PHYSIOLOGY OF THE INVERTEBRATA

THE
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OF
THE INVERTEBRATA

BY

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ETC. ETC.

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TO

PROF. T. H. HUXLEY, LL.D., F.R.S., F.L.S., F.Z.S.

Correspondant de l'Institut de France .
Past-President of the Royal Society, etc. etc.

WHO HAS CREATED A NEW EPOCH IN BIOLOGY; AND WHOSE
GENIUS HAS DONE SO MUCH TO AWAKEN THE KEENEST
INTEREST IN THE STUDY AND POPULARISATION
OF SCIENCE

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AS

A TOKEN OF ADMIRATION AND RESPECT

BY

THE AUTHOR

PREFACE.

> "*Physiology is to a great extent applied physics and chemistry.*"
> PROF. HUXLEY.
>
> "*A true knowledge of biology must be based on a knowledge of chemistry and physics.*"—M. M. P. MUIR.
>
> "*Biology being the science which deals with the matter and energy of living things, manifestly rests on physics and chemistry, since it involves the application of the laws and principles of these sciences to the special case of living matter.*"—R. J. H. GIBSON.
>
> "*Chemistry lies at the basis of physiology.*"—A. BINET.
>
> "*It is impossible that physiology can ever acquire a scientific foundation without the aid of chemistry and physics.*"—J. VON LIEBIG.

THE branch of biology detailed in the following pages has had only a few workers; for the reason that the majority of biologists are not chemists, and consequently have not the necessary manipulative skill in applying a science like chemistry to the solution of biological problems.

The true functions of the various organs of the *Invertebrata* have always been, until recent years, more or less problematical. Morphology and histology alone could not answer correctly the questions involved; but physiology with chemical and physical methods of research have illuminated very many obscure problems concerning the functions of the various organs and tissues of the *Invertebrata*; and no doubt they are destined to play an important part in the elucidation of many problems still requiring solution.

The following work gives an account of some of the most important researches on the subject, which have been published during the past fifteen or twenty years; and I have also included an account of my own researches in the present volume, more especially as these have appeared in the *Proceedings* of the Royal Societies of London and Edinburgh, and have also attracted the attention of the Académie des Sciences (l'Institut de France), to the extent that its Council thought proper to award me an "honourable mention" in connection with the *Prix Montyon,* which is given annually for researches in experimental physiology and physiological chemistry. Besides, several well-known biologists have informed me that a work on the physiology of the *Invertebrata* would be a welcome addition to biological literature. Consequently, I hope that this work (although I am fully cognisant of its many imperfections and shortcomings) may prove of some utility to those scientists and students who are desirous of investigating biological problems involving the applications of chemistry and physics.

I take this opportunity of expressing my gratitude and best thanks to Sir Richard Owen, K.C.B., F.R.S., for the great interest he has always taken in my investigations, and for the many letters of friendly criticism which I have received from him.

I am also grateful to Mr. F. E. Beddard, F.R.S.E.; the Rev. W. H. Dallinger, LL.D., F.R.S.; Mr. H. H. Dixon (of the University of Dublin); Prof. J. C. Ewart (of the University of Edinburgh); Prof. Léon Fredericq (of the University of Liège); Dr. A. Giard (of Paris); Mr. S. T. Griffiths;

Mr. A. Johnstone, F.G.S. (of the University of Edinburgh); Dr. C. A. MacMunn, F.C.S.; Prof. P. Mantegazza (of the University of Rome); Dr. A. C. Maybury, F.G.S.; Prof. A. von Mojsisovics (of the University of Gratz); Mr. E. B. Poulton, F.R.S.; Dr. G. J. Romanes, F.R.S.; Prof. G. O. Sars (of the University of Christiania); and Dr. C. Zeiss, for valuable assistance in various parts of the book.

My obligations are due to the President and Council of the Royal Society of Edinburgh for the loan of certain wood-blocks used in illustrating my own papers on the *Invertebrata*, and which were originally printed in the Society's *Proceedings*.

In conclusion, I here record the name of my sister (Miss Mildred H. Griffiths), for her help in preparing, under my direction, certain drawings for the illustrations. Figures 32 and 33 are supplied by Dr. Carl Zeiss, optician, Jena, from his catalogue of microscopes.

A. B. GRIFFITHS.

EDGBASTON, *Feb.* 1892.

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THE

PHYSIOLOGY OF THE INVERTEBRATA.

CHAPTER I.

INTRODUCTION.

ANIMAL *physiology* may be defined as that branch of biology which is concerned in the elucidation of the various functions which take place in the animal economy. It is a branch of study quite distinct from morphology, chorology, and ætiology; and as a separate branch of biological science we propose to treat it in the following pages.

Researches undertaken to investigate accurately the proper physiological functions of the various organs and tissues of the *Invertebrata* were greatly needed; and it is only during the last few years that certain biological chemists—fully equipped with the necessary manipulative skill—have considerably advanced this important but much-neglected branch of biology.

If one studies any particular organ from only one aspect, incomplete or erroneous conclusions are apt to be drawn. For instance, the vesicular tissue lying in the rectal loop in *Ascidia*, and in some species extending over the intestine, is well known to be renal in function. This vesicular tissue is a true kidney *physiologically*; *morphologically* it is another matter, and depends upon one's definition of a true kidney. *Embryologically* these vesicles are the remains of a part of the original colon.

As more attention has been paid to the morphology of the *Invertebrata*, it is not our object to speak of that branch of the subject further than is necessary; but in some cases the function of an organ or a tissue cannot be comprehended without referring to its anatomy.

According to the great apostle* of biological thought, "the actions of living matter are termed its *functions;* and these functions, varied as they are, may be reduced to three categories. They are either—(1) Functions which affect the material composition of the body, and determine its mass, which is the balance of the processes of waste on the one hand, and those of assimilation on the other. Or (2) they are functions which subserve the process of reproduction, which is essentially the detachment of a part endowed with the power of developing into an independent whole. Or (3) they are functions in virtue of which one part of the body is able to exert a direct influence on another, and the body, by its parts or as a whole, becomes a source of molar motion. The first may be termed *sustentative*, the second *generative*, and the third *correlative* functions. In the lowest forms of life the functions which have been enumerated are seen in their simplest forms, and they are exerted indifferently, or nearly so, by all parts of the protoplasmic body; and the like is true of the functions of the body of even the highest organisms, so long as they are in the condition of the nucleated cell, which constitutes the starting-point of their development. But the first process in the development is the division of the germ into a number of morphological units or blastomeres, which eventually give rise to cells; and as each of these possesses the same physiological functions as the germ itself, it follows that each morphological

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* Prof. Huxley.

unit is also a physiological unit, and the multi-cellular mass is strictly a compound organism, made up of a multitude of physiologically independent cells. The physiological activities manifested by the complex whole represent the sum, or rather the resultant, of the separate and independent physiological activities resident in each of the simpler constituents of that whole.

"The morphological changes which the cells undergo in the course of the further development of the organism do not affect their individuality; and, notwithstanding the modification and confluence of its constituent cells, the adult organism, however complex, is still an aggregate of morphological units. Nor is it less an aggregate of physiological units, each of which retains its fundamental independence, though that independence becomes restricted in various ways.

"Each cell, or that element of a tissue which proceeds from the modification of a cell, must needs retain its sustentative functions so long as it grows or maintains a condition of equilibrium; but the most completely metamorphosed cells show no trace of the generative function, and many exhibit no correlative functions. Contrariwise, those cells of the adult organism which are the unmetamorphosed derivatives of the germ exhibit all the primary functions, not only nourishing themselves and growing, but multiplying and frequently showing more or less marked movements."

The cell theory, first ably worked out by Schwann, has led physiology, aided by chemical means, to scrutinise more profoundly the mechanism of the vital acts; it has taught it to refer them to their ultimate agents—that is, to the histological elements themselves, which vary in function and in form in complex beings, and which we must consider as playing a part in the mechanism of organised beings analogous to that of atoms in chemical molecules.

In the lowest animals all functions are performed by all tissues: the sarcode of an amœba assimilates, breathes, excretes, and reproduces—for no special part is set aside for the functions of digestion, of respiration, of excretion, of reproduction. There seems to be in the lowest Invertebrates a confusion of organic materials and functions. Many of the *Protozoa* are endowed with motility and sensibility, with a sort of instinct;* and yet, as far as we know at present, they are destitute of muscular and nervous elements. Possibly the sarcode is the rudiment, still undivided, of muscular fibre.

But as we ascend gradually from lower to higher forms the differentiation becomes more marked, and we find particular parts of the body reserved for special actions. But this differentiation passes through various stages before arriving at the most differentiated forms of animal life. As already stated, the single cell of the amœba performs many functions; and even when an organ has arrived at such a stage that it is quite distinct, it may have a dual or triple function—as, for instance, the pentagonal pyloric sac of *Uraster rubens* (one of the *Asteridea*) has been proved to have a dual function.† It is a digestive gland as well as an excretory organ, separating the nitrogenous products of the waste of the tissues, &c., from the blood in the form of uric acid, which is to be found in the five pouches of that organ. In *The Origin of Species* (chapter vi.) Darwin mentions the fact that "numerous cases could be given among the lower animals of the same organ performing at the same time wholly distinct functions: thus, in the larva of the dragon-fly . . . . the alimentary canal respires, digests, and excretes." But as we pass from the lower to the higher forms of animal life the various organs have special functions assigned them. This rule not only applies to the physiological functions of various organs, but also to their ana-

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* See Binet's *Psychic Life of Micro-Organisms.*

† See Dr. A. B. Griffiths' papers in the *Proceedings of Royal Society of London*, vol. 44, p. 325; and the *Proceedings of Royal Society of Edinburgh*, vol. 15, p. 111.

tomical elements. The more simple is the organisation of an animal, taken as a whole, the simpler is also the structure of each of the orders of anatomical elements. For example, the muscular fibres of the *Radiata*, *Annulosa*, and *Mollusca* are simpler than the same elements in the crab (Robin). But in the higher animals there is a complete differentiation of parts into organs having special physiological functions and varied degrees of structure. In fact, the important law of Von Baer —"the law of progress from the general to the special"— reigns supreme in the organic world.

In the higher Invertebrates the various organs are localised in different parts of the body. One area is restricted to digestion, another to circulation, a third to respiration, and a fourth to reproduction. The more highly organised the animal, the more divided is its body into separate and distinct organs, each endowed with its own special function.

The main object of this volume will be to consider in detail the physiological functions of the various organs in the *Invertebrata;* but as it is impossible to investigate functions without a knowledge of the organs performing them, we shall refer (when necessary to a proper understanding of the mechanism described) to their anatomy.

As we shall have to allude to numerous classes, &c., of animals, a classification of the *Invertebrata* will hardly be out of place in concluding the present chapter.

The following tables are founded on the classifications of Professor Huxley:—

PROTOZOA.

- Monera.
- Protoplasta.
- Gregarinida.
- Catallacta.
- Infusoria.
- Foraminifera.
- Radiolaria.
  - (*a*) Heliozoa.
  - (*b*) Cytophora.

METAZOA.

I. ZOOPHYTIC SERIES.			II. ECHINODERMAL SERIES.	III. ANNULOID SERIES.	
Porifera or Spongida.	Cœlenterata.		Echinodermata.	Trichoscolices.	Annelida.
	Hydrozoa.	Actinozoa.			
Myxospongiæ	Siphonophora	Octocoralla	Holothuridea	Turbellaria	Myzostomata
Ceratospongiæ	Discophora	(*a*) Pennatulidæ	Asteridea	Rotifera	Gephyrea
Silicispongiæ	Hydrophora	(*b*) Gorgonidæ	Ophiuridea	Trematoda	Hirudinea
Calcispongiæ	Hydrocorallina	(*c*) Alcyonidæ	Echinidea	Cestoidea	Oligochæta
		(*d*) Helioporidæ	Crinoidea		Polychæta
		(*e*) Tubiporidæ	Cystidea		(*a*) Errantia
		Hexacoralla	Edrioasterida		(*b*) Tubicola
		(*a*) Actinidæ	Blastoidea		
		(*b*) Antipathidæ			
		(*c*) Zoanthidæ			
		(*d*) Perforata*			
		(*e*) Fungida*			
		(*f*) Aporosa*			
		Tetracoralla (Rugosa*)			

* Madreporaria.

METAZOA—*continued.*

IV. Arthrozoic Series.							
Nematoscolices.	Chætognatha.	Arthropoda.					
		Onychophora.	Myriapoda.	Insecta.	Arachnida.	Crustacea.
Nematoidea	Sagitta	Prototracheata	Protosyngnatha	Thysanura	Pentastomida	Eurypterida
Nematorhyncha			Chilopoda	Orthoptera	Arctioca	Xiphosura
Acanthocephala			Archipolipoda	Palæodictyoptera	Pycnogonida	Trilobita
			Diplopoda	Rhynchota	Acarina	Phyllopoda
				Diptera	Araneina	Cladocera
				Lepidoptera	Arthrogastra	Ostracoda
				Neuroptera		Copepoda
				Hymenoptera		Rhizocephala
				Coleoptera		Cirripedia
						Amphipoda
						Isopoda
						Stomapoda
						Anomoura
						Brachyura
						Macroura

METAZOA—*continued.*

V. Malacozoic Series.			VI. Pharyngopneustal Series.
Malacoscolices.		Mollusca.	
Polyzoa.	Brachiopoda.		
Podostomata Phylactolæmata Gymnolæmata Pedicellinea	Tretenterata Clistenterata	Lamellibranchiata Scaphopoda Polyplacophora Heteropoda Gasteropoda (*a*) Pulmogasteropoda (*b*) Branchiogasteropoda Pteropoda Cephalopoda (*a*) Dibranchiata (*b*) Tetrabranchiata	Hemichordata Urochordata (Tunicata)

If animals are looked upon as machines for doing work, they differ from one another in the extent to which this work is subdivided. "Each subordinate group of actions or *functions* is allotted to a particular portion of the body, which thus becomes the organ of those functions; and the extent to which this division of physiological labour is carried differs in degree within the limits of each common plan, and is the chief cause of the diversity in the working out of the common plan of a group exhibited by its members. Moreover, there are certain types which never attain the same degree of physiological differentiation as others do.

"Thus, some of the *Protozoa* attain a grade of physiological complexity as high as that which is reached by the lower

Metazoa. And notwithstanding the multiplicity of its parts, no Echinoderm is so highly differentiated as a physiological machine as is a snail. . . . . It is not mere multiplication of organs which constitutes physiological differentiation; but the multiplication of organs of different functions in the first place, and the degree in which they are co-ordinated, so as to work a common end, in the second place. Thus, a lobster is a higher animal, from a physiological point of view, than a *Cyclops*, not because it has more distinguishable organs, but because these organs are so modified as to perform a much greater variety of functions, while they are all co-ordinated towards the maintenance of the animal by its well-developed nervous system and sense-organs. But it is impossible to say that, *e.g.*, the *Arthropoda*, as a whole, are physiologically higher than the *Mollusca*, inasmuch as the simplest embodiments of the common plan of the *Arthropoda* are less differentiated, physiologically, than the great majority of Mollusks." (Huxley.)

CHAPTER II.

THE CHEMISTRY OF PROTOPLASM.

Before commencing our study of the physiology of the *Invertebrata* in detail, we offer a few remarks concerning the chemical nature and supposed composition of protoplasm,* or albumin. As the complex molecule of albumin is the basis of all physiological functions—in fact, "the physical basis of life"—no apology is needed in bringing this chapter before the attention of our readers.

Many chemists have submitted albumin to ultimate analyses. Among these may be mentioned the following:—

	Dumas and Cahours.	Würtz.	Lieberkühn.	Griffiths.	Mülder.	Scherer.	Rüling.	Schützenberger.
Carbon . .	53·4	52.9	53·3	53·5	53·4	54·3	53·1	52.6
Hydrogen . .	7·1	7.2	7·1	7.2	7.0	7.1	7.0	7.1
Nitrogen . .	15.8	15.6	15·7	15.8	15·7	15·9	—	16.3
Oxygen . .	—	—	22.1	—	22.3	—	—	—
Sulphur . .	—	—	1.8	1.7	1.6	—	1.3	1.8

Besides the above elements, there is always present in protoplasm a small, but variable, amount of ash, which contains phosphorus and other elements in infinitesimal quantities.

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* From πρῶτος (first), and πλάσμα (formed substance).

Albumins are incapable of being crystallised, or, if they are present in some tissues in an apparently crystalline condition, they are not crystals in the true sense of the word. These pseudo-crystals are readily recognisable beneath a microscope, for they dissolve in a dilute solution of potash, and are stained yellow by nitric acid.

A solution of iodine colours albumin or protoplasm brown, while sulphuric acid colours it red. Carmine deeply stains *dead* protoplasm, but has no action on living protoplasm. Dilute mineral acids and alcohol coagulate albumin; but it is soluble in concentrated hydrochloric acid. According to Dr. F. Hoppe-Seyler,* albumin has a specific rotatory power of from -35.5° to -56°. A temperature of about 50° C. coagulates albumin; *i.e.*, it is converted into an isomeric modification by the action of heat, as well as by *dilute* acids, as already stated.

Albumin combines with hydrochloric, sulphuric, phosphoric, and acetic acids, forming albuminates. It also combines with certain bases and salts, forming similar compounds. It was the albuminate of potash which gave Lieberkühn the means of ascertaining the empirical formula of this complex chemical compound. Lieberkühn's formula for albumin is represented as follows:—

$$C_{72}H_{112}N_{18}O_{22}S.$$

The above formula gives no idea of the atomic constitution of albumin.

Dr. C. Schorlemmer, F.R.S. (*Rise and Development of Organic Chemistry*, p.123) says: "The enigma of life can only be solved by the discovery of the synthesis of an albuminous compound." The direct synthesis of albumin has not yet been performed; but during the past nine or ten years some excellent work has been done by Loëw and Bokorny in this line of research, which opens a vast field of inquiry for the physiological chemist. These chemists have paved the

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* *Handbuch der Physiologisch- und Pathologisch-Chemischen Analyse.*

way for the synthesis of this compound; and in their researches* on living and dead protoplasm, they have arrived at the conclusion that living protoplasm contains an aldehydic group of elements. In their experiments on the living protoplasm of the fresh-water algæ, *Spirogyra* and *Zygnema*, growing in spring-water containing 0.1 per cent. of dipotassium phosphate and ammonium nitrate, Loëw and Bokorny found that the living cells had the power of reducing silver from very dilute alkaline solutions of salts of that metal. Dead cells do not give this reaction.

Loëw and Bokorny have experimented (with the same result) upon the cotyledons of *Helianthus annus*, the epidermal hairs of plants, the sap of the pine and oak, the cells of fruits, fungi, and also many of the *Infusoria*. They conclude from these observations that living protoplasm contains an aldehydic group of elements, whereas there is no such group in dead protoplasm.

Reinke (*Berichte der Deutschen Chemischen Gesellschaft*, vol. 14, p. 2144; vol. 15, p. 107) says that the aldehydic nature, as tested by an alkaline silver solution, is only a property of the protoplasm of the chlorophyll, for he failed to find it in the protoplasm of cells in unopened buds; therefore he thinks it is probable that it is formed only in the presence of sunlight by the chlorophyll corpuscles.

Mori (*Chemisches Centralblatt* [3], vol. 13, p. 565) considers that formic aldehyde is the first product of assimilation, for he detected (by the action of a solution of silver nitrate) a substance which reduced the nitrate in plants containing chlorophyll which had been exposed to sunlight. When the same plants were left for about forty-eight hours in a dark place, so that on applying the test again the first products of assimilation might be used up, no reduction of silver nitrate

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* *Die Chemische Kraftquelle im lebenden Protoplasma;* also *Berichte der Deutschen Chemischen Gesellschaft*, vol. 14, p. 2508; vol. 15, p. 695; *Pflüger's Archiv für Physiologie*, vol. 25, p. 150; vol. 45, p. 199; and *Bot. Centr.* 1889, p. 39.

took place. Therefore, both Reinke and Mori support Baëyer's theory that formic aldehyde is formed by chlorophyll under the influence of light from the carbonic acid of the atmosphere in the presence of water:

$$\left\{\begin{matrix} CO_2 = CO + O \\ H_2O = H_2 + O \end{matrix}\right\} = O_2 + \left\{\begin{matrix} H \\ COH. \end{matrix}\right.$$

Dr. Kretzschmar (*Biedermann's Centralblatt für Agricultur-Chemie*, 1882, p. 830), on the other hand, states that the protoplasm of living and dead cells reduces silver from an alkaline solution of the salts of that metal, and so concludes that this reagent fails to distinguish between living and dead protoplasm.

The author * has also shown that the alkaline solutions of copper (cupric) and silver salts are reduced by both living and dead protoplasm. In fact, these reagents fail to distinguish between living and dead protoplasm, but these investigations do not disprove Loëw and Bokorny's idea that protoplasm (*i.e.*, living and dead) contains an aldehydic group of elements; but this particular group of elements is only one of many combinations of elements forming the complex molecule of albumin.

When we study the decomposition of albumin (both animal and vegetal) by the agency of different chemical reagents, we begin to see that its chemical constitution is not represented by any simple group of elements. Many of the substances found in the animal body are products of the metabolism of protoplasm—*e.g.*, urea (CN_2H_4O), creatine ($C_4H_9N_3O_2$), creatinine ($C_4H_7N_3O$), cholesterine ($C_{28}H_{44}O_2$), uric acid ($C_5H_4N_4O_3$), guanin ($C_5H_5N_5O$), leucin ($C_6H_{13}NO_2$), tyrosin ($C_9H_{11}NO_3$), &c.

Professor P. Schützenberger (*Comptes-Rendus*, vol. 106, p. 1407) has shown experimentally that when albumin is boiled with barium hydroxide, it yields leucin, leuceïn, and the products of hydration of urea and oxamide; and Dr. W.

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* *The Chemical News*, vol. 48, p. 179; *Journal of Royal Microscopical Society*, 1884, p. 249; *Journ. Chem. Soc.* 1884, p. 202.

Palladin (*Berichte der Deutschen Botan. Gesellschaft*, vol. 6, p. 296), and Drs. Schulze and Kisser (*Landw. Versuchs-Stat.*, vol. 36, p. 1), have shown that vegetal protoplasm can be made to yield tyrosin, leucin, xanthine, hypoxanthine, and similar compounds, which are undoubtedly some of the products of the decomposition of albumin occurring in the bodies of living animals. If protoplasm or albumin gives rise to such compounds as the above, we have good reason to believe that its constitution is more complex than Loëw and Bokorny would have us suppose. Many of the substances formed during the decomposition of albumin have been artificially prepared in the laboratory. For instance, leucin is very largely diffused in the animal organism, and has been obtained artificially by oxidising amylic alcohol with potassium bichromate and sulphuric acid, and then distilling, when the following reaction occurs:

$$\underset{\text{[Amylic alcohol.]}}{2C_5H_{11}HO} + O_2 = \underset{\text{[Valeric aldehyde.]}}{2C_4H_9COH} + 2H_2O.$$

When valeric aldehyde is treated with ammonia, valeral ammonia is formed, and if the latter compound is digested with hydrocyanic and hydrochloric acids it is converted into leucin:

$$(a)\quad C_4H_9.COH + NH_3 = \underset{\text{[Valeral ammonia.]}}{C_4H_9CH(NH_2)OH.}$$

$$(b)\quad C_4H_9CN(NH_2)OH + HCN + H_2O =$$

$$\underset{\text{[Leucin.]}}{C_4H_9CN\left\{\begin{matrix}NH_2\\COOH\end{matrix}\right.} + NH_3.$$

Amido-isovaleric acid (a substance which occurs in the pancreas of the ox), amido-butyric acid, and amido-propionic acid, have been obtained by Schützenberger* from albumin; and all these substances have been obtained artificially in the laboratory.

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* See *Comptes-Rendus*, vols. 81 and 84.

Dr. Guckelberger (*Liebig's Annalen*, vol. 64, p. 39) obtained caproic, valeric, butyric, propionic, acetic, and formic acids by oxidising albumin with potassium bichromate and sulphuric acid. As these organic acids can be obtained artificially from cyan-alcohols, it has been stated that albumin or protoplasm is a compound of cyan-alcohols or cyanhydrins united to a benzene nucleus.

By looking upon albumin as built up of cyan-alcohols, we can readily account for the formation of such compounds as glycocine, leucin, the acids of the $C_nH_{2n+1}COOH$ series, as well as those of the lactic series—occurring in the animal body.

In the year 1828 Wöhler converted ammonium cyanate into urea; and Dr. Pflüger (*Pflüger's Archiv*, vol. 10, p. 337), in calling attention to the great molecular energy of the cyanogen compounds, suggested that the functional metabolism of protoplasm by which energy is set free, may be compared to the conversion of the energetic unstable cyanogen compounds into the less energetic and more stable amides. In other words, that "ammonium cyanate is a type of living, and urea of dead nitrogen, and the conversion of the former into the latter is an image of the essential change which takes place when a living proteid dies."*

Dr. P. W. Latham, in "The Croonian Lectures" for 1886, ably argues from experimental data that albumin or protoplasm has the following constitutional formula:

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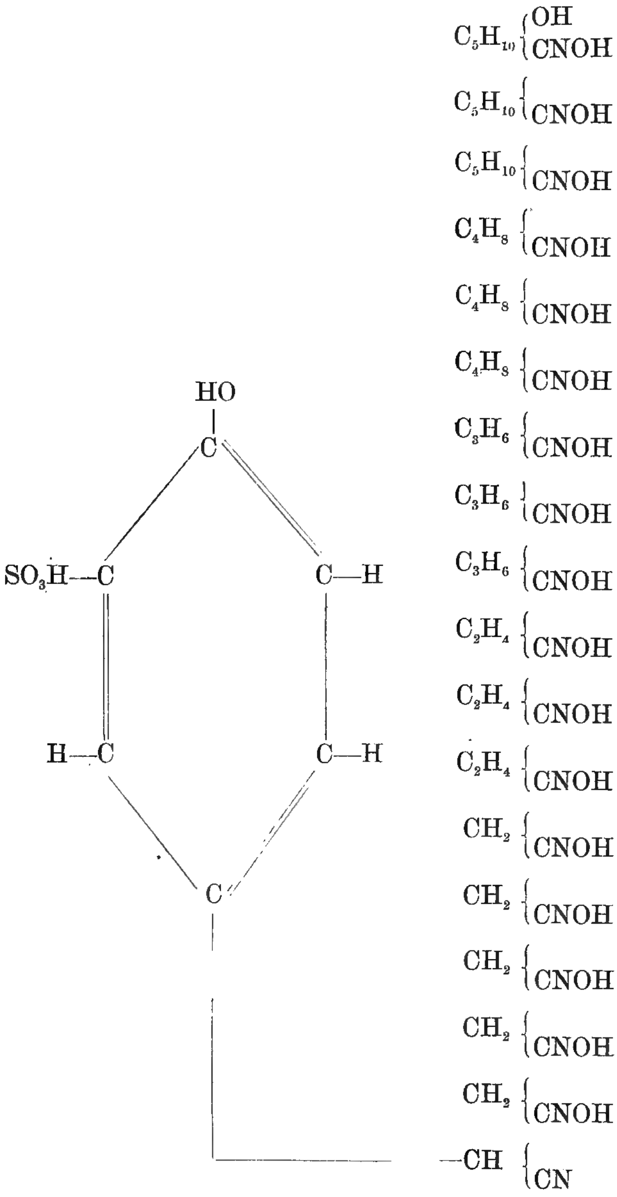
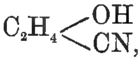
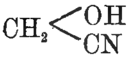
* See Foster's *Text-book of Physiology* (4th ed.), p. 749.


C5H10 OH CNOH
C5H10 CNOH
C5H10 CNOH
C4H8 CNOH
C4H8 CNOH
C4H8 CNOH
C3H6 CNOH
C3H6 CNOH
C3H6 CNOH
C2H4 CNOH
C2H4 CNOH
C2H4 CNOH
CH2 CNOH
CH2 CNOH
CH2 CNOH
CH2 CNOH
CH2 CNOH
—CH CN
HO
C
SO3H—C
C—H
H—C
C—H
C

This substance, whose composition is $C_{72}H_{118}N_{18}O_{22}S$, differs from Dr. Lieberkühn's empirical formula ($C_{72}H_{112}N_{18}O_{22}S$) only by six atoms of hydrogen.

According to Latham, albumin "is a compound of cyan-alcohols united to a benzene nucleus, these being derived from the various aldehydes, glycols, and ketones, or that they may be formed in the living body by the dehydration of the amido-acids; that from a body so constituted all the different substances may be obtained which have been extracted from albuminoid tissues; that lactic acid is obtained in two ways, either from  $C_2H_4<\begin{matrix}OH\\CN,\end{matrix}$ or from changes and condensation in  $CH_2<\begin{matrix}OH\\CN\end{matrix}$ with the simultaneous development of carbonic anhydride, a result which is brought about when a muscle contracts or when it dies; and that urea may be obtained from one series of cyan-alcohols with the production of a cyan-alcohol higher in the series.

"Such a compound of cyan-alcohols therefore, presenting so much resemblance in its properties to albumin, cannot differ very widely (though perhaps not absolutely correct) from the molecular constitution of albumin.

"Taking this view, then, of the constitution of albumin, the following may be given as a summary of the nutritive changes: The amido-acids—glycocine, leucin, tyrosin, &c.—in passing from the alimentary canal to the liver, are dehydrated, forming a series of cyan-hydrins or cyan-alcohols attached to a benzene nucleus, and then pass into the circulation. In the tissues these cyan-alcohols, partly by condensation, partly by hydration and oxidation, give rise to the various effete products which are eliminated from the system in the form of carbonic acid and urea."

There is no doubt that the theory of protoplasm being a complex molecule,* derived from various aldehydes, glycols,

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* See also a paper by Dr. P. Schützen in the *Comptes-Rendus*, tome 112, p. 198.

and ketones, aids us considerably in understanding the origin of various secretory products found in the *Invertebrata* as well as in the *Vertebrata.*

Living protoplasm is a substance which is constantly undergoing chemical changes. It is the chemical and physical properties of this complex substance, diversely modified, which underlie all the vital functions—nutrition, secretion, growth, reproduction, motility, &c. Of these functions the most important is nutrition, the double and perpetual movement of molecular renovation of the living substance. Without nutrition there can be no growth, no reproduction, no movement, and in fact no physiological function whatsoever. It has been stated that "life can be conceived of as reduced to its most simple expression, to mere nutrition. A being capable of nourishing itself, and destitute of every other property or function, which, after all, is only a simple extension of the nutritive property, its life will be only an individual life;" a time will come when the nutritive functions will have less energy—then "the nutritive residue, incompletely expulsed, will impregnate the living tissues and liquids obstructing them." Such obstruction necessarily interferes with physiological activity, and ultimately ends in complete arrest. When this stage arrives, the organism, no longer capable of adjusting its "internal relations to external relations,"* undergoes those chemico-biological changes which finally result in its molecules (as new combinations) once more re-entering the mineral kingdom—or the world of inanimation. On the other hand, if the nutritive activity of a living organism "is sufficiently energetic to rise, as it were, to excess, even to growth and reproduction, the being is sure of living in its offspring; it fills its place in the innumerable crowd of living beings, and can even, according to the doctrine of evolution, become the source of a superior organised type, can ascend in the hierarchy of life."

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* Mr. Herbert Spencer's definition of "life."

From what has been said in this chapter it will be gathered that "a mass of living protoplasm is simply a molecular machine of great complexity; but it must not be supposed that the differences between living and not-living matter are such as to bear out the assumption that the forces at work in the one are different from those which are to be met with in the other. Considered apart from the phenomena of consciousness," Professor Huxley says, "the phenomena of life are all dependent upon the working of the same physical and chemical forces as those which are active in the rest of the world."

CHAPTER III.

DIGESTION IN THE INVERTEBRATA.

Digestion in General.

In this chapter we have to trace the function of *digestion* from its lowest or most general form to that stage when it nearly approaches in complexity the digestive process occurring in the backboned animals.

Digestion is that process whereby food is taken into an organism, and there made fit to become part thereof—*i.e.*, the digested food becomes assimilation, for in the living organism, however low in the animal scale, there is never any repose. The organism has to reckon with its environment; oxidation is always going on, therefore the digested food is employed in the work of reparation and of reconstruction. Animal organisms cannot live without constantly absorbing complex organic substances. As they cannot manufacture these substances, they obtain them from other animals or from plants; hence we may divide even the lowest animals into either carnivorous, herbivorous, or omnivorous forms.

For the process of digestion the organism is furnished with either a general or a special apparatus, whose office consists in forming a kind of physiological kitchen to modify the raw materials, which renders them more suitable for assimilation or absorption. This apparatus is the digestive system.

Many of the lowest animals are comparable to the lowest plants—in fact, the two great kingdoms may be said to overlap, for there is no sharp line of demarcation, as far as digestion is concerned, between the *Protozoa* and the *Bacteria*. For instance, if one compares the *Gregarine* (a parasite) to a bacterium or any other fungus, both forms live by assimilating the products of decomposed organisms, or rather organic matter; thus showing that the lowest members of the animal kingdom are closely allied to the lowest members of the vegetal kingdom.

The mode of nutrition among the lowest animals is not uniform—a fact which ought not to appear remarkable when we bear in mind that these animals are made up of all manner of heterogeneous beings that have nothing in common save the microscopic smallness of their bodies and the simplicity of their structure. In the animal kingdom three main types of nutrition may be distinguished:—

(1) Holophytic or vegetal nutrition.
(2) Saprophytic or endosmosis nutrition.
(3) Animal nutrition.

The first type of nutrition or digestion is found in animal cells that contain chlorophyll, and that nourish themselves by forming assimilable substances from ingredients taken from the medium in which they live. It should be borne in mind that the function of chlorophyll in the animal as well as in the vegetal kingdom is essentially that of nutrition, and not of respiration; although we shall see later in this volume that many of the animal chromophylls (using the word in its widest sense) have respiratory as well as other functions.

A large number of the lower animals contain chlorophyll, but these animals are met with chiefly among the *Flagellata*. Their assimilative or digestive organs bear the name of chromatophores. These chromatophores are small granular masses of protoplasm impregnated with a colouring substance. In the centre of the chromatophore is a small bright globule which is said to possess the same chemical reactions as nuclein. Dr. Schmitz has named this small globule pyrenoid.* The function of the pyrenoid is the formation of starch and similar carbohydrates. This is a process of digestion akin to the vegetal kingdom.

It is interesting to note that "the *Euglenæ* (belonging to the *Flagellata*) might nourish themselves as animals do, for they have a mouth and a digestive apparatus. The buccal, or oral, aperture opens in the anterior end at the base of the flagellum, and is connected with a short gullet or œsophagus (Fig. 1). Nevertheless the *Euglena* is never seen using its mouth for swallowing alimentary particles. A curious problem is involved here. If it is true, as has been claimed, that it is the function that makes the organ, how do we explain the existence, and especially the genesis, of this digestive apparatus, which performs *no* function?"

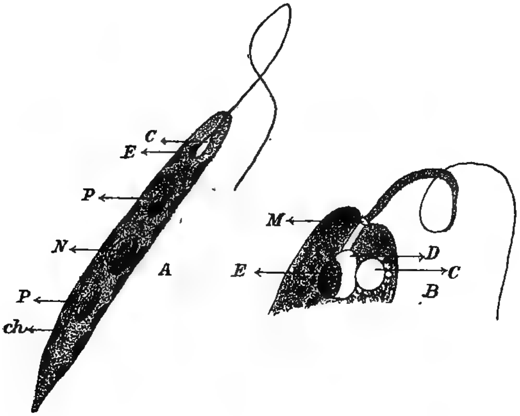

FIG. 1.—EUGLENA.

A = C, contractile vacuole; E, eye or ocular spot; P, disk of paramylone; N, nucleus; Ch, chromatophores.

B = M, mouth; E, eye; D, contractile reservoir; C, contractile vacuole.

The second type of nutrition or digestion in the animal

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* From πυρὴν, a nucleus.

kingdom is that of saprophytic or endosmosis nutrition. It occurs in the *Gregarinida*, &c., and is the simplest type of nutrition, for the organism simply nourishes itself by absorbing, through the whole surface of its body, the liquids containing decomposing or digested animal and vegetal substances.

The third and highest type of nutrition occurs in all animals except those coming under the previously mentioned types. In the highest type of nutrition the organism "seizes solid alimentary particles, and nourishes itself after the fashion of an animal, whether it be by means of a permanent mouth, or by means of an adventitious one, improvised at the moment of need."

Before describing in detail the great physiological functions, it may be stated that "in organised beings, from the lowest to the highest, the most differentiated, there is a graduated hierarchy. From the physiological confusion which exists at the lowest step of the ladder we pass, step by step, through a series of organic models, better and better finished, to the most perfect specialisation. Nothing is more interesting than this seriation of organs, especially from the point of view of the great doctrine of evolution, which more and more vivifies all the branches of natural history."

THE PROTOZOA.

(*a*) The *Gregarina*.—This animal (Fig. 2, A) infests the interior of cockroaches, earthworms, and other Invertebrates. It well illustrates an example of endosmosis or saprophytic nutrition, for it absorbs or imbibes fluid nutriment by every part of its surface, and most probably the effete matter is likewise given out at every part of its surface.

Although the anatomical structure of the *Gregarina* gives it a higher rank in the zoological scale than the *Amœba*, the latter organism is certainly its superior in the matter of digestion. It may be stated that the gradual specialisation of different functions do not follow the same lines in the animal series. Nor will the advance of particular functions keep pace with the advance in anatomical structure. As far as structure is concerned, the *Gregarina* ranks higher than the *Amœba.*

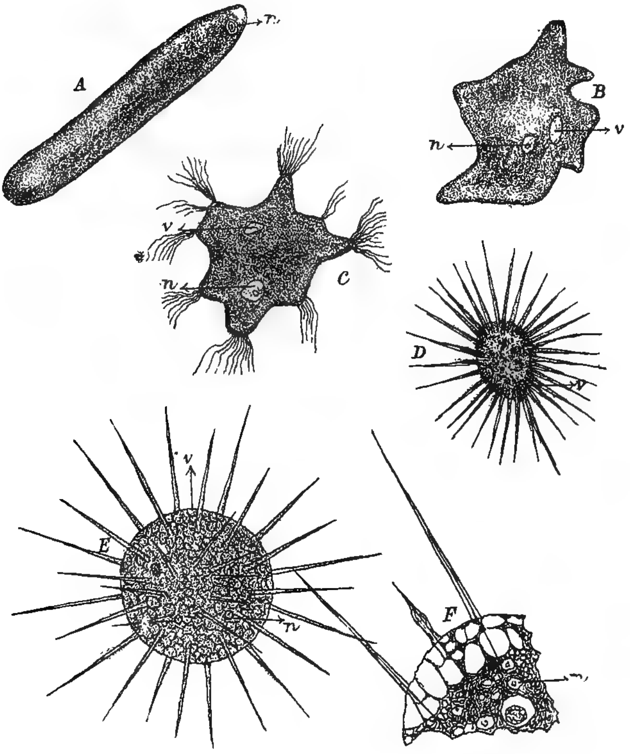

FIG. 2.—VARIOUS PROTOZOA.

A = Gregarina. B = Amœba. C = Magosphæra. D = Actinophrys.
E = Actinosphærium. F = Part of E highly magnified.
v = contractile vacuole. *n* = nucleus.

(*b*) The *Amœba.*—In the *Protoplasta,* to which the *Amœba* belongs, we have a distinct advance in the mechanism of digestion, for in this order one beholds the very birth of the digestive function.

The *Amœba* (Fig. 2, B) seizes its food by extending some portion of its cell. The extended portion is known as a pseudopodium. The pseudopodium, after seizing the particles of food, retract, and the food becomes incorporated in the interior of the cell, which has the property of digesting and absorbing the nutritive portion of the food and ejecting the non-digested portion.

In some forms of the *Protoplasta* pseudopodia are extended from any part of the protoplasmic cell; whereas in others (*e.g.*, *Pamphagus*) these non-differentiated prehensile organs are extended from one particular region only of the cell. In *Arcella* and *Difflugia*, having an external covering or shell, the pseudopodia are extended only from the single opening present in each shell.

There is another point of difference between the *Gregarina* and the *Amœba*—namely, the latter organism has a contractile vacuole. It is possible that this vacuole is in some way directly connected with the function of digestion, but there is no doubt that it performs more than one function, for the author has shown that at times the contractile vacuole of the *Amœba* acts as a renal organ (see later in this volume).

As far as the function of digestion is concerned in the *Protoplasta*, every part of the protoplasm may be made to serve as a digestive cavity in enveloping the food particles. "A mouth region and an anal region are marked off for each particular particle of food, but there is no mouth and there is no anus."

(*c*) The *Foraminifera*.—These complex *Protozoa* may be looked upon as colonies of *Amœbæ* connected together and surrounded by a complex shell. They have been divided into the *Perforata* and the *Imperforata*, according to whether the shell is either perforated or imperforated. In the former class, the shell contains many apertures, through which the pseudopodia of the particular individual dwelling within that division of the shell are protruded. In the *Imperforata* "the food for the whole colony is seized and taken in by the pseudopodia given off by the individual segment found in the last-formed, and therefore most free cavity of the shell."

Nearly all the *Foraminifera* are marine animals; whereas the *Amœbæ* chiefly inhabit fresh water, although some are found in the sea.

(*d*) The *Catallacta.*—There is a morphological difference between this order and the *Protoplasta,* although the mechanisms of their digestive functions are closely allied.

Magosphæra (Fig. 2, C) which represents the *Catallacta,* protrudes pseudopodia which are broad at the base, while the other extremities break up into a number of very fine filaments. We may term these secondary pseudopodia. *Magosphæra* has a well-marked contractile vacuole.

(*e*) The *Radiolaria.*—One of the most common of this order is *Actinophrys* (the sun-animalcule). It has stiffish pseudopodia, "which radiate from all sides of the globular body." *Actinophrys* (Fig. 2, D) has a contractile vacuole, but secretes no shell. In *Actinosphærium* (Fig. 2, E) the "central part of the protoplasm is distingushed from the rest by containing a number of endoplasts" (nuclei). Most of the *Radiolaria* are simple and solitary organisms, but *Sphærozoum* and *Collosphæra* form colonies.

In the case of *Actinophrys sol* any part of the body serves as a way of entry for food; in fact it is a pantostomate being (W. S. Kent).

(*f*) *Infusoria.*—Under this head Professor Huxley includes—

Infusoria flagellata (the "Monads").
Infusoria tentaculifera (the *Acinetæ*).
Infusoria ciliata.

