produced are wholly distinct in section, but elsewhere several are in communication. The two mesenteries included within each loculus belong to adjacent pairs, no exosepta being present. × 140.

FIG. 143.—Section through a mesenterial filament and the swollen part of the mesenterial endoderm immediately behind. × 320.

FIG. 144.—Section through another filament, in which many of the cells on the left side are filled with granular contents. × 320.

FIG. 145.—Section through a part of a mesenterial filament in which the cells have all become enlarged and glandular, the modification having also affected the swollen endoderm behind (see p. 473). Three granular gland cells are found in the section, in addition to the clear gland cells. × 400.

FIG. 146.—Section through a mesentery containing two ova. × 300.

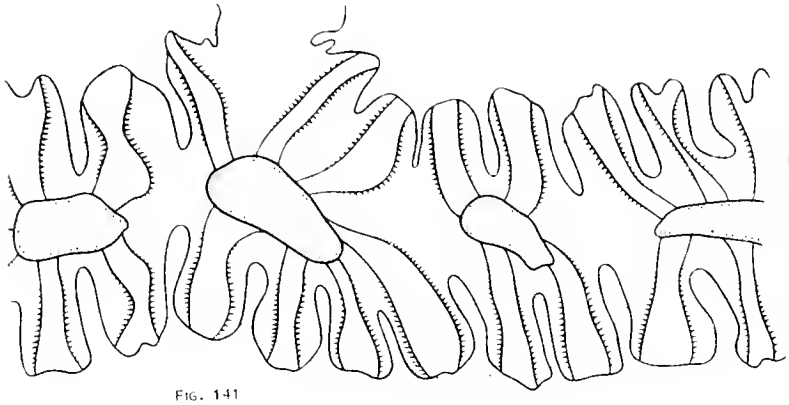


FIG. 141

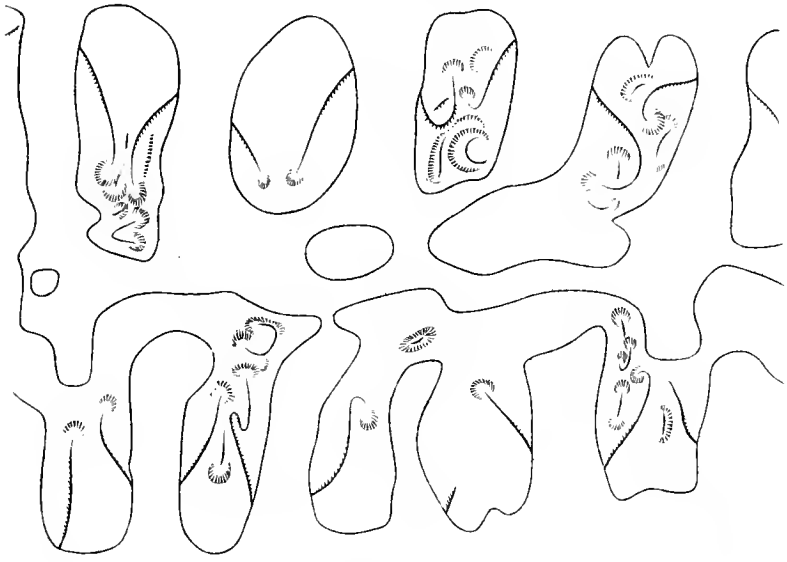


FIG. 142.

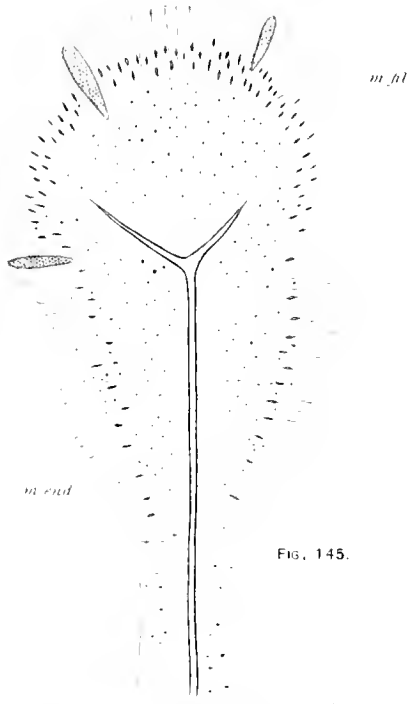


FIG. 145.