The *Infusoria* are the well-known inhabitants of water containing decomposing vegetable matter. These organisms differ entirely from those previously described, inasmuch as they have a permanent aperture—the mouth. Beyond this aperture there is a distinct tube—a short œsophagus, which is closed at one end, for it does not dilate into a stomach. Although there is no further differentiation of this primitive alimentary canal, it forms a distinct advance on the forms so far described. The posterior end of the œsophagus is closed by the protoplasmic mass of the cell. Food particles are brought to the mouth by means of the vibrating flagellum or flagella in the *Infusoria flagellata*, or by tentacula in the *Infusoria tentaculifera*, or by cilia in the *Infusoria ciliata.*

In *Monas vulgaris*, one of the *Flagellata*, the food is dashed by a sudden jerk directly against the oral aperture or mouth, and the base of the flagellum presses the food particles into it. According to Cienkowsky, bacteria, micrococci, and other forms, which constitute the food of the *Monas*, "are pulled into the latter's neighbourhood by strokes of the flagellum"; and Drs. Dallinger and Drysdale remark that certain forms of the *Flagellata* are most voracious creatures. "The 'field' in their neighbourhood is rapidly cleared of dead and living bacteria, simply devoured by them. It is probable that this capacity for absorbing nutriment, which must give large advantage in the struggle for existence, explains the amœboid condition so common at what will be seen to be such an important period in the development of the monads." *

Noctiluca (Fig 3, A) is another genus of the *Flagellata.* It is extremely abundant in the upper layers of the waters of the ocean, "and is one of the most usual causes of the phosphorescence of the sea." Phosphorescence is associated with the function of digestion or nutrition, for many micro-organisms will not "phosphoresce" unless supplied with certain foods.† *Noctiluca* is a free swimmer. It is globular in form, and possesses a strong flagellum. The central protoplasmic mass is connected by many radiating filaments with the external layer, and contains a gastric or food

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* See Drs. Dallinger and Drysdale's paper in *Monthly Microscopical Journal*, 1875, p. 194.

† Dr. A. B. Griffiths' book: *Researches on Micro-Organisms*, p. 165.

vacuole, where the food is retained until digested. There is no contractile vacuole.

The *Infusoria tentaculifera*, or *Acinetæ* (Fig. 3, B), are organisms that move about very little—some of them being fixed to a pedicle their whole life. These organisms possess tentacula, or suckers, and are entirely different from the radiating pseudopodia of the *Radiolaria*. Each tentaculum is a tube (containing a granular fluid) which terminates

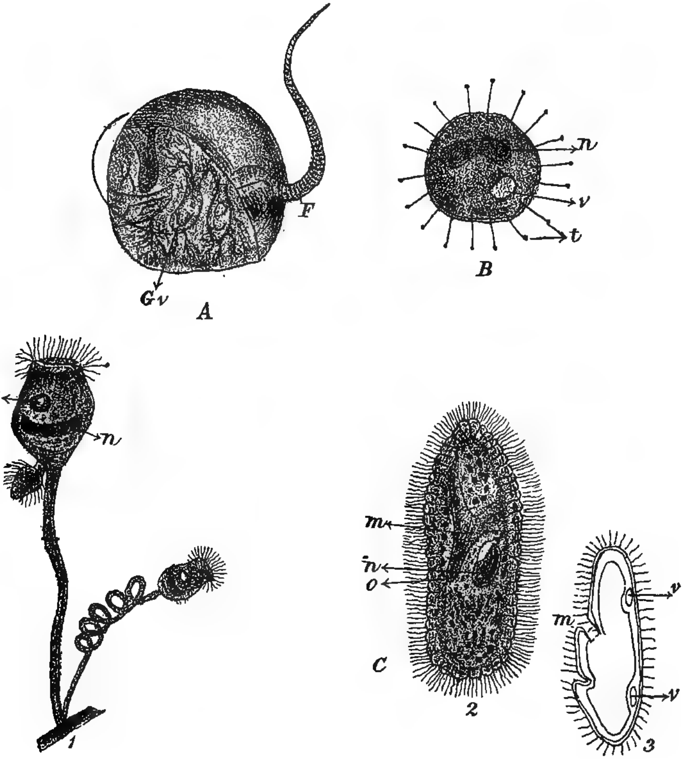

FIG. 3.—TYPES OF INFUSORIA.

Representing the *Flagellata*, the *Tentaculifera*, and the *Ciliata*.

A = Noctiluca. B = Acineta. C 1 = Vorticella. C 2 and 3 = Paramœcium.
G*v* = Gastric vacuole. F = Flagellum. *t* = Tentacles. *n* = Nucleus.
v = Contractile vacuole. *m* = Mouth. *o* = Œsophagus.

externally in a slight knob, the latter being pierced with a small air-hole. These knob-like projections are used for seizing the prey. The protoplasm of the captured infusorium slips slowly through the tentacula,* and is gathered together in the interior of the *Acineta* in the form of small globules. Therefore we have in these tentacula a direct advance on the flagella of the monads and the pseudopodia of the forms already described, inasmuch as the former are not only prehensile organs, but act as suckers.

The *Acinetæ* possess one or more contractile vacuoles, and in this respect differ from the monads.

The *Infusoria ciliata* are characterised by having numberless cilia (Fig. 3, C). These cilia are either localised to the oral side of the body, or form a zone round it, or are scattered over its external surface.

In all the *Infusoria ciliata* there is an oral region, or mouth, an œsophagus which leads into the central protoplasmic mass, and there is an anal region. In this division of the *Infusoria* the differentiation into parts has gone so far as to produce a mouth, an œsophagus, and an anal region; but the alimentary canal is broken, for the œsophagus and anal region do not form one continuous tract. The *Infusoria ciliata* have contractile vacuoles.

In the *Vorticellæ* (Fig. 3, C) "the oral region presents a depression, the vestibule from which a permanent œsophageal canal leads into the soft semi-fluid endosarc, where it terminates abruptly; and immediately beneath the mouth, in the vestibule, there is an anal region, which gives exit to the refuse of digestion, but presents an opening only when fæcal matters are passing out." The *Vorticellæ* possess a contractile vacuole as well as several gastric or food vacuoles. The latter are filled with a clear fluid containing the swallowed bodies (algæ, &c.). The food vacuoles do not remain stationary, but are conveyed round the inner part of the body, so that the particles of food contained in these vacuoles undergo digestion.

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* See Stein's *Der Organismus der Infusionsthiere*, vol. 1, p. 76.

In the *Paramœcia* (Fig. 3, c) the oral region or mouth is situated near the anterior end of the body, and an anal aperture is observable in a definite part of the body during the excretion of the undigested portion of the food. There is also an œsophagus which passes into the endosarc, or the semi-fluid portion of the protoplasmic mass. In the endosarc the particles of food give rise to food vacuoles which undergo a rotatory movement round the endosarc; this movement being caused by the contractility of the ectosarc or "cell-membrane." During the rotation of the food vacuoles digestion proceeds; the nutritive portion of the food being absorbed, while the indigestible residuum is ejected through the improvised anus. As already stated, there is no actual anal aperture; but there is a very distinctly marked *region* where the effete matter is ejected. Therefore, in *Paramœcium* there is an oral aperture, an œsophagus, a distinct course for the food, though there is no intestine, and an anal region, though no permanent opening. We have in the higher *Ciliata* a beginning of a true alimentary canal, although of a simple form; and even the *tract* of the moving food vacuoles has been described as "a rudimentary *intestinal* canal."

In the *Paramœcia* there are two contractile vacuoles, situated anteriorly and posteriorly in the ectosarc; the physiological function of these cavities will be considered later; but they have probably a dual function—one of these being that of a renal organ.*

THE PORIFERA OR SPONGIDA.

These are animals having many cells, and are the lowest in the zoological scale of the *Metazoa*. The body cavity (gastro-vascular space) serves alike for digestion and circulation; and it may be remarked that, "with the exception of certain parasites, and the extremely modified males of a few species,

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* The author's paper in the *Proceedings of Royal Society of Edinburgh*, vol. 16, p. 133.

all these animals possess a permanent alimentary cavity, lined by a special layer of cells."

The histological structure of an adult sponge is comparable in certain details to the *Amœbæ* and to the *Infusoria flagellata*, for adult sponges are partly composed of aggregations of amœbiform cells and partly of flagellate cells. But in the embryonic condition a sponge is comparable to an embryo *Hydrozoon*, and is consequently unlike any form belonging to the *Protozoa*.

The body of these animals has a spongy consistence, and is usually strengthened by a calcareous, silicious, or fibrous skeleton.* All over the surface of the body are minute inhalent apertures, through which the water, bearing food particles, passes into the gastro-vascular space or body-cavity. This body-cavity is lined internally with flagellate cells.

Besides the inhalent apertures, there may be one or many exhalent apertures (oscula). The former are comparable to the intercellular spaces of plants, and are formed by the separation of one cell from another. These apertures or pores are not constant, for "they may be temporarily or permanently closed, and new ones formed in other positions."

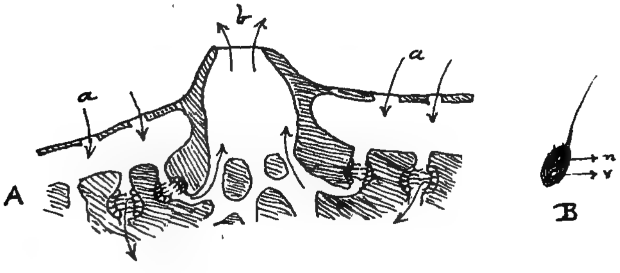

FIG. 4.—DIAGRAM OF SECTION OF SPONGILLA.
(*After* HUXLEY.)

A, *a* = inhalent apertures. *b* = exhalent aperture; the arrows indicate the direction of the currents. B = an endoderm cell.

The waste materials or excretory matters of each cell are

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* The *Myxospongiæ* are devoid of a skeleton.

thrown into the gastro-vascular cavity, and collectively expelled through the exhalent aperture or apertures (Fig. 4, A), as the case may be.

The *Porifera* are composed of three layers: the ectoderm (of flat epithelial cells), the mesoderm, and the endoderm (of long flagellate cells, Fig. 4, B). Besides a flagellum, a single endodermic cell contains one or more contractile vacuoles and a nucleus. It is possible that these endodermic cells have the power of digesting the food particles, and thereby rendering the food into such a state that it is readily absorbed. The gastro-vascular cavity, with its internal lining of endodermic cells, is a rudimentary form of digestive system.

THE CŒLENTERATA.*

This class of the *Metazoa* is divided into two sub-classes—the *Hydrozoa* and the *Actinozoa*. They have a mouth, a gastro-vascular cavity, but no inhalent or exhalent apertures; in this point they differ from the *Porifera*.

The morphological characteristic of the *Cœlenterata* is a body with a constant cavity, which may be considered a digestive cavity, but sometimes it is badly differentiated.

In the case of the *Hydra*, it was formerly stated that if the animal were turned inside out, it can digest with what was previously its external surface: that is, the ectoderm and endoderm were interchangeable. But recent Japanese experiments have shown that this organism is more specialised than was originally supposed to be the case; and it has been shown that when turned inside out, the *Hydra* again turns itself back to its normal condition, so that the functions of its inner and outer surfaces are not interchangeable. Although in the *Hydra* the digestive cavity is somewhat badly differentiated, in many of the *Hydrozoa* the digestive system is divided into three parts—viz., an œsophageal portion, a

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* κοῖλος, ἔντερον.

dilated portion, and a narrowed portion, which ultimately terminates in a cæcum.

The *Hydrozoa* which live in colonies, have an intestinal tube in common—that is, the tube acts for the whole tribe of organisms; while in the *Siphonophora* (one of the four orders of the *Hydrozoa*) "certain members of the colony specially adapt themselves for the digestive function. For that purpose they come to bear the form of dilatable sacs, and are in communication interiorly with the digestive cavity common to all the tribe."

In the *Actinozoa* the body cavity is hardly more differentiated than that of the *Hydrozoa*, for it is still a gastro-vascular cavity, but is divided by vertical partitions (mesenteries) into a number of intermesenteric chambers which communicate with each other at the bottom of the gastro-vascular cavity. The mouth or oral aperture of the *Actinozoa* serves both for the reception of food and the rejection of excreta.

The mesenteries of the *Actinozoa* are divided into primary and secondary; the former being longer than the latter. The secondary mesenteries, which are situated between the primary, have on their free edges twisted and coiled filaments. These mesenteric filaments secrete a fluid which has digestive properties.

The *Actinozoa* may be divided into two groups—the *Coralligena* and the *Ctenophora*. Most of the *Coralligena* "are fixed temporarily or permanently, and may give rise to (by gemmation) tuft-like or arborescent zoanthodemes. The great majority possess a hard skeleton, composed principally of carbonate of lime." This group of the *Cœlenterata* has a digestive or somatic cavity divided by mesenteries.

The *Ctenophora* are free swimming organisms, and never give rise to colonies. They possess a mouth or oral aperture, an œsophagus, and a gastro-vascular canal system, which communicates with the exterior by two aboral apertures.

So far we have seen, in this general study of the digestive function of the *Invertebrata*, this function performed by the whole of the body (*Gregarina*); by any portion thereof (*Rhizopoda*); by a mouth, an œsophagus, and a tolerably definite portion of the sarcode of the body, without, however (after the œsophagus), any distinct tube (*Infusoria*); by an oral aperture or mouth, and a distinct alimentary canal, one with a somatic or body cavity (*Hydra*); by an oral aperture and a distinct alimentary canal suspended in, distinct from, but communicating with the somatic cavity (*Actinia*).

THE ECHINODERMATA.

In this class, physiological differentiation in the digestive apparatus has taken an important step forward. In the *Holothuridea* there is a mouth and an œsophagus leading into an alimentary canal, but it is not differentiated into a stomach and intestine. The alimentary canal is simply a tube with oral and aboral apertures.

In the *Asteridea*, there is an oral aperture or mouth, and an œsophagus leading into a wide stomach which has five sacs round its periphery. The intestine is short and terminates in an anus. In each ray there are two pyloric cæca.

The *Ophiuridea* have a mouth, gastric sac or stomach without cæca, and there is *no* intestine or anus.

In the *Echinidea* there is a mouth provided with so-called teeth (masticatory apparatus), and the intestine is long and terminates in an anus. There is no differentiation into a stomach and appendages.

The *Crinoidea** have an oral aperture which leads into a short, wide œsophagus. There is a large, coiled, and sacculated alimentary canal which terminates in an anus.

In the *Cystidea* there is an aboral as well as an oral aperture.

Therefore, to summarise the *Echinodermata*, we may say

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* See Prof. Sars's papers, *Mémoires pour servir à la connaissance des Crinoïdes vivants*, 1868.

that there is a digestive cavity or alimentary canal with an oral aperture, and usually an anus; also a water-vascular system, and a true vascular system.

THE TRICHOSCOLICES.

This class of the Annuloid Series is divided into the following orders:—the *Turbellaria*, *Rotifera*, *Trematoda*, and *Cestoidea*.

(1) The *Turbellaria* possess a mouth or oral aperture, and an alimentary canal,* but there is no anus, except in the higher forms. The mouth is either at the anterior or posterior end of the body, or sometimes it is situated in the middle. The alimentary canal is lined by an endoderm, and between the endoderm and ectoderm there is a mesoderm consisting of muscular and connective tissues. The alimentary canal of the *Turbellaria* is either straight or branched.

(2) The *Rotifera*, or the "wheel-animalcules," have a funnel-shaped oral aperture or mouth situated on one side, or in the middle, of the trochal disc. The mouth of these organisms is a great advance on all the forms previously described. Its internal lining, as well as the trochal disc, are abundantly provided with cilia, and at the posterior end of this cavity there is a muscular pharynx (mastax) with an armature consisting of four distinct pieces. The muscular pharynx and its appendages are used in the mastication of the prey seized by the ciliated trochal disc. The pharynx leads into a short œsophagus (also provided with cilia) which passes into a digestive cavity or stomach. The stomach then passes into a short intestine. Opening into the anterior part of the stomach are two large glandular tubes having a pancreatic function. The intestine, which usually opens externally by a cloaca, has numerous lateral diverticula

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* With the exception of *Convoluta*, for in this form an alimentary canal can hardly be said to exist.

(cæca). However, in some of the *Rotifera*, as, for example, *Notommata*, the alimentary canal is blind or closed at the posterior end; and the males of some forms are entirely devoid of any digestive apparatus. The whole of their brief life is devoted to reproduction.

(3) The *Trematoda* are all parasitic animals, having one or more suckers upon the ventral side of the body, and behind the mouth. The mouth leads into a muscular pharynx, which opens into a more or less elongated œsophagus, and terminates in a branched intestine. There is no anus.

In *Amphiptyches* and *Amphilina* the alimentary canal is entirely absent; and on the authority of Professor P. J. Van Beneden* it "becomes aborted in the adult *Distoma filicolle.*"

(4) The *Cestoidea*, or tape-worms, are examples of *reversions* to a very low type of digestion, although in other respects these animals are comparatively high in the zoological scale. They live by the imbibition of partly digested food of the animals whose intestines they infest.

In the words of Professor Huxley,† "it is obvious that the *Cestoidea* are very closely related to the *Trematoda*. In fact, inasmuch as some of the latter are anenterous, and some of the former are not segmented, it is impossible to draw any absolute line of demarcation that the *Cestoidea* are either Trematodes which have undergone retrogressive metamorphosis, and have lost the alimentary canal which they primitively possessed; or that they are modifications of a Trematode type, in which the endoderm has got no further than the spongy condition which it exhibits in *Convoluta* among the *Turbellaria*, and in which no oral aperture has been formed; or, lastly, it is possible that the central cavity of the body of the embryo *Tænia* simply represents a blastocœle. If the *Cestoidea* are essentially Trematodes, modified by the loss of their digestive organs, some trace of the digestive apparatus ought to be discoverable in the embryo tape-

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* *Mémoire sur les Vers Intestinaux* (1858).

† *The Anatomy of the Invertebrated Animals*, p. 213.

worm. Nevertheless, nothing of the kind is discernible, unless the cavity of the saccular embryo is an enterocœle. And if this cavity is a blastocœle, and not an enterocœle, it may become a question whether the tape-worms are anything but gigantic morulæ, so to speak, which have never passed through the gastrula stage."

THE ANNELIDA.

The second class of the Annuloid Series contains the following orders: the *Myzostomata*, *Gephyrea*, *Hirudinea*, *Oligochæta*, and *Polychæta*.

(1) The *Myzostomata* are parasitic unsegmented worms. There is a mouth, through which a proboscis is protruded. The mouth passes into a straight alimentary canal terminating in a cloaca. The alimentary canal has numerous lateral cæca.

(2) The *Gephyrea* are marine unsegmented worms* with a more or less cylindrical body. The oral aperture or mouth is either terminal, or has a ventral aspect. In some forms the mouth is provided with a proboscis, or is surrounded by tentacula; and it passes into a pharynx, which opens into either a straight or coiled intestine. The anus is always situated dorsally, and in *Phoronis* it is close to the mouth.

(3) The *Hirudinea*.—The leeches are more or less segmented worms, provided with a sucker at the anterior end of the body. Most species have a second unperforated sucker situated posteriorly, and there are a few of the *Hirudinea* with lateral suckers. The mouth of *Hirudo medicinalis* is armed with chitinous teeth, and opens into the pharynx, which is provided with glands. The sucking action of the animal is produced by the contraction of the muscles which suspend the pharynx. The pharynx passes into a slender œsophagus, which leads into a very long stomach; and from

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* In the larvæ of *Chætifera* (belonging to the *Gephyrea*) there are traces of segmentation.

the stomach a narrow intestine passes to the anus, which is situated dorsally. The stomach is produced into a number of lateral cæca, or diverticula.

The alimentary canal of *Malacobdella* is "a simple tube bent several times upon itself."

(4) The *Oligochæta*—The earthworm and certain fresh-water worms belong to this order. The body is elongated, rounded, and segmented. The mouth is a small aperture, leading into a buccal cavity, and into which true salivary glands open. This cavity or sac passes into a pharynx, which is continued into a straight œsophagus bearing three pairs of lateral diverticula (the œsophageal glands). About the region of the fifteenth segment the œsophagus opens into a dilated portion of the alimentary canal called the crop or proventriculus. The crop leads into the gizzard or stomach, which is provided with strong muscles. The gizzard is succeeded by the intestine, which terminates in an anus.

(5) The *Polychæta.*—In this order the alimentary canal "rarely presents any marked distinction into stomach and intestine." The mouth opens into a muscular pharynx, which is capable of being protruded as a proboscis; and in *Polynöe* and other genera the proboscis is provided with papillæ and chitinous teeth. The pharynx leads into a straight tubular intestine. In certain genera of the *Polychæta* there are long cæca which form lateral appendages to the intestine. The function of these cæca is of a pancreatic nature; while the pair of glandular organs appended to the base of the proboscis in *Nereis* are true salivary glands. The anus, in many Annelids, is not terminal, but is situated in the centre of a raised papilla on the dorsal side of the animal.

THE NEMATOSCOLICES.

This class of the Arthrozoic Series is divided into three orders: the *Nematoidea*, *Nematorhyncha*, and *Acanthocephala.*

(1) The *Nematoidea.*—The "thread-worms" possess elongated, rounded bodies. They are not segmented organisms. The anterior end is sometimes furnished either with hooks and spines within the oral cavity, or with papillæ around the mouth. The mouth leads into a muscular pharynx, lined with chitin, which then proceeds into a narrow œsophagus—the latter passing into a long intestine which terminates in an anus* situated ventrally. There is no dilatation of the alimentary canal to form a stomach.

(2) The *Nematorhyncha.*—This order contains the following genera among others: *Chætonotus*, *Chætura*, *Dasyditis*, and *Turbanella.* These organisms are allied to the *Rotifera*, "but they differ from them in the absence of a mastax, and in the disposition of the cilia, which are restricted to the ventral surface of the body." Professor Huxley says: "On the whole, however, I think that, notwithstanding the cilia of the *Gastrotricha*,† the closest affinities of the *Nematorhyncha* are with the *Nematoidea*, and I therefore place them among the *Nematoscolices.*"

(3) The *Acanthocephala.*—The animals of this order, and particularly *Echinorhynchus*, are parasitic, for in the sexless condition they infest the *Invertebrata*, while in the sexual state they are found infesting the *Vertebrata.*

There is neither a mouth nor an alimentary canal in *Echinorhynchus.* This is another example of reversion to a low type of digestion. No doubt nutrition is performed by the absorption or imbibition of fluid nutriment through the external walls of the body.

THE CHÆTOGNATHA.

This class of the Arthrozoic Series is represented by only one genus—the *Sagitta.*

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* *Mermis* has no anus.

† One of the two groups into which the *Nematorhyncha* have been divided.

The *Sagitta* have rounded, elongated, unsegmented bodies. There is a head, at the anterior end of which is the mouth. On each side of the mouth is situated several strong, curved, chitinous spines, which are said to act as jaws. The mouth passes into a straight alimentary canal which terminates in an anus situated ventrally and anteriorly to the caudal region. The caudal region ends in a fan-like "fin" of delicate setæ. No salivary glands or pancreatic follicles appear to exist in *Sagitta*. The endoderm of the alimentary canal possibly performs the function of a digestive gland.

The genus *Sagitta* includes several species of vermiform animals which live near the surface of "the ocean in all parts of the world."

THE ARTHROPODA.

This is the third and last class of the Arthrozoic Series, and is divided into the *Onychophora*, *Myriapoda*, *Insecta*, *Arachnida*, and *Crustacea*. These divisions are again subdivided (see the table given in Chapter I.).

(1) The *Prototracheata*.—The only genus is *Peripatus*, and, due to the important investigations of Professor H. N. Moseley, F.R.S,* *Peripatus* has been referred to the *Arthropoda*. All the species of this genus have a well-developed tracheal system. There is a distinct head, with several tentacula; the mouth is situated ventrally beneath a large projecting suctorial lip, and is provided with a pair of mandibles or jaws. There is also a short oral papilla attached to the head on each side of the mouth. The mouth or oral aperture leads into a muscular pharynx; then follows a short œsophagus, which passes into a wide and long stomach. The stomach leads into a short intestine terminating in an anus situated at the posterior end of the body. There appears to be no salivary glands or pancreatic follicles.

(2) The *Chilopoda*.—On referring to the classification given in the first chapter of the book it will be observed that the

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* *Philosophical Transactions of the Royal Society*, 1874.

Myriapoda have been divided into four orders; and as two of these contain only fossil genera they do not come under our notice.

In the *Chilopoda* (centipedes) the body is usually long and segmented; each segment carrying a pair of many-jointed limbs. The first and second pairs of limbs are masticatory, while the fourth pair are known as poison-claws. The head is flattened and the mouth is constructed for biting. The mouth leads into a long œsophagus, followed by an alimentary canal which is usually straight, somewhat like the intestinal tube of caterpillars. There is a pair of salivary glands (Fig. 5) which pour their contents into the mouth.

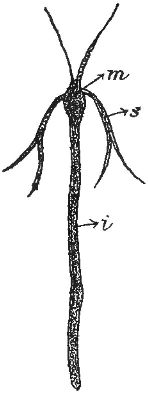

FIG. 5.

ALIMENTARY CANAL OF THE CHILOPODA.

m = mouth. *s* = salivary glands. *i* = intestine.

(3) The *Diplopoda* or *Chilognatha* (millipedes) have rounded bodies, which are segmented. There are two pairs of limbs on each segment except the anterior one. The first pair of maxillæ is represented by a four-lobed buccal plate or under-lip. The digestive system (like the *Chilopoda*, is a simple tube with salivary glands.

(4) The *Thysanura* represent the first order of the *Insecta*, and are said to resemble the young *Blattæ*. The mouth is provided with mandibles and maxillæ. The alimentary canal is divided into a buccal, a median, and a terminal portion. There are well-marked salivary glands, and according to Sir John Lubbock *Lepisma* is provided with four Malpighian tubules; but certain genera of the *Thysanura* (*e.g.*, *Japyx*, *Campodea*) are devoid of these excretory organs.

(5) The *Orthoptera* comprise the cockroaches, crickets, dragon-flies, may-flies, grasshoppers, &c. The body is divided (like all the *Insecta*) into head, thorax, and abdomen.

In *Blatta* the mouth leads into an œsophagus which gradually dilates into a large crop (ingluvies). The crop passes into a small gizzard or proventriculus, and then into a wide tubular stomach, the so-called chylific ventriculus, which leads into the small intestine or ileum, followed by the large intestine or colon, and the rectum; the latter terminating in the anus, which is situated between the podical plates. To the anterior end of the stomach are attached seven or eight pyloric cæca; and from the posterior end of the stomach are several Malpighian or urinary tubules (from twenty to thirty). The mouth of *Blatta*, which has a ventral aspect, is provided with a pair of well-developed salivary glands and receptacles. Each gland is divided into two lobes composed of numerous acini. The proventriculus contains six principal teeth, and between each pair of teeth are five smaller teeth. These teeth or ridges are produced by the folding of the chitinous lining of the crop, which passes into the proventriculus. The ileum is separated from the large intestine or colon by a circular valve; and the walls of the rectum are raised into six ridges projecting into the interior. These ridges are the rectal glands.

The mouth of *Blatta* is situated between "the labrum in front, the mandibles and maxillæ at the sides, and the labium, with the large lingua, or hypopharynx, behind." In all the *Orthoptera* the mouth is constructed on the above plan, but the *Physopoda** "present a modification which is transitional to the Hemipteran mouth. There is a proboscis directed backwards, and formed by the union of the labrum with the labium, which last is provided with palps, though they are sometimes very small."

The labrum, labium, mandibles, and maxillæ of the *Insecta* are, in the main, subservient to the functions of taking in or crushing food. In the carnivorous *Libellula depressa*, the alimentary canal is short and there is neither crop nor gizzard, but the so-called chylific ventriculus is present.

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* A sub-order to which *Thrips* belongs.

(6) The *Palæodictyoptera* are found only in the fossil condition.

(7) The *Rhynchota* form an order of the *Insecta* having a suctorial mouth in the form of a jointed rostrum. The order includes the bugs (land and water), *Aphides*, *Cicada*, &c. They all suck the juice of plants or the blood of animals. According to Huxley, " there is a usually sharp and pointed labrum, while the mandibles and maxillæ are mere tubercles, surmounted by long chitinous pointed styles, of which there are four. The labium is usually represented by a median, jointed, fleshy, elongated body, the anterior face of which presents a longitudinal groove in which the mandibles and maxillæ are enclosed. Neither the maxillae nor the labium are provided with palps." With such an arrangement of parts one can readily understand the suctorial power of the *Rhynchota* ; for it may be mentioned that the *Cicadæ* perforate the bark of the trees on which they live, and exhaust their sap. The structure of these mandibles, maxillæ, &c., are also well adapted for piercing the skin and sucking the blood of animals.

The *Rhynchota* have a crop, either forming an appendage to the œsophagus, or forming an anterior dilatation to the so-called chylific ventriculus, which in the *Cicadæ* is of great length.

(8) The *Diptera*.—This order includes the fleas, flies, gnats, crane-flies, &c. The mouth is suctorial, and is therefore constructed on a somewhat similar plan to the last-mentioned order; but the maxillæ have palps. In the house-fly " the labrum, mandibles, and maxillæ coalesce at their origins to constitute the base of the proboscis, which is mainly formed by the confluent second maxillæ."

The mouth leads into a narrow œsophagus which passes into a crop situated upon the stomach. This is followed by a small intestine which is convoluted, and then a short rectum provided with two lateral glandular bodies—the so-called rectal glands.

(9) The *Lepidoptera*.—In this order " the labrum and the mandibles abort, and the labium is represented only by a

triangular plate which bears two large palps." The maxillary palps in the *Lepidoptera* are greatly elongated, and form a sucking proboscis. The crop projects from the side of the

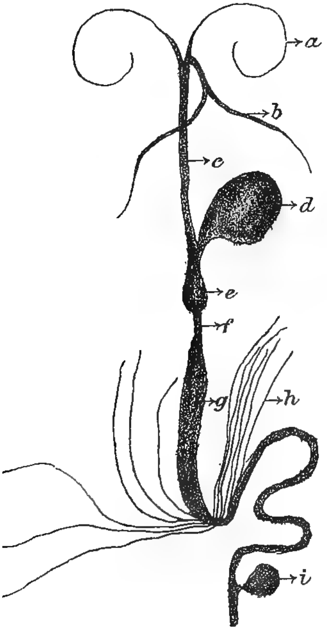

FIG. 6.—ALIMENTARY CANAL OF THE LEPIDOPTERA.

a = proboscis (maxillæ). *b* = salivary glands. *c* = œsophagus. *d* = crop. *e* = chylific ventriculus. *f* = small intestine. *i* = rectum. *h* = Malpighian tubules. *g* = large intestine.

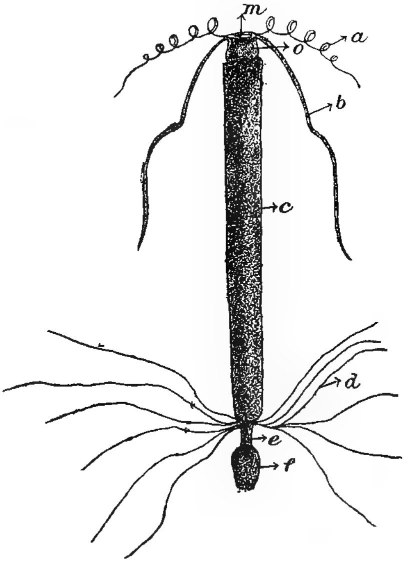

FIG. 7.—ALIMENTARY CANAL OF THE LARVAL LEPIDOPTERA.

m = mouth. *o* = œsophagus. *a* = salivary glands *b* = spining glands. *c* = 'chylific stomach. *d* = Malpighian tubules. *e* = intestine. *f* = rectum.

long œsophagus (Fig. 6). The "chylific" ventriculus is very small, but is sacculated. The small intestine is short and passes into the wide rectum. In the larvæ of the *Lepidoptera* the œsophagus is short and wide (Fig. 7), and passes to a long chylific stomach. The intestine is short, and terminates in the rectum. Both in the larval and perfect state there are well-developed salivary glands and Malpighian tubules. The former secrete the silk-like material in which the larvæ invest themselves on turning into the pupal state.

(10) The *Neuroptera.*—In this order the mouth parts are masticatory, although sometimes also suctorial. The alimentary canal is somewhat similar to that of the *Lepidoptera.* There are eight free Malpighian tubules.

(11) The *Hymenoptera* is the order to which bees, wasps, and ants belong. The mouth parts are for biting (ants), and licking (bees). The labial palps are long and slender; "there are two large paraglossæ, and between them a median, annulated, setose, cylindrical organ proceeds, which either represents the lingua, or is an independent prolongation of the ligula. *Functionally this organ is a tongue, and enables the bee to lap up the honey on which it feeds.* The mandibles and maxillæ are employed as cutting and modelling instruments, but appear to have little or nothing to do with mastication, properly so called."

In the bee the mouth opens into a slender œsophagus, which extends the whole length of the thorax, and at whose posterior end it dilates into the large honey-bag (Fig. 8). Before any honey passes into the stomach the so-called valve (*i*)* must be withdrawn by a special action. The "valve" then returns to its usual position, and thereby converts the crop (*b*) into a special receptacle for collecting nectar until the bee reaches its hive. In the crop the nectar or honey undergoes a change which prevents it (to a certain extent) undergoing acetic fermentation. When the bee reaches its hive the honey is regurgitated into waxen cells. The stomach or chylific ventriculus (*c*) is very long and leads into a short intestine (*e*), and then into a wide, distensible rectum (*g*).

The poison of the *Hymenoptera* is a fluid containing formic acid (H_2CO_2), which is secreted by a gland and retained in a receptacle connected with the sting. The sting is nothing more than a modified ovipositor.† In the larval bee the

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* *Vide* next chapter.

† See Lacaze-Duthiers's *Recherches sur l'armure génitale femelle des Insectes.*

alimentary canal consists only of a short but wide œsophagus, a large chylific ventriculus, and from four to six Malpighian tubules. There is no intestine or anus.

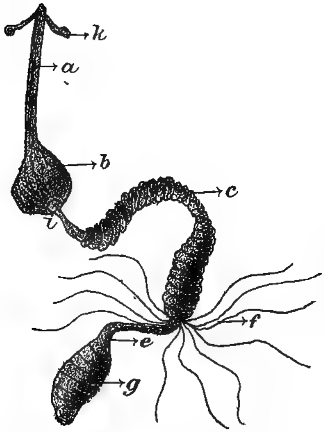

FIG. 8.—ALIMENTARY CANAL OF BEE (*Hymenoptera*).

a = œsophagus. *b* = honey-bag.
c = stomach. *e* = ileum. *f* = Malpighian tubules. *g* = rectum.
i = valvular opening of stomach.
k = salivary glands.

(12) The *Coleoptera* (beetles) have masticatory mouths, and the alimentary canal is framed on the same type as the *Orthoptera*; but in the larval condition of the *Coleoptera* the gizzard is entirely absent. In most herbivorous *Coleoptera* the chylific ventriculus of the larval form is much shorter than in the perfect insect or imago, and has appended at both ends a number of cæcal tubes. But the latter disappear during the metamorphosis.*

"The alimentary canal is most simple in the *larvæ of insects* in which, as in worms, it usually extends, without convolutions, from one end of the body to the other; in a few larvæ, as that of the bee, it has only the anterior opening or mouth, and the opposite or anal orifice is not developed until the pupal state. In all *mature* insects the alimentary canal presents the two distinct apertures: it is simplest in the carnivorous larviform Myriapods†; present more numerous and distinct constrictions and divisions in the Hexapods, and increases in complexity and length as the food requires most preparation in order to effect its conversion into the animal nutrient fluid."

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* With the exception of the genus *Hister*, for traces of these cæcal tubes are to be found in the perfect insect.

† Not true insects.

(13) The *Pentastomida* is the first order of the *Arachnida*—one of the five divisions of the Arthropoda. The only genus is the parasitic *Pentastomum*. In the sexual state, the vermiform *Pentastomum* is found in the nasal cavities of the *Carnivora,* while in the sexless condition it infests the liver and lungs of the *Herbivora* and *Reptilia.* There are ambulatory limbs, the only appendages are four hooks, two on each side of the mouth or oral aperture. The alimentary canal is very simple, at the anterior end of which is a slender œsophagus and at the posterior end the anus.

(14) The *Arctisca* or *Tardigrada.*—Like the previously mentioned order, the *Arctisca* are low-organised members of the *Arachnida;* yet there is an advance not only in the alimentary canal, which is more in keeping with the highly developed digestive system of the *Insecta,* but in the presence of rudimentary legs.

The genus *Macrobiotus* is found in moss and in sand. The mouth (Fig. 9) is suctorial, which is situated at the end of a rostrum, and is provided with two styles. It leads into a short œsophagus which passes into a muscular pharynx. The ducts from two well-defined salivary glands discharge their contents into the posterior part of the oral cavity. The pharynx leads into a wide alimentary canal which gradually narrows to the anus.

(15) The *Pycnogonida.*—The alimentary canal of these marine animals is very different from that of the two previously mentioned orders. The œsophagus leads into a more or less circular stomach which sends off very long diverticula or cæca into the legs. There is a short rectum terminating in an anus.

(16) The *Acarina.*—This order includes the mites and ticks. The alimentary canal is short and straight; but the stomach is produced into several cæcal appendages. Salivary glands are sometimes present. In *Ixodes* the salivary glands are situated on the sides of the anterior part of the body, and pour the secretion into the mouth at the base of the

labium. Malpighian tubules are also sometimes present. The alimentary canal terminates in an anus which is either situated at the posterior end of the body or near the middle of the abdomen.

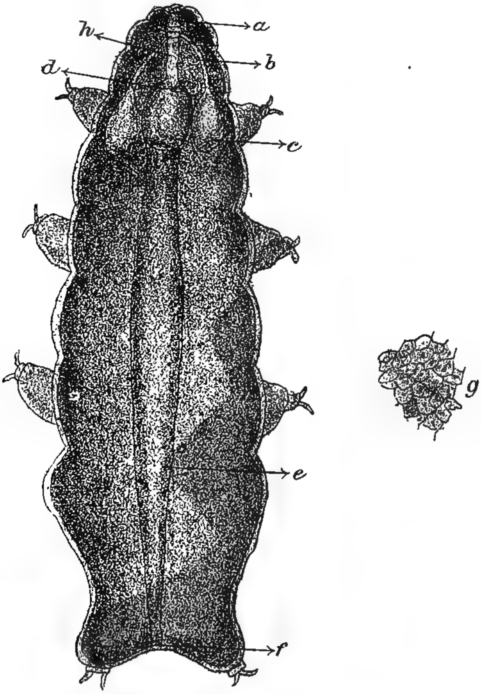

FIG. 9.—ALIMENTARY CANAL OF MACROBIOTUS.

a = mouth or oral cavity. *b* = salivary duct. *c* = salivary gland.
h = œsophagus. *d* = pharynx. *e* = alimentary tract or intestine.
f = anus. *g* = microscopical structure of salivary gland.

(17) The *Araneina* are *Arachnida* with sub-chelate cheliceræ, and possess a poison gland which opens in the terminal joint. They have from four to six spinning glands situated at the posterior end of the abdomen.

"The spiders are remarkable for the minuteness of the pharynx and œsophageal canal. Savigny believed that in some species there existed three pharyngeal apertures, through which the juices expressed from the captured insect by the action of the maxillary plates were filtered, as it were, into the narrow œsophagus. In *Mygale*, however, there is only one aperture." The œsophagus leads into a stomach produced into several lateral appendages, which sometimes extend into the limbs. The stomach of *Tegenaria domestica*, and other species, is capable of great distension, and passes directly into the intestine, which dilates into a rectum and then terminates in an anus. Into the intestine open several so-called biliary ducts. The latter are thrown off from a large organ (Fig. 10) situated on either side of the intestine, but which is greatly concealed by large masses of adipose tissue occupying the sides of the abdomen. This organ has not the function of a liver, for its secretion is of a pancreatic nature.

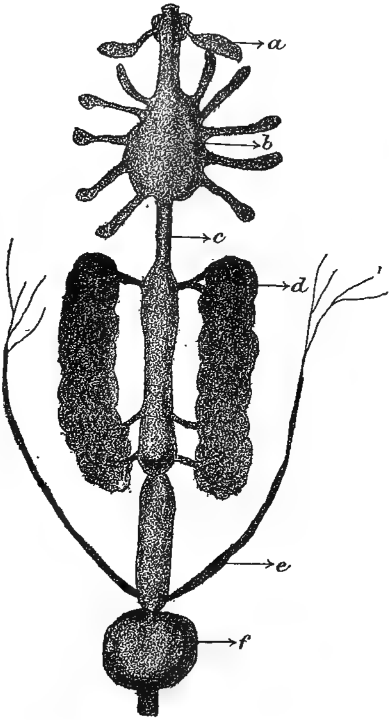

FIG. 10.—DIAGRAM OF THE ALIMENTARY CANAL OF PHOLCUS RIVULATUS.

a = salivary glands. *b* = stomach.
c = intestine. *d* = so-called liver.
e = Malpighian tubules. *f* = rectum.

In front of the rectum open two long slender tubes which often branch; these are the Malpighian tubules. Salivary glands are also present. Spiders are carnivorous animals, and the females are sometimes addicted to cannibalism.

They devour their "Romeos," if the latter are in the least obnoxious.

(18) The *Arthrogastra*.—In this order, to which the scorpion belongs, "the mouth is situated between the labrum in front, the bases of the pedipalpi and those of the first two pairs of ambulatory limbs at the sides and behind." It is a very small aperture and leads into a pharyngeal sac with chitinous walls. The pharynx passes into a narrow œsophagus, and into this two ducts from large salivary glands discharge the secretion. The intestine forms practically a straight tube which terminates in an anus. As in the *Araneina*, numerous so-called biliary ducts open into the intestine. The pancreas or digestive gland (the so-called liver) is extremely well developed in *Scorpio*, occupying all the spaces between "the other organs in the enlarged part of the body, and even extending for some distance into the narrow posterior somites."

All the *Arthrogastra* have a distinctly segmented abdomen.

(19) The *Eurypterida* form an order of extinct *Crustacea*, consequently it does not come under our description.

Before alluding to the other orders, it may be stated that the *Crustacea* have been subdivided into the *Gnathopoda*, *Pectostraca*, and *Malacostraca*. The *Gnathopoda* have been further divided into the *Merostomata*, *Branchiopoda*, and *Lophyropoda*. These three divisions comprise seven orders, commencing with the *Eurypterida* and ending with the *Copepoda*.

(20) The *Xiphosura*.—Of this order the only existing representative is the genus *Limulus* (the king crabs). The mouth of *Limulus* is provided with a small labrum, a rudimentary metastoma, and six pairs of lateral appendages which terminate in chelæ. It is situated in "the centre of the sternal surface of the anterior division of the body; the anus opens on the same surface, at the junction between the middle division and the telson." The œsophagus is continued from the mouth forwards and upwards, and then dilates into

a stomach, the posterior end of which gradually lessens in diameter and finally passes into the intestine. The stomach is lined internally with a dense rugged membrane. "The distinction between the stomach and intestine is effected, as Van der Hoëven has shown, by a conical valvular pylorus, which projects into the commencement of the intestine. The hepatic mass, composed of contorted slender cæca, which with the generative glands fills the greater part of the cephalo-thoracic cavity and also extends into the abdomen, pours its secretion into the commencement of the intestine by two ducts on each side."

The so-called liver or hepatic mass is a very large organ in the *Crustacea;* but its secretion answers chemically to that of a pancreas—in fact, this organ is nothing more than a pancreas or digestive gland. In *Limulus* there is a short rectum opening into a kind of cloaca.

(21) The *Trilobita* form an extinct order of *Crustacea.*

(22) The *Phyllopoda.*—In this order the alimentary canal, as represented by *Apus*, is very simple. The mouth is situated anteriorly on the ventral side of the body, and leads into a vertical œsophagus which finally bends back into a small stomach. The stomach passes into a straight intestine, the latter terminating in an anus situated below the terminal segment. The pancreas (the so-called liver) is situated in the head, and consists of many cæcal tubules branching from the stomach. There are two salivary glands whose secretion is poured directly into the stomach, these glands being situated above that organ.

Dr. G. O. Sars (the distinguished Professor of Natural History in the University of Christiania) has very fully described the digestive system of *Cyclestheria hislopi*,* a new generic type of bivalve *Phyllopoda.*

In *Cyclestheria hislopi* the mouth, "located between the masticatory parts of the mandibles, is generally covered

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* See *Christiania Videnskabs—Selskabs Forhandlinger*, 1887, No. 1, pp. 28 and 40.

below by the labrum. It leads to a short and narrow œsophagus, which ascends almost perpendicularly to the intestine, in the inner cavity of which it forms a distinct mammillar projection. The walls of the œsophagus are highly muscular, and its contours wavy from the strong circular muscles. Besides numerous fine muscular bundles forming a continua-

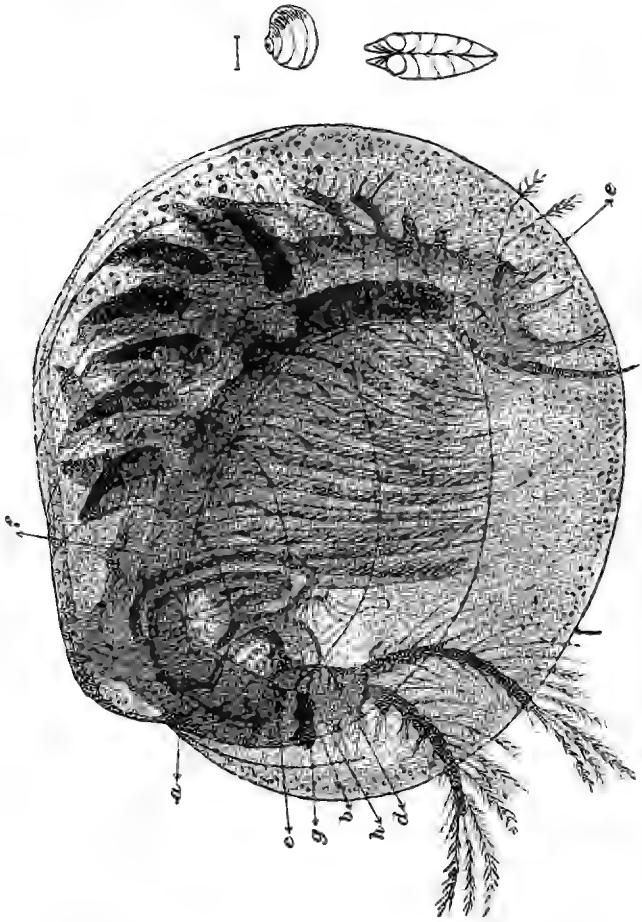

FIG. 11.—ALIMENTARY CANAL, &c., OF CYCLESTHERIA. (*After* Dr. G. O. SARS.)
a = alimentary canal (intestine). *b* = œsophagus. *c* = mandible. *d* = labrum. *e* = anus.
f = shell-gland. *g* = eye. *h* = position of brain. (× about 24 diameters.)

tion of the transverse muscles of the labrum mentioned above are found adjoining its anterior wall. The intestine (Fig. 11), as in the other forms of the *Phyllopoda*, constitutes a rather wide and uniform tube, running along the axis of the body, but very slightly dilated in its anterior part, that curves more or less abruptly downward, according to the attitude of the head. The foremost part of the intestine, extended within the preoral part of the head, expands at the end on either side to a very short and broadly rounded cæcum, quite simple, without any trace of folds or lobes, and communicating with the intestinal cavity by a wide opening."

In *Cyclestheria hislopi* there is no pancreas or so-called liver filling up a great part of the anterior end of the body. The total want of this organ is a striking feature, as it is present in all other known bivalve *Phyllopoda*. In this respect *Cyclestheria* occupies a lower rank than the *Branchipodidæ*, in which the digestive tubules are found to be at least more or less distinctly folded or lobed. "The structure of the intestinal tube (of *Cyclestheria*) is that usually met with, its walls being rather thin and surrounded by numerous circular muscles. At the end of the trunk the intestine terminates with a well-defined rectum, traversing the caudal part close to its ventral side, and opening at its extremity between the two caudal claws. The latter part of the intestinal canal is very strongly muscular and generally devoid of contents, except when at intervals the excrements are expelled from the anal orifice."

According to Dr. Sars, the food of *Cyclestheria* consists of vegetable matter (*e.g.*, *Algæ*, *Desmidiæ*, *Diatomeæ*, and *Confervæ*). The contents of the alimentary canal are of a yellow colour in its anterior part, becoming gradually darker posteriorly, and the excreta are invariably of a dark-brown colour. "The *food* is conveyed to the mouth by the rhythmical movements of the legs, which give rise to a whirling motion, whereby any small particles suspended in the surrounding water are sucked between the valves and brought into the narrow conduit running along the ventral side of the trunk between the bases of the legs. The particles are here successively thrown forward, chiefly by the aid of the coxal lobes of the legs, till they reach the oral region, where they are partly pushed into the mouth by the aid of the maxillæ, partly caught by the protracted labrum, and by the retraction of that part brought immediately within the reach of the mandibles. When the animal is feeding, the latter organs are found to move almost incessantly, their molar surfaces being at short intervals closely applied against each other and their bodies revolved, so as to cross and triturate the particles. At the same time the labrum is lowered at short reprises and then thrown back against the mandibles, thus continually conveying new particles within the reach of the mandibles. The swallowing movements of the œsophagus when transferring prepared food to the intestine, are very distinctly observed through the shell, whereas the intestine itself does not seem to perform any perceptible peristaltic movements."

(23) The *Cladocera.*—In this order, to which *Daphnia* belongs, the alimentary canal does not differ very much from that of the *Phyllopoda.* Many of the Australian *Cladocera* have been recently investigated by Dr. G. O. Sars.* In *Latonopsis australis*, *Simocephalus australiensis*, *Macrothrix spinosa*, and *Ilyocryptus longiremis*, the alimentary canal is a simple tube traversing the body, whereas in *Dunhevedia crassa* and *Alona archeri* the alimentary canal forms in the middle of the body a double loop before passing to a dilatation in front of the muscular rectum. A large dilatation or sac is also present in *Ilyocryptus longiremis,* but there are no loops. A sac of smaller size is observable in all the above-mentioned forms, and is situated in each case in front of the rectum. The intestine or alimentary canal of *Macrothrix spinosa* is dilated in its anterior part; and the digestive tube of *Simocephalus australiensis* is provided with two large incurved

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* *Christiania Videnskabs—Selskabs Forhandlinger*, 1888, No. 7.

cæcal appendages. The ducts from these appendages open into the anterior end of the alimentary canal. These cæcal appendages are not present in any of the other Australian forms mentioned above. The anus in these forms is situated behind or above the caudal claws. For a further description of the *Cladocera* the reader is referred to an excellent paper, entitled "Oversigt af Norges Crustaceer med forelobige Bemærkninger over de nye eller mindre bekjendte Arter," by Dr. Sars.*

(24) The *Ostracoda.*—"The alimentary canal of the *Ostracoda* is provided anteriorly with an apparatus of hard parts resembling in many respects the gastric armature of the *Isopoda*, aad gives rise to two hepatic cæca."

In *Cyprinotus dentato-marginatus*, the alimentary canal consists of three principal parts: a narrow, muscular œsophagus ascending almost perpendicularly from the oral aperture, the intestine proper, and a very short rectum opening just in front of the caudal rami. "The intestine proper exhibits two considerable dilatations, the anterior, lying in the foremost part of the body, almost globular in form, the posterior somewhat larger and more oval, both defined by a well-marked median instriction, just above the great adductor muscle of the shell. From the anterior division of the intestine two slender cæcal appendages are given off, each being received between the lamellæ of the corresponding valve and running diagonally backwards to the infero-posteal corner." These cæcal appendages, of a green colour, are, *à priori*, pancreatic in function. The kidney or shell-gland in the *Ostracoda* is very small.†

(25) The *Copepoda.*—The mouth leads into a straight and simple alimentary canal. In *Cyclops*, which is probably the most common form of the *Copepoda*, there is no distinct

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* *Christiania Videnskabs—Selskabs Forhandlinger*, 1890, No. 1, pp. 30–53.

† For a detailed description of many genera and species of the *Ostracoda*, see a paper by Dr. G. S. Brady, F.R.S., in the *Transactions of the Royal Society of Edinburgh*, vol. 35, p. 489; and one by Dr. Sars in *Christ. Vidensk Selsk. Forhandl.*, 1889, No. 8, pp. 5-58; and 1890, No. 1, pp. 54–76.

digestive gland or pancreas. In *Diaptomus orientalis*, first described by Dr. Brady,* the anterior portion of the intestine is dilated; but, speaking generally, the digestive system of the *Copepoda* is a simple tube devoid of appendages.

(26) The *Rhizocephala* form the first order of the *Pectostraca;* and they are parasitic organisms. The body is sac-like, and, unlike the majority of the *Crustacea*, is devoid of limbs and segmentation. The mouth is funnel-shaped, and is surrounded by chitin. There is no alimentary canal. In fact, we have in this order one of the reversions to a very low type of digestion.

(27) The *Cirripedia* contain the barnacles (*Lepas*) and the acorn-shells (*Belanus*).

The mouth in *Lepas* faces the posterior end of the body and leads into a short œsophagus, which dilates into a stomach. The stomach passes into the intestine, which is bent upon the former organ. The intestine tapers gradually to the anus, which is situated at the base of the caudal appendage. The stomach is covered by small branched glands which are pancreatic in function.

The food of the barnacles (consisting of small marine animals) is brought to the mouth by the currents produced by the cirri. In the words of Prof. Huxley, "a barnacle may be said to be a crustacean fixed by its head, and kicking the food into its mouth with its legs."

The majority of the *Cirripedia* are hermaphrodites, but in the so-called supplemental or complemental male of *Scalpellum vulgare* (one of the *Balanidæ* or sessile *Cirripedia*) there is neither mouth nor alimentary canal. In *Scalpellum ornatum* the complemental males have no mouth; but in *Scalpellum rostratum* these males have a well-developed alimentary canal.†

(28) The *Amphipoda* have a laterally compressed body with branchiæ attached to the thoracic limbs. The mouth opens into a straight and simple alimentary canal. The ducts of

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* *Linn. Soc. Journ. Zool.*, vol. 19, p. 296.

† See Darwin's *Monograph of the Cirripedia.*

the pancreas (the so-called liver) discharge the secretion into the anterior part of the alimentary canal. There are in some of the *Amphipoda* Malpighian tubules which open into the posterior part of the alimentary canal.*

(29) The *Isopoda*.—In this order, to which the wood-louse belongs, the body is usually broad, depressed, or vertically flattened, and more or less arched. The alimentary canal is similar to that of the *Amphipoda*. Fig. 12 represents the digestive system of *Oniscus* (the wood-louse). It forms a straight tube, the masticatory portion being strongly armed. Two ducts, leading from a pair of cellular pancreatic follicles on each side of the alimentary canal, pour the digestive fluid into the anterior portion of the canal. The number of these follicles is variable in other genera of the *Isopoda*, but in *Oniscus* there are always four, two on each side of the alimentary canal. Sometimes there are one or two tubules which open into the posterior part of the intestine. The function of these appendages is of the same nature as the Malpighian tubules of the *Insecta*.

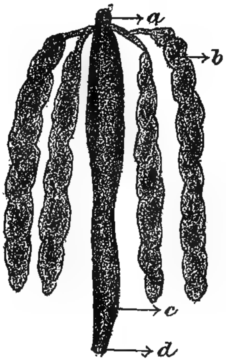

FIG. 12. — ALIMENTARY CANAL OF ONISCUS.

a = masticatory portion.
b = pancreatic follicles.
c = intestine. *d* = anus.

(30) The *Stomapoda* are elongated. *Crustacea* having a short, cephalo-thoracic shield which does not entirely cover all the thoracic segments. In the genus *Squilla* there are five pairs of maxillipeds, and three pairs of backwardly turned biramous thoracic feet. The alimentary canal, somewhat dilated in its anterior part, is a long cylindrical tube,

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* Many new species of the *Amphipoda* have been described by Sars in the *Christiania Vidensk. Se'sk. Forhandl.*, 1882, No. 16, pp. 75–115.

into which numerous pairs of pancreatic follicles discharge the digestive fluid. The intestine becomes narrower at the posterior end, and terminates in an anus situated behind the twentieth somite.

(31) The *Anomoura* form a small order containing the hermit-crabs (*Paguridæ*). They are distinguished from the *Macroura* in having an uncalcified and soft integument. The appendages of the body are more or less abortive through disuse, while those of the sixth somite are modified to form claspers. By means of the claspers the hermit-crabs are capable of holding on to the columellæ of the shells of Molluscs which the *Paguridæ* inhabit. The inner part of the *Anomoura* are somewhat similar in structure to those of the *Macroura.*

(32) The *Brachyura.*—This order includes the crabs. The abdomen is small and without a caudal "fin." It is curved round against the channelled ventral surface of the thorax. The mouth lies between the mandibles, and is a wide aperture, bounded by the labrum in front and the metastoma behind. It leads into a wide but short œsophagus. The œsophagus opens almost ventrically into a large stomach of globular form. The walls of the stomach, as well as those of the œsophagus, are lined by a chitinous extension of the exoskeleton—the so-called teeth. The function of these chitinous teeth is to divide and macerate the food before it passes into the intestine. The posterior part of the stomach of the *Brachyura* gradually lessens in diameter, and then leads into the intestine. "The intestine passes backwards with a slight vertical bend to the base of the penultimate abdominal segment." The so-called liver, which is essentially pancreatic in function,* consists of two symmetrical halves. This large bilobed organ extends the whole length of the cephalo-thorax; and the numerous cæcal tubes (arranged in tufts), of which it is composed, are clearly seen under the surface of water. The cæcal tubes of each half of the digestive organ lead into a

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* Dr. Griffiths' paper in the *Proceedings of Royal Society of Edinburgh,* vol. 16, page 178.

"bile-duct," which opens into the anterior portion of the intestine.

(33) The *Macroura* form the last order we have to consider of the *Crustacea*. To this order belong the lobster (*Homarus*), crayfish (*Astacus*), and shrimp (*Palæmon*).

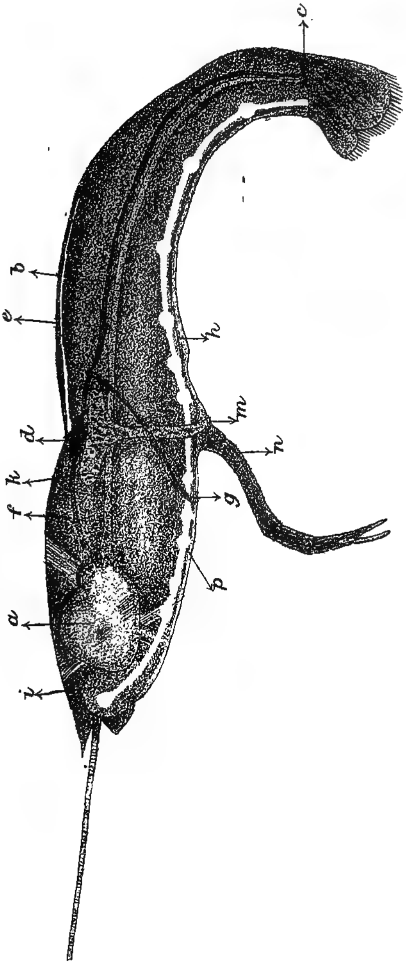

FIG. 13.—THE CRAYFISH (ASTACUS FLUVIATILIS).

a = stomach. *b* = intestine. *c* = anus. *d* = heart. *e* = superior abductor artery. *f* = ophthalmic artery. *g* = sternal artery. *h* = inferior abdominal artery. *i* = green gland. *k* = genital gland (♀). *m* = opening of genital duct. *n* = second ambulatory limb. *p* = nervous system.

The alimentary canal is well defined, especially the stomach.

As an example of the *Macroura*, we describe in detail the alimentary canal of *Astacus fluviatilis* (the fresh-water crayfish). The mouth lies behind the mandibles, and is a wide aperture bounded by the labrum in front and the metastoma behind. This oral aperture leads into a wide but short œsophagus situated on the ventral side of the head. The œsophagus opens almost vertically into a large stomach divided into cardiac and pyloric portions. The pyloric portion, dilated dorsally in a cæcum, passes directly into a long tubular intestine, which dilates into a small rectum, and finally terminates in an anus (Fig. 13). The only lateral appendage to the alimentary canal of *Astacus* is the so-called liver (Figs. 14 and 16), whose ducts open on each side of the pylorus. This so-called liver is in reality a digestive gland or pancreas, and consists of numerous cæcal tubes, whose microscopical structure is represented in Fig. 16. There are no other cæcal appendages to the alimentary canal of *Astacus*; in this respect the crayfish differs from the *Brachyura* and some other *Macroura*. But it may be stated that “in many *Crustacea* the digestive canal is surrounded by cells filled with oily or fatty matter of a yellow or blue colour; they may be compared to an omentum, and probably serve as a store of nutriment, to be drawn upon during the moult, or when food is scarce.”

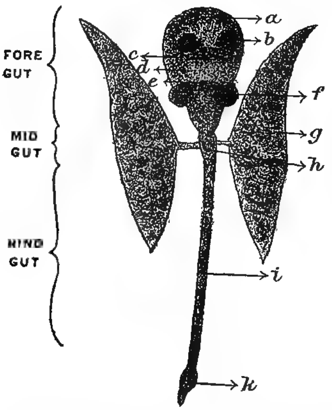

FIG. 14.—ALIMENTARY CANAL OF ASTACUS.

a = cardiac part of stomach. *b* = anterior gastric muscles. *c* = cardiac ossicle. *d* = pyloric part of stomach. *e* = pyloric ossicle. *f* = posterior gastric muscles. *g* = so-called “liver.” *h* = cæcum. *i* = intestine. *k* = rectum.

There are no salivary glands in *Astacus fluviatilis*. As the stomach of the crayfish (Fig. 15) is far in advance of any previously described, it is important that a full detailed description of it should be given. As already stated, the stomach of *Astacus* is divided into cardiac and pyloric portions. The internal walls of the anterior half of the cardiac portion are membranous and are invested with numberless minute hairs; but in the posterior half the walls are strengthened by calcified and chitinous ossicles which are so arranged as to form a gastric mill or gizzard. Professor Huxley * describes the gastric mill of *Astacus* in the following

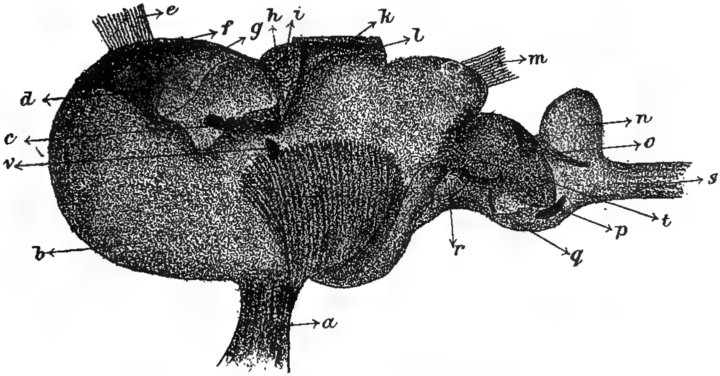

FIG. 15.—LONGITUDINAL SECTION OF STOMACH OF ASTACUS.

a = œsophagus. *b* = position of gastrolith. *c* = lateral tooth. *d* = pterocardiac ossicle. *e* = anterior gastric muscle. *f* = cardiac ossicle. *g* = urocardiac process. *h* = zygocardiac ossicle. *i* = pre-pyloric ossicle. *k* = median tooth. *l* = pyloric ossicle. *m* = posterior gastric muscle. *n* = cæcum. *o* = median pyloric valve. *p* = aperture of "bile" duct. *q* = lateral pouch. *r* = cardio-pyloric valve. *s* = intestine. *t* = lateral pyloric valve *v* = small inferior tooth.

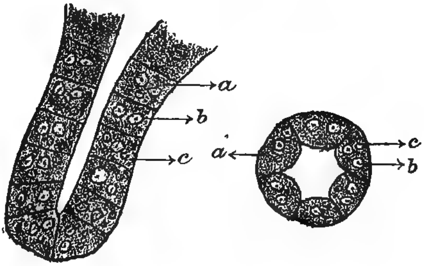

FIG. 16.—STRUCTURE OF SO-CALLED LIVER OF ASTACUS.

a = epithelium cells. *b* = so-called hepatic cells. *c* = ferment cells.

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* *The Anatomy of Invertebrated Animals*, p. 318.

words: "It consists, in the first place, of a transverse, slightly arcuated cardiac plate, calcified posteriorly, which extends across the whole width of the stomach, and articulates at each extremity by an oblique suture with a small curved triangular antero-lateral or pterocardiac ossicle. On each side, a large, elongated postero-lateral or zygocardiac ossicle wider posteriorly than anteriorly, is connected with the lower end of the antero-lateral ossicle, and, passing upwards and backwards, becomes continuous with a transverse arcuated plate, calcified in its anterior moiety, and situated in the roof of the anterior dilatation of the pyloric portion; this is the pyloric ossicle. These pieces form a sort of six-sided frame, the anterior and lateral angles of which are formed by movable joints, while the posterior angles are united by the elastic pyloric plate.

"From the middle of the cardiac piece a strong calcified urocardiac process extends backwards and downwards, and, immediately under the anterior half of the pyloric ossicle, terminates in a broad, thickened extremity, which presents inferiorly two strong rounded tuberosities, or cardiac teeth. With this process is articulated obliquely upwards and forwards, in the front wall of the anterior dilatation of the pyloric portion, and articulates with the anterior edge of the pyloric ossicle, thus forming a kind of elastic diagonal brace between the urocardiac process, and the pyloric ossicle. The inferior end of this pre-pyloric ossicle is produced downwards into a strong bifid urocardiac tooth. Finally, the inner edges of the postero-lateral ossicles are flanged inwards horizontally, and, becoming greatly thickened and ridged, form the large lateral cardiac teeth. The membrane of the stomach is continued from the edges of the pre-pyloric to those of the postero-lateral ossicle in such a manner as to form a kind of pouch with elastic sides, which act, to a certain extent, as a spring, tending to approximate the inferior face of the pre-pyloric ossicle to the superior face of the median process of the cardiac ossicle."

There are four principal muscles (see Figs. 14 and 15) which work this complex stomach. The two anterior gastric muscles attached to the cardiac ossicle, ascend obliquely forwards and are fixed to the inner surface of the carapace. The two posterior gastric muscles attached to the pyloric ossicle are also fixed to the carapace. The food torn to pieces by the mandibles is crushed into a fine state of division in the cardiac portion of the stomach. The thick walls of the pyloric portion are covered internally with long hairs. These project into the interior forming a kind of strainer, which only allows the nutritive juices and finely divided particles to pass into the intestine.

At the sides of the cardiac portion of the stomach, embedded in its tissues, are usually to be found in the summer two calcareous masses or plates, known as gastroliths. At the period when the crayfish moults the gastroliths are also cast. They weigh from two to three grains; what their function may be is still unknown. Possibly, they may be simply deposits due to an excess of calcareous matter in the system.*

We have now come to the end of the great class, ARTHROPODA. The majority of its members, excepting degenerate types, have well-defined digestive apparatuses. Often, as in the *Crustacea* and *Insecta*, the intestinal epithelium is furnished with a hard layer of chitin ($C_{15}H_{26}N_2O_{10}$), sometimes raised into projections destined to crush and macerate the food. The mouth is either suctorial, masticatory, or biting; and in the *Crustacea* certain anterior parts of the intestinal canal become buccal pieces. In some of the lower Arthropods there are present both salivary glands and so-called livers; in others, either one or the other organ is absent—*e.g.*, both salivary glands and "livers" are present in the *Orthoptera*, *Coleoptera*, and *Arthrogastra*. In the *Lepidoptera*, *Arctisca*, and *Dilopoda* only salivary glands are present; and in the *Xiphosura* and *Ostracoda* there are only the so-called livers or digestive

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* See also Irvine and Woodhead in *Proc. Roy. Soc. Edin.*, vol. 16, p. 330.

glands. The "liver" in the lower Arthropods consists of cæcal prolongations of the intestine, but in the higher *Crustacea* it becomes an organ of considerable size. As a rule the salivary glands are better differentiated in the *Insecta* and *Arachnida* than in any of the other classes of the *Arthropoda*. But the large bilobed liver, or, as we prefer to call it, the pancreas, is characteristic of the *Crustacea*, especially the higher forms. It appears that the salivary glands and pancreas are interchangeable, sometimes one replacing the other.

It may be remarked that in many of the *Arthropoda* the alimentation considerably influences both the form and the dimensions of the digestive apparatus. Carnivorous animals have a digestive apparatus which is comparatively short. Caterpillars, which are most voracious, have wide intestines, while the butterflies, which eat little, and only liquid foods, have long and slender alimentary tubes. Certain genera of the *Insecta* (*Ephemera*, *Bombyx*, *&c.*) which are very voracious as larvæ, are in the mature state destitute of organs of manducation. Wholly destined for generation or reproduction, they cannot take any nutriment; hence the brief duration of their lives.

THE POLYZOA.

The *Malacoscolices*, one of the Malacozoic Series, is divided into two great classes—the *Polyzoa* and *Brachiopoda;* and the former class is subdivided into four orders.

The *Polyzoa* have a mouth surrounded with tentacula, an enlarged alimentary canal, sometimes furnished with dentiform projections destined for mastication. Occasionally there exists a sort of stomach.

Most of the *Polyzoa* are microscopic animals; but, living in colonies, they sometimes form conspicuous masses; consequently they bear a resemblance to the Sertularian *Hydrozoa.*

(1) The *Podostomata.*—This order is represented by the genus *Rhabdopleura.* The disc or lophophore is horseshoe-

shaped. In the *Rhabdopleura* the tentacula are narrower, but longer, than any other *Polyzoa;* in this respect they somewhat resemble the *Brachiopoda.* "The mouth is situated beneath the free margin of the disc, on the opposite side to the anus."

(2) The *Phylactolœmata* are all fresh-water *Polyzoa.* The mouth (Fig. 17) is situated on the lophophore, and is surrounded by a number of ciliated tentacula. The mouth leads into an œsophagus which passes into a muscular pharynx. "The particles of food are carried down the inner surface of each tentacle, and the mouth and pharynx expand to receive such as are appropriate, as if by an act of selection. The rejected particles pass out between the bases of the tentacula, or are driven off by the centrifugal currents." The muscular pharynx leads into a capacious stomach. The narrow intestine is continued from the posterior end of the stomach, and terminates in an anus situated near the mouth. The intestine is bent backwards, so that it runs almost parallel with the anterior portion of the alimentary canal. The walls of the stomach are studded with cells or follicles of a pancreatic nature; and its orifice is surrounded by cilia. The food particles are constantly regurgitated into

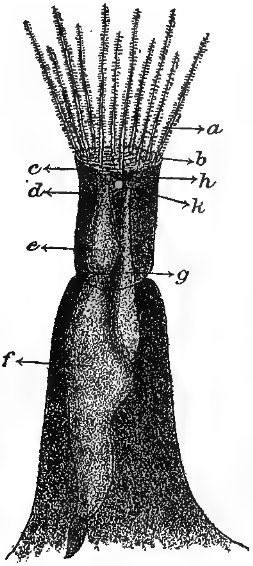

FIG. 17.—ALIMENTARY CANAL OF POLYZOON.

a = tentacles. *b* = lophophore. *c* = mouth. *d* = œsophagus. *e* = pharynx. *f* = stomach. *g* = intestine. *h* = anus. *k* = nervous ganglion.

the middle portion of the stomach (which is sometimes called a gizzard), and, after having undergone a further comminution, are returned to the anterior portion of that organ, where they are kept in constant agitation. These particles finally pass into the intestine. The undigested portion of the food agglomerates into small pellets which are carried upwards and are expelled through the anus.

The alimentary canal of the *Polyzoa* is devoid of salivary glands.

It has been stated that the *Polyzoa* resemble somewhat the Sertularian *Hydrozoa,* but it must be distinctly understood that the *Polyzoon* has not merely a digestive cavity, like the *Hydra* and the *Actinia;* for the digestive apparatus of the former is differentiated into a pharynx, stomach, and intestine provided with an anal aperture. In fact, the *Polyzoon* has a complex and highly developed digestive system. Then, again, the Polyzoan tentacula differ from those of the *Hydrozoa* and *Actinozoa,* in being somewhat stiff and provided with cilia.

(3) The *Gymnolœmata* are marine *Polyzoa,* except *Paludicella,* which is a fresh-water form.

(4) The *Pedicellinea.*—In this order the buds, produced by gemmation, become detached from the original stock.

THE BRACHIOPODA.

This class is divided into two orders, the *Tretenterata* and the *Clistenterata.* They are all marine animals "provided with a bivalve shell, and are usually fixed by a peduncle, which passes between the two valves in the centre of the hinge line, or the region which answers to it in those Brachiopods which have no proper hinge."

(1) The *Tretenterata* have no hinge. The mouth or oral aperture leads into an œsophagus, which passes into a stomach provided with pancreatic follicles. From the stomach passes the intestine, which opens into the cavity of the pallium or mantle on the right side of the mouth. The alimentary canal

is suspended in a spacious perivisceral cavity. "The walls of this cavity are provided with cilia, the working of which keeps up a circulation of the contained fluid." In *Lingula* the intestine is long, and forms two bends before it terminates in the pallial cavity.

(2) The *Clistenterata* have a hinge uniting the two valves of the shell. In the *Terebratula* the mouth opens downwards into the pallial chambers, and is situated in the middle line, about one-third of the length of the shell from the hinge. The mouth of the *Brachiopoda* has no rudiments of a maxillary or dental apparatus. The œsophagus in *Terebratula* is short, and is situated between the anterior portions of the so-called liver. The stomach is an oblong organ which is dilated at the cardiac end; the narrower may be spoken of as the pyloric portion, but there is no valvular structure at the pylorus. The cardiac portion of the stomach is surrounded by the so-called liver. The intestine is short, straight, and is continued in a line with the pylorus to the interspace between "the attachments of the adductores longi and cardinales to the ventral valve," where it ends blindly. The so-called liver (pancreas) is a large organ consisting of numerous ramified follicles. There are usually two ducts from this organ, communicating with the cardiac portion of the stomach. The alimentary canal is freely suspended in the body cavity by delicate membranes which stretch from the body walls.

THE MOLLUSCA.

The *Mollusca* form the second division of the Malacozoic Series; and this division comprises seven orders.

(1) The *Lamellibranchiata* include the *Ostrea*, *Anodonta*, *Mytilus*, *Pecten*, *Cardium*, *Mya*, *Unis*, &c. The mouth is bounded by lips, which are usually produced into two labial palps. These palps are ciliated, and by the action of the cilia food particles, which have passed into the branchial chamber, are driven into the mouth. The mouth of a Lamellibranch

carries no organs—jaws or teeth—for the prehension or mastication of food particles. It passes by a short œsophagus (Fig. 18) into an expanded stomach, which is embedded in the so-called liver. At the pyloric end of the stomach a diverticulum of that organ contains a rod-like body—the crystalline style. The function of the crystalline style is most

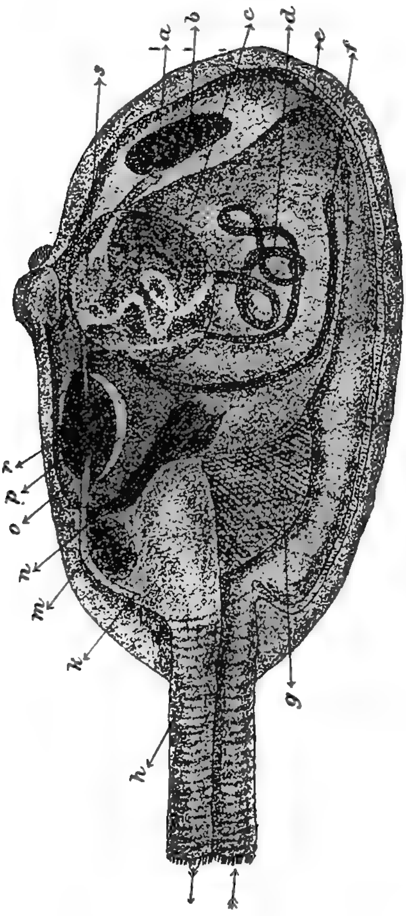

FIG. 18.—ALIMENTARY CANAL, &C., OF MYA (THE GAPER).

a = mouth. *b* = anterior adductor muscle. *c* = so-called liver. *d* = intestine in substance of foot. *e* = foot. *f* = gastric cæcum with style. *g* = gills. *h* = siphons. *k* = anus. *m* = posterior adductor muscle. *n* = posterior retractor muscle. *o* = organ of Bojanus. *p* = heart. *r* = pericardium. *s* = position of stomach embedded in the liver.

likely to mix the food particles with the secretions of the stomach and those poured into it from the ducts of the large digestive gland ("liver"), which surrounds the stomach. The crystalline style is well-developed in *Mya*, *Cytherea*, &c.; but in *Ostrea* it only exists in a rudimentary state as a piece of cartilage; and in *Pholas* it is said to have the form of a folded plate.

The Lamellibranch stomach leads into a long intestine, which turns downwards and makes many convolutions among the so-called liver and genital gland, and again comes into the dorsal region, where it traverses the heart, leaving the pericardium at its posterior end, and ultimately terminates in an anus situated behind the posterior adductor muscle. The anus is placed on a projecting papilla. That portion of the intestine from where it enters the heart to the anal aperture is usually called the rectum. In a transverse section, the intestine is horseshoe-shaped, due to the folding in of its dorsal wall, consequently forming a typhlosole. The so-called liver, which is pancreatic in function, consists of numerous branched cæcal follicles. These are united into ducts which open into the stomach by several irregular apertures. There are no salivary glands in the *Lamellibranchiata.*

(2) The *Scaphopoda.*—In *Dentalium* the mouth is surrounded by many filiform tentacula which play the *rôle* of prehensile organs. The mouth leads into a buccal chamber containing the odontophore—a prehensile rasp-like tongue. The buccal chamber passes into the œsophagus leading into the stomach. The intestine then follows, and after being coiled several times, terminates in an anus behind the root of the foot.

The intestine of the *Scaphopoda* does not traverse the heart, as in the *Lamellibranchiata,* for that organ is entirely absent. The so-called liver is bilobed.

(3) The *Polyplacophora* are vermiform *Mollusca* without eyes or tentacula. In *Chiton* the shell is unlike that of any other Mollusc. It consists of eight calcified plates arranged

in a segmented, imbricated manner one behind the other. The mouth is at one end of the body, and the anus at the other.

(4) The *Heteropoda.*—This order, which includes *Atlanta*, is sometimes immersed in that of the *Gasteropoda.*

It may be remarked in passing that, although the *Lamellibranchiata* have no salivary glands, these organs are frequently present in the *Odontophora*, which include the *Scaphopoda, Polyplacophora, Gasteropoda, Pteropoda*, and *Cephalopoda.*

(5) The *Gasteropoda* are subdivided into the *Pulmogasteropoda* and the *Branchiogasteropoda.*

As an example of the digestive system of the *Pulmogasteropoda* we describe that of *Helix* (the snail).

The alimentary canal, which is much coiled, bends forward to open by an anus in the mantle cavity. The mouth, situated at the base of the head-lobe in front of the foot, is bounded by lips. It leads into a buccal cavity, into which is poured the secretion from two large salivary glands (Fig. 19, A). Then follows the œsophagus, which dilates into a crop or proventriculus. The crop leads into the stomach (provided with a blind cæcal appendage) passing into a long-coiled intestine embedded in a large many-lobed organ—the so-called liver, which opens by ducts into both the intestine and stomach. The posterior portion of the intestine bends anteriorly and widens into a rectum which opens, by an anal aperture situated on the right side of the body, into the mantle or pallial cavity. The intestine of *Helix* is folded internally so as to form a typhlosole.

The two salivary glands are on each side of the crop, but their ducts open into the buccal cavity. These glands present different degrees of development in different Gasteropods. This is due to the construction of the mouth and the nature of the food. In *Helix* and *Limax* the salivary glands are well-developed organs; but in *Calyptræa* they are simple tubes.

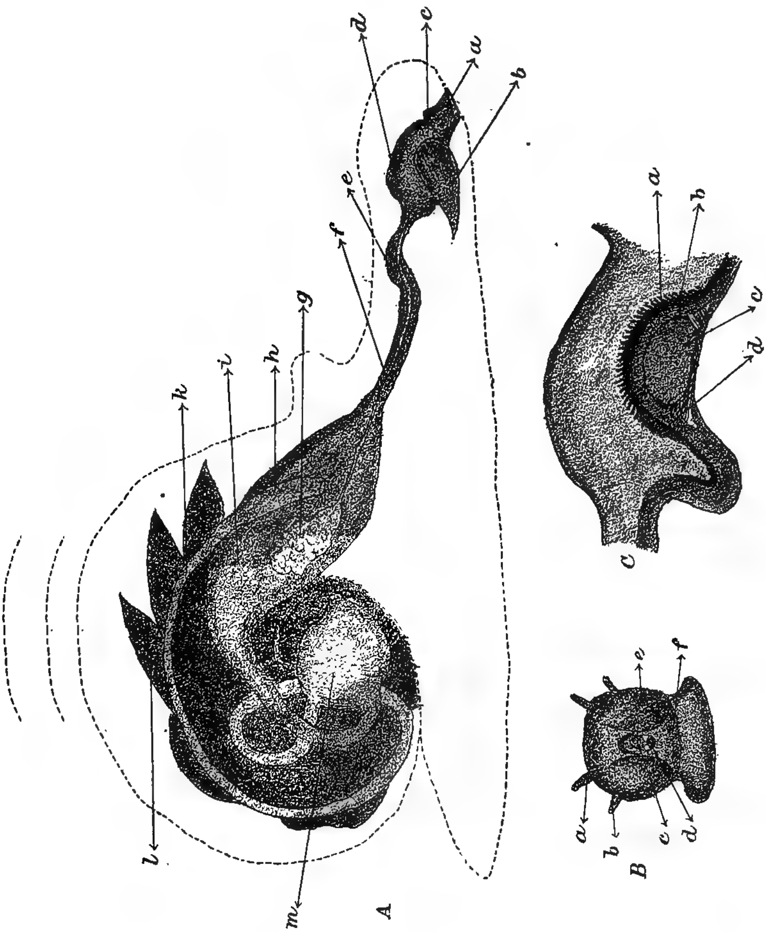

FIG. 19.—ALIMENTARY CANAL OF HELIX ASPERSA.

A. *a* = mouth. *b* = odontophore. *c* = tooth. *d* = buccal mass. *e* = œsophagus. *f* = salivary duct. *g* = salivary gland. *h* = rectum. *i* = crop or proventriculus. *k* = intestine. *l* = liver. *m* = stomach.

B. Buccal Mass. *a* = tentacle (optic organ). *b* = tentacle (olfactory organ ?). *c* = horny jaw. *d* = mouth. *e* = lateral lip. *f* = circular lip.

C. Longitudinal Section of Buccal Mass. *a* = odontophore. *b* = radular membrane. *c* = odontophore cartilage. *d* = intrinsic muscle.

The ducts from the large many-lobed "liver" (pancreas) open into the stomach and anterior portion of the intestine. The secretion of this organ is pancreatic in function.

The buccal cavity (Fig. 19, B and C) is furnished with hard masticatory structures. The upper portion is provided with a horny jaw, and on the floor is the odontophore or radula. This odontophore (lingual ribbon) lies over a cartilaginous support (Fig. 19, C). Powerful muscles are attached to this support, and by the alternate expansion and contraction of these muscles the odontophore is worked backwards and forwards. By this mechanism the food taken into the mouth is ground down against the horny palate. The odontophore is a chitinous product of the radular membrane (Fig. 19, C), and is armed with tooth-like projections. The projections are constantly being replaced as they are worn away by the friction which ensues during mastication.

In the *Branchiogasteropoda* (which includes *Buccinum*, *Patella*, *Cypræa*, &c.) the alimentary canal does not, as a rule, vary very much from that of the *Pulmogasteropoda*.

(6) The *Pteropoda* are marine Molluscs. The foot, which is small, is provided with two large, muscular, wing-like fins (epipodia).* In *Hyalæa* the œsophagus dilates into a kind of crop or proventriculus, which is followed by a cylindrical stomach. The intestine is tubular, describes two convolutions in the substance of the liver, and then terminates in an anus situated beneath the right fin.

(7) The *Cephalopoda*.—This order is divided into the *Dibranchiata* and the *Tetrabranchiata;* and the former order is subdivided into the *Decapoda* and the *Octopoda*.

The *Dibranchiata* include *Sepia*, *Octopus*, *Argonauta*, &c. As an example of the digestive system (Fig. 20) we describe that of *Sepia officinalis*. The mouth, armed with two chitinous jaws which overlap each other, is provided with an

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* See Cuvier's *Mémoires pour servir à l'Histoire et l'Anatomie des Mollusques*.

odontophore. It leads into a long œsophagus, which is narrower in the *Dibranchiata* than in the *Tetrabranchiata*, and then dilates into the muscular stomach. The pyloric portion of the stomach communicates with a glandular sac—the pyloric cæcum. The intestine is bent somewhat upon itself, passing towards the neural (ventral) end of the body and terminating in a median anus. One or two pairs of salivary glands are present in the *Dibranchiata*, which pour the secretion into the buccal cavity or the anterior portion of the œsophagus. The so-called liver is a well-developed bilobed organ provided with two ducts, which in the *Decapoda* receive the ducts of a large number of cæcal appendages. It has been considered that these appendages are the rudiments of a pancreas; but there is no doubt that the so-called liver *per se* is essentially pancreatic in function. This organ does not give rise to any of the biliary acids (glycocholic and taurocholic acids) nor glycogen. The colouring matters which the so-called liver contains, do not answer chemically to bilirubin and biliverdin. But its secretion contains leucin, tyrosin, and a ferment (or ferments) which converts starch into glucose.