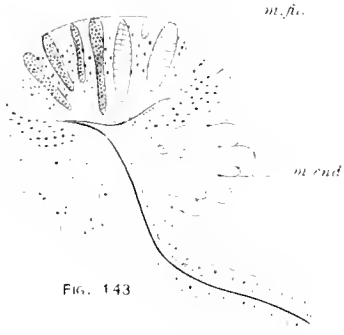


FIG. 143

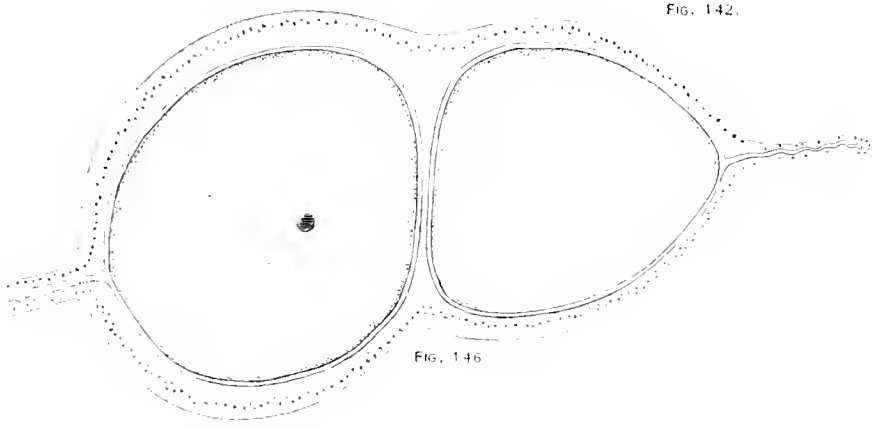


FIG. 146

FIG. 144.

PLATE XXII.

MEANDRINA LABYRINTHICA (Ellis & Solander).

FIG. 147.—Transverse section through two stomodæal ridges opposite the insertion of the mesenteries, showing the difference in histological character between the ectoderm of the ridges and that of the grooves. × 300.

COLPOPHYLLIA GYROSA (Ellis & Solander).

FIG. 148.—Section through the convolutions at the free extremity of a single mesentery; each convolution is terminated by a mesenterial filament. × 70.

OCULINA DIFFUSA Lamarck.

FIG. 149.—Portion of a branch of a living colony, showing the different forms assumed by the polyps on expansion and retraction.

SIDERASTRÆA SIDEREA (Ellis & Solander).

FIG. 150. Retracted polyp. The septa are seen through the partly transparent polypal walls, and superficially the arrangement of the entocœlic and exocœlic tentacles on the disk. The Roman numerals indicate the cycles to which the entotentacles and entosepta belong, the outermost cycle comprising only exotentacles and exosepta. The first, second, and third cycles of entotentacles and entosepta are complete, except that a third-cycle tentacle and septum are wanting in the lower left-hand system. In the upper left-hand system a fourth-cycle entotentacle and entoseptum have appeared.

FIG. 151.—Fully expanded tentacles: *a*, Bifurcated entocœlic; *b*, simple exocœlic. Enlarged.

FIG. 152.—An interseptal lamella from *S. radians*, freed by decalcification and slightly magnified. When *in situ* the lamella lines the two walls of an interseptal loculus and incloses a mesentery; the left vertical border is peripheral, the right central; the curved upper border is in continuity with the disk, the lower is adjacent to a dissepiment. The three vertical rows of apertures represent the spaces formerly occupied by synapticula. × 20.