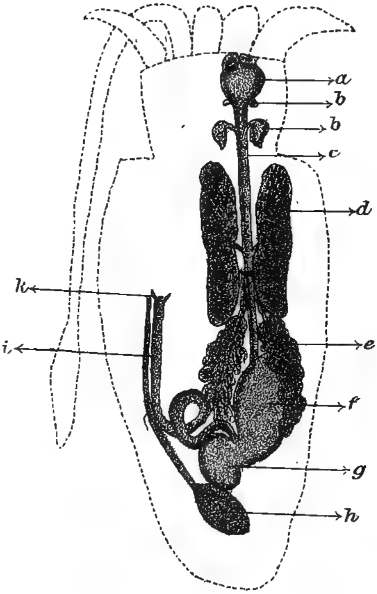

FIG. 20.—ALIMENTARY CANAL OF SEPIA.

a = buccal mass. *b* = salivary glands.
c = œsophagus. *d* = so-called liver.
e = pancreatic follicles (so-called).
f = stomach. *g* = pyloric cæcum.
h = ink-bag. *i* = intestine. *k* = anus.

The ink-bag is a tough, fibrous, glandular sac. It is usually of an oblong pyriform shape, and secretes a brown or black fluid, the colour of which is very durable.

The *Tetrabranchiata* are represented by the only existing genus, *Nautilus*, which is provided with an external chambered siphunculated shell.

Like that of the *Sepia*, the mouth of the *Nautilus* is armed with powerful jaws (Fig. 21). It leads into an œsophagus which dilates into a wide crop. The crop passes into the stomach whose internally chitinous lining is thick and ridged. The cæcum in *Nautilus* is small, and is attached to the anterior portion of the intestine. The intestine makes two abrupt bends and terminates in the branchial cavity. In *Nautilus* there are no salivary glands, unless certain small glandular bodies within the buccal cavity possess that function. The so-called liver is a racemose tetra-lobed gland, and its function is, *à priori*, that of a pancreas.

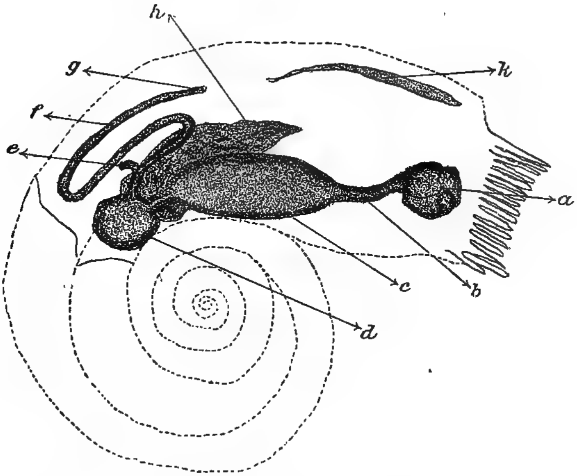

FIG. 21.—ALIMENTARY CANAL OF NAUTILUS.

a = buccal mass. *b* = œsophagus. *c* = crop. *d* = stomach. *e* = "pyloric" cæcum. *f* = intestine. *g* = anus. *h* = so-called liver. *k* = funnel.

The *Tetrabranchiata* have four gills and numerous short retractile tentacula without suckers; while the *Dibranchiata* possess two gills and from eight to ten tentacula with suckers round the head.

From what has been said, it will be seen that the *Mollusca* have a very complete digestive system which is comparable, in a great measure, with that of the *Vertebrata.* In some of the *Mollusca* we find a long œsophagus and enlarged stomach, an intestine with circumvolutions, and a rectum. In others, we observe the stomach arranged more or less after the plan of certain Vertebrates; there are cardiac and pyloric portions, separated by a salient fold. "Sometimes the stomach is furnished with triturating hooklets of varied form. But it is especially by the development of the glandular appendages that the stomach of the *Mollusca* is distinguished from that of the animals hierarchically inferior. These organs, in fact, go on perfecting and complicating themselves more and more in the diverse families of Molluscs, and especially in the more advanced of the Molluscs—the Cephalopods (Cuvier)—there are œsophageal salivary glands with short cæca, a liver (so-called) developed, compact, divided into lobes, provided each of them with an excretory conduit or duct, and all these conduits or ducts open together or separately at the commencement of the median intestine, or into the stomach." But this "liver" is essentially pancreatic in function: the true Vertebrate liver is entirely absent in the *Invertebrata.*

THE PHARYNGOPNEUSTAL SERIES.

This series is divided into two orders—the *Hemichordata* and the *Urochordata* (*Tunicata*).

(1) The *Hemichordata* are represented by a single example —*Balanoglossus,* which is "an elongated, apodal, soft-bodied worm, with the mouth at one end of the body and the anus at the other." The mouth, surrounded by a well-marked lip, leads into a wide œsophagus which opens into a stomach.

From the stomach passes the intestine, which terminates in an anal aperture situated at the posterior end of the body. The mouth is provided with a proboscis.

(2) The *Urochordata* or *Tunicata.*—As an example of this order we describe *Phallusia mentula* (Fig. 22). The oral aperture leads into the pharyngeal-respiratory chamber, from which the œsophagus, situated on the posterio-neural side of the body, selects the food particles introduced into that chamber by the action of small tentacula. The walls of the pharyngeal-respiratory chamber are gathered into ciliated folds, which have a number of slit-like perforations. These act as a kind of sieve. On the hæmal side of the pharynx there is a ciliated groove bounded by two glandular folds (the endostyle). The œsophagus leads into an internal-folded stomach. The intestine, which forms a loop, terminates in an anus situated opposite the atrial or cloacal aperture on the neural side of the body. The Savigny tubules lie upon, and open by a duct into, the stomach. These tubules also ramify over the wall of the intestine, and are pancreatic in function. They are present in nearly all the *Tunicata.**

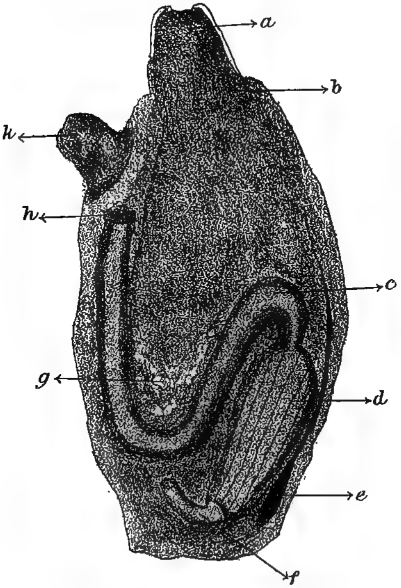

FIG. 22.—ALIMENTARY CANAL OF PHALLUSIA.

a = mouth. *b* = tentacles. *c* = intestine. *d* = stomach. *e* = heart. *f* = œsophagus. *g* = Savigny's tubules. *h* = anus. *k* = atrial aperture.

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* See Chandelon in *Bull. Acad. Belg.*, 1875 ; and Dr. W. A. Herdman in

In *Appedicularia* there is a caudal appendage which contains a notochord; but in the Ascidians the caudal appendage is only present in the larval condition of the animal—a condition closely resembling the tadpole or larval frog. In fact, these animals are degenerated Vertebrates.* Another point in which the Ascidians approach the *Vertebrata* is that the pharynx is also a respiratory cavity.

We have now come to the end of our chapter on Invertebrate digestion in general. Below the *Actinia* the alimentary canal communicates with the body cavity, but with the exception of the *Tunicata*, in all those forms higher (than the *Actinia*) in the animal scale, the body cavity and alimentary canal are entirely separated from each other.

In regard to the masticatory apparatuses; (1) a gizzard is observed in the *Rotifera*, *Oligochæta*, the higher *Insecta*, *Polyzoa*, *Gasteropoda*, and *Cephalopoda*. (2) The complex masticatory apparatus of *Echinus*, with its five jaws, each traversed by a tooth, is probably nothing more than altered epithelium which has become hardened. (3) Hardening of the membrane of the buccal mass is a further advance in the apparatus designed for mastication; as these structures are at the commencement of the alimentary canal, and are separated from the stomach. In the *Annelida* (*e.g.*, *Lumbricus* and *Hirudo*) the so-called jaws are hardened parts of the epithelium of the mouth. These structures may be functionally compared to the teeth of the *Vertebrata*. (4) The *Arthropoda* present a highly developed masticatory apparatus in the jaws, which are appendages of the body segments. "The simplest condition is met with in the *Myriapoda*, as the centipede. A small labrum above the oral aperture, a pair of mandibles or hard crushing jaws, a labium below the oral aperture, with side lobes. The *Arachnida* (spider and scorpion) have labrum and mandibles,

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the *Challenger Reports*, 1882, part i. p. 49; 1886, part ii. pp. 22, 52 and 88; part iii. pp. 22 and 42.

* See Ray Lankester's book, *Degeneration*, p. 41.

and two pairs of more delicate jaws—the maxillæ. These are the side lobes of the labium of the centipede, specialised into distinct lateral jaws. In the *Arachnida*, the mandibles are extended into prehensile and offensive claws. The maxillæ in the spider are related in a remarkable manner to the function of reproduction. The specialisation is therefore incomplete. The *Crustacea* have a labrum, two mandibles, four maxillæ (the second pair representative of the split labium of the *Myriapoda*), and three pairs of maxillipedes (feet-jaws). These last represent the six legs of the *Insecta*. The somites, which in the latter bear motor organs, carry in the *Crustacea* organs that serve for mastication, but they are in structure closely allied to the true legs on the succeeding somites."

In the *Insecta*, the labium, labrum, mandibles and maxillæ are all met with; they present numberless and complex modifications, but for all that are chiefly subservient to the functions of taking in or crushing food. (5) The odontophore or radula of the *Mollusca* forms a still further advance, as it appears to combine the functions of teeth and of a tongue.

As far as a *stomach* is concerned, the first indication of it as a separate organ is observable in some of the *Echinodermata*, *e.g.*, in the *Asteridea*, but the specialisation of the organ is incomplete, inasmuch as it forms a dual function, viz., that of a renal organ as well as being a gastric cavity. There is a true stomach (a dilatation of the alimentary canal) in the *Annelida*, *Arthropoda*, *Polyzoa*, *Brachiopoda*, and *Mollusca*. The crop present in the *Insecta* is simply a cavity which serves to store the food before passing into the stomach. The intestine is straight, and without convolutions in many forms—as, for example, in the *Asteridea*, *Myriapoda*, *Arthrogastra*, &c.—but also in many of the *Mollusca* there is a bend or flexure in the intestine.

CHAPTER IV.

DIGESTION IN THE INVERTEBRATA.

Digestion in Particular.

In the present chapter we describe in *detail* the physiology of the digestive function in certain selected types of all the more important branches of the *Invertebrata.*

THE PROTOZOA.

The *Protozoa* having no differentiated parts, the cell itself performs, among other functions, that of digestion. This function is diffuse in the lower animals, and only becomes specialised or differentiated as we ascend in the zoölogical scale.

THE PORIFERA AND CŒLENTERATA.

Among the animals with cellular differentiation—the *Porifera* and the *Cœlenterata*—the internal cavity of the body (morphologically identical with the alimentary canal, and not with the somatic or body cavity of other animals) has the function of a digestive cavity.

Concerning the function of digestion in *Hydra fusca*, Dr. Greenwood[*] has recently come to the following conclusions: (*a*) the ingestion of solids is performed by slow advance over the prey of lip-like projections of the animal's substance. *Entomostracea*, *Nais*, beetle larvæ, and raw meat prove the most acceptable food; innutritious matter does not act as a stimulus to digestion. (*b*) The digestion of

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[*] *Journal of Physiology*, vol. 9, 317.

enclosed food particles takes place entirely outside the endodermic cells which line the enteric cavity, and among these may be distinguished: (1) pyriform cells destitute of large vacuoles holding secretory spherules during hunger, and these empty during digestive activity; (2) ciliated vacuolate cells, often pigmented: the water of the digestive fluid is probably derived from the vacuoles. (*c*) The pigment occurs as brown or black grains; it has an albuminoid basis. The pigment resists solution in most chemical reagents, but dissolves slowly in nitric acid. (*d*) A reserve substance of an albuminoid nature accumulates during digestion in the basal part of the vacuolated cells, and eventually takes the form of spheres. The excretory pigment probably takes its rise in some residue from this absorbed substance; it is also possible that fat is similarly formed. (*e*) The medium in which digestive activity goes on is probably not acid.

In *Hydra viridis*, which contains chlorophyll,* the mode of nutrition appears to be different from that just described. Gland cells do not form a conspicuous feature in the endoderm of *Hydra viridis*, and consequently digestive secretion is less active.

If the vacuolated cells of the endoderm of *Hydra fusca* contain a nutritive fluid we may reason, *à priori*, that the food vacuoles of the *Protozoa* probably contain a digestive fluid; at any rate the food particles nearest to these vacuoles are always becoming smaller in size, showing that digestion is proceeding.

In *Hydra viridis* chlorophyll has probably a secretory as well as a respiratory function. The same remark applies to the chlorophyllogenous *Protozoa*. "Professor Huxley first showed the presence of "yellow cells" in *Thalassicolla*, which have also been found in almost all Radiolarians. These bodies Haëckel† considered as secreting cells or digestive glands, comparable to the liver cells of *Amphioxus*, and those

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* The chloroplastids of Prof. E. Ray Lankester, F.R.S.

† *Die Radiolarien*, p. 136.

of *Velella* and *Porpita*, as described by Voigt. Subsequently Haëckel found starch in these cells, and concluded that this fact supported the idea of the nutritional function previously assigned to them by himself.*

"Cienkowski† in 1871 endeavoured to show that the yellow cells of Radiolarians were parasitic algæ, since they survived the death of their host, and multiplied subsequently, passing through an amœboid and encysted state."

There is no doubt that the "yellow cells" do survive for some time in the bodies of dead Radiolarians; but in regard to *Hydra* and *Spongilla*, Prof. E. Ray Lankester‡ has shown that "the chlorophyll corpuscles of these animals are not algæ at all (as stated by Dr. Brandt§), but differ in no essential respect from the chlorophyll bodies of plants."

Dr. C. A. MacMunn‖ has shown that "the chlorophyll bodies of *Spongilla*, *Hydra*, *Paramœcium*, *Ophrydium*, *Vortex viridis*, and *Stentor polymorphus* are of different size, colour, and give different reactions, and a different spectrum, from the 'yellow cells' of *Actiniæ*. With regard to size, the 'yellow cells' of *Anthea cereus* were found to measure 12μ ($= 12 \times \frac{1}{1000}$ mm.), or 13μ down to 10μ; while in *Paramœcium* they measured from 6μ down to 3μ—*i.e.*, less than half the size of the former; in *Hydra viridis* mostly from 6μ to 4μ. The colour is a dull brownish-yellow in the 'yellow cells' of *Anthea*, &c.; while it is a fine green in the *Infusoria* and *Hydra*. The spectrum in *Spongilla*, in *Hydra*, and in the *Infusoria* is that of plant chlorophyll; while in the 'yellow cells' it is that of chlorofucin."

The chief function of animal chlorophyll and allied pigments is that of respiration; but it is probable that these pigments play an important part in sexual selection, in

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* *Jena Zeitsch.* 1870, p. 532.

† *Archiv. Mikro. Anat.* 1871.

‡ *Quarterly Journal of Microscopical Science*, vol. 22, p. 229.

§ *Monatsb. Akad. Wiss. Berlin*, 1881.

‖ *Proceedings of Birmingham Philosophical Society*, vol. 5, pt. 1, p. 212.

mimicry, or act as "screens" for the protection of underlying cells, for protective purposes; and possibly, though not probably, they may have a nutritional function, as suggested by Haëckel. Whatever may be the true function or functions of animal chlorophyll, one thing is certain—that the pigment is manufactured in the body of the animal containing it. In the words of Dr. MacMunn: "I would ask investigators to pause before they decide that when an animal chlorophyll is met with, it has been simply eaten by the animal, and deposited unchanged in its tissues; they must remember that the radicle of chlorophyll, like the radicles of other pigments, may be furnished by the action of the digestive juices of the animal on some substance furnished by the plant, and that the animal laboratory is capable of building up molecules quite as large as that of chlorophyll. Our own hæmoglobin is not the unchanged hæmoglobin of our food; what is derived from it is broken up and then regenerated; and it shows an ignorance of physiology to suppose that chlorophyll should be an exception to a general rule."

Reverting once more to the *Porifera*, Dr. Léon Fredericq* has extracted from a large number of sponges a ferment analogous to trypsin or pancreatin. This ferment acts upon starch, fats, and albuminoids. The author of the present work fully confirms Fredericq's researches. The ferment contained in and manufactured by the cells of the *Porifera* converts starch into glucose. It forms an emulsion with neutral fats, and finally decomposes them into fatty acids and glycerol (glycerine). The ferment also converts albuminoids into peptones, which become partially converted into leucin and tyrosin. There is no doubt that the cells of the *Porifera* secrete a ferment in every way analogous to the pancreatic ferment of higher forms.

THE ECHINODERMATA.

Fredericq has also obtained similar results with many

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* *Archives de Zoologie Expérimentale*, tome 7, p. 400.

species of the *Actiniæ*, only the digestive ferment secreted by the cells of these animals does not appear to have the same degree of activity as that extracted from the *Porifera*. Its action is much slower.

The digestive apparatus of *Uraster rubens* (one of the *Asteridea*) has been examined by the author. The *walls* and contents of the wide sacculated stomach, and its five sacs do not contain digestive ferments; for the digestive fluid is

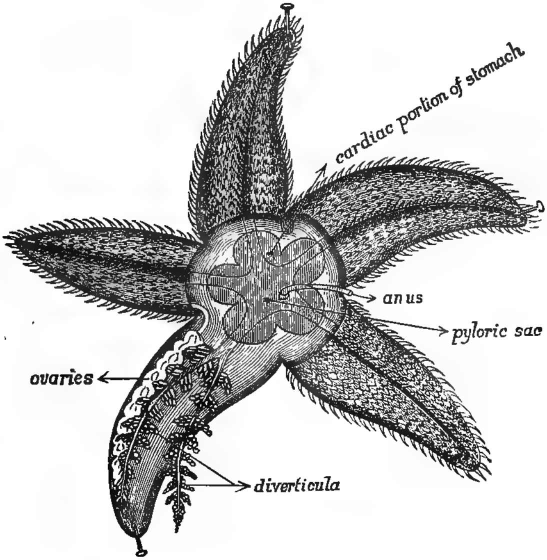

FIG. 23.—STOMACH AND PYLORIC CÆCA OF URASTER.

derived from the pyloric cæca situated in each ray. The pyloric sac, or stomach, gives off five radial ducts, each of which divides into two tubules (Fig. 23) bearing a number of lateral follicles, whose secretions are poured into pyloric sac and intestine.*

The secretion (of the cæca) was obtained from a large number of star-fishes, and gave the following reactions:—

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* *Proceedings of Royal Society of Edinburgh*, vol. 15, p. 111; and *Proceedings of Royal Society of London*, vol. 44, p. 325.

(*a*) The secretion forms an emulsion with oils yielding subsequently fatty acids and glycerol.

(*b*) The secretion decomposes stearin, with the formation of stearic acid and glycerol—

$$C_{57}H_{110}O_6 + 3\ H_2O = 3\ C_{18}H_{36}O_2 + C_3H_8O_3.$$

(*c*) The secretion acts upon starch paste with the formation of dextrose. The presence of dextrose was proved by the formation of brownish-red cuprous oxide, with Fehling's solution.

(*d*) The secretion dissolves coagulated albumin (hard white of egg).

(*e*) Tannic acid gives a white precipitate with the secretion.

(*f*) When a few drops of the secretion of the pyloric cæca are examined chemico-microscopically, the following reactions are observed:—On running in, between the slide and cover-glass, a solution of iodine in potassium iodide, a brown deposit is obtained; and on running in concentrated nitric acid upon another slide containing the secretion, yellow xanthoproteic acid is readily formed. These reactions show the presence of albumin in the secretion of the organ in question.

(*g*) The presence of albumin in the secretion was further confirmed by the excellent tests of Dr. R. Palm.*

(*h*) The soluble enzyme or ferment secreted by the cells of the pyloric cæca was extracted by the Wittich-Kistiakowsky method.† The isolated ferment converted fibrin (from the muscles of a young mouse) into leucin and tyrosin.

(*i*) The albumins in the secretion are not converted into taurocholic and glycocholic acids; for not the slightest traces of these biliary acids could be detected by the Pettenkofer and other tests.

(*j*) No glycogen was found in the organ (*i.e.*, the cæca) or its secretion.

From these investigations, which have been repeated on

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* *Zeitschrift für Analytische Chemie*, vol. 24, pt. 1.

† *Pflüger's Archiv für Physiologie*, vol. 9, pp. 438–459.

other genera besides *Uraster*, the pyloric cæca or diverticula of the *Asteridea* are proved to be pancreatic in function.

Dr. L. Fredericq (the distinguished Professor of Physiology in the University of Liège) has obtained similar results, but by an entirely different method. Fredericq obtains various aqueous extracts (neutral, alkaline, and acid) of the cæca previously hardened in alcohol. These extracts each contain the digestive ferments. They digest cooked and raw fibrin exceedingly well in alkaline extracts. This action is less active in neutral extracts, and is almost *nil* in acid extracts.

The pyloric cæca of the *Asteridea* are consequently digestive organs—their function being similar to that of the pancreas of the *Vertebrata.*

Dr. MacMunn[*] has shown that these pyloric cæca "contain a large quantity of enterochlorophyll, mostly dissolved in oil, which may possibly act in supplying oxygen to the tissues of the animal, perhaps from the waste carbon dioxide." If this be correct, the pyloric cæca perform a dual function—that of a digestive and a respiratory organ.

It may be stated that the stomach or pyloric sac of *Uraster rubens* is a digestive cavity and a renal organ[†]—*i.e.*, it has a dual function. Darwin states, in *The Origin of Species* (chap. vi.), that "numerous cases could be given among the lower animals of the same organ performing at the same time wholly distinct functions; thus, in the larva of the dragon-fly and in the fish—*Cobites*—the alimentary canal respires, digests, and excretes."

THE TRICHOSCOLICES.

Dr. Fredericq has investigated the nature of digestion in *Tænia serrata* (one of the *Cestoidea*), which inhabits the small intestine of the dog. His experiments were conducted in the following manner:—Three tape-worms, killed by chloro-

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[*] *Proc. Birmingham Philosop. Soc.* vol. 5, pt. i. p. 214.

[†] See Dr. A. B. Griffiths' paper in *Proceedings of Royal Society of London*, vol. 44, p. 326.

form, were washed in water, and then cleaned by means of a brush. They were cut into small pieces and left to harden, for twenty-four hours, in a large quantity of absolute alcohol. Aqueous extracts (neutral, alkaline, and acid) were made of the hardened pieces; but each extract was found to be completely inactive as a digestive fluid. Fibrin remained intact in them during many days.

These extracts had a milky appearance, due to an intense fluorescence, which immediately suggested the presence of glycogen. A solution of iodine (in water) converted these extracts into brown-coloured liquids. They formed a precipitate in the presence of alcohol, which was dissolved by copper sulphate and potash.

Finally, the addition of saliva caused the opalescence to disappear, and at the same time the liquid became rich in glucose, as proved by Fehling's solution. It must be distinctly understood that this glycogen is not present in the internal fluids of the tape-worm's body, but is present in the integument of that animal. Glycogen is also present in the integument of the *Nematoidea.*

It is seen from these investigations that the *Cestoidea,* and possibly the *Trematoda* as well, do not contain any traces of digestive ferments, either pepsin, trypsin, or diastatic ferment.

The juices of the small intestine in which *Tœnia serrata* lives are, nevertheless, rich in ferments; but these ferments, having little diffusive power, do not pass the barrier which the external skin of these *Entozoa* offers them. This was proved in the following manner:—Some *Ascares marginatœ* (belonging to the *Nematoidea*), obtained from the small intestine of a dog, were placed, some intact and others cut into pieces, into an artificial pancreatic juice.* Those which were left intact remained in the juice without apparent change; but those cut into pieces were almost completely

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* The aqueous extract of a dog's pancreas which had been hardened in alcohol.

digested or dissolved—only leaving the horny integument (hyalin). This integument did not appear to be formed of chitin, for it was rapidly attacked by a boiling solution of potash.

THE ANNELIDA.

(*a*) The *Hirudinea*. For this purpose Fredericq cut into pieces twelve horse-leeches (*Hæmophsis vorax*), and from these pieces he prepared two extracts, one acid and the other alkaline. Fibrin was digested (in twelve hours) in the alkaline extract, but was unaltered in the acid extract.

The author of the present volume has obtained similar results with *Hirudo medicinalis*. Digestion, therefore, in the *Hirudinea* is somewhat similar to the pancreatic digestion in the *Vertebrata*.

(*b*) The *Oligochæta*. In this order, represented by *Lumbricus terrestris*, the digestive system (Fig. 24) is more highly developed than in any other animal already alluded to in the present chapter.

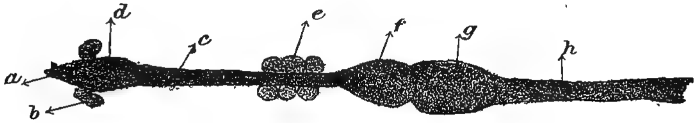

FIG. 24.—DIAGRAM OF ANTERIOR PORTION OF ALIMENTARY CANAL OF LUMBRICUS.

a = mouth. *b* = salivary glands (?). *c* = œsophagus. *d* = pharynx.
e = calciferous glands. *f* = crop. *g* = gizzard. *h* = intestine.

If the head or anterior portion of *Lumbricus* (as far as the sixth segment) is severed from the body, and that part of the alimentary canal which it contains is dissected out of the head, and is placed on starch, it will be converted into glucose, but it has no action on fibrin. From this there is no doubt that the saliva is poured into the pharynx. This secretion bathes the food (which is of a mixed nature) during its passage through the œsophagus. Attached to the sides of the posterior end of the œsophagus are three pairs of calciferous glands. These glands secrete a substance extremely rich in calcium carbonate. The function of these glands in secreting calcium carbonate is to neutralise the vegetable acids of the food, for the digestive fluid of *Lumbricus* is inactive unless alkaline. The food and fluids in the crop of the earthworm are always alkaline. In the crop the food matter is stored before it passes into the gizzard, whose powerful muscular walls and thick chitinous lining crush any food-stuffs that require mastication or grinding. The posterior portion of the gizzard has thinner walls, and leads into the long glandular intestine, which is lined with columnar cells. The intestine is almost enveloped in a yellowish glandular tissue—the so-called liver. This organ is essentially pancreatic in function.*

There is no doubt that the *principal* digestive fluid of worms is of the same nature as the pancreatic juice of the *Vertebrata*. Dr. Léon Fredericq (*Archives de Zoologie Expérimentale*, vol. vii. p. 394) proved this in the following manner:—

A large quantity of worms, chopped into small pieces, are treated with strong alcohol. The alcohol is left to act for many hours; and then decanted. The alcoholic extract is used in the examination for biliary acids. The insoluble residue is pressed between several folds of filter paper, dried in air, and finally pulverised in a mortar. The pulverised residue is divided into several parts, the object being to prepare several aqueous extracts (neutral, alkaline, and acid). The dilute acid solutions used in preparing the acid extracts are made from hydrochloric acid and water (the degrees of concentration being from six to twelve cc. of HCl per litre of water). The divided residue (previously alluded to) is allowed to macerate in the fluids for twenty-four hours; and then filtered. The filtered liquids are placed in separate test-tubes in each of which a small piece of fibrin has been

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* Dr. A. B. Griffiths' paper in *Proc. Roy. Soc. Edinb.*, vol. 14, p. 237.

suspended. The test-tubes are then placed in an incubator* heated to about 40° C. At the end of an hour or so, the fibrin which is in the alkaline extract has almost entirely disappeared; leaving only a small quantity of finely divided *detritus*. This liquid contains peptones.

The neutral extract acts in a similar manner, except that the fibrin is dissolved a little more slowly; it takes from five to six hours to complete the digestion. This liquid also contains peptones.

The most concentrated acid extract has no action on the fibrin, which swells, but remains intact during many days. On the other hand, the fibrin is dissolved more or less completely in the dilute acid extracts, but to do this it requires from thirty-six to forty-eight hours.

The ferment in which *Lumbricus* dissolves the fibrin acts well in a neutral solution, better in an alkaline solution, and badly or not at all in an acid solution; these properties entirely resemble those of trypsin or the pancreatic ferment.

The neutral extract converts starch into glucose. The aqueous extract, therefore, contained a substance or ferment which acts in a similar manner to diastase.

Fredericq having dissected a large earthworm (under water), removed the whole of the alimentary canal, and obtained from the intestine a fluid which is slightly alkaline and readily digests fibrin. This alkaline fluid is secreted by the glandular tissue which almost covers the intestine. The organ has been termed a "liver," whereas it is a true pancreas. The names "bile" and "liver" have been employed at random by a great number of those who have investigated the anatomy of the *Invertebrata*. Nevertheless the principal characteristics of the bile (pigments and biliary acids) have never been discovered with exactitude in any animals lower than the cranial Vertebrates. There is nothing in this fact which ought to surprise us, because it is

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* Like the incubators used in bacteriological laboratories. See Griffiths' *Researches on Micro-Organisms*, p. 17.

established that the colouring matters of the *bile* are derived from one of the products of the decomposition of hæmoglobin (probably of hæmochromogen), a substance which is not found, except very rarely in the *Invertebrata.*

The earthworm is one of these animals rich in hæmoglobin, consequently one would suppose that liver pigments and biliary acids would be present in this Invertebrate animal.

The alcoholic filtrate from the macerated worms (already referred to) would contain (if present) these pigments and acids. This filtrate is very rapidly discoloured on exposure to daylight, but, besides the colouring matter which is sensitive to light, it often contains traces of chlorophyll (from food).

The alcoholic filtrate is evaporated to dryness on a water bath, and the residue treated with ether. The ethereal solution is reserved for future examination, while the insoluble residue (in ether) is dissolved in a small quantity of water. The filtered aqueous solution is now used in testing for biliary acids by the Pettenkofer test; but not the slightest trace of these acids is detected in *Lumbricus.* The reaction of Gmelin and Tiedemann, employed in detecting the presence of biliary pigments, was applied without success to the fresh juices and organs of *Lumbricus;* also to the alcoholic extracts (from which the alcohol had been evaporated).

The ethereal extract previously obtained was found to contain cholestrine and fatty globules.

In addition to the pancreatic ferment, the author has detected indol (C_8H_7N) as well as leucin and tyrosin in the fresh juices and organs obtained from about 4 lbs. of earthworms. This is an additional proof of the pancreatic nature of the digestive fluid of *Lumbricus.*

Although biliary pigments are entirely absent in the *Oligochæta,* other pigments are present. Most likely the pancreatic tissues, which almost envelop the intestine of *Lumbricus,* contain enterochlorophyll.

In the words of Dr. MacMunn (*loc. cit.*, p. 189), "the radicle indol is furnished by the action of pancreatic ferments upon food proteids; and as the so-called liver of Invertebrates is really a pancreas in at least some of its functions, possibly some such radicle may be changed by a ferment furnished by the 'liver' into enterochlorophyll."

Not only is the digestive fluid of *Lumbricus* capable of acting upon starch (as already stated), but it readily attacks cellulose; this fact agrees perfectly with the kind of food-stuffs which the earthworm consumes.

(*c*) The *Polychæta.*—In *Nereis,* a pair of salivary glands are appended to the base of the proboscis. The secretion obtained from a large number of these glands readily converted starch into dextrose.

Concerning the digestive fluid of *Nereis pelagica* (a marine species), Dr. L. Fredericq performed the following experiments:—Sixty of these worms, which had been preserved in alcohol for six months, were dried and pulverised. From the pulverised mass the various aqueous extracts (neutral, alkaline, and acid) were prepared. Fibrin was dissolved after a few minutes in the alkaline extract; at the end of a little longer time in the neutral extract; but remained intact for many days in the acid extract. The liquid resulting from the digestion gave distinctly the reactions of peptones with copper sulphate and potash.

The same experiments repeated with fresh specimens of *Nereis* gave the same results. The digestive power of the alkaline extract is considerable; for it can digest, in less than two hours, a quantity of fibrin equal to the weight of the worms employed in making the extract.

THE INSECTA AND ARACHNIDA.

We now proceed to the *Insecta* and *Arachnida,* and, as examples of these two classes, we describe in detail the physiology of the alimentary canal in the *Orthoptera*, *Lepidoptera*, *Hymenoptera*, and the *Araneina*.

(*a*) The *Orthoptera*.—The alimentary canal of *Blatta* (the cockroach) is very highly developed. The salivary glands (Fig. 25, *a* and *b*) of the cockroach are situated on each side of the œsophagus and crop, and extend posteriorly as far as the abdomen. They are about one-third of an inch in length, and composed of acini (Fig. 25, *b*). Accompanying the glands are two salivary receptacles, one on either side of the crop. A quantity of the secretion* was extracted by crushing about sixty glands of cockroaches, which had been recently killed. The secretion was alkaline to test-papers. A portion of the secretion was added to a small quantity of starch, which was converted into glucose in twelve minutes.

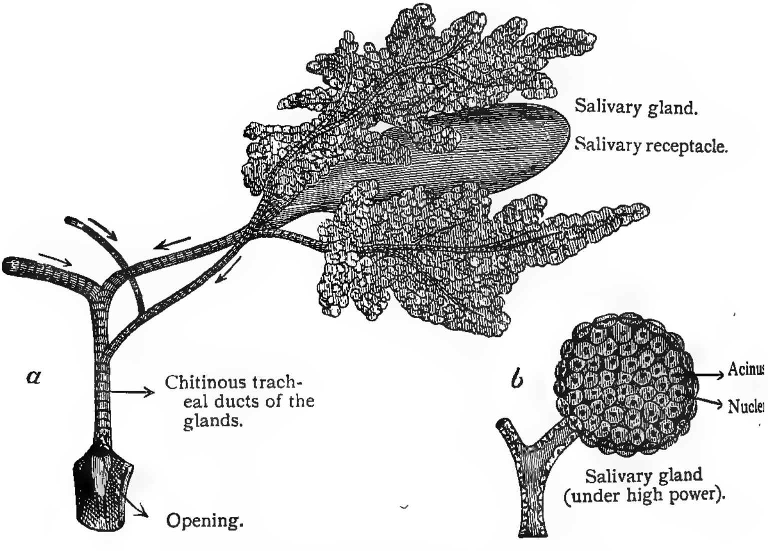

FIG. 25.—(*a* and *b*) SALIVARY GLAND OF BLATTA.

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* Griffiths, in *Proc. Roy. Soc. Edinb.*, vol. 14, p. 234; and *Chemical News*, vol. 52, p. 195.

The presence of glucose was proved by the formation of red cuprous oxide by the action of Fehling's solution.

Another portion of the secretion was distilled in a miniature retort (made of glass tubing) with dilute sulphuric acid. To the distillate ferric chloride was added, which produced a red colour, indicating the presence of sulphocyanates.

The secretion of these glands yields a small quantity of ash, which contains calcium phosphate.

The soluble ferment of this secretion may be isolated by precipitating an infusion of the glands obtained from a large number of these insects with dilute phosphoric acid, adding lime-water, and filtering. The precipitate is then dissolved in distilled water, and re-precipitated by alcohol. This precipitate converts starch into glucose, but has no action on fibrin; in other words, it has a similar action to ptyalin —the ferment of the saliva of the higher animals. It is probable that in *Blatta* there are terminations of the nerves in these salivary glands. It may be that these nerve-endings affect the protoplasmic substance of the cells forming the ferment, which has the property of converting starch into glucose.

The crop of *Blatta* simply acts as a receptacle to store up the rapidly swallowed food until time is afforded for the food to be passed on to the true stomach.

The gizzard or proventriculus has been described in the last chapter. It is considered by some to be an internal masticatory apparatus, but M. Plateau[*] considers that the proventriculus of *Blatta* acts simply as a strainer.

The chylific ventriculus may be termed the true stomach of *Blatta*, for it is probable that digestion is more active in this than in any other part of the alimentary canal. It is lined with epithelium, and often contains peptones.

The pyloric cæca, situated in front of the chylific ventri-

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[*] See his papers on the digestion in the *Myriapoda*, *Insecta*, and *Arachnida*, published in the *Bulletin de l'Académie Royale des Sciences de Belgique*, 1874–78.

culus, have been directly proved by the author* to be pancreatic in function. The secretion from these cæca flows into the chylific ventriculus, where digestion proceeds.

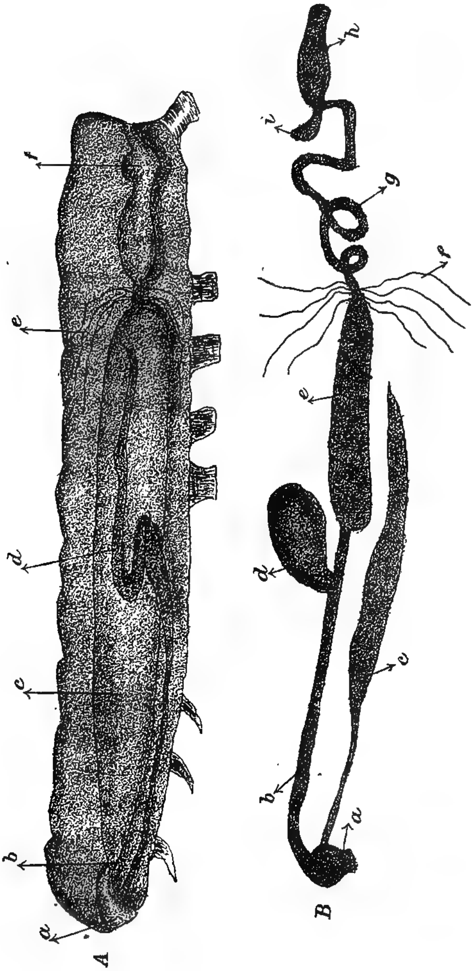

FIG. 26.—ALIMENTARY CANAL OF PONTIA BRASSICÆ. × 3.

A. Larva. *a* = pharynx. *b* = œsophagus. *c* = stomach. *d* = salivary gland. *e* = Malpighian tubules. *f* = rectum.

B. Perfect State. *a* = pharynx. *b* = œsophagus. *c* = salivary gland. *d* = crop. *e* = stomach. *f* = Malpighian tubules. *g* = intestine. *h* = rectum. *i* = cæcum.

In the carnivorous *Libellula* (the dragon-fly) there is no crop or gizzard, only the chylific ventriculus is present; the

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* Griffiths, in *Proc. Roy. Soc. Edinb.*, vol. 14, p. 237.

fluids within this organ are always slightly alkaline, and an infusion of about twenty of these organs readily converted starch into glucose, and digested fibrin.

(*b*) The *Lepidoptera.*—As an example of this important order we describe the physiology of the alimentary canal of the larva and imago of *Pontia brassicæ* (the large white cabbage butterfly).

The alimentary canal of the larva (Fig. 26, A) agrees closely with the general Lepidopterous type. The mouth opens into a pharynx lined by a dark, firm cuticula, and into the latter open two ducts from a pair of well-developed salivary glands. These glands form elongated tubes, gradually diminishing in diameter towards the posterior ends. The œsophagus is very narrow and short. It leads into a long chylific stomach, which opens into a short duct. Behind the stomach the intestine consists of four parts: first, a short, constricted piece; second, a dilated, oval division; third, the short rectum; and fourth, the anal tube. The stomach has an epithelium lining, which is thrown up into folds so as to form imperfectly differentiated glandular follicles.

At the posterior end of the stomach are the Malpighian tubules.

Fig. 26, B, represents the alimentary canal of the imago of *Pontia.* The pharynx passes into a narrow, but long, œsophagus leading to the crop or food receptacle.

This crop is entirely absent in the larval, but is developed in the pupal stage. The stomach is much smaller than in the larva, but its lining is also thrown up into glandular follicles. The posterior end of the stomach leads into a long and peculiarly coiled small intestine. The intestine passes into the wide terminal division, the rectum, from the front end of which there is a curved blind cæcum or pouch.

In the imago of *Pontia* there are also a pair of well-developed salivary glands.

The secretion of the salivary glands is alkaline to test-papers, and readily converts starch into glucose. It has, however, no action on fibrin. It contains sulphocyanates, proved by the red colour produced by ferric chloride with a drop of the secretion. The stomach of both the larva and imago contains glandular follicles. These secrete a digestive fluid, which answers in every way to that of a Vertebrate pancreas. The Malpighian tubules are well-developed in the imago, as well as in the larva of *Pontia*. Their function is that of a renal organ, but this subject will be considered in detail in our chapter on *excretion*. It may be stated in passing, that according to Dr. B. T. Lowne, F.L.S.,* the Malpighian tubules of *Calliphora erythrocephala* (the blow-fly) are "hepatic" in function. If by hepatic he means that these tubules have the function of a Vertebrate liver, his conclusions are erroneous, for neither biliary acids nor glycogen are present in these tubules. Again, if Dr. Lowne means by "hepatic" that they have a pancreatic function, this is also erroneous, because these tubules do not yield any digestive ferment or ferments. On the other hand, the Malpighian tubules of the *Diptera*, including *Calliphora*, readily yield uric acid; and there is little doubt that they are physiologically the kidneys of the animal; although, concerning their place of development from the alimentary canal, as well as from other considerations, they are the homologues of hepatic organs (liver).

(*c*) The *Hymenoptera*.—The structure of the alimentary canal of *Apis* (the bee) has already been given. The long stomach is furnished internally with small glandular follicles, and by making an alkaline extract of the stomachs obtained from a large number of bees (which had been kept for some time without food), the extract contained a ferment which hydrolyzes starch, and digests fibrin, although feebly. In fact, it answers to the characteristic tests of trypsin or pancreatin. An alcoholic extract of the bee's stomach does

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* *The Anatomy, Physiology, Morphology, and Development of the Blow-fly* (1890).

not contain the smallest trace of biliary acids, pigments, or glycogen.

Dr. A. von Planta* has recently investigated the juice, or the sticky substance, which the working bees store in the cells of the larvæ of the queens, drones, and workers. Leuckart† regarded it as the product of the true stomach (see Fig. 8*c*) of the working bees, which they vomit into the cells in the same way that honey is vomited from the honey-bag (see Fig. 8*b*). Fisher and others regarded it as the product of the salivary glands of the bees. Schönfeld has more recently shown that Leuckart's original view is the correct one. He showed that the saliva can be easily obtained from the salivary glands of the head and thorax, and that it is very different from the food-juice deposited in the cells by the bees; and that, moreover, the juice is similar, both chemically and microscopically, to the contents of the bee's true stomach; he showed also, from the consideration of certain anatomical and physiological peculiarities of the bee, such as the position of the mouth, the inability of the bee to spit, &c., that the view of this substance being saliva is quite untenable. Certain observers have to this replied, that a bee cannot vomit the contents of its true stomach, because of a *valve* which intervenes between it and the honey-stomach or bag (see Fig. 8*i*); but Schönfeld has shown that the structure, mistaken for a valve, has not the function of one, but is in reality an internal mouth, over which the animal has voluntary control, and by means of which it is able to eat and drink the contents of the honey-stomach when necessity or inclination arises. By light pressure on the stomach, and stretching out the animal's neck, the contents of the stomach can be easily pressed out.