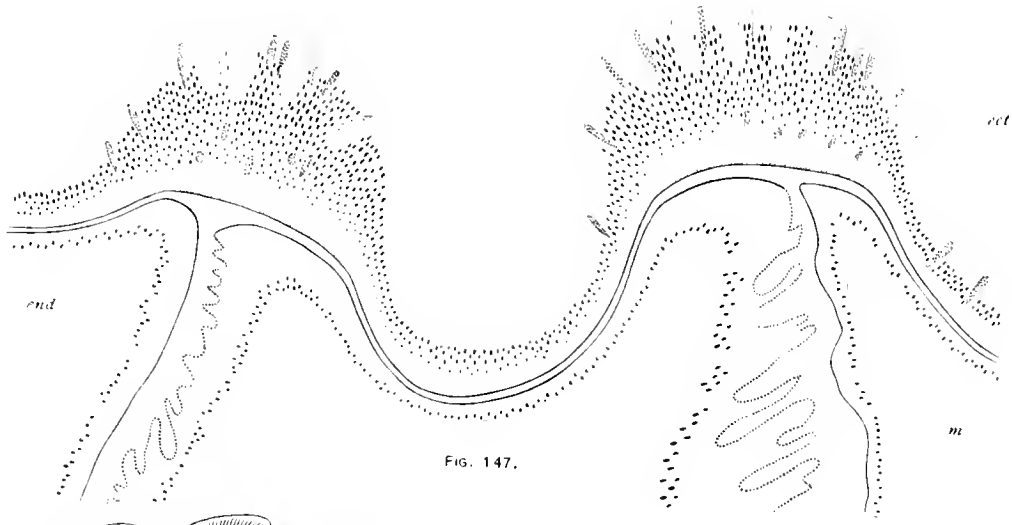


FIG. 147.

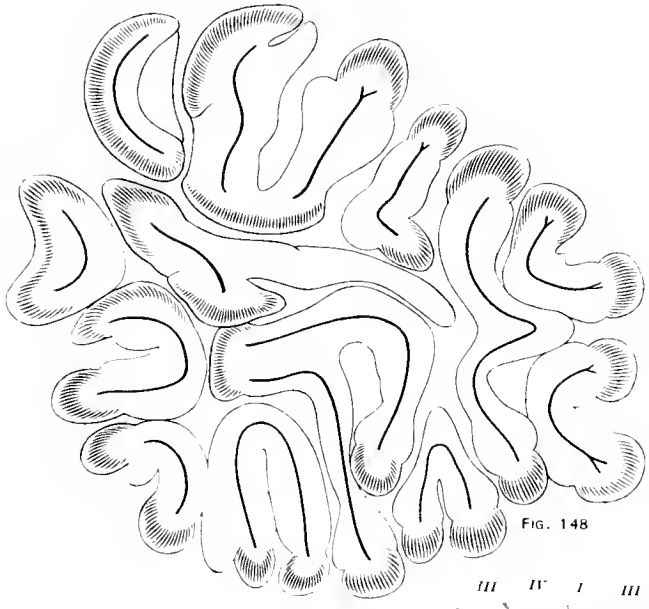


FIG. 148

FIG. 149.

FIG. 151

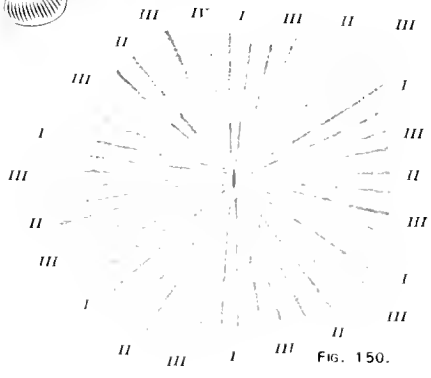


FIG. 150.

FIG. 152.

J. E. D. del.

PLATE XXIII.

SIDERASTRÆA SIDEREA (Ellis & Solander).

FIG. 153.—Transverse section through the stomodæal region of an adult polyp. Six pairs of complete mesenteries constitute the first cycle, six alternating pairs the second cycle, and only ten pairs are present in the third cycle. At this level the mesenteries nowhere extend as far as the peripheral limits of the interseptal loculi. Both mesenteries and loculi are interrupted by the synapticula which connect adjacent septa. Septa occur within both the entocœles and exocœles, and in some cases are fused at their central termination. × 100.

FIG. 154.—Transverse section through the upper part of the disk of a retracted polyp. The discal walls are resting directly upon the tissues covering the septal edges. The simple apical knobs of two exocœlic tentacles (represented diagrammatically) are seen lying directly over the edge of the exosepta. × 110.

FIG. 155.—Transverse section through the lower part of the disk of the same retracted polyp. The section at this level includes the synapticula, which are seen perforating the mesenteries, and an entocœlic tentacle with two apical knobs, one on each side of the entoseptum. × 110.

FIG. 156.—Tangential section through a part of the peripheral region of a polyp, exhibiting the short vertical extent of the mesenteries, and also the slight increase in thickness of the skeletotrophic tissue from above downward. The column wall rests directly upon the tissues covering the septa, and is thrown into ridges and grooves corresponding with the septa and mesenteries. × 70.

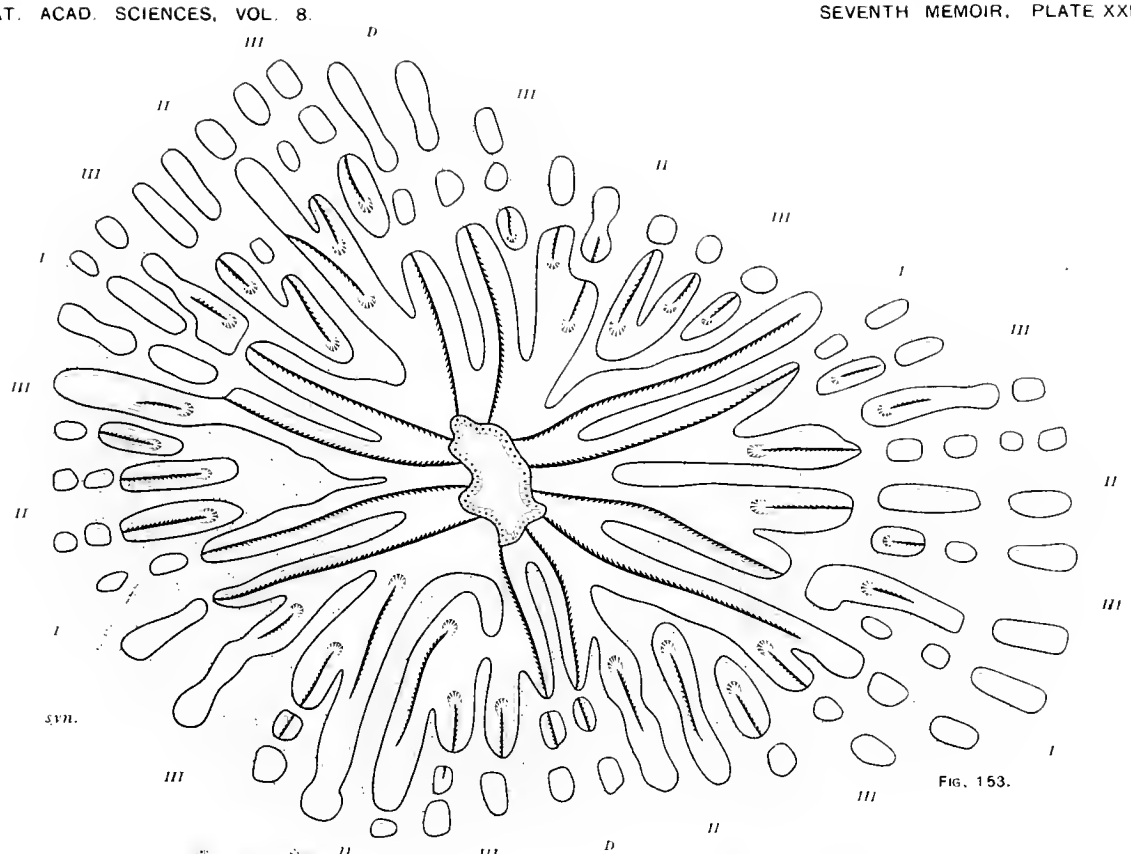


FIG. 153.