Dr. A. von Planta's investigations entirely confirm Schönfeld's view, that the food-juice comes from the bee's true stomach. The subject was investigated from the point of

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* *Zeitschrift Physiol. Chemie*, vol. 12, p. 327.

† *Deutsche Bienenzeitung*, 1854–5.

view of its chemical composition, and care, also, was taken to investigate, individually, the juice as occurring in the cells of three varieties of bees—queens, drones, and workers.

Some preliminary microscopical examinations of this substance yielded the following results, which are quite in accord with the subsequent chemical analyses:—

(1) The food of the queen-bee larvæ is the same during the whole of the larval period; it is free from pollen grains, which have been reduced to a thickish but homogeneous juice by the digestive action of the bee's stomach.

(2) The food of the larval drones is also, during the first four days of the larval period, free from pollen, and appears to have been completely digested previously. After four days their food is rich in pollen grains, which have, however, undergone a certain amount of digestion. The food-stuff of the larvæ is probably formed from bee-bread.

The following table gives the average percentages obtained from several analyses:—

		Food-stuff of—		
		Female or Queen Bees.	Drones or Males.	Neuters or Working-Bees.
Water		69.38 %	72.75 %	71.63 %
Total solids		30.62 ,,	27.25 ,,	28.37 ,,
In the Solids	Nitrogenous matter	45.14 ,,	43.79 ,,	51.21 ,,
	Fat	13.55 ,,	8.32 ,,	6.84 ,,
	Glucose	20.39 ,,	24.03 ,,	27.65 ,,
	Ash	4.06 ,,	2.02 ,,	—

All these food-stuffs are rich in nitrogen; all were of a greyish white colour; and that of the queen-bee was the stickiest, while that of the working-bees was the most fluid. The greater part of the nitrogenous matter of the food was proteid. The sugar present was always invert-sugar, whereas the sugar in pollen grains is invariably sucrose.

The preceding table shows certain differences in the composition of the different kinds of larval food, more especially in the composition of the solids present. Its composition is, moreover, quite different from that of the bee's saliva, which contains no sugar. The difference between the proportional amount of the different solids present in the different forms of larval food is a constant one, and no doubt this variation has in view the particular requirements of the larvæ in question. Certain small but constant differences were also observed in the chemical composition of the food of the larval drones during the first four days and at subsequent periods.

Not only is there a difference in the quality, but there is also one in the quantity of the food supplied. The juice from 100 queen-bee cells yielded 3.6028 grammes of dry matter, that from 100 drones' cells 0.2612 gramme, and that from 100 workers' cells, 0.0474 gramme.

(*d*) The *Araneina.*—As the spider's web has indirectly to do with digestion a few remarks on the subject may not be out of place. There is no doubt that "one of the most characteristic organs of the *Araneina* is the arachnidium, or apparatus by which the fine silky threads which constitute the web are produced. H. Meckel,* who has fully described this apparatus as it occurs in *Epeira diadema*, states that, in the adult, more than a thousand glands, with separate excretory ducts, secrete the viscid material, which, when exposed to the air, hardens into silk. These glands are divisible into five different kinds, and their ducts ultimately enter the six prominent arachnidial mammillæ, which, in this species, project from the hinder end of the abdomen. Their terminal faces are truncated, forming an area beset with the minute arachnidial papillæ by which the secretion of the glands is poured out."

The secretion of these glands is insoluble in water, and has a nitrogenous basis. Web-spinning has several objects in

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* *Müller's Archiv*, 1846.

view: (1) it is a means by which the spider obtains a livelihood; (2) it is subservient to propagation of the species*—the silk being used as a cocoon for the reception of eggs, a nest for the young, as well as forming aëronautic gossamer lines for the dispersion of the young brood on the approach of maturity; (3) in the genus *Hydrachna* (belonging to the *Acarina*) it serves to attach the moulting individual to an aquatic plant by the anterior part of the body, when it struggles to withdraw itself from its exuvium; (4) it forms a home for the spider.

The secretion of the salivary glands of *Tegenaria domestica* (the common house-spider) contains a diastatic ferment and sulphocyanates. These were proved by the tests previously given.

The so-called "liver ducts" of *Tegenaria domestica* have been investigated by Mr. A. Johnstone, F.G.S.,† and the author,‡ with the following results:—

When examined microscopically these ducts are seen to consist of cellular tissue; and the secretion is poured into the intestine. The secretion obtained from a large number of animals, as well as an extract made of the intestines of a very large number of spiders, gave the following reactions:—

(1) The secretion and extract form emulsions with neutral oils, yielding subsequently fatty acids and glycerol.

(2) The secretion and extract decompose stearin with the formation of stearic acid and glycerol:—

$$C_{57}H_{110}O_6 + 3H_2O = 3C_{18}H_{36}O_3 + C_3H_8O_3.$$

(3) The secretion and extract act upon starch paste with the formation of dextrose. The presence of dextrose was proved by the formation of red cuprous oxide with Fehling's solution.

(4) The secretion and extract dissolve coagulated albumin with the formation of peptones, which are readily recognised

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* See Dr. H. C. McCook's *American Spiders and their Spinning Work.*

† Demonstrator in Geology in the University of Edinburgh.

‡ *Proceedings of Royal Society of Edinburgh*, vol. 15, p. 113.

by the rose colour produced in the cold by potash and copper sulphate.

(5) Tannic acid produces a white precipitate with the secretion.

(6) When a few drops of the secretion of these ducts were examined chemico-microscopically, the following reactions were observed: on running in a solution of iodine (in potassium iodide) between the slide and cover-glass, a brown deposit was obtained; and on running in concentrated nitric acid, on another slide containing the secretion, yellow xanthoproteic acid was formed. These reactions prove the presence of albumin in the secretion of the organ in question. The presence of albumin was further confirmed by the tests of Palm.*

(7) The soluble ferment, or enzyme, secreted by the cellular tubes was extracted, although with some difficulty, by the Wittich-Kistiakowsky method. This ferment converts fibrin into leucin and tyrosin.

(8) The albumins in the secretion and extract are not converted into taurocholic or glycocholic acids, for not the slightest traces of these biliary acids could be detected by the Pettenkofer and other tests.

(9) The secretion contains approximately four per cent. of solids. The slight residue (solids), which contains some combination of sodium, effervesced on the addition of dilute acid.

(10) No glycogen was found in the secretion or extract.

From these investigations, which have been repeated on several occasions, the so-called liver of the *Araneina* is proved to have a similar function to the pancreas of the *Vertebrata.*

THE CRUSTACEA.

(1) The *Brachyura.*—As a type of this order, the alimentary canal of *Carcinus mœnas* will be considered in detail.

This animal is a voracious feeder; its food consists of

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* *Zeitschrift für Analytische Chemie*, vol. 24, pt. i.

animal and vegetable substances. These contain albuminoids, fatty and starchy matters, and earthy salts. The food is torn to pieces by means of the chelæ. The wide and short œsophagus leads into a large globular stomach containing chitinous teeth, the object of these teeth being to sub-divide the food so that it may be acted upon by the digestive fluid poured into the intestine. The only lateral appendage of the alimentary canal of *Carcinus* is the so-called liver. It is an organ of considerable size, and consists of two symmetrical halves. Its secretion has the following reactions:—

It decomposes fats and oils with the formation of glycerol and fatty acids. It converts starch into dextrose, and dissolves albumin. The action of the secretion upon milk is to render it transparent. The secretion contains leucin and tyrosin, no doubt produced by the metamorphoses of certain albuminous substances. In the words of Prof. M. Foster, F.R.S.,[*] "one result of the action of the *pancreatic juice* is the formation of considerable quantities of leucin and tyrosin." These organic compounds are not formed in a liver, for they are "dehydrated in a *true* liver, forming a series of cyanhydrins or cyanalcohols attached to a benzene nucleus, which then pass into the circulation."

The principal mineral ingredient found in the ashes (incinerated at a low temperature) of the so-called liver of *Carcinus* was sodium carbonate. In the ash of a Vertebrate liver the chief mineral constituents are potassium and phosphoric acid.

The soluble ferment is readily extracted by the Wittich-Kistiakowsky method, or by the method recently introduced by Dr. N. Kravkoff.[†] This method consists in precipitating the soluble ferments and albuminoids by means of ammonium sulphate. By treatment with alcohol, the albuminoids become insoluble, and the ferments are then extracted with water. The ferment so extracted converts fibrin into leucin and tyrosin; as well as hydrolyzes starch.

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[*] *Text-book of Physiology*, (4th ed.), 438.

[†] *Journal of Russian Chemical Society*, 1887, p. 387.

The secretion of the so-called liver of *Carcinus* does not contain glycocholic and taurocholic acids, or glycogen.

By using the methods of M. Zaleski* for ascertaining the presence of ferrous, ferric, and ferrosoferric compounds in a true liver, the author of the present volume could *not* detect the presence of iron in the organ or its secretion.

From the above reactions the conclusion to be drawn is, that this bilobed organ is essentially pancreatic in function.†

THE MACROURA.

The general details of the alimentary canal of *Astacus* have been described in the last chapter. The principal organs are the stomach and the "liver."

The gastric juice of the crayfish has recently been investigated by M. Stamati.‡ By means of a gastric fistula, the gastric juice can be easily collected from the crayfish. This secretion is of a yellowish colour, somewhat opalescent, and alkaline to test-papers. It digests fibrin, rapidly forming peptones which give the ordinary reactions: it also transforms starch into glucose. It appears also that fats are emulsified and fatty acids liberated. This so-called gastric juice of M. Stamati was in fact nothing more than the secretion of the "liver," which pours its secretion into the anterior part of the intestine, and no doubt finds its way into the pyloric portion of the crayfish's stomach. After the stomach of *Astacus* has been thoroughly washed out with water, an extract of the organ does not digest fibrin, nor does it act upon starch. This proves that Stamati's gastric juice was in reality the secretion of the "liver."

The so-called liver of *Astacus fluviatilis* has been proved by the author § to be pancreatic in function. Its secretion

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* *Zeitschrift für Physiologische Chemie*, vol. 10, pp. 453–502.

† Dr. A. B. Griffiths' paper in *Proc. Roy. Soc. Edin.*, vol. 16, p. 178.

‡ *Comptes Rendus de la Société Biologique*, [2], t. 5, p. 16.

§ Griffiths' paper in *Proc. Roy. Soc. Edin.*, vol. 14, p. 237.

contains about five per cent. of solids, and readily digests fibrin and hydrolyzes starch.

Similar reactions to the above are also produced by the so-called livers of *Homarus* and *Palæmon*. There is no doubt that the "liver" of the *Macroura* is a true pancreas.

THE LAMELLIBRANCHIATA.

Dr. Léon Fredericq has investigated the alimentary canal of *Mya arenaria* (see Fig. 18) and *Mytilus edulis* (the mussel). The secretions of the so-called livers of these two animals digest fibrin analogous to the pancreas of higher forms.* When neutral and alkaline extracts of the organ are prepared, they have the characteristic reactions already given under the head of *Carcinus mœnas*; but Fredericq states that he has extracted glycogen from the secretion of the "liver" of *Mya*. It is, however, probable that glycogen is only present in this organ and other tissues of *Mya* during certain periods of growth. It may be remarked that in *Carcinus*, where development is achieved by sudden bounds—by moultings—the "liver" contains glycogen during these periods of rapid growth, but at other times there is not the slightest trace of the carbohydrate in that organ or any part of the alimentary canal.

The contents of the digestive canal of *Mya* are acid. This acid is chlorohydric acid, and is found chiefly in fluids obtained from the stomach. It is possible that the function of the stomach, as a separate digestive organ, becomes more differentiated in the *Lamellibranchiata*. Is it possible that it gives rise to a secretion similar to the gastric juice of higher forms?

The so-called liver of *Ostrea*, *Pecten*, *Anodonta*, and *Cardium* functionates as a true pancreas.

Dr. C. A. MacMunn† has extracted enterochlorophyll from

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* *Proc. Roy. Soc. Edin.*, vol. 14, p. 237.

† *Philosophical Transactions of Royal Society*, 1886, pt. i, p. 235.

the "liver" pigments of certain genera of the *Mollusca*, as well as from a large number of other Invertebrates. Among the *Mollusca* experimented on were—*Mytilus*, *Ostrea*, *Anodonta*, *Cardium*, *Unio*, *Octopus*, *Buccinum*, *Patella*, *Helix*, and *Limax*. In some Molluscs—as *Patella*—the "liver" contains enterohæmatin besides enterochlorophyll. It might be suggested in reference to the discovery by Fredericq of glycogen ($C_6H_{10}O_5$) in the "liver" of *Mya* that it was produced by the enterochlorophyll present in the organ; as enterochlorophyll is allied to chlorophyll. But MacMunn (*loc. cit.*, p. 257) states that he has made "various sections of Invertebrate 'livers' obtained from animals feeding and fasting, but never obtained a trace of starch ($C_6H_{10}O_5$) or cellulose with iodine in iodide of potassium, Schulze's fluid, or with iodine and sulphuric acid. These experiments were made on the 'livers' of *Helix aspersa*, *Anodonta cygnea*, *Patella vulgata*, *Ostrea edulis*, *Mytilus edulis*, *Astacus fluviatilis*, the cæca of star fishes, &c. The precautions recommended by Geddes* of previously digesting the tissues in alcohol, and in caustic potash, and neutralising with acetic acid, having been adopted in each case."

It appears that the "enterochlorophyll occurs dissolved in oil globules, also in granular form, and sometimes dissolved in the protoplasm of the secreting cells of the 'liver.'" The probable function of this and other pigments will be alluded to in a subsequent chapter.

THE GASTEROPODA.

The secretion of the salivary glands of *Helix aspersa* has been examined by the author.† It contains a ferment which converts starch into glucose. The ferric chloride test failed to show the presence of sulphocyanates. The mineral ingredients found were calcium and chlorine; but no phosphates

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* *Proc. Roy. Soc. Edin.*, vol. 11, p. 377.

† *Ibid.*, vol. 14, p. 235.

or carbonates could be detected in the salivary glands of *Helix*. Similar results have been obtained with the salivary glands of *Limax flavus*, and *Limax maximus*.

The so-called livers of *Helix aspersa*, *Limax flavus*, and *Limax maximus* are pancreatic in function.

Dr. M. Levy* has recently carefully examined the so-called liver of *Helix pomatia*. The weight of its organic constituents is very constant, being the same in summer and winter, and in great measure they are the same in kind in all periods of the year. The alcoholic extract of the gland when examined by the spectroscope gave the spectrum of enterochlorophyll. The digestive ferments present are a diastatic, a peptic, but not a tryptic one. The peptic ferment appears to be identical with the late Dr. Krukenberg's helicopepsin. The diastatic ferment disappears during the winter sleep; it is capable of digesting raw starch, but has no action on cellulose. A fat emulsifying action is shown by the secretion in the summer-time, but this also disappears during hibernation.

The ferment, by means of which this action is brought about, is not identical with the one described by Dr. Schmiedeberg† as histozyme. Histozyme, which was separated from pigs' kidneys, is concerned in the splitting up of hippuric acid. The snail's ferment has no such action. According to Dr. Levy, glycogen with sinistrin is generally present in the organ, but all tests for *bile* gave a negative result. Jecorin was also absent. Dr. Levy has separated the following substances from the so-called liver of *Helix pomatia*:—

In the alcoholic extract	Enterochlorophyll	
	Lecithin	
	Oleic acid	
	Fatty acids	
	Ash	Chlorine
		Phosphoric acid
		Sulphuric acid.
In the ethereal extract	A trace of fat.	

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* *Zeit. Biol.*, vol. 27, p. 398.

† *Archiv. Exper. Path. und Pharm.*, vol. 14.

In the aqueous extract
- Sugar
- Globulin (coagulating at 66° C.)
- Glycogen
- Sinistrin
- Hypoxanthine*
- Ash
  - Potassium
  - Sodium
  - Calcium
  - Magnesium
  - Iron (traces)
  - Manganese
  - Chlorine
  - Phosphoric acid
  - Sulphuric acid.

In winter animals, silica was also found as an ash constituent.

Dr. Fredericq has investigated the nature of the secretions of the salivary glands and "liver" of *Arion rufus.* The secretion of the salivary glands readily acts upon starch, but has no action upon fibrin and neutral oils. The secretion of the "liver" is a brown liquid, and can be collected in a sufficiently large quantity by killing a large number of fresh snails. It suffices to dissect them lengthways to extract the viscera, and to collect the liquid which flows from the cut end of the intestine. If the secretion is extracted after the animals have just been feeding, it is most likely that the secretion will be slightly acid (acidity due to food); in that case the digestion of fibrin takes about twenty-four hours. On the other hand, if the secretion is extracted when alkaline, or if the acid secretion is rendered slightly alkaline by a small quantity of sodium carbonate, its activity is greatly increased. In an acid solution the ferment is inactive, and this is readily observed when a small quantity of acidulated water is added to the digestive fluid of the snail, for it completely stops the digestion of fibrin.

The "liver" and its secretion furnish a diastatic ferment transforming starchy matters into glucose. The so-called

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* And other bases precipitable by phosphotungstic acid.

liver of *Arion rufus*, as well as *Helix*, is a digestive gland which is comparable to the pancreas of the *Vertebrata*. It contains neither biliary pigments nor biliary acids. If one considers that the Vertebrate liver is not a digestive gland in the proper sense of the word, since neither bile nor an infusion of hepatic tissues contains digestive ferments, we may conclude that the name of liver is in no way applicable to the digestive gland of the *Gasteropoda*.

It is stated by Barfurth that the liver of the *Gasteropoda* performs the functions of a hepato-pancreas. It is certainly pancreatic in function; but there are no chemico-physiological reasons for saying that it also possesses a hepatic function.

The salivary glands and "liver" of *Patella vulgàta* have been investigated by the author.* The limpet (*P. vulgata*), with its conical shell adhering to the rocks of our coasts, is well known to every sea-side wanderer. This member of the *Gasteropoda*, has been the subject of many scientific memoirs in ancient and modern times. Amongst naturalists, Aristotle was the earliest who gave an account of some of the limpet's habits, and Cuvier was the first to describe its anatomy. Although this interesting little animal has attracted the attention of many naturalists, it is only within the last decade that the true functions of its internal organs have been satisfactorily worked out.

The "liver" of *Patella vulgata* is a yellowish saccular gland, and the greater bulk of this organ is encircled by the superficial coil of the intestine. Its secretion acts upon starch-paste converting the starch into glucose, as proved by Fehling's solution. The sècretion, as well as the organ itself produces an emulsion with oils and fats, yielding subsequently glycerol and fatty acids. The soluble ferment secreted by the columnar cells of the epithelium of the gland is readily extracted by either the Wittich-Kistiakowsky or Kravkoff

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* Dr. Griffiths in *Proceedings of Royal Society of London*, vol. 42, p. 393; vol. 44, p. 328.

methods. The isolated ferment, as well as the organ and its secretion, digest fibrin.

Neither the organ nor its secretion contains biliary acids or glycogen. From these investigations there is no doubt that the so-called liver of *Patella vulgata* is similar in function to the pancreas of the Vertebrate division of animal life.

The two salivary glands of *Patella* are well-marked, and situated anteriorly to the pharynx, lying beneath the pericardium on one side and the renal and anal papillæ on the other. They are of a yellowish-brown colour, and give off four ducts. The secretion of these glands was examined by the same method applied to the salivary glands of *Sepia officinalis* (see later in this chapter), and with similar results.

The following table represents the constituents found in the salivary secretions of the two orders of the *Mollusca* :—

+ = Present. — = Absent.

	Cephalopoda.	Gasteropoda.	
	Dibranchiata.	Pulmogasteropoda.	Branchiogasteropoda.
Soluble diastatic ferment	+	+	+
Mucin	+		+
Sulphocyanates . .	+	?	+
Calcium phosphate .	+	?	+
Calcium	+	+	+
Chlorine	?	+	?

The "liver" and salivary glands of *Buccinum* (whelk) have similar functions as the same organs in *Patella*.

THE CEPHALOPODA.

In a memoir published in the *Chemical News*, vol. 48, page 37, and the *Journal of the Chemical Society*, 1884, page 94, the author gave an account of a peculiar excretory product found in the Sepia's "liver." This product was proved to be albumin in pseudo-crystalline aggregations when examined under the microscope. These bodies are not of a constant occurrence in this organ of *Sepia officinalis.*

Two years after the publication of the above-mentioned memoir the author* made a thorough examination of this organ in *Sepia* which substantiated and extended the observations of Krukenberg,† Fredericq,‡ and Jousset de Bellesme.§

After carefully dissecting the organ out of the cavity of the body of a fresh *Sepia,* the following experiments were performed:—

(1) A small portion of the organ was placed on starch-paste. The starch granules disappeared, with the exception of the celluloid covering, and on treating with water, and testing the solution with Fehling's solution, sugar in the dextrose form was found.

(2) The organ gave an akaline reaction to litmus paper.

(3) When a small portion of the organ was agitated with a small quantity of oil, an emulsion was produced—this emulsion had first an alkaline reaction, and after some time became acid, owing to the formation of butyric and other acids of the fatty series.

(4) The action of it on milk was to render the milk transparent in four hours; 15 cc. of milk were rendered transparent by 6 milligrammes of the organ.

(5) A chemico-microscopical examination of the secretion of the organ revealed the presence of albumin.

The Isolation of the Ferment.—The process used to obtain the ferment or ferments (in a crude state) from the secretion of the organ was that devised by Wittich and used by Kistiakowsky‖ in his researches on pancreatic ferments.

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* *Proceedings of Royal Society of Edinburgh,* vol. 13, p. 120.

† *Untersuch. Physiol. Inst. Heidelberg,* Bd. 1, p. 327 [1878].

‡ *Bull. Acad. Sciences Belgique,* tome 56, p. 761 [1878]; *Revue Intern. Sciences,* t. 3, p. 263 [1879].

§ *Comptes Rendus,* t. 88, pp. 304, 428 [1879].

‖ *Pflüger's Archiv. für Physiologie,* vol. 9, p. 438.

The process consists in hardening the organ in alcohol for three days, and then cutting it up into very small pieces, extracting with glycerol and filtering.

On the addition of alcohol to the filtrate, the ferment is precipitated.

The action of this ferment or ferments on starch was the complete conversion of the latter into dextrose or right-handed glucose, which was proved by the action of Fehling's solution; and the formation of crystals ($C_6H_{12}O_6$ $NaCl$, H_2O) with a solution of sodium chloride, a distinction from levulose or left-handed glucose, which does not form these crystals with sodium chloride solution. The action of the ferment on fibrin was the formation of leucin (α- amido-caproic acid, $C_6H_{13}NO_2$) and tyrosin (paraoxyphenylamido-propionic acid, $C_9H_{11}NO_3$); for on treating the fermented mass with hot water and filtering, a solution is obtained which contains leucin and tyrosin. When acetic acid was added to this solution, acicular crystals were deposited. These crystals are insoluble in ether, but soluble in boiling water. The aqueous solution produced a red flocculent precipitate on the addition of a neutral solution of mercuric nitrate; this reaction is characteristic of tyrosin.

The acetic acid solution, after precipitating the tyrosin, was evaporated, when leucin was deposited in white shining plates, which melt at 98° C. These crystals of leucin were heated with barium oxide, the result of the action being the formation of amylamine and carbon dioxide:—

$$C_6H_{13}NO_2 = N(C_5H_{11})H_2 + CO_2$$

By digesting the organ itself with boiling water and filtering, the filtrate contained leucin and tyrosin. The ferment has no action on cellulose.

From these investigations, the so-called liver of *Sepia officinalis* is proved to be a pancreas, for the juices of the organ are purely digestive in function, digesting starch, oil, and similar bodies, and transforming fibrin into leucin and tyrosin. Then, again, albumin is present in its secretion, which is characteristic of the pancreatic fluid of the higher animals—no albumin being found in the liver, for albuminoids are decomposed by that organ. No glycocholic and taurocholic acids or glycogen were obtained from the organ. Not the slightest trace of these biliary compounds could be detected in the organ or its secretion.

There is no doubt that these investigations prove that this so-called liver of the *Cephalopoda* is a true pancreas or digestive organ.

The author in his paper entitled, "Further Researches on the Physiology of the Invertebrata,"* gave the following account of the salivary glands of the cuttle-fish: There are two pairs of salivary glands in *Sepia officinalis*. The posterior pair, which are the larger (see Fig. 20) lie on either side of the œsophagus. The secretion of the posterior glands is poured into the œsophagus, while the secretion of the smaller anterior pair of glands passes directly into the buccal cavity. A quantity of the secretion was extracted by using several freshly-killed cuttle-fishes. It was alkaline to test-papers. A portion of the secretion was added to a small quantity of starch, the starch being converted into glucose in fifteen minutes. The presence of glucose was proved by the formation of red cuprous oxide by the action of Fehling's solution. The soluble enzyme, or ferment, contained in the secretion (which is capable of causing the hydration of starch), was isolated by precipitating the secretion with dilute normal phosphoric acid, adding lime-water and then filtering. The precipitate produced was dissolved in distilled water and reprecipitated by alcohol. This precipitate converts starch into glucose.

When a drop of the clear secretion was allowed to fall into a beaker containing dilute acetic acid, stringy flakes of *mucin* were easily obtained. The presence of mucin was confirmed by several well-known tests.

Another portion of the secretion was distilled (with the

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* *Proceedings of Royal Society of London*, vol. 44, p. 327.

utmost care) with dilute sulphuric acid, and to the distillate ferric chloride solution was added, which gave a red colour, indicating the presence of sulphocyanates.

The inorganic constituents, as far as the author could make out, consisted only of calcium phosphate. No calcium carbonate could be detected.

There is much in favour of the supposition that the diastatic ferment in these secretions is produced as the result of the action of nerve-fibres (from the inferior buccal ganglion) upon the protoplasm of the epithelial cells of the glands.

THE TUNICATA.

The very fine, branched, and ampullated tubules (sometimes known as Savigny's tubules), ramifying over the wall of the intestine in nearly all the *Tunicata*, form a digestive gland, which is certainly pancreatic in function. The common duct of this gland opens into the stomach. The latter organ always contains a secretion having similar chemical properties to those produced by the pancreatic tubules.

The two following tables summarise our studies of the salivary glands and the so-called livers of the *Invertebrata*:—

(a) THE SALIVARY GLANDS.

+ = Present. – = Absent.

	Oligochæta.	Orthoptera.	Lepidoptera.	Hymenoptera.	Araneina.	Gasteropoda.		Cephalopoda.
						Pulmogasteropoda.	Branchiogasteropoda.	Dibranchiata.
Diastatic ferment .	+	+	+	+	+	+	+	+
Mucin . .	?						+	+
Sulphocyanates . .	?	+	+		+	?	+	+
Calcium phosphate .	?	+				?	+	+
Calcium . .		+				+	+	+
Chlorine .		–				+	?	?
Calcium carbonate						–		–

(*b*) THE SO-CALLED LIVER (EITHER DIFFERENTIATED OR NOT).

(+ = Present. − = Absent.)

	Porifera.	Echinodermata.	Trichoscolices.	Hirudinea.	Oligochæta.	Orthoptera.	Lepidoptera.	Hymenoptera.	Araneina.	Brachyura.	Macroura.	Lamellibranchiata.	Gasteropoda.*	Cephalopoda.†	Tunicata.
Diastatic ferment	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+
Pancreatin	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+
Peptones			−	+	+	+	+			+	+	+	+	+	+
Leucin			−	+	+	+	+							+	+
Tyrosin			−	+	+	+	+							+	+
Albumin			−	+	+	+	+							+	+
Taurocholic acid	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Glycocholic acid	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Glycogen	−	−	−	−	−	−	−	−	−	−	−	+ (?)	− (?)	−	−
Sodium										+	?		+		

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* See also Levy's investigations on the "liver" of *Helix pomatia*, already given.

† Blundstone states that the glycogenic function is performed in the *Mollusca* by the connective-tissue cells.

The chief digestive glands of the *Invertebrata* are the pancreas (the so-called liver) and the salivary glands. There appears to be no organ, from the lowest to the highest Invertebrate animal, corresponding with the Vertebrate liver. Dr. C. Letourneau, in his *La Biologie*, says: "Does the *pancreas* exist in the Invertebrates? This is a question of comparative physiology which still waits for a reply. We do not begin clearly to recognise the pancreas except in fishes, and then only in a rudimentary state." After the recent researches of Krukenberg, Fredericq, Jousset de Bellesme, Plateau, Hoppe-Seyler, as well as those of the author, the problem now requiring solution is the following:—Does a true *liver* exist in the *Invertebrata?* The pancreas appears to be the chief digestive organ of the earlier forms of animal life.

On the other hand, some biologists look upon the Vertebrate liver, pancreas, and salivary glands as differentiated bodies of an original pancreas of the *Invertebrata.* But have not many forms of the lower animals similar salivary glands to those found in the *Vertebrata?* And is not the so-called liver of the *Invertebrata* a true pancreas, capable of producing the same chemical and physiological reactions as the pancreas of higher forms?

CHAPTER V.

ABSORPTION IN THE INVERTEBRATA.

IN Chapters III. and IV. the processes of digestion in the *Invertebrata* were considered in detail. The digested food becomes tissue; but before this is attained the said digested food, which is still enclosed in the alimentary canal (if present), must first pass through its walls and gain entrance into the blood or tissues. This process is known as *absorption.*

The function of absorption in the *Vertebrata* is carried on by a distinct set of vessels, but these are entirely wanting in the *Invertebrata.* In the higher animals absorption takes place partly in the stomach and partly in the intestine. "The mucous membrane of the stomach and intestine contains an abundant supply of capillaries; the walls of these vessels are only one cell thick; consequently the soluble peptones and sugar will diffuse readily into their interiors." In the intestine the area of absorption is largely increased by means of the villi in the *Vertebrata,* and by means of the typhlosole in those Invertebrates whose intestine is provided with such an arrangement.

There are no openings in the substance of the villi and typhlosoles; consequently the nutritive fluids pass directly through their substance by a kind of transudation or imbibition (endosmosis). Every animal membrane will absorb certain fluids with greater or less facility. Thus most of them will absorb pure water more abundantly than a solution of sodium or potassium chloride; or a solution of sugar more readily than one of gum; and the same liquid will be absorbed more readily by one membrane, and less so by others. Thus every membrane has a special power of absorption for certain fluids, which it will take up in greater or smaller quantity, according to their nature and composition. In all cases, however, there is a natural limit to this quantity, beyond which absorption will not continue.

In the higher animals there is absorption by the blood-vessels and absorption by the lacteals; but, as already stated, there are no *distinct vessels* in the *Invertebrata* set apart for the function of absorption. In the lower *Mollusca, Echinodermata*, &c., the digested food is absorbed by the walls of the alimentary canal. In the higher *Mollusca* and *Arthropoda*, the digested food or nutritive fluids are absorbed by the blood-vessels in the walls of the alimentary canal. In both of the above cases, the two functions of absorption and digestion are not completely differentiated from each other.

In the *Invertebrata* the digested food is brought into contact or close relationship with the various tissues in three ways:

(1) The food particles (as in *Amœba*), during the process of digestion, are brought into contact with the tissues (using the term in its widest sense), that are to be nourished or renovated by them. In this case there is a fusion of the two functions of absorption and digestion. The digested food immediately becomes tissue.

(2) The digested food or nutritive fluid transudes through the walls of the alimentary canal into the somatic or body cavity, and is consequently absorbed by the walls of, and the organs suspended in, that cavity. In this case, the nutritive fluid passes through a transitory condition, in such a state being known as the "chylaqueous" fluid. The so-called chylaqueous fluid is found in the body cavity, and is never enclosed in any distinct vessels; it undoubtedly represents the blood of the higher animals.

(3) The digested food contained in the alimentary canal is

absorbed by the blood-vessels distributed on the walls of the digestive system. Through the medium of blood-vessels the products of digestion are carried to all parts of the body. In this case there is a fusion of the functions of absorption and circulation; the products of digestion become incorporated with the blood ere they reach the tissues for which they are destined.

Therefore, in the *Invertebrata* the function of absorption does not exist as an entirely separate function, as one finds in the *Vertebrata*. It is either fused with the function of digestion or the function of circulation.

THE PROTOZOA.

The *Gregarinida*, being parasitic organisms, pass their existence in the chyle or nutritive fluid of the higher animals. They absorb by the whole surface of their bodies the nutritive fluids of their hosts; such fluids are already in such a state as to form a nutritive material for these low organisms. Probably the nutritive material does not undergo any further change after passing into the body of a *Gregarina*. "Perhaps no other animals present such a complete want of differentiation between the functions of digestion and absorption" as do the *Gregarinida*.

In the *Rhizopoda* (*e.g.*, *Amœba*) food is taken in at any part of the cell, but only at one region of the cell at one given time—*i.e.*, the whole surface of the cell can ingest food, but only one portion of it ingests at a time. In these animals the intimate contact of the food particles, absorbed within the living substance, is aided by the contractions of the sarcode, by the emission and retraction of the pseudopodia. The sarcode of these organisms absorbs nutrient matter from the food particles. There is no distinct channel through which the food particles pass. What causes the sarcode to absorb nutrient matter from the heterogeneous materials introduced into the cells by the pseudopodia? There is no doubt that it is due to the excitability* or irritability† of the cell, caused indirectly by the presence of food particles.

Speaking of the *Rhizopoda*, M. Richet says that "irritability is their life complete." The presence of food particles excites digestion and absorption, but only the digested particles are absorbed. This power of selection is possessed by the protoplasm of the cell; it is a physiological property of that complex substance whose composition has already been alluded to in the early part of the work.

In the compound *Rhizopoda*, only certain regions of the sarcode take in food particles. "The food so ingested passes through more or less of a compound *Rhizopoda* in a similar fashion to that met with in the simple forms."

In the *Infusoria* the food particles may possibly undergo a preliminary digestion in the short œsophagus (*e.g. Paramœcium*). After this the food gives rise to food vacuoles in the sarcode. These food vacuoles undergo a rotatory movement round the cell, just below the cuticular layer. "Only the sarcode immediately in contact with the food vacuoles, as they pass round, can be regarded as truly absorptive. Here is, then, the first marking off of a region (only a region) of the sarcode, whose work is that of absorbing nutrient materials from the food, and transferring them to other parts of the sarcodic body."

THE PORIFERA.

In the *Porifera* the food particles, along with water, enter through the inhalent apertures, and pass into the gastro-vascular cavity, which is lined with flagellate cells; but the functions of digestion and absorption in the *Porifera* do not differ very much from those occurring in the *Rhizopoda*.

THE CŒLENTERATA.

In the *Hydrozoa* the function of absorption is somewhat

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* See Dr. Romanes' *Mental Evolution.*

† Richet's *Essai de Psychologie Générale.*

more complicated than in the *Rhizopoda.* The digestive and somatic cavities are not differentiated, for they form one common cavity. The digested food is absorbed by the cells of the endoderm. In the *Protozoa* the function of absorption is effected by the sarcode, whereas in the *Hydrozoa* the "sarcode" becomes differentiated into cellular membranes, the internal one (endoderm), lining the digestive cavity. The endoderm of the *Hydrozoa* is the absorptive layer and is the means of transferring the absorbed fluids to the ectoderm.

Although there are many points in the mode of absorption in the *Hydrozoa* comparable to those of the *Rhizopoda,* yet the former class marks a distinct advance on that of the latter; for the food is first digested in the "chylaqueous" fluid contained in the digestive and somatic cavity, whereas in the *Rhizopoda* the food particles are brought into actual contact with the sarcode, which performs both the functions of digestion and absorption.

In the *Actinozoa* the function of absorption comes under the second method already described. The digested food transudes through the linings of the digestive cavity, or passes directly through the posterior aperture into the somatic cavity. The somatic cavity, which is distinct from the digestive cavity,* contains a "chylaqueous" fluid. This fluid consists largely of water, and contains albuminoid spherules, which are possibly the precursors of the white corpuscles of chyle and of blood in the higher animals.

The nutrient matter of the digested food, having passed into the somatic cavity, is absorbed by the endodermic cells of that cavity and by the mesenteries.

THE ECHINODERMATA.

As far as the function of absorption in the *Echinodermata* is concerned, there is very little difference from that of the

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* In *Actinozoa* the digestive cavity is suspended in the somatic cavity.

Actinozoa. The alimentary canal, or digestive system, is suspended in the somatic cavity; and the digested food transudes through the walls of the former into the latter. The nutrient fluid is then absorbed by the walls of the somatic cavity, as well as by the various organs suspended therein. The somatic or peritoneal cavity in the *Asteridea* contains a watery corpusculated fluid. The corpuscles are nucleated cells; this fluid therefore represents the blood of the higher animals.

It will be noticed that in the *Actinozoa*, as well as in the *Echinodermata*, the function of absorption is distinct from that of digestion, but it is not performed by any special organs.

THE CESTOIDEA.

As already stated, the *Cestoidea* are reversions to a lower or simpler type. They are immersed in the chyle or the tissues of the higher animals; consequently they absorb the digested food, &c., by the whole of the external surface. Although these animals are much higher in the zoological scale than the *Gregarinida*, there is in the functions of digestion and absorption a close analogy between these two orders. In both, the processes of absorption and digestion are not differentiated.

THE ANNELIDA.

The digestive tube is suspended in the perivisceral cavity. The digested food transudes into this cavity, and there becomes mixed with a colourless corpusculated fluid. This fluid fills the perivisceral cavity, and is analogous to the blood of other Invertebrates. This colourless fluid is not contained in any vessels, although there is in *Lumbricus*, for example, a red fluid contained in a well-developed system of vessels, in addition to the colourless fluid already mentioned.

The nutrient matters, after having passed into the perivisceral cavity or chambers—as the perivisceral cavity is generally divided into chambers by means of thin muscular mesenteries—are absorbed by the pseudo-hæmal vessels, as well as by the various tissues, &c., suspended in the perivisceral cavity.

THE MYRIAPODA AND INSECTA.

In these two classes of the *Invertebrata* there is a distinct advance, in the mode of absorption, on all the forms alluded to in the present chapter.

Over the external surface of the alimentary canal there are distributed blood-vessels; and the nutrient matter of the food is chiefly absorbed by these vessels, and more especially by those carrying venous blood. Here the digested food is absorbed by distinct vessels, although there may be some transudation directly into the somatic or body cavity, especially in some of the lower orders of these two classes.

The vessels which absorb the digested food are not special vessels (like the lymphatics of the *Vertebrata*) set apart for the function of absorption, for they perform the ordinary function of veins, as well as "carrying away from the tissues of the alimentary canal the effete products resulting from the work of those tissues. But in addition to this there is laid upon them the office of receiving the fresh material introduced into the system through the alimentary canal. These vessels are not only transmitting blood, but are absorbing 'chyle'; there is a fusion of the functions of absorption and circulation."

THE ARACHNIDA.

The function of absorption in this class is performed in a similar manner to that of the *Myriapoda* and *Insecta.* The digested food passes into the veins, and is conveyed to the dorsal vasiform heart.

THE CRUSTACEA.

The digested food passes from the intestine into the blood-vessels or veins, which are distributed on its walls. No other vessels are known to convey the digested food into the circulatory system "than the irregular venous receptacles which are in contact with the parietes of the intestine."

THE POLYZOA AND BRACHIOPODA.

The function of absorption in the *Polyzoa* and the *Brachiopoda* is not so highly differentiated as the *Myriapoda*, *Insecta*, *Arachnida*, and *Crustacea*. In the latter, the digested food passes into vessels, or, in other words, into the circulatory system; but as there are no vessels in the *Polyzoa* and the *Brachiopoda*, the function of absorption is analogous to that of the *Actinozoa*. There is an alimentary canal suspended in a somatic or body cavity. The digested food transudes through the walls of the digestive system, and is then absorbed by the external endoderm of the body cavity, as well as by the organs suspended therein.

THE MOLLUSCA.

The function of absorption in the *Mollusca* is placed under the head of our third category. The digested matter is absorbed by vessels, but these perform the dual functions of absorption and circulation.

There are no special absorbent vessels in the *Invertebrata*. But although there is no special apparatus set apart for absorption, the nutrient fluids, absorbed by either the sarcode, somatic linings, or blood-vessels, are spread wherever they are required, the distribution being in some animals effected slowly, in a way analogous to absorption. In others the distribution of the nutrient fluids is accomplished rapidly by the establishment of currents, which serve also to remove the excretory products eliminated from the organs. This originates another function, the circulation of the blood, and another set of organs by which this is performed.

CHAPTER VI.

THE BLOOD IN THE INVERTEBRATA.

IN animals of the simplest structure all the fluids of animal economy resemble one another. "It seems, indeed, to be only water charged with a certain amount of organic particles; but in animals higher in the scale of being, the humours cease to be of the same nature, and there is one, distinct from all the others, destined to nourish the body; this fluid is the blood. It not only nourishes the body, but is the source whence are drawn all the secretions, such as the saliva, urine, bile, and tears." In the *Mammalia*, *Aves*, *Reptilia*, *Amphibia*, *Pisces*, and in most of the *Annelida*, the blood is of a red colour. But in the greater number of the *Invertebrata* the blood presents various colours and densities, being often thin or watery, and slightly yellow or green, brown, rose-coloured, or lilac. The majority of the *Invertebrata* have white blood; *e.g.*, the *Insecta*, *Crustacea*, *Mollusca*, &c.

The blood of the *Invertebrata*, like that of the *Vertebrata*, is not homogeneous, for it consists of a transparent or semi-transparent liquid, and a number of small, solid corpuscles, which float in this liquid.

In the higher animals the corpuscles are of two kinds, red and colourless; but in the *Invertebrata* there are, as a rule, only colourless corpuscles. The red blood of Annelides is different from the red blood of the *Vertebrata*, inasmuch as the plasma is coloured, and the corpuscles are colourless in the former, while in the latter the plasma is colourless, and there are present coloured and colourless corpuscles. The perivisceral fluid of the *Annelida* is colourless, and contains colourless nucleated corpuscles.

The corpuscles in the blood of the *Invertebrata* are of different sizes, and the size varies much in the same individual. The size of the corpuscles in the earthworm and leech are as follows:—

Lumbricus	$\frac{1}{112}$ inch in diameter.
Hirudo	$\frac{1}{2800}$ inch in diameter.

Their form, however, is generally spherical; and their surface has a raspberry appearance.

In the higher *Invertebrata* the blood clots after a variable period of time.

Drs. J. B. Haycraft and E. W. Carlier* have recently examined the coagulation of the blood in certain forms of the *Invertebrata*. According to their investigations, "in Invertebrate blood the clot is formed, at any rate for the greater part, by the welding together of blood-corpuscles. These throw out processes, which interlace to form a solid mass." Haycraft and Carlier have examined the blood of a crab and a sea-urchin.

"Crab's blood clots in about five minutes, when the opaque pinkish fluid becomes water-clear, with a branching clot within it. During and after coagulation the clot becomes of a brown-black colour, from the development within the corpuscles of a pigment."