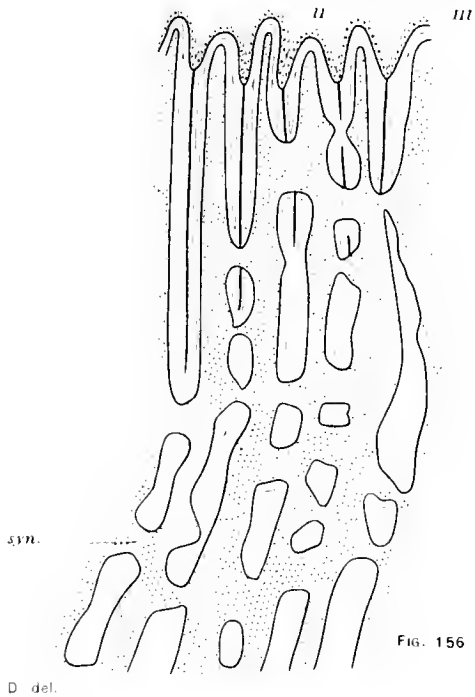


FIG. 156

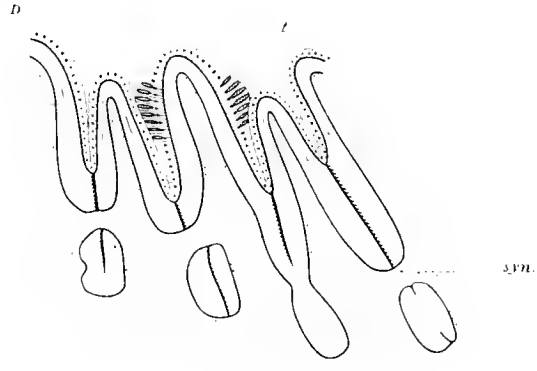


FIG. 155.

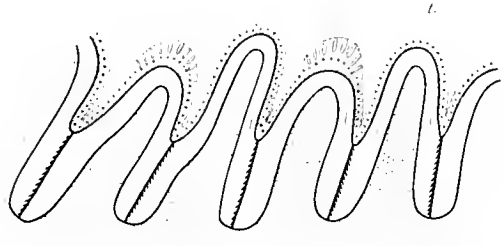


FIG. 154.

J. E. D. del.

PLATE XXIV.

SIDERASTRÆA SIDEREA (Ellis and Solander).

FIG. 157.—Portion of the skeletotrophic wall with a mesentery attached, from the middle region of a polyp. The mesoglœa of the mesentery is greatly swollen and striated at the extremity where it comes in contact with the skeleton, and the calicoblast layer, very broad elsewhere, is here absent. × 400.

FIG. 158.—Transverse section through an incomplete mesentery in the stomodæal region. The incipient mesenterial filament, the mesoglœal plaitings supporting the retractor muscle, and the glandular character of the mesenterial endoderm are represented. The peripheral end of the mesentery has already undergone resorption toward its fixed extremity, and is free from the skeletotrophic tissues and greatly narrowed. × 300.

FIG. 159. Transverse section through a mesentery, a short distance below the stomodæal region, along with its attachment to the skeletotrophic tissues. The mesenterial filament is here fully developed. The calicoblast layer is as broad as the endodermal layer, and is highly granular and vacuolated; a portion of the skeletal matrix is persistent on the right side. The mesoglœa is expanded along the line of attachment of the mesentery to the septal invagination. × 300.