"The blood of the sea-urchin varies very much in the number of corpuscles present in the different specimens. In most cases, when allowed to coagulate, the clot is very small, and not easy to demonstrate in a few drops of blood."

The blood of the higher Invertebrates generally darkens rapidly on exposure to air. For example, Mr. E. B. Poulton, F.R.S.,† has shown that the blood of Lepidopterous larvæ and

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* *Proc. Roy. Soc. Edinb.*, vol. 15, p. 423.

† *Proceedings of Royal Society*, 1885, p. 294.

pupæ becomes black: and Dr. C. A. MacMunn[*] has shown that the blood of *Helix pomatia* assumes a blue tinge on exposure to air.

Concerning the composition and nature of the Invertebrate blood generally, further remarks will be given later in this chapter.

THE PROTOZOA AND PORIFERA.

These animals are without blood, for no part of the sarcode can be regarded as blood. The sarcodic substance lining the canals, which traverse the skeleton of the *Porifera*, is also devoid of any fluid analogous to the blood of the higher *Invertebrata.*

In some of the *Cestoidea* and allied forms the blood or nutritive fluid found "in those interstices of the mesoderm that represent the somatic cavity of other animals, is said to be free from corpuscles." The simplest form of Invertebrate blood is present in the *Nematoidea.*

In the *Polyzoa* the fluid contained in the perivisceral cavity consists largely of water, and has but few, if any, corpuscles. This nutritive fluid (the chylaqueous fluid of some writers), derived in the first instance from the food that has been digested in the alimentary canal, and which has transuded through the walls of that canal, is, without doubt, analogous to the blood of higher forms.

In the *Hydrozoa,* which are provided with blood, the blood is of a very watery nature. The amount of fibrin is extremely small; consequently the fluid is non-coagulable, and it is almost devoid of corpuscles. That the so-called chylaqueous fluid is analogous to the blood of higher forms is demonstrated by the fact that the perivisceral fluid of the *Annelida* yields on investigation "not only albumin and fibrin, but crystals which are derived from the water that constitutes so large a part of the nutritive fluid."

From the above remarks it will be observed that the blood

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[*] *Quarterly Journal of Microscopical Science,* 1885.

of many of the *Invertebrata* is devoid of corpuscles; and the young of many of these animals (which in the adult form have corpusculated blood) have blood without corpuscles. This is another fact which proves that "development is a progress from the general to the special, from the lower to the higher form, and that the earlier stages of the history of higher animals are similar to the adult forms of lower ones."

Although many forms of the *Invertebrata* have blood devoid, or nearly devoid, of corpuscles, other forms have corpusculated blood.

THE ACTINOZOA AND ECHINODERMATA.

The "chylaqueous" fluid in the *Actinozoa* and *Echinodermata* is analogous to the blood of higher forms. In both these classes the blood is corpusculated; some of these corpuscles are distinct cells with wall and nucleus, but the majority of the corpuscles in the blood of the *Actinozoa* and *Echinodermata* are of a very rudimentary nature. "They are probably small masses of matter with no definite limiting membrane on their exterior, akin, perhaps, to the albuminous molecules in our chyle."

THE MYRIAPODA.

In this class the blood is contained in some part of its course in blood-vessels. It contains three distinct corpuscles, which are devoid of cell-walls. "The simplest kind are pellucid central nuclei invested by a few granules. Next rank the oat-shaped corpuscles, where the nucleus is still very evident. The third and most perfect form presents a central nucleus, surrounded and almost obscured by a large number of granules. As yet no definite cell-wall is to be seen on the exterior of the granules."

THE ANNELIDA.

The perivisceral cavity, communicating with the excretory or segmental organs, contains a corpusculated fluid which is nutritive. The corpuscles are oval, flat, granular, colourless bodies without a limiting membrane. Besides these corpuscles, the blood of the *Annelida* contains "actual cell corpuscles of fusiform shape, and devoid of granules. Here, then, are some corpuscles with a true wall, but all the solid, floating particles of the blood are not yet of that high order of structure."

The fluid present in the pseudo-hæmal system or vessels of the *Annelida* contains a substance allied to hæmoglobin; and according to Dr. MacMunn, this red colouring matter functionates in a similar manner to the histohæmatins of other Invertebrates, *i.e.*, it has a respiratory function. It will be noticed, that there is in the case of the pseudo-hæmal system of the *Annelida* a fusion of the functions of circulation and respiration. This hæmoglobin is dissolved in the fluid and does not belong to the corpuscles. It is questionable whether this "respiratory blood," as Prof. Huxley* calls it, possesses any nutritive properties; it appears to be entirely devoted to the function of respiration.

In the *Gephyrea*, represented by *Sipunculus*, the blood corpuscles contain a coloured fluid between the external wall and the central nucleus. This is the first appearance of a coloured corpuscle, but it differs essentially from the coloured corpuscles of the *Mammalia*, for in the latter the colouring matter is distributed throughout the corpuscle.

Prof. E. Ray Lankester, F.R.S.,† has shown that the perivisceral cavity of *Sipunculus nudus* contains a pale madder-like colouring matter, "which is due to a large number of coloured corpuscles from $\frac{1}{3500}$ to $\frac{1}{4000}$ of an

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* *The Anatomy of the Invertebrated Animals*, p. 57.

† *Proceedings of Royal Society*, vol. 21, p. 71.

inch in diameter, and that this colouring matter, also found in other parts of the worm, is not hæmoglobin."

Delle Chiaje showed that in *Sipunculus balanorophus* and *S. echinorhynchus* "the arterial blood is red, the venous brown. G. Schwalbe* found that the body fluid of *Phascolosoma elongatum* (a Gephyrean) is a bright-rose or greyish-red colour, and is cloudy owing to the presence of morphological elements, and that on standing in the air it gets darker and darker until it assumes an intense Burgundy-red colour. By long standing in the air this colour goes into a dirty brown owing to decomposition, and in drying the whole assumes a dirty green colour. Krukenberg† found the blood of *Sipunculus nudus* to contain the same colouring matter as that observed by Schwalbe; he finds that it is the oxygen of the air which brings about the colour change, and that the colour is removed by CO_2. This colouring matter gives no absorption band either in the oxidised or reduced condition. Krukenberg calls this pigment hæmerythrin, and the chromogen belonging to it hæmerythrogen. The colouring matter is decomposed by H_2S. The oxygen in the oxidised blood-pigment seems, according to Krukenberg, to be more firmly fixed than in oxyhæmoglobin. Milne-Edwards‡ in 1838 discovered that certain Annelids possessed green blood, his observations being made on *Sabella*.

"Prof. Ray Lankester § on examining the blood of *Sabella ventrilabrum* and *Siphonostoma* (sp. ?) with the spectroscope discovered the interesting fact that it only gives a banded absorption spectrum, but is capable of being oxidised and reduced, and it behaved in such a way with potassium cyanide and ammonium sulphide, as to have led him to conclude that hæmoglobin and this colouring matter (chlorocruorin) 'have a common base in cyanosulphæm, and perhaps

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* *Archiv. für Mikr. Anat.*, vol. 5, p. 248, *et seq.*

† *Vergleich. Physiol. Studien*, p. 85.

‡ *Annales des Sciences Naturelles*, 1838, vol. 10, p. 190.

§ *Journal of Anatomy and Physiology*, 1868, p. 114; 1870, p. 119.

in Stokes' reduced hæmatin.'* . . . . Prof. Lankester could not obtain derivatives of chlorocruorin, owing, as he has stated, to the apparent instability of this body, which decomposes rapidly."

Dr. MacMunn has recently examined spectroscopically the behaviour of chlorocruorin with certain reagents, but his investigations will be described later in this chapter, when we consider in detail the chromatology of the Invertebrate blood.

The red blood of *Lumbricus* can be made to yield crystals of oxyhæmoglobin (Fig. 27), and a solution of these crystals gives an absorption spectrum (Fig. 28).

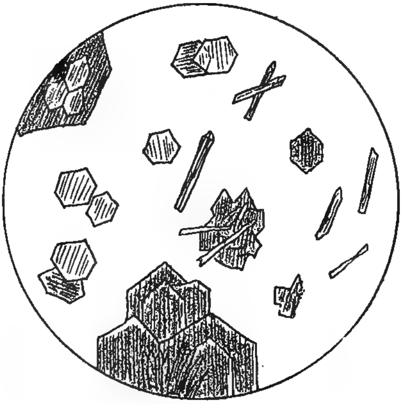

FIG. 27.—CRYSTALS OF OXYHÆMOGLOBIN FROM BLOOD OF LUMBRICUS.

Hæmoglobin is also present in special corpuscles of the blood of *Glycera* (one of the *Polychæta*); as well as in the vascular fluid of *Nephelis* and *Hirudo*. It appears that this particular colouring matter is spectroscopically identical with Vertebrate hæmoglobin.

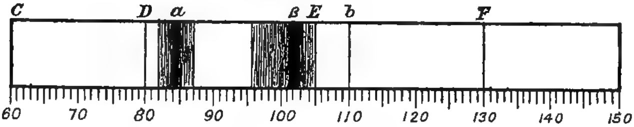

FIG. 28.—ABSORPTION SPECTRUM OF OXYHÆMOGLOBIN FROM BLOOD OF LUMBRICUS.

THE INSECTA.

In a large number of insects the blood is colourless; although sometimes it is of a green, yellow, or red hue. This colour

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* Hæmochromogen.

is not due to the flat, oat-shaped, granular corpuscles with their well-defined walls and nuclei, but is due to the liquid in which they float.

In the case of Phytophagous larvæ, Mr. E. B. Poulton, F.R.S.,* has shown that they owe their colour and markings to two causes:—(1) "Pigments derived from their food-plants, chlorophyll and xanthophyll, and probably others; (2) pigments proper to the larvæ or larval tissues made use of because of some (merely incidental) aid by either or both of these groups of factors. It may be generally stated that all green colouration without exception, is due to xanthophyll. All other colours (including black and white) and some yellows, especially those with an orange tinge, are due to the second class of causes. . . . . Derived pigments often occur dissolved in the *blood*, or segregated in the subcuticular tissues (probably the hypodermic cells), or even in a chitinous layer, closely associated with the cuticle itself."

In some cases, the colour of the blood changes before the pupal stage is reached, while in others it remains the same as in the larval condition. On this point Mr. Poulton (*loc. cit.*, p. 277) says:—"the superficial derived pigments of *Sphinx Ligustri* become brown in the dorsal region, before pupation, while the colour of the blood is unchanged. In *Dicranura Vinula* the whole larva becomes reddish-brown, and in this case the green blood changes to brownish-yellow. The true larval pigment also changes before pupation, except when it is cuticular. Thus the larva of *E. Angularia* becomes transparent by the disappearance of dark pigment, and the green blood gives its colour to the larva. The green colour of the blood is generally retained in the pupal state, and it is often of great importance."

According to Mr. Poulton, the blood of Phytophagous larvæ and pupæ is acid to litmus-paper, with the exception of that of *Ephyra punctaria*, which seemed to be neutral. This acid, which is volatile, is readily extracted with ether; but its

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* *Proc. Roy. Soc.*, 1885, p. 270.

nature has not been determined. The corpuscles of Phytophagous blood are amœboid.

Coagulation.—"The blood clots after a very variable period of time, but generally darkens in about five minutes, ultimately forming a solid black clot which is due to oxidation. If blood be sealed in a tube, the small quantity of oxygen present will form a thin black film on the surface of the blood, and the action then ceases." Mr. Poulton has shown "how blood can be kept indefinitely without clotting in a section of tube with a cover-glass over one end, and the other cemented to a glass slide." He has kept "the blood of *Pygæra Bucephalus* in this way for a month, quite unchanged, and on then breaking off part of the cover-glass a thick black crust was formed on the surface, while the blood beneath became translucent instead of clear and transparent. On removing the crust a second thin one was formed, but on removing this, no further coagulation took place. If in sealing up blood, or placing it in a tube section, a bubble of air is accidentally included, coagulation takes place round the bubble, but not elsewhere. This black substance is the normal clot, for the injured places on larvæ which have healed are always black, notably the horns of *Sphinx* larvæ which have been nibbled off by others of the same species. The coagulation takes place after the addition of water, or of a saturated solution of neutral salt (sodium sulphate). The occurrence of a reducing agent in the blood appears to be very remarkable, but it is possible that the substance is capable of again yielding up its oxygen, and so acting as a carrier. It has been observed that if fresh blood be added to that which is turning black on the surface, the black clouds are redissolved. If this be not so, it is difficult to see how the blood can be the internal medium for the supply of oxygen in these animals, and one is tempted to the supposition that in the tracheal system we have a means for the supply of oxygen direct to the tissues." Another suggestion which occurred to Poulton was that "the coagulation is a very similar process to the darkening of cuticular pigment on larvæ, and the darkening of the pupal covering. It has always been assumed that this darkening is due to light, but it takes place rapidly and completely in pupæ buried several inches under ground, in compact and opaque cocoons, or sometimes in the heart of a tree." Furthermore, Poulton has never observed that darkness made the least difference to the darkening of pupæ. It is, therefore, "very probable that this will also prove to be due to oxidation, and possibly to the formation of a substance similar to the black clot of the blood."

Poulton has observed that "the brown and colourless blood darkens as well as the green."

The Action of Reagents.—The action of (*a*) alcohol (fifty per cent.) on the blood of *P. Bucephalus* was to precipitate proteids; and if the mixture is shaken, "the proteids and pigments are precipitated as yellowish-green clouds, and in a few minutes the upper part of the liquid becomes blue, and ultimately black, from the formation of coagulum. The proteids are decolourised and sink, the alcohol remaining yellow with xanthophyll (the chlorophyll disappearing). Absolute alcohol does not lie on the top of the blood (like diluted alcohol), but mixes with it at once. (*b*) Chloroform behaves in the same manner as ether, but it dissolves nothing coloured from the green coagulum; the latter contracts in a few hours, and a clear blue liquid appears between it and the sides of the tube. The exposed surface of the coagulum (the chloroform having sunk to the bottom) rapidly becomes black. (*c*) Distilled water, like weak spirit, lies on the top of the blood with a cloud of precipitated proteid (probably globulin) above the junction. On shaking, the cloud disappears, and the blood only seems diluted; if now more water be added (altogether many times the volume of the blood), in a few minutes the whole fluid becomes cloudy, remaining dark-greenish. On filtering, a blue solution comes through, which slightly darkens for some hours. With less water the blood coagulates normally, although after a longer interval of time. (*d*) Carbon disulphide had no effect for a considerable time. Eventually the blood was coagulated (green) but nothing coloured was dissolved out."

The Action of Heat.—"The blood of the pupa of *Sphinx Ligustri* was heated in a glass tube in a water-bath; no change was seen till the temperature reached 132° F., when part of the blood became slightly dim. By 141° the whole of the blood was distinctly cloudy, but it was not till 180° that the blood became quite coagulated—solid-looking and opaque, the proteids being yellow with xanthophyll. In the interstices of the clot was a clear yellow fluid. The xanthophyll in the coagulum was easily extracted by ether or alcohol."

Dr. L. Fredericq* has also investigated the nature of the blood in the *Insecta.* He experimented upon the blood of the larvæ of *Oryctes nasicornis* (belonging to the *Coleoptera*). The blood was extracted by making a small slit (with fine scissors) across the skin of the back and the walls of the dorsal vessel; into this slit a slender glass canula was inserted when the blood of the animal immediately rose in the tube. The blood is a colourless liquid having somewhat the aspect of the lymph of the *Mammalia*, and holding in suspension a large number of colourless globules which slightly interfere with its transparency. The blood of *Oryctes* quickly coagulates. This coagulation is not arrested by the addition of sodium chloride, magnesium sulphate, &c. But a slightly elevated temperature (54° C.) sufficed to prevent coagulation.

When exposed to the air the blood of this insect becomes a dark brown colour; but the brown colour has not the same intensity throughout the fluid; it is of a deeper colour in the vicinity of the mass of globules. Light has no action in changing the colour; the change being due to oxidation. After being coagulated with hot water, the blood of *Oryctes*

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* *Bulletins de l'Académie Royale de Belgique*, 3e série, tome i.

changes to a brown colour in contact with air. But the coagulum produced by alcohol is not acted upon by air.

When the oxidised or brown blood is examined by the spectroscope, it does not show any characteristic absorption bands.

At first sight the blood of *Oryctes* appears to contain a substance acting under the influence of oxygen in a similar manner to hæmoglobin or hæmocyanin. The substance which becomes brown in air, does not probably play any *rôle* in the respiration of the animal. The blood in the vessels is perfectly colourless; the brown colour which is produced after it has been extracted from the body is probably a cadaveric or *post mortem* phenomenon comparable to the spontaneous coagulation which equally occurs in this liquid. In fact, the colourless substance, which becomes brown on exposure to air is not contained in the blood which circulates, but is formed at the moment of spontaneous coagulation. If one carefully plunges the larvæ of *Oryctes* into warm water (50° to 55° C.) for a quarter of an hour before opening it, the blood extracted from the dorsal vessel neither coagulates nor colours in air.

The production of the colourless substance (susceptible of becoming brown in contact with air) has probably been prevented by the temperature of 50° to 55° C. For when once this substance has been produced, the temperature of boiling is incapable of preventing its combination with oxygen, and a change of colour which it indicates.

Finally, the most important fact which proves that the phenomenon of colouration does not play any *rôle* in the respiration of the animal, is that the brown substance once formed constitutes a stable combination, which is not decomposed by acids or alkalies, and is not decolourised when placed *in vacuo* or in a sealed tube.

The phenomenon of colouration which the blood of the larvæ of *Oryctes* presents when it is exposed to air, appears to be a cadaveric phenomenon, and as already stated, comparable to spontaneous coagulation. The substance which becomes brown in air does not form any intermediate vehicle between the exterior air and the tissues which require it. The existence of such an intermediate vehicle is most doubtful, especially when one bears in mind the anatomical disposition of the respiratory apparatus in the *Insecta*, *i.e.*, the air penetrates by the tracheæ among all the living tissues. By means of the tracheæ the function of respiration is carried on in every part of the body.

The Crustacea.

Dr. Léon Fredericq* has examined the blood of various *Crustacea*. The blood of crabs, lobsters, &c., which live in the sea, has exactly the same taste as sea water; which leads one to suppose that the blood or nourishing fluid of these animals has the same saline composition as the waters in which they live.

According to an analysis of Backs, and cited by Pelouze and Fremy,† the water of the North Sea contains a little more than three per cent. of soluble salts:—

Sodium chloride . .	2.358
Potassium chloride . .	0.101
Magnesium chloride . .	0.277
Magnesium sulphate . .	0.199
Calcium sulphate . .	0.111
	3.046

It tastes strongly salt and bitter.

In support of the idea that the blood of certain *Crustacea* living in the North Sea, has the same saline composition as the medium in which they live, Fredericq obtained the following result after analysing the blood of an Ostend lobster (*Homarus vulgaris*):—

3.040 per cent. of soluble ashes.

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* *Bulletins de l'Académie Royale de Belgique*, 3^e série, tome iv.

† *Traité de Chimie*, 3^e éd., tome 1, p. 252.

The blood of a large female lobster (bled by making a cut in the claws) weighed 26.49 grammes. This blood was dried at a moderate heat in a covered crucible; then heated to complete carbonisation. The porous carbon was exhausted with warm water. The filtered solution was evaporated to dryness, the residue allowed to cool in a dessicator, and weighed with the usual care. The 26.49 grammes of blood yielded 0.8055 gramme of soluble salts, equal to 3.040 per cent.

23.01 grammes of the blood of the crabs (*Carcinus mœnas*) of Roscoff yielded 0.708 gramme of soluble salts, equal to 3.07 per cent.

The crabs (*C. mœnas*) of Roscoff living in sea water of a density of 1.026 were also examined; 14.78 grammes of the blood of these animals yielded 0.445 gramme of soluble salts, equal to 3.001 per cent.

The hermit crab (*Platycarcinus pagurus*) of Roscoff, whose blood had a density of 1.037, was examined by Fredericq; 13.54 grammes of this blood yielded 0.419 gramme of soluble salts or equal to 3.101 per cent. In the case of another hermit crab the blood had a density of 1.036, and 31.08 grammes of it yielded 0.965 gramme of soluble salts, equal to 3.104 per cent.

In the case of the sea crayfish (*Palinurus vulgaris*) of Roscoff, 22.94 grammes of blood yielded 0.666 grammes of soluble salts, equal to 2.9 per cent.

In the case of *Maja squinado* of Roscoff, 15.60 grammes of blood yielded 0.476 gramme of soluble salts, equal to 3.045 per cent.

The sea water of Roscoff in which the above Crustaceans lived was also analysed with the following results:—27.312 grammes of sea water yielded on evaporation 0.929 gramme of saline residue which is equal to 3.401 per cent. In another determination 26.266 grammes of the same water yielded 0.894 gramme of saline residue, which is equal to 3.407 per cent.

The *Maja squinado* of Naples lives in sea water which is exceptionally rich in saline matter; 20.669 grammes of this water yielded 0.821 gramme of saline residue, equal to 3.9 per cent; 14.807 grammes of the blood of *Maja* yielded 0.498 gramme of soluble salts, equal to 3.37 per cent.

Not only has Fredericq examined the blood of various Crustaceans inhabiting sea water but he has also examined the blood from those living in brackish and fresh water.

6.48 grammes of the blood of *Carcinus mœnas* inhabiting brackish water yielded 0.096 gramme of soluble salts, equal to 1.48 per cent.

To examine the blood of fresh water Crustaceans seven crayfishes (*Astacus fluviatilis*) were used in the experiments. A large quantity of blood was obtained by making an incision in the claws. Its taste was only slightly saline; 23.453 grammes of it yielded 0.221 gramme of soluble salts, that is less than one per cent. (0.94 per cent.)

The following table gives a summary of the results obtained concerning the saline matter of the blood of various Crustaceans and the medium in which they live:—

PROPORTION OF SALINE MATTER IN THE BLOOD OF CRUSTACEANS.

	Blood.		Water in which the Animals lived.	
	Density.	Percentage of soluble salts.	Density.	Percentage of salts.
Astacus fluviatilis	—	0.940	—	fresh water
Carcinus mœnas	—	1.480	?	brackish water.
,, ,,	—	1.650	1.007	about 0.9
,, ,,	—	1.560	1.010	,, 1.3
,, ,,	—	1.990	1.015	,, 1.9
,, ,,	—	3.001	1.026	3.40
,, ,,	—	3.007	—	3.40
Homarus vulgaris	—	3.040	1.026	3.41
Platycarcinus pagurus	1.037	3.101	1.026	3.40
,, ,,	1.036	3.104	1.026	3.40
Palinurus vulgaris	—	2.900	1.026	3.40
Maja squinado	—	3.045	1.026	3.40
,, ,,	—	3.370	?	3.90

The blood of crabs living in brackish water contains a smaller percentage of saline matter than those living in sea water; and the blood of crayfishes living in rivers contains only a very small amount of saline matter—generally less than one per cent.

According to the above investigations it appears that there is an exchange of salts, forming a kind of equilibrium between the composition of the blood and the external medium in which these Crustaceans live. This equilibrium is the result of the simple laws of diffusion.

Among the fresh water Crustaceans the albuminoid substances of the blood probably retain a little more of the soluble salts than is contained in the external medium.

It is probable that this exchange of dissolved salts is established by the respiratory organs—the branchiæ. The delicate walls of the branchiæ, which separate the blood from the external medium, allow the respiratory gases to pass by simple diffusion: and most likely these delicate walls act in a similar manner to a dialyzer with easily diffusible salts. The albuminoid substances of the blood do not pass into the external medium.

The nourishing fluids, to which the illustrious physiologist —Claude Bernard—gave the name of "milieu intérieur," have not (with the animals previously mentioned) the constant chemical composition and independence of the conditions of the "milieu extérieur" which characterises the blood of the higher animals.

Among fishes (*Pisces*) the branchial walls allow equally to pass the oxygen and carbonic anhydride of respiration. One can therefore understand that there is a similar exchange of salts between the blood and the external medium. But experience proves that it is the *inverse* of that which takes place among the Crustaceans and other Invertebrates; for the blood of marine fishes has a saline composition which is entirely different from that of sea water. The blood of a sole, a haddock, and a weever does not contain more soluble salts than the blood of fresh water fishes.

Among fishes the interior fluid constituting the blood is isolated more or less from the external medium in which the animal lives. In regard to this there is an advance on that which occurs among Invertebrates.

The blood of the *Crustacea* contains corpuscles which are very well defined. They are oval in shape, granular, and present a very distinct wall externally and nucleus within.

THE MOLLUSCA.

The blood of the lower *Mollusca* (*Lamellibranchiata* and *Gasteropoda*) is corpusculated, but the nuclei (which are generally present) are sometimes very indistinct.

The percentages of saline matter contained in the blood of *Anodonta* and *Mytilus* were found to be the following* :—

	I.	II.	III.	IV.	Average.
Anodonta cygnea . . .	1.002	0.998	1.006	0.996	1.000
Mytilus edulis . . .	1.796	1.799	1.810	1.800	1.801

It will be observed that the blood of the fresh water mussel contains a smaller amount of saline matter than that of the marine form.

The blood of the *Mollusca* is principally colourless, but Dr. L. Cuénot† has recently shown that the blood from the heart of *Aplysia depilans* (one of the *Gasteropoda*) has a distinct rose colour, due to the presence of 0.636 per cent. of an albuminoid which is precipitated by alcohol, acids, mercuric chloride, and the usual reagents. Its colour has no relation to the presence of oxygen, and it seems improbable that it plays any part in respiration. When the blood is dialyzed,

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* See Dr. Griffiths' paper read before the Royal Society of Edinburgh on June 1, 1891 (*P. R. S. E.*, vol. 18, p. 288).

† *Comptes Rendus*, vol. 110, p. 724.

or exposed for a long time to air, it decomposes spontaneously, part of the albuminoid remaining in solution and part separating in a white, flocculent form. This albuminoid is entirely distinct from hæmocyanin, and has been called hæmorhodin. If the blood is concentrated *in vacuo* and heated, it becomes opalescent at 58° C., and coagulates completely at about 70° C.

The blood of *Aplysia punctata* is quite different, and contains 1.77 per cent. of a perfectly colourless hæmocyanin which is not affected by air, and coagulates at about 76° C. This albuminoid probably plays no part in the absorption of oxygen.

In the *Gasteropoda*, *Cephalopoda*, as well as in the *Crustacea* and *Arachnida*, the function of respiration is brought about by an albuminoid substance analogous to hæmoglobin, but contains copper instead of iron. This substance, which Fredericq* named hæmocyanin, combines with oxygen, forming a very unstable combination.

The blue colouring matter of the blood of *Octopus vulgaris* is due to the absorption of oxygen, for if the blood is placed *in vacuo* it loses its colour, but regains it in the presence of air or oxygen. Hæmocyanin occurs in the arteries of the living *Octopus*.

Krukenberg† examined the blood of *Sepia officinalis*, *Carcinus mænas*, *Homarus vulgaris*, *Squilla mantis*, as well as other species of the *Mollusca* and *Crustacea*, and observed that the blood becomes blue by shaking with oxygen or air; and that the blue colour disappears more or less with carbonic anhydride. "Krukenberg also found great differences in the blood of individual Gasteropod Molluscs, which led him to assume that perhaps the oxygen in such cases is in a firmer combination with the hæmocyanin than is the case in Crabs and Cephalopods. He also made the interesting observation

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* *Archives de Zoologie Expérimentale*, 1878; see also Fredericq's *La Lutte pour l'Existence*, p. 84.

† *Vergleich. Physiol. Studien*, 1st R., 3 Abh., 1880, S. 72.

that the blood of Crabs and Cephalopods on treatment with carbonic oxide became colourless, but regained its blue colour on shaking with air. This behaviour is different from that of hæmoglobin when similarly treated. It was further found that blood which had become blue by the reception of oxygen if allowed to stand in a test-tube exposed to the air did not lose its blue colour from above downwards, but from below upwards, whence he concludes that the blueing is not due to suspended particles, but to the presence of a chromogen which becomes blue by the reception of oxygen. . . . . He could find no hæmocyanin in the blood of several Molluscs (*e.g.*, *Tethys fimbria*, *Doris tuberculata*, *Aplysia depilans*, &c)."

Although the blood of the higher Invertebrates, as a rule, contains copper, in some this element is replaced by manganese. Krukenberg has shown that the blood of *Pinna squamosa* (one of the *Lamellibranchiata*) as well as the organ of Bojanus are rich in manganese. If a borax bead is dipped into the blood of *Pinna* and then heated in the oxidising blowpipe flame, the bead becomes a distinct violet colour, and in the reducing flame it remains colourless.

It is probable that copper, manganese, and possibly other metals play the same part in the blood of the *Invertebrata* as iron plays in the *Vertebrata*.

The author* of the present volume has also extracted copper from the blood and organs of *Sepia officinalis;* but the process was entirely different from those of Fredericq and Krukenberg.

In the majority of the *Invertebrata* the carrier of oxygen to the tissues is hæmocyanin contained in the blood; but in many of the *Annelida*, as well as in nearly all Vertebrates, the transport of oxygen from the surrounding medium (air or water) to the living tissues is made by means of the hæmoglobin of the blood.

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* See Dr. Griffiths' paper in *Chemical News*, vol. 48, p. 37; *Journal of Chemical Society*, 1884, p. 94.

This substance (as is well known) forms an oxygenised combination which is very unstable, and which is carried by the blood across the tissues of the animal, and is there dissociated, yielding its oxygen to the elements of those tissues which require it.

Prof. Ray Lankester discovered that in some Annelids the hæmoglobin is replaced by a green-colouring matter (chlorocruorin).

Reverting once more to the saline matter contained in the blood of the *Mollusca*, the author* obtained the following results (*i.e.*, percentages) :—

		I.	II.	III.	Average.
Pulmogasteropoda.	*Helix pomatia* . .	1.065	1.072	1.069	1.068
	Helix aspersa . .	1.079	1.080	1.062	1.077
	Limnæus stagnalis .	1.200	1.203	1.210	1.204
	Limax flavus . .	1.122	1.100	1.115	1.112
	Limax maximus . .	1.119	1.127	1.114	1.120
Branchio-gastero-poda.	*Buccinum undatum* .	1.699	1.710	1.698	1.702
	Patella vulgata . .	1.706	1.721	1.719	1.715
Cephalo-poda.	*Sepia officinalis* . .	2.840	2.862	2.851	2.851
	Octopus vulgaris .	3.004	3.032	3.020	3.018

Dr. L. Fredericq† found 3.016 per cent. of soluble and insoluble salts in the blood of *Octopus vulgaris*.

The author of the present volume has submitted to analysis the ashes of the blood of several Invertebrate animals. The ashes were obtained by incinerating the blood, partially covered in a platinum dish, at a very low tempera-

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* A paper read before the Royal Society of Edinburgh on June 1, 1891.

† *Bulletins de l'Académie Royale de Belgique*, 3^e série, tome iv.

ture. By so doing the alkaline metals are not volatilised as they are when a high temperature is used.

The following results represent the averages of three analyses in each case :—

	Cancer pagurus.	*Carcinus mænas.*	*Astacus fluviatilis.*	*Palinurus vulgaris.*	*Homarus vulgaris.*
Copper oxide (CuO)	0.22	0.19	0.20	0.18	0.18
Iron oxide (Fe_2O_3)	trace	trace	—	—	trace
Lime (CaO)	3.55	3.57	3.58	3.79	3.54
Magnesia (MgO)	1.91	1.89	1.88	1.90	1.89
Potash (K_2O)	4.97	4.78	4.82	4.92	4.77
Soda (Na_2O)	43.90	44.91	44.96	43.98	44.99
Phosphoric acid (P_2O_5)	4.90	4.86	4.81	4.87	4.84
Sulphuric acid (SO_3)	2.90	2.81	2.75	2.86	2.81
Chlorine	37.65	36.98	37.00	37.50	36.96
	100.00	99.99	100.00	100.00	99.98

	Anodonta cygnea.	*Mytilus edulis.*	*Pinna squamosa.*	*Sepia officinalis.*	*Octopus vulgaris.*
Copper oxide (CuO)	0.23	0.22	trace	0.24	0.21
Manganese oxide (MnO_2)	—	trace	0.19	—	—
Iron oxide (Fe_2O_3)	—	—	trace	—	—
Lime (CaO)	3.61	3.72	3.70	2.31	2.40
Magnesia (MgO)	1.82	1.86	1.83	1.51	1.55
Potash (K_2O)	4.90	4.80	4.86	4.92	4.90
Soda (Na_2O)	44.18	43.90	44.02	45.40	45.31
*Lithium	trace	—	—	—	—
Phosphoric acid (P_2O_5)	4.89	4.82	4.79	4.90	4.88
Sulphuric acid (SO_3)	2.80	2.76	2.73	2.81	2.83
Chlorine	37.55	37.92	37.88	37.90	37.92
	99.98	100.00	100.00	99.99	100.00

There is no doubt, from the above analyses, that copper plays an important part in the blood of the *Invertebrata;* in fact it plays a similar *rôle* to that of iron in the blood of the higher *Vertebrata.*†

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* Detected by the spectroscope.

† See Dr. Griffiths' paper read before the Royal Society of Edinburgh on June 1, 1891.

THE CHROMATOLOGY OF THE BLOOD OF THE INVERTEBRATA.

We have already alluded to some of the colouring matters contained in the blood of the *Invertebrata*, but as a considerable amount of work has been done in this direction, we propose to describe more fully the results obtained in this important subject.

In England the two great authorities on the colouring matter of the Invertebrate blood are Dr. C. A. MacMunn, and Mr. E. B. Poulton, F.R.S. Both of these scientists have presented us with a valuable series of investigations which we now proceed to describe.

The colour of the blood in the *Invertebrata* "does not as a rule belong to the corpuscles, but to what in them answers to the liquor sanguinis of Vertebrates, although there are many exceptions. In some hæmoglobin occurs. Thus, Prof. Lankester has shown* that in *Glycera*, *Capitella*, and *Phoronis*, and in *Solen legumen*, it is found in special corpuscles; while in the vascular fluid of others it is found dissolved, *e.g.*, with certain exceptions in some chætopod Annelids, in some Leeches (*Nephelis*, *Hirudo*), in *Polia sanguirubra* (a Turbellarian), in the special vascular system of a marine parasitic Crustacean observed by E. van Beneden, in the general blood-system of the larva of the Midge (*Chironomus*), in the general blood-system of the Mollusc *Planorbis*, and in the general blood-system of the Crustaceans, *Daphnia* and *Cheirocephalus*."

Hæmoglobin is also present in the blood of *Lumbricus Arenicola*, and *Eunice*; and it has already been stated that this hæmoglobin is spectroscopically the same as that found in Vertebrate blood.

The blood obtained from five hundred earth-worms (*Lumbricus terrestris*) was treated with benzene, which readily dissolves the colouring matter. The mixture was allowed to stand for twenty-four hours at 0° C.; when it separated into two distinct layers. The one containing the colouring

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* *Proceedings of Royal Society*, vol. 21, p. 71.

matter was then separated from the other; and about one-sixth of its volume of pure absolute alcohol was added. After filtration the alcoholic extract was exposed to − 12° C., when red crystals were obtained. These crystals yielded the following results on analysis:—

	Blood of *Lumbricus*.			Blood of Dog.
	I.	II.	III.	
Carbon	53.91	53.86	—	52.85
Hydrogen	7.02	7.10	—	7.32
Nitrogen	—	—	—	16.17
Sulphur	0.41	0.37	—	0.39
Iron	—	—	0.39	0.43
Oxygen	—	—	—	21.84

The above analyses prove that the colouring matter of the blood of *Lumbricus* is comparable chemically to that of a Vertebrate animal, like the dog.*

Although hæmoglobin is present in the blood of certain Invertebrates, the chief constituent in the blood of the majority of these animals is HÆMOCYANIN, a compound said to be analogous to hæmoglobin, but containing copper instead of iron.

It is well known that "the blood of many Molluscs and Arthropods is of a blue colour after exposure to the air, and this is in most cases due to the presence of hæmocyanin."

(1) The *Echinodermata*.—Dr. MacMunn† has examined the blood of *Holothuria nigra*. It does not contain hæmoglobin, but when examined with the spectroscope it strongly absorbed the violet end of the spectrum but gave no bands. The colouring matter of the blood "is soluble in absolute

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* Griffiths in *Proc. Roy. Soc. Edinb.*, 1891 (June 1).

† *Quarterly Journal of Microscopical Science*, vol. 30, p. 60.

alcohol, forming a deep yellow solution, giving an ill-defined band at the blue end of the green, beginning to be feebly shaded at about λ 526, darker at λ 507, and extending to about λ 474. On evaporation it left a reddish residue soluble in ether, in chloroform, and other lipochrome solvents, and when in the solid state it became a transient blue with nitric acid, blue, green, and brownish with sulphuric acid, and greenish-yellow with iodine in potassic iodide. Therefore, the blood of *Holothuria nigra* contains a red lipochrome like that of certain Crustaceans, as Dr. Halliburton* has discovered." Dr. MacMunn also found this red lipochrome or luteïn in the digestive gland of *H. nigra;* and states that he has no doubt that it "is built up in the digestive gland and carried in the blood current to be deposited in other parts of the body, though what its *rôle* may be when deposited there, it is difficult to say. It is not easy to see of what use so much brilliant coloration as exists within the body of *Holothuria nigra* can be, except that the lipochrome is changed into some other constituent. If it be respiratory, as tetronerythrin is believed by Merejkowsky† to be, we could see some reason for its existence," but as Dr. MacMunn has repeatedly shown, "what has been called tetronerythin does not exist in two states of oxidation. Merejkowsky would doubtless call the red lipochrome of *H. nigra* tetronerythrin without hesitation; but since he published his results our knowledge of these fat pigments has undergone a change; for we now know that there are a great number of pigments, formerly, with regard to their supposed respiratory properties, included under the name tetronerythrin, which are distinguishable from each other, and which cannot any longer be called tetronerythrin, the rhodophan of the retina ‡ is not respiratory, nor is the true tetronerythrin in the so-called 'roses' around the eyes of certain birds, respiratory." The

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* *Journal of Physiology*, vol. 6.

† *Bulletin de la Société Zoologique de France*, 1883, p. 81.

‡ Kühne in *Untersuchungen a. d. Physiol. Instit. d. Univ. Heidelberg*, Bd. 1, Heft 4, und Bd. 4, s. 169–248.

lipochromes included under the name tetronerythrin by Merejkowsky “ fail to respond to the test used in determining whether any pigment is respiratory or not, namely, change of colour and spectrum under the influence of reducing agents.”

Dr. MacMunn* has also investigated the brown colouring matter of the perivisceral fluid of *Echinus* (*esculentus ?*) and *sphæra.* This colouring matter gave two bands, one between D and E covering E, and the other between *b* and F, the first of which became decidedly darker after the addition of ammonium sulphide. MacMunn named this pigment echinochrome, and it has a respiratory function.

Since his discovery of echinochrome, MacMunn has made some valuable observations on the perivisceral fluid of *Strongylocentrotus lividus.* On opening a specimen a pale red fluid exudes from the perivisceral cavity. “ In a short time a clot forms ; this becomes gradually darker in colour and it contracts more and more, until all its connections with the side of the containing vessel are broken, and it finally shrinks into a small brown-red mass. The corpuscles are carried down by this clot, and it is to them, not to the plasma, that the colouring matter belongs.” Prof. P. Geddes † (who has worked out the morphology of the corpuscles of the perivisceral fluid of various Echinoderms) has shown that the finely granular, pale corpuscles run together to form plasmodia, and that it is to their fusion that the clotting is due.

“ The corpuscles present all degrees of coloration, from a brilliant red, through a pale orange, to colourless. The red ones are nucleated and of irregular shape, and rapidly throw out amœboid processes, so also do the others. The nucleus is strongly refracting and gives the corpuscles the appearance of a round hole having been punched in it. The red corpuscles measure from $\frac{1}{1500}$ inch in long diameter × $\frac{1}{3000}$ inch in short, down to $\frac{1}{3000}$ in long × $\frac{1}{6000}$ in short, while several

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* *Proceedings of Birmingham Philosophical Society*, vol. 3, p. 380.

† *Proc. Roy. Soc.*, 1880.

measure $\frac{1}{3000}$ in both diameters. The pale ones $\frac{1}{1500} \times \frac{1}{2000}$ down to $\frac{1}{3000} \times \frac{1}{6000}$; the latter are multinucleated.

"The pigment itself in the fresh state showed no distinct bands, but treated with caustic potash in the solid condition the colour changed to dark purple" and showed the bands in the spectrum *a* (Fig. 29).

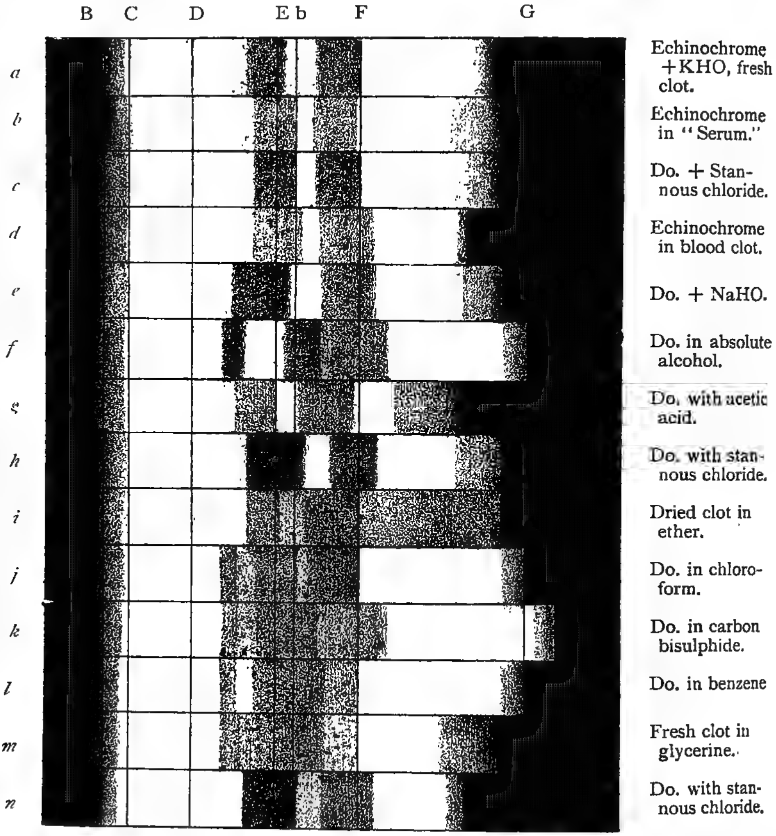

FIG. 29.—SPECTRA OF PERIVISCERAL FLUID OF STRONGYLOCENTROTUS LIVIDUS. (*After* C. A. MACMUNN.)

MacMunn says that the deepening of colour which echinochrome undergoes on exposure to the air must be in part due to the oxidation of a chromogen, if so we may infer the existence of such, and name it echinochromogen.