FIG. 160.—Portion of the skeletotrophic wall from the lower region of the polyp. It differs but little from its character in the upper part of the polyp. × 400.

AGARICIA FRAGILIS Dana.

FIG. 161. Transverse section through a polyp immediately below the stomodæal region. No regular alternation of larger and smaller mesenterial pairs can be established, and no directives occur. At the upper right-hand corner two mesenteries are united by their free extremity. × 70.

FIG. 162. Transverse section through the upper part of a portion of two retracted polyps. The polypal walls all round are practically resting upon the septo-costæ. In the middle left of the section the exsert septo-costæ are seen in section free from the calicinal wall, and the mesenteries of the two adjacent polyps are continuous. The gastro-colonic cavity of the two polyps are likewise in communication along the sides of the septo-costæ. On the upper right the mesenterial chambers and mesenteries have been broken up by the formation of synapticula. × 70.

FIG. 163.—Radial section of a portion of the disk showing a slight tentacular prominence. × 110.

FIG. 157.

FIG. 163.

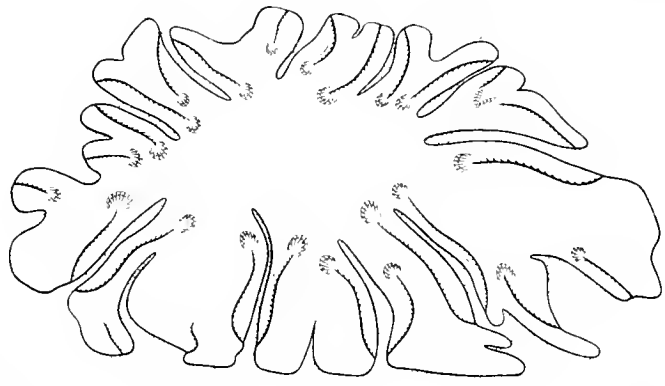


FIG. 161.

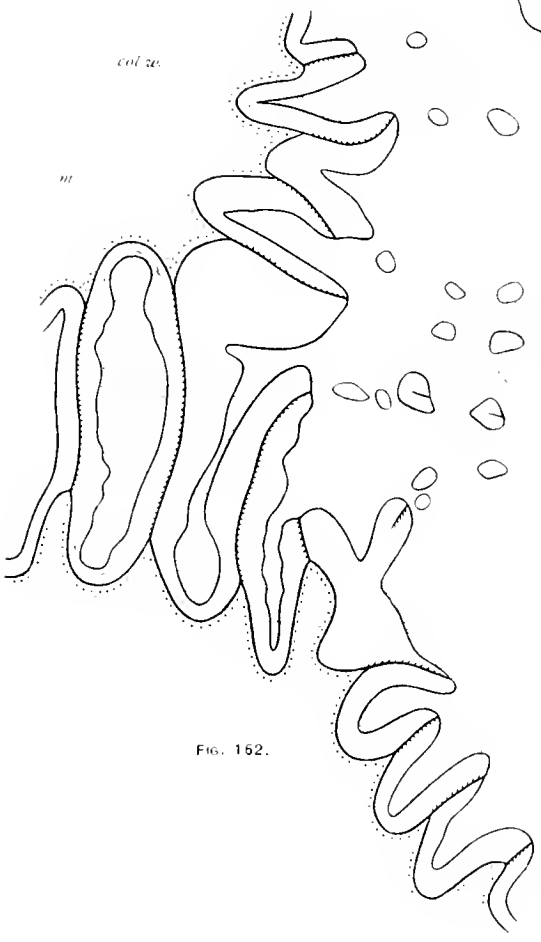


FIG. 162.

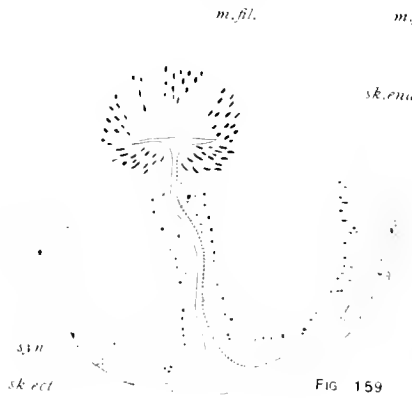


FIG. 159

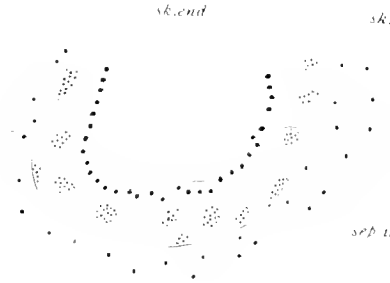


FIG. 160

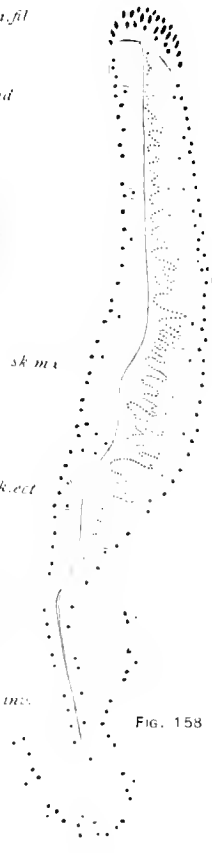


FIG. 158

PLATE XXV.

AGARICIA FRAGILIS Dana.

FIG. 164.—Transverse section through the stomodæal region of a polyp with seven pairs of complete mesenteries and seven alternating incomplete pairs. The upper part of the section, with the transversely shortened mesenteries, is the aspect toward the middle of the colony, the lower is toward the periphery. The septal invaginations are both entocœlic and exocœlic. No directives are present. × 70.

AGARICIA AGARICITES (Linnæus).

FIG. 165.—Vertical section through a freshly extruded larva. On the right side the stomodæal ectoderm is in continuity with the mesenterial filament of a mesentery extending the whole length of the larva. Zooxanthellæ are mainly aggregated in the endoderm around the stomodæal invagination; a few occur within the oral ectoderm. The larval cavity is wholly occupied by a vacuolated tissue; the ectoderm at the aboral extremity is greatly modified from that elsewhere, nervous elements being very prominent and gland cells sparse. × 250.

FIG. 166.—Transverse section through the stomodæal region of a larva. Four pairs of complete mesenteries and two incomplete pairs are present, but no endodermal cavity is yet formed. × 300.

FIG. 167.—Transverse section through the same larva, shortly below the stomodæal region. All the six pairs of mesenteries are filamentiferous, including the fifth and sixth pairs, which are throughout free from the stomodæum. Divisions in the vacuolated tissue are seen associated with the mesenteries. × 300.

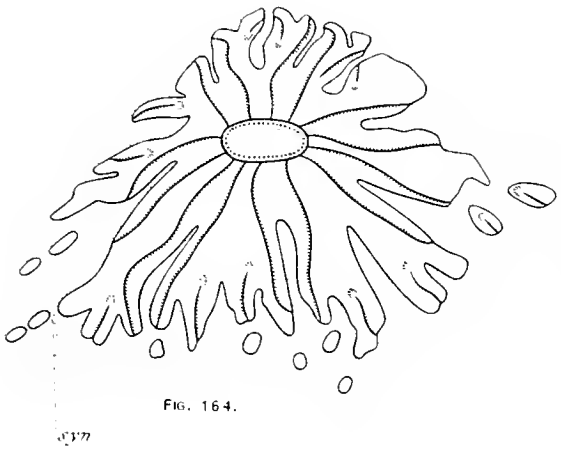


FIG. 164.