Echinochrome differs from the blood pigments of most Invertebrates, as it is readily dissolved by a great number of solvents.

It can be obtained in solution and isolated by two methods:—"(*a*) The fresh blood-clot can be extracted with the solvents mentioned before, or (*b*) the clot may be separated from the serum by filtering, the pigment dried at the temperature of the air (as it changes by using heat) and the dried pigment thus obtained treated by solvents. By the adoption of the latter method it can be obtained in a purer condition."

"The 'serum' after separation of the clot is a faint yellow colour and shows two faint bands in the green, but if allowed to stand some time in contact with the clot it becomes a faint violet red," and then gives the spectrum seen in Fig. 29, *b*. On the addition of stannous chloride to the serum dark bands (Fig. 29, *c*) make their appearance. These bands have the following positions, λ 541.5 to λ 532 and λ 506 to λ 486.5. In the oxidised condition the serum has a spectrum of the same kind but the bands are feebler. The serum is "faintly acid or neutral, faintly opalescent on heating, opalescent with absolute alcohol, and faintly so with ether."

Spectra Fig. 29, *d* and *e* are those of the brownish-red clot, after standing in contact with the serum and with sodium hydroxide respectively.

The red alcoholic solution of the clot gives the spectrum represented in Fig. 29, *f*. These bands read: first, λ 557 to λ 545.5; second, λ 524.5 to λ 501; third, λ 494.5 to λ 475. On the addition of ammonium sulphide two new bands make their appearance. The first is from λ 531 to λ 507; and the second, λ 494.5 to λ 475, the colour of this solution being changed to yellow, and on shaking with air remained the same.

On the addition of acetic acid to an alcoholic solution of the fresh clot, the spectrum given in Fig. 29, *g* is seen. "The spectrum of the original absolute alcohol solution is that of the neutral pigment, as can be proved. Hydrogen peroxide did not affect the bands. Hydrochloric acid produced the same effect as acetic acid; the bands reading: first, λ 545.5 to λ 529.5; second, λ 511.5 to λ 488. When the alcohol solution is treated with stannous chloride the colour changes to yellow, and two very well-marked bands appear (Fig. 29, *h*). Dark part of the first band, λ 535 to λ 511.5; second, λ 496.5 to λ 477. Sodium hyposulphite changed the colour to yellow, but the original bands could be seen, although faint."

Dr. MacMunn has also examined solutions of echinochrome in chloroform, water, ether, carbon disulphide; some of the spectra of these solutions are given in Fig. 29.

Echinochrome is only partially soluble in water and alcohol, but is soluble in chloroform, ether, benzene, glycerol, carbon disulphide, and petroleum ether. It is capable of existing in two states of oxidation, therefore its function is of a respiratory nature. Echinochrome has not been obtained in the crystalline condition.

(2) The *Annelida.*—The blood of many Annelids contains hæmoglobin; some contain pigments allied to chlorophyll, while others contain lipochromes.

The blood of *Arenicola piscatorum* (one of the *Polychæta*) contains, besides hæmoglobin, a lipochrome or lipochromes. Dr. MacMunn obtained a dark brown-green extract by treating this worm with a solution of caustic potash. This solution gave no bands. But he has extracted from the digestive system and the integument of *Arenicola* certain lipochromes, which have well-defined absorption spectra.

The spectrum of the blood of *Nereis Dumerillii* consists of a single band like that of reduced hæmoglobin. The spectrum of an aqueous solution of the blood of this worm consisted of two feeble bands; "the first was like that of the first of oxyhæmoglobin, but the second was rather narrower than is the second blood-band. These bands read approximately: the first, from λ 584.5 to λ 574, the second, about λ 550.5 to λ 536, and a third one at the blue end of the green, from about λ 507 to λ 474 (?) was visible. Sulphide of ammonium caused these bands to disappear," but Dr. MacMunn could not then detect that of reduced hæmoglobin.

The various colouring matters contained in the blood and organs of certain worms are given in the following table:—

	Chlorocruorin.	Lipochromes.	Chlorophyll or allied pigments.	Hæmoglobin.
Polynöe . .	—	present	—	absent
Aphrodite . .	—	—	—	present
Nereis . .	—	present	—	—
Sabella . .	present	—	—	—
Siphonostoma .	present	—	—	—
Serpula . .	present	—	—	—
Cirratulus . .	—	present	—	present
Terebella . .	—	present	—	present
Lumbricus .	—	present	—	present
Hirudo . .	—	—	—	present
Chætopterus .	—	absent	present	—
Arenicola . .	—	present	—	—
Pontobdella .	—	—	present	—
Glycera . .	—		—	present
Phoronis . .	—	—	—	present

Dr. MacMunn has examined the green fluid (containing chlorocruorin) of *Sabella* by means of the microspectroscope. The spectrum (Fig. 30, *a*) consists of a dark band before D, and a feeble one between D and E. The green blood has "a reddish tinge with reflected gaslight, and in most cases is green with transmitted daylight, and reddish with transmitted gaslight. On dilution with water this fluid gave two bands:

the first from λ 618 to λ 593, the second from λ 576 to λ 554.5." On adding ammonium sulphide, the spectrum Fig. 30, *b* is produced. The first of these bands extends from λ 625 to λ 596.5 (?), but this, and also the second band, says MacMunn,

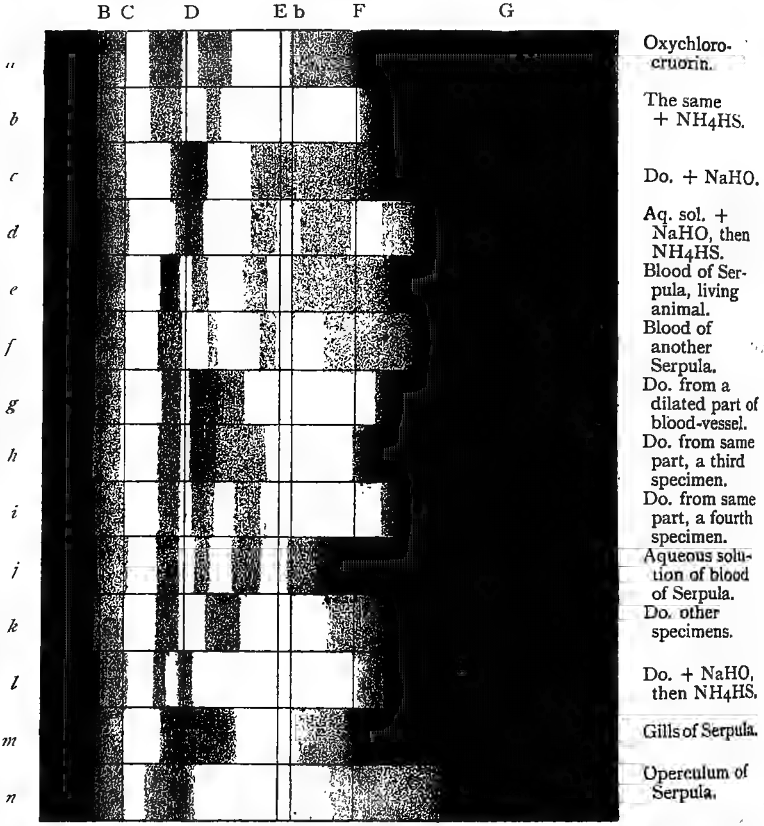

Fig. 30.—Spectra of the Blood of Sabella and Serpula. (*After* C. A. MacMunn.)

"were very faint." After the addition of sodium hydroxide to this solution, a dark band is seen covering D, "which recalls to mind the band of alkaline hæmatin (Fig. 30, *c*), and this band extends from λ 595 to λ 576."

When the blood is treated with alcohol and potassium hydroxide and filtered, a yellow-coloured solution is obtained "free from bands, but on adding ammonium sulphide a band appears covering D" (Fig. 30, *d*). "On treating aqueous solutions with acetic acid the bands faded away, and the colour of the solution changed to a brownish colour (gaslight)."

MacMunn tried the action of alcohol acidulated with sulphuric acid on chlorocruorin, and obtained a greenish solution, which showed a faint shading in the green, too indistinct to map.

"Hence none of the decomposition products of hæmoglobin or hæmatin could be obtained, the pigment, as Prof. Lankester had already shown, being destroyed by the reagents required to produce acid hæmatin and hæmatoporphyrin. The blood of the pseudo-hæmal system of *Serpula contortuplicata* presents some resemblance to that of *Sabella.* There are slight differences in the blood spectra of some specimens, which doubtless are due to the pigment being present in different states of oxidation, and on comparing some of these spectra with those of the histohæmatins and with the decomposition products of hæmoglobin, a striking likeness is apparent."

"On putting a *Serpula* into the compressorium, and bringing gentle pressure to bear on the upper surface of the animal, and examining with the microspectroscope, using a good achromatic substage condenser, a series of spectra are obtained when the various parts of the animal are moved under the objective; what these parts are is seen by looking down the left-hand tube of the microscope. In this way we can differentiate the blood-vessels, intestine, gills, operculum, and other parts, and study the spectrum of each."

With the pseudo-hæmal system of *Serpula*, MacMunn obtained a spectrum represented in Fig. 30, *e*. The band before D is like that of Lankester's chlorocruorin, but the first after D and also the second are different.

An aqueous solution of the blood from the pseudo-hæmal system is yellow by daylight, reddish-yellow by gaslight, and its spectrum is represented in Fig. 30, *e*. The band before D was from λ 620.5 to λ 593, the second about λ 583.5 to λ 572, the third uncertain (about λ 551 to λ 532). After the addition of ammonium sulphide, "the only band seen with certainty was that before D, which seemed slightly nearer the violet." In an alcoholic solution only a faint band was visible from about λ 501 to λ 477.

In a specimen in which the blood appeared a bright carmine-red colour, MacMunn obtained the spectrum represented in Fig. 30, *f*. The second band of this spectrum resembles the first band of hæmochromogen, and is really the same as Fig. 30, *b*.

Fig. 30, *g* represents the spectrum of the blood from a dilated part of the principal blood-vessel of *Serpula*. "The darkness of the second band at once distinguishes the pigment from chlorocrurorin." Fig. 30, *h* and *i* also represent the spectra of the blood from the same part of a third and fourth specimen.

"An aqueous solution of blood obtained from a dozen specimens, whose blood gave the above spectra, was yellow, and showed the three bands represented in Fig. 30, *j*, and these gave the following readings:—First band, λ 618 to λ 593; second, λ 582 to λ 570.5; third, λ 551 to λ 529.5 (?) On treatment with sulphide of ammonium the solution became slightly greener; no bands could then be seen after D, and that before it was very faint. Hence it would appear that the two- and three-banded spectrum denotes the oxidised state.

"In some *Serpulæ*, whose blood was not red but brown, the bands before and after D reminded one of chlorocruorin (Fig. 30, *k*). An aqueous solution of the blood of these specimens had a reddish tint by gaslight, and gave three bands, which read as follows:—First, λ 620.5 to λ 595; second, λ 538.5 to λ 570.5; third, λ 551 to λ 532. On adding sulphide of ammonium, the band before D read λ 620.5 to λ 598, and a second band was visible after D, which could not be measured. On adding to this reduced fluid some caustic soda, at first the only change produced was the disappearance of the faint band after D; but, after standing, the spectrum given in Fig. 30, *l* appeared, of which the bands read: first, λ 623 to λ 607; second, λ 596.5 to λ 579. This shows that the *blood* of these *Serpulæ* did not contain the same kind of chlorocruorin as *Sabella*, but a pigment very closely related to it, probably nearer to hæmatin than it."

MacMunn has also investigated spectroscopically the gills and opercula of *Serpula*. The pigment present is allied to, if not identical with, tetronerythrin. The use of this pigment is not of a respiratory nature. "It is not unlikely that, especially when its likeness to Kühne's chromophanes is taken into consideration, it may be of use in absorbing rays of light concerned in some obscure photochemical process." *

From what has been said, it will be seen that the blood of the *Annelida* contains various pigments; and that hæmoglobin and the lipochromes are uniformly distributed among these animals. Krukenberg† observes: "Chlorophane und rhodophane tragen auch bei Würmern in manchen Fällen viel zu einer lebhaften pigmentirung bei."

(3) The *Insecta*.—Mr. E. B. Poulton, F.R.S., has examined spectroscopically the blood of Lepidopterous larvæ and pupæ. He used Zeiss' microspectroscope in these researches, which was found "to be extremely delicate and convenient on all occasions." As a means of illumination a paraffin lamp was at first used, "and it acted very well for the less refrangible half of the spectrum, but in all later work bright sunlight was alone employed, because of its immense superiority at the violet end."

Concerning Zeiss' and other microspectroscopes used in researches on the chromatology of the Invertebrate blood, a description of these instruments will be given later in the present chapter.

The greatest care is required in obtaining the blood of insects so as to prevent any admixture with food particles of

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* *Quarterly Journal of Microscopical Science*, 1885.

† *Grundzüge einer vergl. Physiol. d. Farbstoffe und der Farben*, 1884, p. 137.

the alimentary canal or any secretions. As the blood in Lepidopterous larvæ exists under considerable pressure, it is readily obtained by making a minute prick in the hypodermis. In larvæ, Mr. Poulton generally pricked the distal parts of the claspers; and then examined a drop of the blood under the microscope to see if any food particles were mixed with it. The blood should be perfectly clear, containing only colourless corpuscles, fat-cells, and minute spherules of fat.

The blood of pupæ was obtained by making a prick in the cuticle of the wings. The blood at once issues, being under considerable pressure. "The whole of the blood was obtained by pushing the abdominal segments inwards, and ultimately by gradually increasing compression of the pupa. Owing to histolytic changes, the weak and thin-walled digestive tract is broken, and a red fluid escapes, which is mixed with the last of the blood. By carefully watching for the first appearance of the red fluid, the blood may be obtained in a perfectly pure state, exactly resembling that of the larva in clearness and in microscopic contents. The blood is received into sections of glass tubes of various lengths, with the ends carefully ground. One end is cemented with Dammar varnish to a glass slide, and when the tube is filled with blood a cover-glass is placed upon the open end, and becomes fixed by the drying of the blood. In most cases the blood so prepared will keep for months without change. If, however, air be admitted, an opaque black clot is formed on the surface, and the rest of the blood becomes cloudy. It will also keep indefinitely in sealed tubes."*

Mr. Poulton has examined the blood of the larvæ of *Phlogophora meticulosa.* These larvæ assume various shades of colour between green and brown. The green blood was taken up by a capillary tube (0.75 mm. internal diameter); and allowed to stand four days, during which time it was reduced to about half its volume (due to evaporation). The tube was then sealed. The spectrum produced by using a

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* *Proc. Roy. Soc.*, vol. 38, p. 283.

paraffin lamp was the following: "a broad band in the red, of which the extreme edges extended from 64.5–68.5, and when this band was best seen the violet end was cut off at 51, and the green was darkened to 52. There was no absorption of the red end. When the blood was fresh and less concentrated, the blue came through on the violet side of the darkening at 51, thus showing a broad dark band between this part and the green. A more concentrated sample of similar blood, prepared in the same way and at the same time, gave a darker band in the red with the same limits, but with more defined edges. The violet end was similarly absorbed. There were indistinct traces of a broad dim band about 59–61.5."

"The fresh blood of another individual of the same species which was dark greenish-brown, due to a combination of subcuticular pigment and green blood, was examined in a capillary tube. The compound character of the larval colouring was proved by gentle pressure. The pale green blood with a thickness of about 1 mm. gave the band in the red from 65–68, the violet end, being completely absorbed at 45, darkened to 51 (when the slit was narrowed so as to render the band distinct). A greater thickness of blood darkened the band, and cut off the violet end at 50, darkening to 52 (when the band was distinct). A still greater thickness produced more marked results with nearly the same limits. On widening the slit, no blue appeared at the absorbed end, The dark band now seemed to extend to 68.5. The whole spectrum was much dimmed, but this was probably due to the accidental presence of fat in the blood. In this case the thickness of fluid was 3.3 mm., and the colour was bright green."

The fresh blood of a dark-brown larva (*P. meticulosa*) produced a spectrum with a faint band in the red. After the blood had been exposed to the air for 2½ hours it became brown, but the spectrum was not altered.

The spectrum of the green fluid contents of the alimentary canal of another brown individual of the same species showed a band in the red from 65.5–68.5, while the blue was cut off at 50, darkened to 52.

Poulton remarks that "this observation upon the green fluid from the digestive tract is important, because it serves to identify the chlorophyll in the blood with that taken in as food. It is likely, however, that a greater thickness of fluid and the use of sunlight would bring out some differences between the derived pigment dissolved in the digestive secretions, and that united with a proteid in the blood. . . . . It seems quite certain that the derived pigments of the blood and tissues are only protective, and play no further part in the physiology of these organisms. Thus there are no marked differences between the physiological processes of the brown and green individuals of the same brood in a dimorphic species, or in the processes of a green larva, which has become brown, or *vice versâ*. It seems that the pigments are entirely harmless, and are often retained when they would have no effect upon colour. Thus, in *Pygæra Bucephalus*, the blood is bright green, although the larva and pupa are entirely opaque, while the eggs are white. It is possible that in this case the conspicuous colours—which warn enemies that the species is distasteful—have been recently acquired, and in consequence of the complete opacity, there would be no advantage in losing the colour of the blood."

In the experiments just mentioned, Poulton used a paraffin lamp as a means of illumination, but he afterwards found that by the aid of sunlight the spectra were further developed.

The concentrated green blood of the larva of *P. meticulosa*, when examined by sunlight, gave the spectrum represented in Fig. 31, sp. 1. "The band in the red, reaching from 64.5–68, was very black, except at the edges. When this band was most distinct and clear, the violet end was absorbed to 51, darkened to 52. On opening the slit a little, the blue came through (though dimmed) at 48, the violet end being absorbed at 43. When the slit was very narrow, traces of

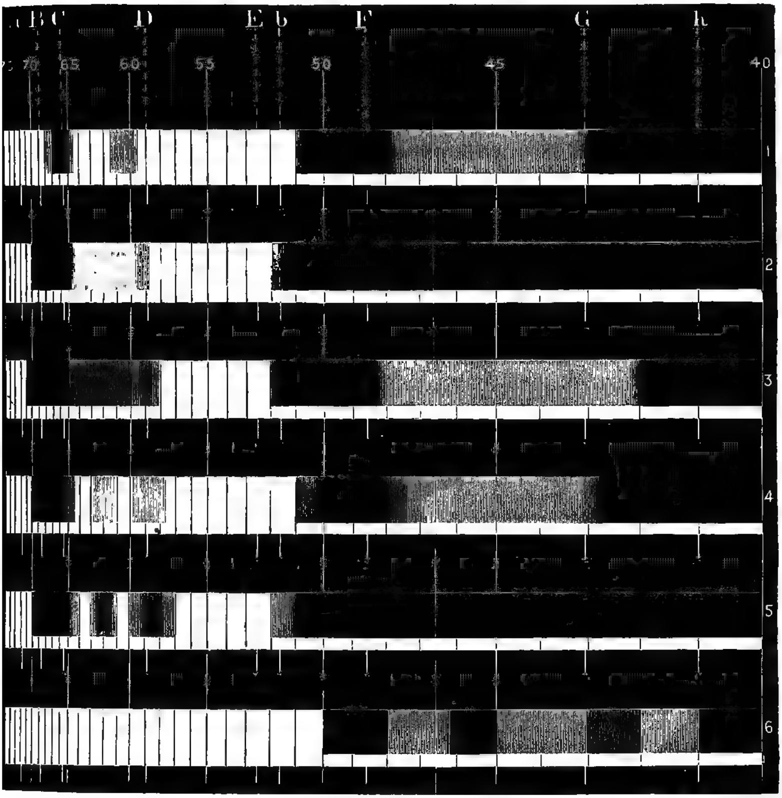

FIG. 31.—SPECTRA OF THE BLOOD OF LEPIDOPTEROUS LARVÆ AND PUPÆ. (*After* E. B. POULTON.)

Spectrum 1.—The blood of the larva of *P. Meticulosa* (green variety) examined in a thickness of about .75 mm. by sunlight. The blood had been allowed to remain in an open capillary tube for about four days, and was then sealed up after it had evaporated to half its bulk.

Spectrum 2.—The fresh and unaltered blood of the pupa of *S. Ligustri*, examined in a thickness of 35 mm. by sunlight.

Spectrum 3.—The fresh and unaltered blood of the pupa of *P. Bucephalus*, examined in a thickness of 23 mm. by sunlight.

Spectrum 4.—Two fresh calceolaria leaves, gently compressed, and examined by sunlight.

Spectrum 5.—Five ditto ditto.

Spectrum 6.—The fresh and unaltered blood of the pupa of *S. Ligustri*, examined in a thickness of 3 mm. by illumination from the bright sky near the sun.

another band, from 59.5–61.5, were faintly seen. . . . . The two chief bands and the absorption of the violet end were also seen in the blood of a living larva by passing the light through one of the claspers."

Poulton has also examined the blood of the pupæ of the *Pygæra Bucephalus*, *Sphinx Ligustri*, *Chærocampa Elpenor*, *Smerinthus Ocellatus*, *Smerinthus Tiliæ*, *Smerinthus Populi*, *Dicranura Vinula*, *Papilio Machaon*, *Ephyra Punctaria*, and the ova of *Ennomos Angularia*, *S. Tiliæ*, *S. Ocellatus*, and *Sphinx Ligustri*. He has also made a comparison between the spectra of the pigments contained in the blood of Lepidopterous larvæ and pupæ, and the spectra of unaltered plant pigments (see Fig. 31).

The spectrum of the green blood of the pupa of *P. Bucephalus* is represented in Fig. 31, sp. 3. "The characteristic band in the red ends sharply at 71, gradually at about 64.5, passing into a lesser absorption of the red, which is continuous with the second band, extending from about 58–60.5, but with very indistinct limits. When these appearances are best seen, the violet end is completely absorbed to 52, darkened to 52.5. On opening the slit a little, the dimmed blue comes though from 48–42. The band in the blue now sharply ends at 52, gradually at 48. Diminishing the thickness of the blood to 8 mm. (the previous thickness being 23.5 mm.) produces nearly the same spectrum, the band in the red being a little narrower, while the band at D cannot be detected. On diminishing the thickness still further to 1 mm., another band appears in the violet. The spectrum is as follows: The characteristic band from 65–70; the chief band of the blue end, 48–51; the second band of the blue end, 45–46.75; the violet being absorbed at 41. The second band of the blue end is much fainter than the first band, and it is not seen in a thickness of 5 mm."

Fig. 31, sp. 2, represents the spectrum of the fresh blood of the pupa of *Sphinx Ligustri*. The characteristic band extends from 70 to 64.5, becoming gradually continuous with a less absorption, extending to D, of which "the part from 59–60 corresponds to the second band of the less refrangible part of the spectrum and the third band of true chlorophyll. The violet end is completely absorbed from 51.5, dimmed to 52, but on widening the slit a little, blue comes through on the violet side of 48, but very dimly." With a thickness of 3 mm. the blood gives no absorption of the red, but shows three bands at the violet end (Fig. 31, sp. 6). The blood of the pupa of *S. Ligustri* is a yellow colour in those individuals which have fed upon privet in the larval state, and greenish-yellow in those which have fed upon lilac. "Comparing the spectra of the blood from pupæ of which the larvæ had fed upon different foods, it was found that the lilac-fed individuals showed greater effect at the red end than the privet-fed individuals, while the converse was true of the violet end. The comparison was made in a thickness of about 8 mm. and by sunlight."

The table on p. 164 gives the spectra of the blood obtained from various Lepidopterous pupæ.

After adding absolute alcohol to the blood of the pupa of *S. Ocellatus*, a bright yellow solution of xanthophyll was obtained, which gave "the characteristic spectrum (shifted to the violet) 49–47, 45.25–44, the violet being absorbed at 42."

Alcoholic extracts of the ova of *E. Angularia*, *S. Tiliæ*, *S. Ocellatus*, and *Sphinx Ligustri* gave each the spectrum of xanthophyll.

Poulton has made a comparison of the above results with those yielded by unaltered plant pigments. In Fig, 31, sp. 4 and 5, are given the spectra of two and five calceolaria* leaves (superposed) respectively. "Comparing these two spectra with those of *green* blood (Fig. 31, sp. 1, 2, and 3), the resemblance is seen to be very great, the chief differences being in the second and third bands of the red end, which are continuous (Fig. 31, sp. 2 and 3), while the third is developed

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* The same results were seen in the leaves of other plants.

Pupæ.	Colour of Blood.	Thickness in mm. of Blood examined.	Spectra with Sunlight.	Remarks.
C. Elpenor . .	Reddish-brown	23	Band from 69·5–65; chief band, 50·5–48; second, 46.25–45; third, 43–42; violet end absorbed at 41.	
D. Vinula . .	Reddish-brown	2.75	No bands visible, but violet end absorbed up to 50.	Light of paraffin-lamp used.
P. Machaon. .	Yellow	3·5	Chief band, 50–48; second, 46.25–45; third, 43–42; violet end absorbed at 41.	Spectrum same from all varieties.
S. Tiliæ . .	Green	5	Band, 64.5–70; violet end absorbed to 50, dimmed to 51; no blue came through on widening.	Light of paraffin-lamp used.
,, . .	,	1	Band, 66–99; violet end absorbed to 49, darkened to 51; blue came through on widening.	
S. Populi . .	Yellowish-green	5	Band, 66–69; violet end cut off at 51, darkened to 52.	
S. Ocellatus .	,,	4	Chief band, 48–50.3; second, 46.75–45; third, 43–42.	

before the second (Fig. 31, sp. 1). Considering the chemical change which must have taken place in the chlorophyll during digestion, rendering possible the passage of the walls of the digestive tract, and considering its chemical union with a proteid constituent of the blood, the resemblances of the spectra are very striking; in fact, the two spectra are far nearer to each other than the ordinary spectrum of chlorophyll in alcoholic solution is to the unaltered chlorophyll of leaves."

Alcoholic solutions of chlorophyll are very unstable, the reason being that the alcohol precipitates the proteid which was orginally united to the colouring matter in the living plant or animal. Consequently, in the alcoholic solution the combination is no longer the same.

Both the chlorophyll and xanthophyll in caterpillars' blood are united chemically with a proteid; hence their great stability. The separation of these pigments from the proteid is at once effected by the addition of alcohol. The former pass into solution, while the latter is precipitated. The solution of the pigments is very fugitive; an alcoholic solution of chlorophyll changing in a few seconds, so rapidly is it acted on by light.

"But while the pigments exist unchanged in the blood of many larvæ for a long time, in other species they are entirely destroyed during the comparatively short period preceding ecdysis, when some green larvæ become brown; and conversely the pigments may appear in the blood equally suddenly. The former change must be due to an active destruction or excretion of the pigments, and is probably also accompanied by changes in the digestive tract, whereby no more pigment is passed through its walls. And so also the proportions of xanthophyll and chlorophyll may be changed during the life of a caterpillar."

From Poulton's interesting investigations it will be observed that Lepidopterous larvæ and pupæ make use of a modified chlorophyll, as well as other plant pigments, derived from their food, because of the protective [*] colour which they acquire from its presence in their blood and tissues.

(4) The *Arachnida.*—Professor Ray Lankester [†] has shown that the blood of *Scorpio* becomes blue on exposure to air. It contains hæmocyanin. The blood of *Epeira*, *Tegenaria*, and *Pholcus* also contains hæmocyanin.

(5) The *Crustacea.*—Concerning the blood of the *Crustacea*, Genth in 1852 first observed the blue colour of the blood of *Limulus cyclops*; and in 1857, Professor Haeckel [‡] observed that the blue blood of *Homarus* became, after many hours' exposure to the air, a violet colour.

In 1873, Rabuteau and Papillon [§] experimented on the blood of crabs, and found that it became blue in contact with air, but lost this property when submitted to the action of carbonic anhydride. It, however, recovered its blue colour on shaking with air. "Jolyet and Regnard [‖] showed in 1877 that on shaking crabs' blood with air it showed a beautiful blue or brownish colour, according to the manner in which it was examined; it gradually loses this colour, becoming reddish and then feebly yellow; but on treatment with pure oxygen its original colour is restored. They found two colouring matters in crabs' blood: one is blue, and is precipitated by alcohol with the albumin of the blood; the other is reddish, and remains in the alcoholic filtrate."

In 1879, Dr. Léon Fredericq [¶] proved that the blue blood of *Homarus* contained hæmocyanin, and that it was blue with reflected and brown with transmitted light. The blue pigment —hæmocyanin—is a proteid containing copper. The red pigment in crabs' blood is also present in the blood of *Homarus*. But this pigment does not belong to the proteid constituents of the blood; it does not contain copper, iron, or manganese,

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[*] From enemies.

[†] *Quarterly Journal of Microscopical Science*, 1878, p. 453.

[‡] *Müller's Archiv*, 1857, p. 511, Anm. i.

[§] *Comptes-Rendus*, t. 77, p. 137.

[‖] *Archives de Physiologie*, 2 série, t. 47.

[¶] *Bulletins de l'Académie Royale de Belgique*, 2 série, t. 47.

and it has nothing to do with the change in the colour of the blood.

It may be remarked in passing that Dr. W. D. Halliburton, F.R.S.,* has shown that the blood plasma of *Homarus* contains a red pigment, which is soluble in alcohol, ether, and chloroform; but it is possible that this pigment belongs to the histohæmatins which Dr. MacMunn has found to be pretty generally distributed in the tissues and organs of the *Invertebrata*.

The blood of *Homarus*, *Cancer*, *Carcinus*, and *Astacus* does not show any absorption bands when examined by the microspectroscope. The blood in all these animals contains hæmocyanin.

The blood of *Apus*, one of the *Phyllopoda*, is of a red colour, and, according to Lankester, this colour is due to hæmoglobin. Another Crustacean which has red or violet blood is *Gammarus*.

(6) The *Polyzoa*.—Several of the *Polyzoa* contain lipochromes; and in *Flustra foliacea* MacMunn † has shown there exists a chlorophylloid pigment which is soluble in alcohol. The spectrum of this pigment somewhat resembles that of modified chlorophyll. The alcoholic solution is a yellow colour, and has a red fluorescence. Its chief dark band reads from λ 681·5 to λ 656, its darker part from λ 678 to λ 662. "It showed another before D; the third chlorophyll band was missing, and there was one lipochrome band."

(7) The *Mollusca*.—The blood of many Molluscs contains the pigment hæmocyanin.

In 1816, Erman simply recorded the fact that the blood of *Helix* was of a blue colour. Harless and Von Bibra ‡ (in 1847) stated that the blood of *Helix pomatia* acquired a blue colour on exposure to air, but this colour was discharged by shaking the blood with carbonic anhydride. They also

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* *British Medical Journal*, 1885.

† *Proc. Physiol. Soc.*, 1887; and *Quart. Journ. Micro. Science*, vol. 30, p. 79.

‡ *Müller's Archiv*, 1847, p. 148.

observed "that ammonia removed the blue colour, which came back on neutralising with hydrochloric acid. They stated that this blood contains copper, but no iron; but Gorup-Besanez* found iron also in its ash."

In 1858, Dr. Witting recorded in his paper, "Ueber das Blut einiger Crustaceen und Mollusken,"† that the blood of *Unio pictorum* had a slight blue tinge. Similar observations were made by Rouget‡ in 1859 on the blood of *Octopus vulgaris.*

In 1867, the late Dr. Paul Bert§ described the blood of *Sepia* as "feebly bluish, especially in the veins of the gills, and that it acquired a bright blue colour on exposure to air. This colour belongs to the plasma, and is not lost by boiling."

Rabuteau and Papillon‖ in 1873 examined the blood of *Octopus*, which became blue on exposure to air. They also examined spectroscopically the blood of this animal, and arrived at the conclusion that it gives no bands. But the most remarkable paper on the blood of *Octopus vulgaris* is that of Dr. Fredericq,¶ published in 1878. He proved that the blood contained hæmocyanin, and that the substance was a proteid combined with copper. There is no doubt that the blueing of the Molluscan as well as Crustacean blood is due to the oxidation of hæmocyanin, and that hæmocyanin is the carrier of oxygen within the system.

The blood of *Helix* and *Arion* was also shown by Fredericq to contain hæmocyanin, and to give no absorption bands.

Among the *Mollusca*, the late Dr. Krukenberg** examined the blood of *Eledone moschata*, *Sepia officinalis*, *Limnæus*

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* *Lehrbuch der Physiologischen Chemie*, p. 369.

† *Journal für Practische Chemie*, Bd. 73, s. 121–132.

‡ *Journal de la Physiologie*, t. 2, p. 660.

§ *Comptes-Rendus*, t. 65, p. 300.

‖ *Comptes-Rendus*, t. 77, p. 137.

¶ *Bulletins de l'Académie Royale de Belgique*, 2 série, t. 46.

** *Vergleichend-physiologische Studien*, 1st Reihe, 3 Abth., 1880, s. 72.

stagnalis, *Helix pomatia*, and *Helix aspersa*; and in all these he observed that the blood became blue by shaking with air and oxygen, and that the blue colour disappeared in the presence of carbonic anhydride. Krukenberg states that in the blood of the three last-named Molluscs there exists a body *very nearly related to*, but different from, hæmocyanin; but there is no doubt that hæmocyanin exists in the blood of these animals.

Krukenberg could find no hæmocyanin in the blood of *Tethys fimbria*, *Doris tuberculata*, *Aplysia depilans*, and *Pleurobranchus*.

Many years ago the blood of *Anodonta cygnea* was examined by Schmidt,* who described it as colourless; but the blood of this Lamellibranch contains, without doubt, hæmocyanin.

Among the *Mollusca*, MacMunn† has examined the blood of *Helix pomatia*, *Helix aspersa*, *Paludina vivipera*, and *Limnæus stagnalis*. The blood of these animals gave no absorption bands when examined by the microspectroscope.

"The blood of *Helix aspersa* was found to be a bluish-white colour by daylight, but by gaslight it had a purplish tinge; after twenty-four hours' standing that had disappeared, and it was then very slighly brownish. Examined in a deep layer, no bands could be seen; on treatment with ammonia, the blue colour persisted, and no bands came into view. With acetic acid the blue colour persisted, and no bands appeared. After repeated filtering the blue colour remained; hence it can hardly have been due to particles in suspension. On treatment with reducing agents the blue colour was lost, and no bands appeared."

The blood of *Helix pomatia* "assumed a distinct blue tinge on exposure to air, and gave no absorption bands, but absorbed a little of the violet end of the spectrum. On treatment with ammonia its colour was not so well marked,

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* Lehmann's *Handbuch der Physiologischen Chemie.*

† *Quarterly Journal of Microscopical Science*, 1885.

and it had a faintly reddish tinge, but no bands could be seen, nor after treatment with acetic acid, which did not remove the colour. On treatment with ammonium sulphide the blue colour disappeared, and could not be again brought back by shaking with air for some time; the fluid had assumed a bronze colour, and with gaslight a faint violet tint, but no bands were seen."

The blood of *Limnæus stagnalis* assumed a whitish-blue colour on exposure to air, "gave no bands, nor after treatment with ammonia, acetic acid, or ammonium sulphide; the last discharged the colour completely, which could not be restored on shaking with air."

The blood of *Paludina vivipara* "is frequently exuded when the animal is pricked with a needle or otherwise irritated, and is of a blue colour. It is quite free from bands. Ammonia slightly diminishes the colour, but does not remove it; acetic acid does not remove it. With neither reagent nor ammonium sulphide could any distinct bands be obtained."

The blood of the majority of the *Mollusca* contains hæmocyanin, that of a few contains hæmoglobin (*e.g.*, *Planorbis*), while that of others, according to Krukenberg, is devoid of either of these substances.

Microspectroscopes.

As the examination of the colouring matters of the blood necessitates the use of a microspectroscope, we now proceed to describe two forms of this important instrument of research.

The one used by Mr. E. B. Poulton, F.R.S., in his investigations on the blood of the *Lepidoptera* is illustrated in Fig. 32. This instrument has the slit mechanism between the lenses. The upper achromatic lens is adjustable to the slit; an Amici prism is placed over the eyepiece, and the whole connected with the body by a clamping screw. The mechanism worked by the screw F is for contracting and expanding the slit by the symmetrical movement of both edges. This opens so widely as to permit a view of the whole visual field. The slit is shortened by the screw H, so that when the comparison prism is inserted the aperture is contracted to such an extent that the image of the object under investigation completely fills it. There is a comparison prism, with lateral frame and clips to hold the compared object and the mirror; all these parts are fixed in a drum combined with the eyepiece. Above the eyepiece there is an Amici prism of great dispersion, which turns aside on a pivot, leaving the eyepiece unobstructed for adjustment to an object K; the axial position of the prism is indicated by the spring L, which keeps it in place. A scale is projected on the spectrum by means of a small scale-tube and mirror attached to the mount of the prism. The divisions of the scale give the wave-lengths of that section of the spectrum on which they fall in fractions of a micromillimetre, whereby the second decimal place may be read off directly, and the

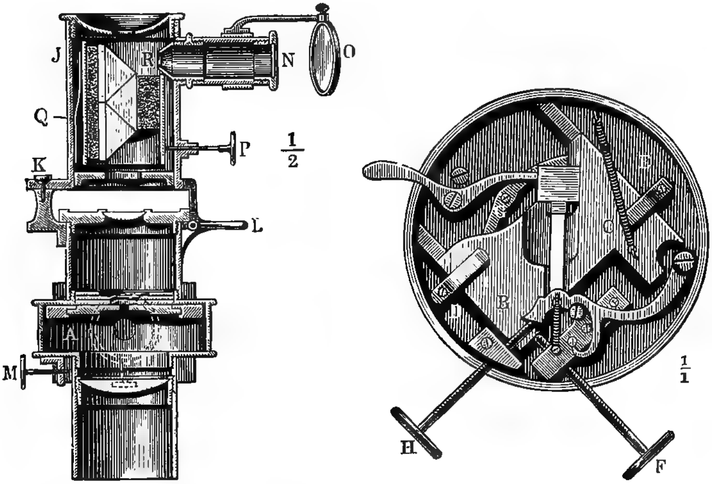

FIG. 32.—THE ABBE-ZEISS MICROSPECTROSCOPE.

1 = Microspectroscope (half actual size). 2 = Drum with mechanism of the slit (actual size).

third calculated by estimation. The position of the scale relative to the spectrum is adjusted by a screw P on the jacket of the Amici prism.

Fig. 33 represents Dr. Engelmann's microspectrometer, which is constructed on the principle of Vierordt's spectrophotometer for quantitative microspectrum analysis. In place of the eyepiece, the box A is attached to the body of the microscope by the tube R; it contains two independent, conaxial, movable slits in juxtaposition, which are symmetrically opened and closed by opposed reverse-threaded screws. The width of each slit is read off on the drums T and T′ accurately to 0·01 mm., and by estimation to 0·001 mm. One slit is occupied by the image of the object under investigation, and the other by light from the source

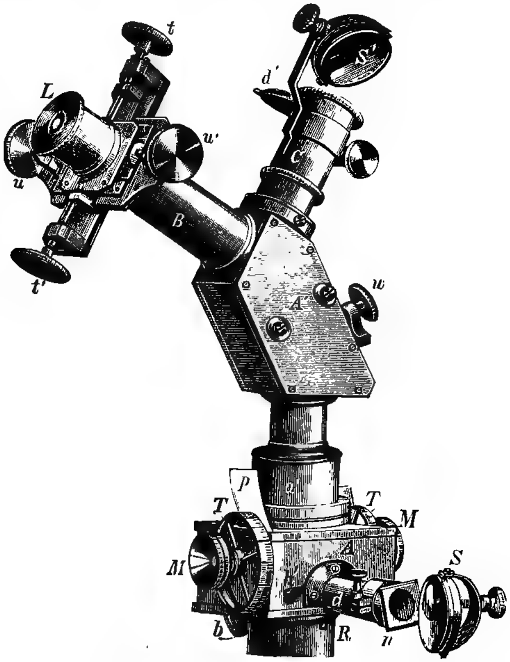

FIG. 33.—THE ENGELMANN MICROSPECTROMETER.

of comparison, which is brought to it by a superimposed reflecting prism and lateral tube *d* with collimator lens, diaphragm carrier *n*, and mirror S, or incandescent lamp.

In the upper opening of the box A is placed either an eyepiece in a sliding jacket, which is accurately adjusted to the slit; or, instead of this (after proper adjustment of the image of the specimen in the objective slit) the spectroscopic apparatus *a*′A′B C, which is fixed in the proper azimuth by an arresting mechanism. This apparatus consists of the box A′ which on one side (the upper end of *a*′) contains a collimator lens *l*, to render parallel the cone of rays proceeding from the objective before they fall on a Rutherford prism P of great dispersion. By the lens *l*′ on the other side (at the

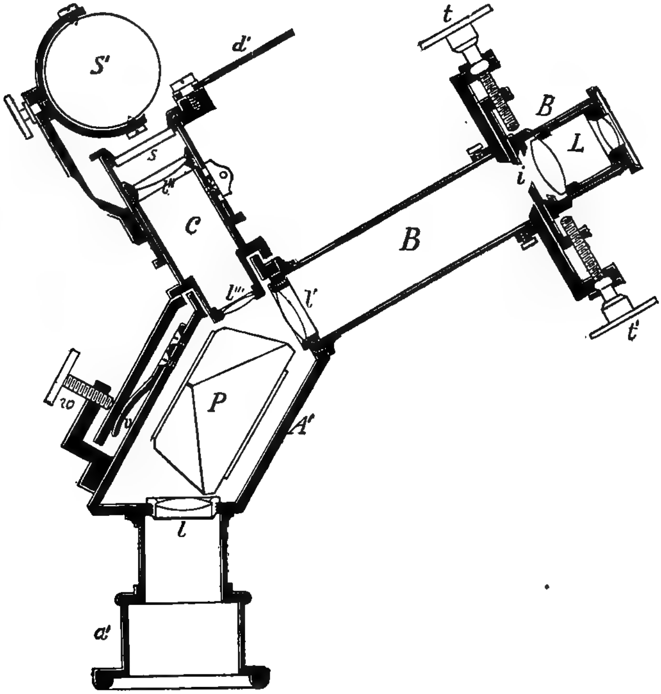

FIG. 33.—THE ENGELMANN MICROSPECTROMETER.

lower end of B) the parallel rays proceeding from the prism are again brought to a focus, and this real spectrum is observed by an eyepiece L. By two slit mechanisms at right angles to each other, actuated by the screws *tt'*, *uu'* in the focal plane of the eyepiece, the visual field can be limited at pleasure according to the procedure of Vierordt.

By means of two lenses shown at C an image of a wave-length scale is projected on the spectrum by reflection from the end-surface of the Amici prism, which is illuminated by the mirror S' and put out of action by closing the shutter *d'*. Adjustment of this scale is made by inclining the whole scale-tube C with the screw *w*, which is opposed by a counter-spring *v* (Fig. 33).