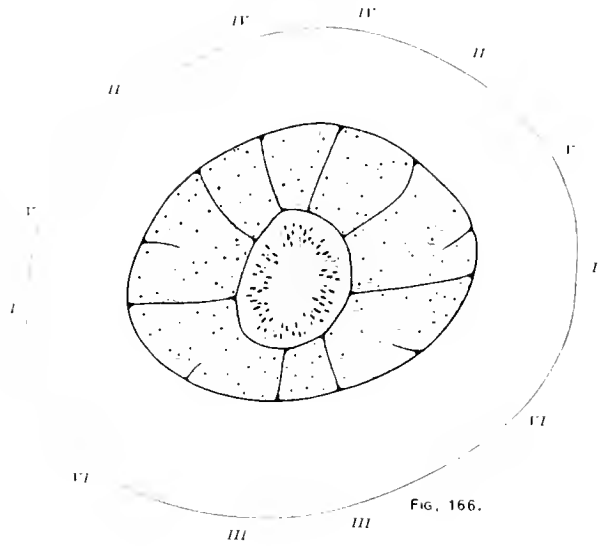


FIG. 166.

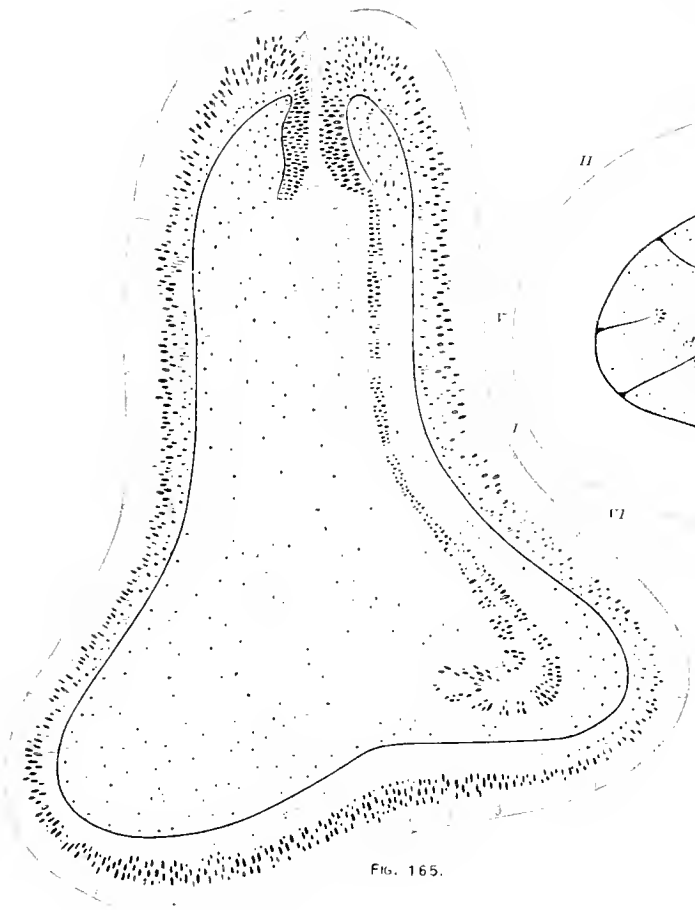


FIG. 165.

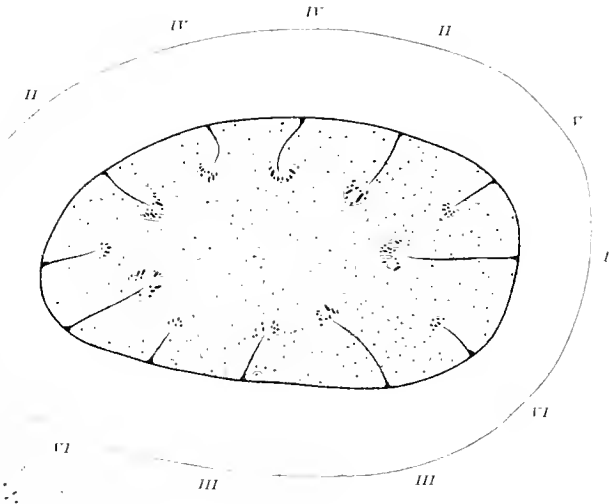


FIG. 167.

J. E. D. del.