Both of these instruments are of the utmost importance for investigating the chromatology of the *Invertebrata.*

Although Dr. MacMunn* uses the microspectroscope, he says that, "when the amount of material is sufficient for the purpose, it is best to measure the position of bands by the *chemical spectroscope* and reduce the readings to wave-lengths by means of a curve plotted out on logarithm paper, as directed in Watts' *Index of Spectra.* Similarly, the readings of others can be reduced to wave-lengths by laying a scale—say of millimetres—along the top of their maps, and noting the readings of the Fraunhofer lines, and then, by means of an index of spectra (such as Watts'), finding the wave-length of these lines, and laying them down in accordance with these data on the logarithm paper. One can also detect an error in the map of any observer by this method. 'So delicate is this graphical method of detecting error, that by its means we might very readily detect error in tables of logarithms or trigonometrical functions.' In using the diffraction grating it is nearly a straight line, and Sir George Stokes, F.R.S., says that by using the reciprocals of the wave-lengths instead of the numbers themselves, one has a straight line instead of a curve."

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* *Proceedings of Birmingham Philosophical Society,* vol. 5, p. 180.

Dr. MacMunn uses in his researches three spectroscopes—(1) a microspectroscope, (2) a Hilgers's "Student's Kensington Spectroscope," and (3) a large spectroscope with one dense flint-glass prism, which is replaceable by a reflection diffraction grating. He has curves adapted to each, so that he can easily correct any error of observation by comparison. "The wave-length record of bands has raised the chromatology of plants and animals from a state of chaos to one which is daily assuming shape and symmetry, and we are now beginning to perceive relationships and the shadows of generalisations which when made will undoubtedly be of great help to biology."

From the above remarks it will be seen that the spectroscope is an instrument of the greatest value not only to the chemist and physicist, but also to the biologist and physiologist. "Until the spectroscope was applied to physiology no one knew what the true colouring matter of the blood was, and the chaotic state of medical knowledge with regard to the cause of the colour of the various animal secretions (of which survivals are still found in many text-books) is sufficiently proved by a perusal of the older text-books, in which one finds the pretended knowledge of the authors cloaked under the adoption of meaningless names, which may have, at the time they were written, brought conviction home to those incapable of judging for themselves, but which show us now what physiological chemistry alone could do, unaided by spectroscopic analysis, in detecting animal pigments and enabling us to follow their metabolism" (MacMunn).

THE GASES OF THE BLOOD.

Very little is known concerning the composition and nature of the gases in the blood of the *Invertebrata.*

The author* has ascertained the approximate composition

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* A paper read before the Royal Society of Edinburgh on June 1, 1891; and also in *Revue Générale des Sciences pures et appliquées*, 1891, p. 395.

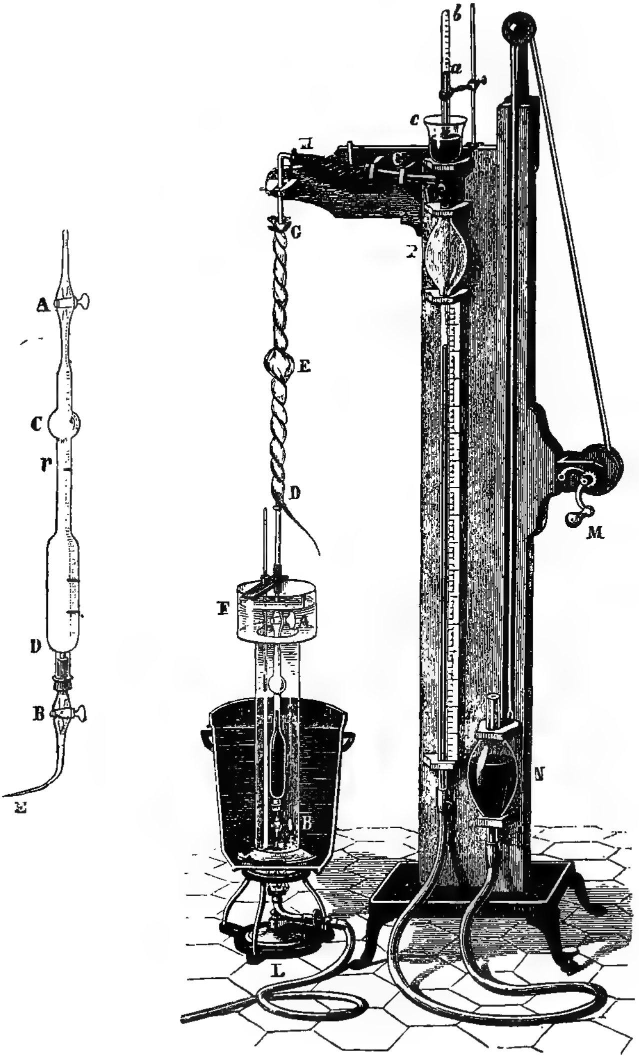

FIG. 34.—APPARATUS FOR EXTRACTING THE GASES OF THE BLOOD.

of the gases in the blood of certain Invertebrate animals. The apparatus used for this purpose was that of Gautier slightly modified (Fig. 34); and the method allows the collection of the blood *in vacuo* (from the time of leaving the vein, &c.) without any alteration in its composition. The glass receiver ACD (left-hand figure), in which the vacuum is made, has a canula E fastened to its lower end. The canula is drawn out into a fine capillary point, which is pushed into the artery, vein, or under the hypodermis, as the case may be. After introducing the canula into the blood system, the tap B is opened, and the blood rises into the receiver. The gases are evolved almost immediately, and by means of the pump they are collected over mercury in the tube *ab*, where their composition is ascertained.

After the introduction of the blood into the receiver the tap B is turned off; the receiver is then attached to the pump. Before opening the tap A, the receiver is placed in a bath of water heated to about 40° C. The heat assists in the liberation of the gases from the blood. Coagulation is prevented by previously introducing a small quantity of sodium chloride into the receiver (*i.e.*, before the introduction of the blood).*

The pump and pneumatic trough do not require description, as they are of the usual kind. The volume of the mixed gases collected at *ab* having been ascertained, the percentage of each gas is estimated by the ordinary methods of gas analysis. The carbonic anhydride is absorbed by potash, the oxygen by pyrogallic acid, whilst the amount of nitrogen is represented by what remains.

(*a*) *Blood of Sepia officinalis.*

A hundred volumes of the blood of the cuttlefish contained the following volumes of the three gases—the volumes being reduced to 0° C. and 760 mm.:—

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* The liberation of carbonic anhydride is accelerated by previously introducing into the receiver a small quantity of a hot solution of tartaric acid.

	I.	II.	III.	IV.	V.	VI.
Oxygen	13.26	12.91	13.14	14.62	14.21	14.34
Carbonic anhydride . .	30.12	31.21	32.10	30.14	29.12	29.89
Nitrogen	1.60	2.00	1.51	1.41	1.73	1.23

The nitrogen is simply dissolved in the blood, but the oxygen and carbonic anhydride are partly dissolved and partly in a state of loose chemical combination with certain constituents of the blood. The oxygen, with the hæmocyanin, and possibly the greater part of the carbonic anhydride, is united to certain salts contained in the blood.

(*b*) *Blood of Cancer pagurus.*

The blood was obtained from very large individuals by opening the carapace, and passing the capillary point of the canula directly into the heart.

A hundred volumes of the blood yielded the following volumes of oxygen, carbonic anhydride, and nitrogen after being reduced to 0° C. and 760 mm.:—

	I.	II.	III.	IV.
Oxygen	14.79	14.88	14.96	14.85
Carbonic anhydride . . .	28.62	27.21	27.14	28.39
Nitrogen	1.01	1.20	1.22	1.30

(*c*) *Blood of Palinurus vulgaris.*

A hundred volumes of the blood of this animal gave the following results:—

	I.	II.	III.	IV.
Oxygen	14.62	14.71	14.29	14.76
Carbonic anhydride	30.00	29.62	28.92	29.79
Nitrogen	1.82	1.60	1.20	1.34

(*d*) *Blood of Homarus vulgaris.*

A hundred volumes of the blood obtained from several large lobsters yielded the following results:—

	I.	II.	III.
Oxygen	14.99	14.81	14.85
Carbonic anhydride	31.11	28.84	29.26
Nitrogen	1.76	1.82	1.85

(*e*) *Blood of Octopus vulgaris.*

A hundred volumes of the blood yielded the following results:—

	I.	II.	III.
Oxygen	13.33	13.28	13.65
Carbonic anhydride	30.23	31.29	31.22
Nitrogen	1.45	1.30	1.29

(*f*) *Blood of Acherontia atropos.*

A hundred volumes of the blood of the larvæ of this moth yielded the following results:—

	I.	II.
Oxygen	16.21	16.79
Carbonic anhydride . . .	32.92	34.24
Nitrogen	1.09	1.98

It may be stated that the oxygen and carbonic anhydride in the blood of the *Invertebrata* do not behave according to the law of Dalton (the law of partial pressures) in regard to the absorption of a mixture of gases by a simple fluid. A portion of each gas combines chemically with some constituent or constituents of the blood. It was Magnus* who first demonstrated that the oxygen and carbonic anhydride of the Vertebrate blood did not obey the law of Dalton; and the same is true concerning the gases of the blood of the *Invertebrata*.

Surveying the *Invertebrata* as a whole, we find animals like the *Protozoa* devoid of blood; next, animals, as some *Trematoda* and *Cestoidea*, with blood devoid of corpuscles or solid particles; then such creatures as the *Echinodermata*, where the blood is corpusculated. In some of these forms, the corpuscles merely consist of solid particles of protoplasm, devoid of cell walls and nuclei; while in others the blood contains walled and nucleated corpuscles. In the *Myriapoda* the blood contains three distinct corpuscles, and during a portion of its course is contained in blood-vessels. In the *Crustacea* the corpuscles are walled and nucleated, but are colourless, or nearly so; while in the *Gephyrea* the corpuscles have a limiting membrane, nucleus, and coloured contents.

As a rule, the colouring matter of the Invertebrate blood belongs to the plasma, and not to the corpuscles; but there are exceptions to this rule, which have already been alluded

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* *Poggendorff's Annalen*, vol. 40, p. 583.

to in this chapter. Concerning the colouring matter itself, it offers a greater diversity of individual pigments than the blood of the *Vertebrata.* In some forms we find chlorophyll and allied pigments; while others contain one or more of the following pigments:—Echinochrome, chlorocruorin, hæmocyanin, hæmoglobin, and the lipochromes.

"To contrast the various conditions of the blood corpuscles of the *Invertebrata* with the stages in the development of our own red corpuscles is not without interest. There is a time in the history of the highest mammal when there is no blood developed; there is a time when only fluid blood, destitute of corpuscles, is to be seen; possibly our blood corpuscles commence as minute fragments or protoplasm derived from the digested food. These minute granules may coalesce in the absorbent vessels and form free nuclei; the nuclei may become surrounded by granules, a wall be developed on the exterior of these, and a white corpuscle (leucocyte) would result." The colourless corpuscle, in its turn, is transformed into a red corpuscle; but the history of this transformation belongs to the physiology of the *Vertebrata* rather than to that of the *Invertebrata.*

CHAPTER VII.

CIRCULATION IN THE INVERTEBRATA.

THE circulation of the blood in the higher animals was discovered by Harvey in 1619.

In order to nourish all the parts of the body, it is necessary that the blood should be conveyed to these parts; but the mode in which it is conveyed differs considerably in the lower animals. Among the Invertebrates we find that the mode of circulation becomes more and more specialised as they rise in the zoological scale. From the *Protozoa* to the *Cœlenterata*, the circulatory and digestive systems are still fused together, for they are not differentiated. In the *Echinodermata* and *Annelida* we find the first true blood or vascular system. In most worms one of the blood-vessels forms a pulsating tube, or so-called heart, by which the blood is driven towards the periphery of the body through certain vessels, returning by others. In the *Mollusca* there is a contractile vessel, which has a much closer resemblance to the Vertebrate heart than the above. This heart consists of two or three chambers;—(*a*) One or two auricles, which serve for the reception of the blood, brought to them by the veins; (*b*) the ventricle which serves for the propulsion of the blood into the arteries. ~~It will be noticed from the above remarks that the circulatory system, like all others, was not perfected at once. Nature made numberless attempts, adding successively new pieces to the system, or complicating little by little those which existed already.~~ In other words, the circulatory system became more and more differentiated under the influence of natural selection and the struggle for existence.

As already stated, in the lowest Invertebrates the digestive and circulatory systems are not differentiated, but among the higher Invertebrates these two systems become distinct. The circulatory system only shapes itself after the digestive system; consequently one may look upon the former as an appendage to the latter.

In the higher animals the blood is made to pass through the respiratory organs in order to expose it to the oxidizing action of the air. In certain of the lower animals the air penetrates into the body; but in all the higher animals, and in many of the lower, there exists a complex apparatus for the circulation of the blood: (1) A system of blood-vessels to convey the blood into the various parts of the body. (2) A~~n~~ ~~organ (called the~~ heart) destined to put this fluid in motion. Most animals, from man to the *Annelida*, have a heart.

THE PROTOZOA.

In these creatures there is no true blood, yet there is a curious foreshadowing of a circulation. In the *Rhizopoda** the only structures which may be said to have a circulatory function are the contractile vacuoles. The spaces are filled with a clear fluid, and exhibit fairly regular and rhythmic expansion and contraction (diastole and systole). During the systoles radiating canals or vessels extend from these vacuoles; these widen as the vacuole lessens in diameter. Presently the vacuole begins to expand, whilst the radiating canals become narrower in diameter and ultimately disappear. The contractile vacuole performs more than one function, and among these is probably that of circulation. There is a pulsating central "organ" with conducting canals proceeding therefrom. Does not this look very much like a primitive circulatory system?

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* The *Rhizopoda* includes the *Protoplasta*, *Foraminifera*, and the *Radiolaria*.

"In the *Infusoria*, contractile vacuoles are present, and there is also a curious movement of the outer layer of the sarcode in company with the food vacuoles. It will be remembered that these food vacuoles pass, after quitting the abrupt termination of the œsophagus, through the sarcode along a very definite line. They trace the outline of the infusorial body as they pass along just within the contractile layer of the animal. With them the outer layer of the sarcode is said to move."

THE PORIFERA.

In the *Porifera* or *Spongida*, there is no true blood, but there is a circulation of water carrying food particles and air for respiration. This circulation is brought about by the action of cilia, which cause the currents of water to enter the inhalent pores, and after traversing the internal canals, finally take their exit through the exhalent pores. These currents of water containing nutritive matter act as carriers of tissue-forming materials as well as of waste products, consequently we may regard them as representing the circulatory system among these Invertebrates. Although the water currents in the *Porifera* have a circulatory function, they also perform the functions of respiration and digestion.

THE CŒLENTERATA.

In these animals the blood or nutritive fluid is not contained in any vessels, but is free in the somatic cavity or enterocœle. This fluid is moved by "the contractions of the body, and, generally, by cilia developed on the endodermal lining of the enterocœle." By this means a kind of circulation is constantly maintained. The movements of the body of the animals belonging to the *Cœlenterata* cause a movement of the corpusculated blood in the body cavities, a flux and reflux, a flowing and an ebbing of the nutritive fluid. Here is the most general form of circulation. There are no vessels and no special pumping apparatus, for the whole body is concerned in the performance of this function. "In the compound *Cœlenterata*, this motion of the corpusculated fluid of the body cavity affects also the fluid in those extensions of the body cavities, through the common flesh or cœnosarc, that place in communication the interiors of the various members of the compound animal."

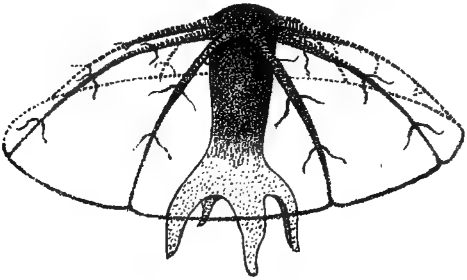

FIG. 35.—CIRCULATION IN MEDUSÆ.

Fig. 35 represents the circulatory system in the *Medusæ*.

THE ECHINODERMATA.

All the *Echinodermata* are furnished with distinct organs of circulation, consisting of a "heart or corresponding organ, and a complicated system of vessels. This circulatory system consists of two vascular rings surrounding the orifice of the digestive tube. These rings are connected with each other, they emit radiating ramifications, and one of them receives vessels proceeding from the intestine." Such is a general description of the circulatory apparatus in the *Echinodermata*, but since the time of Cuvier and Tiedemann "the presence or absence of a blood-vascular system in the *Asteridea* has been alternately asserted and denied." The investigations of Greef,* Hoffmann,† and Teuscher‡ are in favour of "the

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* *Marburg Sitzungsberichte*, 1871–2.

† *Niederländisches Archiv*, vol. 2.

‡ *Jenaische Zeitschrift*, vol. 10.

existence of the anal ring, and of an extensively ramified system of canals, connected with it and with the neural canals." But according to Prof. Huxley, "the facts, as they are now known, do not appear to justify the assumption that these canals constitute a distinct system of blood-vessels." Prof. Huxley doubts the special circulatory function of the neural canals, and he does not consider that the sinus which accompanies the madreporic canal is in reality a heart. He states that this sinus and canals "are mere sub-divisions of the interval between the parietes of the body and those of the alimentary canal, arising from the disposition of the ambulacral vessels and that of the walls of the peritoneal cavity; both of which, as their development shows, are the result of the metamorphosis of saccular diverticula of the alimentary canal, which have encroached upon, and largely diminished, the primitive perivisceral cavity which exists in the embryo. The peritoneal cavity of the body and rays is filled with a watery corpusculated fluid (blood); a similar fluid is found in the ambulacral vessels, and probably fills all the canals."

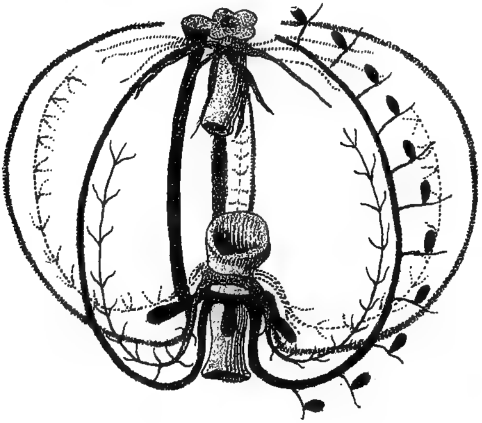

FIG. 36.—CIRCULATION IN ECHINODERMATA (Sea-urchin).

Fig. 36 represents the circulatory system in *Echinus*.

THE TRICHOSCOLICES.

"In the *Turbellaria*, *Trematoda*, and *Cestoidea*, the lacunæ of the mesoderm and the interstitial fluid of its tissues are the only representatives of a blood-vascular system. It is probable that these communicate directly with the terminal ramifications of the water-vascular (respiratory) system. In the *Rotifera*, a spacious perivisceral cavity separates the mesoderm into two layers, the splanchnopleure, which forms the enderon of the alimentary canal, and the somatopleure, which constitutes the enderon of the integument. The terminations of the water vessels open into this cavity."*

THE ANNELIDA.

In the *Annelida* there is a perivisceral cavity (perienteric space) communicating with the segmental or excretory organs. This cavity contains a colourless fluid consisting of a coagulable albuminous plasma and numerous colourless corpuscles. The perivisceral fluid is not only nutritive, but acts as a liquid fulcrum to the muscular movements of the body. If this fluid is let out the power of voluntary motion is lost. It has been stated that "the vermicular motions of the intestine are aided or determined by its resistance and support; it favours circulation by obviating the pressure upon the blood-vessels, which follow the contact of the intestine with the integument, and is, perhaps, the source, or one of the sources, of the blood itself." This fluid contains albumin, fibrin, and certain salts. In addition to the perivisceral cavity and its fluid, there is in most of the *Annelida* a system of vessels with *contractile* walls. These vessels, known as the pseudo-hæmal system, are filled with a fluid, which may be red or green, and corpusculated or non-corpusculated. In some Annelids the pseudo-hæmal system communicates with the perivisceral cavity; but in the majority of these animals it is shut off from it.

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* Huxley's *Anatomy of Invertebrata*, p. 57.

Professor Huxley considers that the perivisceral fluid represents ordinary blood as far as being a carrier of *nutriment* to the tissues; and that the pseudo-hæmal fluid is probably only engaged in the function of respiration; hence the reason that he calls it "respiratory blood."

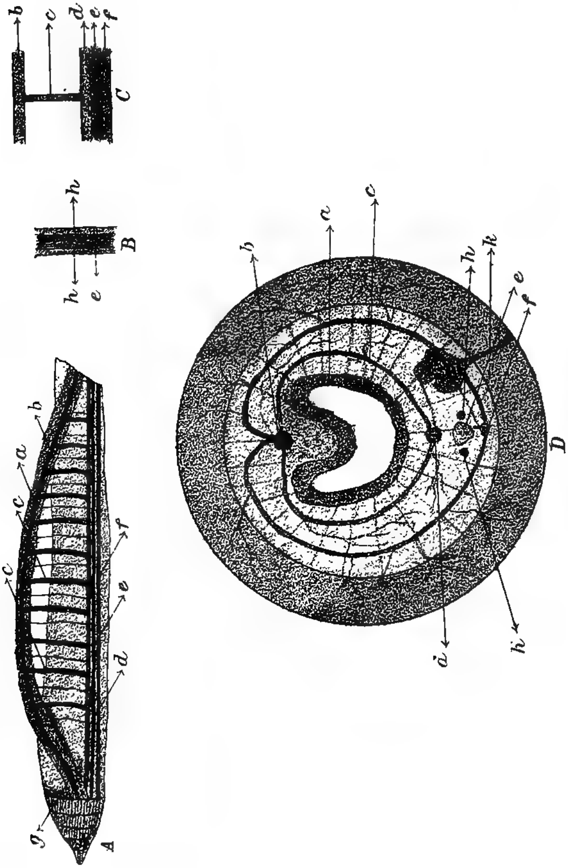

FIG. 37.—THE CIRCULATORY SYSTEM OF LUMBRICUS.

A = Dissection from dorsal side, with the alimentary canal turned on one side.
B = Looking down on nerve with supra-neural vessel removed. D = Transverse section.
a = alimentary canal. b = dorsal vessel. c = transverse vessels. d = supra-neural vessel. e = nerve. f = sub-neural vessel. g = hearts. h = lateral neural vessels. k = segmental organ.

After these general remarks we proceed to detail at length the pseudo-hæmal systems of *Lumbricus* and *Hirudo*.

(*a*) In *Lumbricus*, there are three principal vessels which traverse the body in a longitudinal direction (Fig. 37, A, B, C, D).

The dorsal or supra-intestinal vessel is situated on the dorsal side of the alimentary canal. The supra-neural or sub-intestinal vessel is situated along the ventral side of the alimentary canal; and the sub-neural vessel lies directly beneath the great ventral ganglionic nerve cord. Besides the three principal vessels, there are two lateral neural vessels situated on either side of the nerve (Fig. 37, B). The dorsal vessel (which is contractile, and consequently drives the blood from behind forward) is connected with the supra-neural vessel in nearly every segment by pairs of transverse vessels—*i.e.*, one vessel on each side of the body connects the dorsal to the ventral trunk.

In the anterior portion of the body the longitudinal vessels break up into a blood plexus, consequently in this region (*i.e.*, first seven segments) there are no distinct transverse vessels. Between the seventh and tenth segments, the dorsal vessel becomes dilated into what is known as the "hearts" of *Lumbricus*. These "hearts" contract so as to force the blood from the dorsal to the ventral side of the body. The dorsal vessel also sends out branches to the body wall, mesenteries, and to the walls of the alimentary canal. The supra-neural vessel sends out branches to the nervous system, and also transverse vessels which unite with the sub-neural trunk (Fig. 37, D). Certain transverse vessels also unite the dorsal to the sub-neural vessel; these vessels supply the segmental organs and integument with blood.

(*b*) The body or perivisceral cavity in *Hirudo* is only imperfectly differentiated from the vascular system. It is filled with loose connective tissue in which are dorsal, ventral, and lateral spaces (sinuses) containing blood.

The vascular system (Fig. 38) consists of a ventral blood-vessel or sinus, and two wide lateral vessels which run along the sides of the body. There is also a median dorsal vessel. All these vessels anastomose with each other, and send off branches which also anastomose and give rise to a fine network of blood-vessels situated on the organs of generation, nephridia, and in the muscular mesodermic layer. The red blood contained in these vessels has already been described.

In the *Polychæta* the perivisceral cavity is continued into all the important appendages of the body, consequently they are filled with blood. "The circulation of this fluid is effected partly by the contraction of the body and its appendages, partly by the vibratile cilia, with which a greater or less extent of the walls of the perivisceral cavity is covered. In a great number of *Polychæta* no part of the body is specially adapted to perform the function of respiration, the aëration of the blood probably taking place wherever the integument is sufficiently thin; and, even when distinct branchiæ ordinarily exist, members of the same family may be deprived of them."

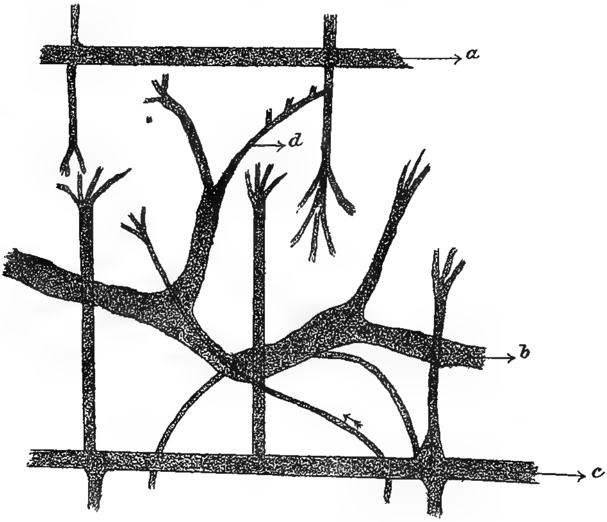

FIG. 38.—DIAGRAM OF THE PSEUDO-HÆMAL VESSELS OF HIRUDO. (*After* GRATIOLET.)

a = dorsal vessel and branches. *b* = lateral vessel and branches.
c = ventral vessel and branches. *d* = branches.

In many of the *Polychæta*, the pseudo-hæmal system is entirely absent (*e.g.*, *Polynoë squamata*), while in others it varies greatly in the arrangement of the principal vessels; "but they commonly consist of one or two principal longitudinal dorsal and ventral vessels, which are connected in each somite by transverse branches. Where branchiæ exist, loops or processes of one or other of the great trunks enter them." The dorsal and ventral vessels are generally contractile; and the direction of the contractions "is usually such that the blood is propelled from behind forwards in the dorsal vessel, and in the opposite direction in the ventral vessel; but the course which it pursues in the lateral trunks is probably very irregular."

THE ARTHROPODA.

The various classes belonging to the *Arthropoda* present a system of vessels, partially at least, shut off from the somatic or body cavity. But the blood-vascular system is not complete in any Invertebrate animal. In some part or parts of the body the vessels will be found to terminate, and the blood will flow through lacunæ or spaces not bounded by any limiting membrane. From this remark it will be observed that the old form of circulation once more comes uppermost—*i.e.*, the blood passes into the general body cavity. This primitive form of circulation is met with in all Invertebrates, but the higher forms have partially developed a system of blood-vessels, which is, however, incomplete, consequently the lower the animal, the more extensive is the lacunar circulation.

In the *Invertebrata*, the arteries have not the three coats, such as are met with in the higher animals. The heart is generally situated in a dorsal position; and its pulsations drive the blood at once over the body generally, and not to the organs of respiration first. "The word 'pericardium,' used by some writers in describing the blood systems of the *Invertebrata*, is an unfortunate and a misleading one. The pericardium of the *Insecta* and *Crustacea* has no homology with the serous membrane, that invests the heart of the Vertebrate animals. It is, in truth, a large venous sinus, surrounding that long segmented vessel in the dorsal region of the body that is generally called the heart. From this sinus, blood passes into the heart by certain lateral openings provided with valves opening inwards. Yet another unfortunate name has been used in this connection. Certain parts of the venous system in the *Insecta* and *Myriapoda* have been designated portal. They represent, however, in no manner the portal system peculiar to the *Vertebrata*."

In the *Arthropoda*, there are no pseudo-hæmal vessels; and "the blood-vascular system varies from a mere perivisceral cavity without any heart (*Ostracoda*, *Cirripedia*) up to a complete, usually many-chambered heart with well-developed arterial vessels. The venous channels, however, always have the nature of, more or less, definite lacunæ. The blood corpuscles are colourless, nucleated cells."*

In all those Arthropods where a heart is present, the blood returns to that organ by the lacunar spaces situated between the organs. These conduits, without special walls, debouch into a so-called pericardiacal reservoir, and the blood penetrates afterwards into the heart by cardiacal clefts. In the *Brachyura* and *Macroura* (Fig. 39) the blood, before returning to the heart, is oxidised in passing through the branchiæ.

In the *Myriapoda*, the heart has many chambers, and it is nearly as long as the body. The blood enters this organ by a pair of clefts, and leaves it partly by the communication with the adjacent chamber, and partly by the lateral arteries. "A median aortic trunk continues the heart forwards, and the lateral trunks encircle the œsophagus and unite into an artery which lies upon the ganglionic chain. The arterial system in the *Chilopoda* is, in fact, as complete as that of the Scorpions."†

In the *Insecta*, circulation is chiefly effected by means of

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* Huxley's *Anatomy of the Invertebrata*, p. 252.

† See Newport in the *Philosophical Transactions of the Royal Society*, 1863.

the heart, which is a tubular organ running along the back of the insect, and hence called the dorsal vessel (Fig. 40). This

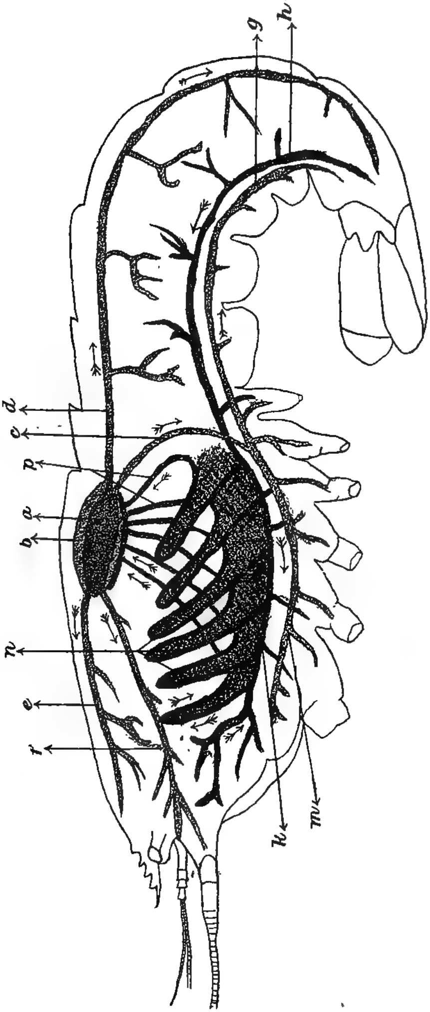

FIG. 39.—CIRCULATORY SYSTEM OF HOMARUS.
(*After* GEGENBAUR.)

a = heart. b = pericardium. c = trunk of ventral artery. d = posterior artery. e = medium and interior artery. f = artery of so-called liver. g = ventral artery. h k = ventral venous sinus. m = anterior portion of ventral artery. n = branchiæ. p = branchial veins.

is formed of a series of sacs opening one into the other, from behind forwards, in such a manner that the folds formed by the junction of the sacs serve as valves to prevent the reflux of the blood. The blood enters the heart from the cavity of the body by a series of valvular openings, when it is gradually driven forwards by the successive contraction of the divisions of the heart, until it escapes in the neighbourhood of the head. After this it is no longer confined within vessels, as neither arteries nor veins have been observed in the *Insecta;* but the blood or nourishing fluid is spread about in the lacunæ and interstices of the organs. Even in these lacunæ the blood is still animated by the action of the heart, and is ultimately forced back until it again reaches that organ. These lacunæ all communicate with a sinus or vessel on the ventral side of the body. Thence the blood passes to the respiratory organs, and then to the so-called pericardium or venous sinus surrounding the heart.

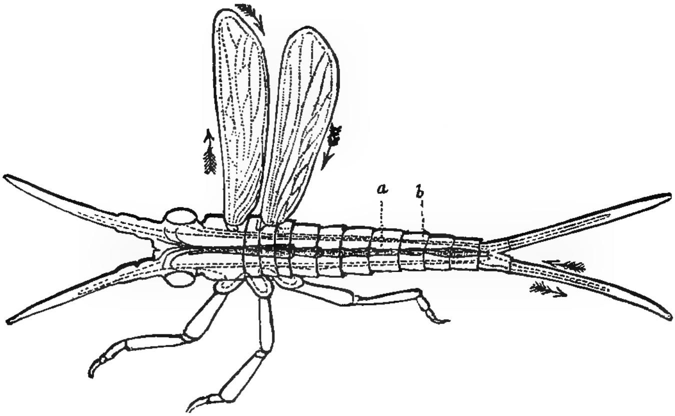

FIG. 40.—CIRCULATION IN THE INSECTA.

a = dorsal vessel or heart. *b* = principal lateral currents.

It may be mentioned that in the *Lepidoptera*, *Orthoptera*, &c., a ventral vessel has been observed. Dr. V. Graber * discovered a ventral vessel in *Stetheophyma grossum* (grasshopper) and various species of *Libellula*, and states that it should be regarded in the light of an artery to a dorsal vein.

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* *Die Insecten*, 1877, vol. 1, pp. 328–345.

Mr. A. H. Swinton* has also observed a ventral vessel (Fig. 41) beneath the intestines in *Sphinx Ligustri.* This vessel is contractile like the dorsal vessel, and unites with the latter at the junction of the thorax with the abdomen. At this junction there is a dilatation of a flat-roundish form. Swinton states that there is a twofold alternating pulsation in this dilatation, that indicated a circular flow of the fluid, as shown by the double-headed arrows (Fig. 41); and which appears to be a rudimentary heart, composed of an auricle and a ventricle, such as exists in the *Mollusca.*

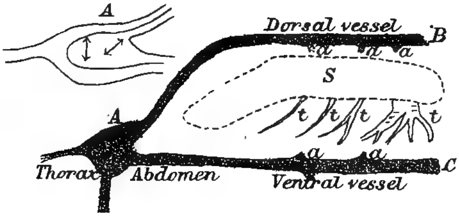

FIG. 41.—CIRCULATION IN THE ABDOMEN OF SPHINX.
(*After* SWINTON.)

A = heart. *B* = dorsal vessel. *C* = ventral vessel. *a* = afferents.
S = intestines. *t* = tracheæ.

The two main vessels have, besides, several afferents, *a*, *a*, and those to the lower one seemed to open each time the flap or fold spasmodically moves upwards; while a central cylindrical duct (B) passes from the heart (A) ventrally into the thorax, where its rhythmical action, says Mr. Swinton, "could be at intervals seen extending as far as the second annulation, although the forms of its vessels were obscured, from the fact that circulation was already partially stayed in this position of the body. Lastly, the ventral and flat-roundish vessels continued to palpitate vigorously long after the valves of the dorsal vessel had ceased to move." Mr. Swinton considers that he has discovered, in this pulsating flat-roundish vessel and its afferents, the *true* heart in the *Lepidoptera.*

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* *Insect Variety: its Propagation and Distribution*, 1880, p. 39.

The *Arachnida* (pulmonary) have a circulatory apparatus, which is to a certain extent well developed. The heart (Fig. 42), situated dorsally, has the form of an elongated vessel, and gives rise to various arteries. The blood having traversed the organs, passes to the lungs, and from thence reaches the heart, following a course similar to that observed in the *Crustacea*. In those *Arachnida* which breathe only by tracheæ (*e.g.*, the mites), the circulatory apparatus is rudimentary; for there appears to be merely a simple dorsal vessel without arteries or veins; and it may be remarked, that in some species the heart or dorsal vessel appears to be entirely wanting.

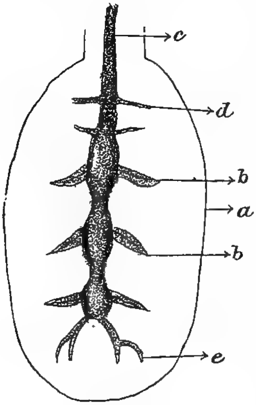

FIG. 42.
HEART OF A SPIDER.

a = abdomen. *b* = lateral pulmonary vessels. *c* = anterior aorta. *d* = transverse branches. *e* = genital arteries.

In some of the lower *Crustacea* the heart is entirely absent. For instance, in the *Copepoda* there is no heart; while in the *Ostracoda* there is either no heart (*Cypris* and *Cythere*), or it is only in a rudimentary form. According to Claus, the heart in *Cypridina*, *Halocryptis*, and *Conchœcia* consists only of a short saccular organ with one anterior and two lateral appendages. The *Cirripedia* have no heart or other circulatory apparatus—that is, as far as is known in the present state of biological science.

Dr. G. O. Sars* has recently investigated the circulatory apparatus in *Cyclestheria hislopi* (see Fig. 11), one of the *Phyllopoda*. The heart of this Phyllopod is located in the dorsal part of the body, and is easily observed in living specimens through the transparent shell. It has the form of an elongated tube traversing no less than four segments of the body, viz., the maxillary segment and the

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* *Christiania Videnskabs-Selskabs Forhandlinger*, 1887.

three first segments of the trunk, its posterior part being, moreover, extended to the middle of the succeeding segment, and its anterior extremity slightly projected within the mandibular segment. It is provided with four pairs of distinctly defined lateral valvular openings, each pair occurring exactly in the middle of the corresponding segment. Here, the heart is connected to the body wall by slender fibres, the intervening parts being slightly instricted, whereby the dorsal as well as the lateral edges of the heart acquire a regular undulated appearance. The heart of *Cyclestheria* has its greatest width across the anterior part, located within the dorsal prolongation of the cervical division, whence it tapers somewhat posteriorly. Its posterior extremity is abruptly truncated and furnished with a rather wide medial opening, whereas the anterior extremity contracts to a short aorta through which the blood introduced into the heart is expelled. The lateral openings of the heart are each surrounded by delicate concentric muscular fibres, and limited by two distinctly defined valvular lips. Likewise at the posterior extremity of the heart a valvular arrangement would seem to occur, and the origin of the aorta is marked off by two narrow lips closing and opening at regular intervals. Of any other distinctly defined blood-vessels, Dr. Sars could not find any trace, the blood circulating simply within the lacunar interstices between the muscles and the connective tissues. In the shell, these lacunar interstices have a very complicated arrangement, forming a richly anastomosing network of what Dr. Sars calls "blood-rooms." Along the dorsal line, however, the presence of a well-defined longitudinal blood-sinus may be readily determined.

The blood of *Cyclestheria* is colourless, and contains numerous small rounded corpuscles, the course of which may be traced with comparative ease, especially in young transparent specimens. By the contraction of the heart (about 150 per minute) the blood is expelled exclusively from its anterior extremity, which is prolonged so as to form a short aorta, which has at its base a valvular apparatus. This apparatus opens and closes at regular intervals. On leaving the open end of the aorta, the blood flows in two different directions, one part anteriorly, the other posteriorly. The considerable quantity of blood conducted to the anterior part of the body is seen to flow down the sides of the head, partly supplying its several appendages, partly running straight back along its ventral side to the region of the adductor muscle of the shell. Here the blood enters the valves, being received within the complicated system of canals occurring between their two lamellæ. The other principal arterial current is seen running from the heart backwards along the dorsal side of the trunk, immediately above the intestine; and, on reaching the tail, it bends round and flows anteriorly along the ventral side, sending off, in each segment, lateral currents to the branchial legs. The blood thus conducted to the various parts of the body and shell returns to the heart by two different ways. The considerable quantity of blood introduced within the canal-system of the shell is at last received by two longitudinal sinuses passing along its dorsal side, the anterior rather short, the posterior occupying the greater part of the dorsal line. In the anterior sinus the blood flows backward, in the posterior, forward; the two currents meeting at the place where the body is connected with the shell dorsally. Here both currents suddenly bend down, the one on the anterior, the other on the posterior side, and pour out the blood into the pericardial sinus, whence it passes into the heart through the lateral valvular openings. The remaining part of the blood, introduced into the trunk and the tail, is at last received within a large sinus, occupying the upper part of the dorsal side of the trunk and divided from the arterial dorsal sinus by a longitudinal ligament extending from the lower side of the heart to the tail. This blood-sinus is apparently fed in each segment of the trunk by a pair of ascending currents from the branchial legs. The blood contained in the above-mentioned sinus flows from behind forward, or in an opposite direction to that contained in the arterial sinus, and for the most part is introduced into the heart through its posterior extremity, though some would also seem to enter the posterior pair of the lateral valvular openings.

Sars says that the course of the blood within the several limbs is not easy to examine in *Cyclestheria hislopi*, for they (the limbs) are concealed for the greater part by the shell. In the antennæ, however, which at times are more or less completely exserted beyond the shell, the blood can be distinctly seen passing along the upper edge of each branch to the extremity, then turning round, and flowing back along the lower edge to the scape (Sars).

In the higher *Crustacea*, the heart and circulatory apparatus are far better defined than in the lower orders of this class. The heart of *Homarus* is a powerful quadrate organ, and the arteries are large, definite in number and in distribution. There are contractile expansions ("gill-hearts") at the base of the blood-vessels conducting the blood to the branchiæ. The heart consists of a single contractile cavity, and the arteries in the higher *Crustacea* are closed tubes; but the venous blood passes back through the interstices between the organs of the body, until it reaches certain cavities or reservoirs situated at the bases of the limbs (Fig. 43); therefore the venous blood bathes all the organs. From the reservoirs or sinuses the blood passes to the branchiæ, where it becomes aërated by contact with the water,

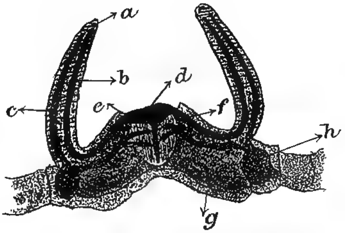

FIG. 43. — VERTICAL SECTION OF A CRUSTACEAN, SHOWING THE COURSE OF THE BLOOD.

a = gill. *b* = vessels which collect the aërated blood from gills. *c* = vessels conducting venous blood to gills. *d* = heart. *e* = carapace. *f* = branchiocardiac vessels. *g* = sternum. *h* = venous sinus.

and then passes through proper vessels to the heart. It will be seen that the circulation in the higher forms is semi-vascular and semi-lacunar.

The circulatory apparatus of *Astacus* is well defined. The heart is situated dorsally and behind the stomach. It is surrounded by the so-called pericardium, which is in reality a blood-sinus; consequently the heart is suspended in a blood-sinus. There are six apertures in this organ provided with valves which open inwards. These allow the blood to enter the heart during the diastole, and prevent its egress, except by the arteries, during the systole. There are six arterial trunks provided with valves at their commencement, their object being to prevent the regurgitation of the blood. These arteries ramify minutely, but the capillary system has not been investigated with anything like satisfaction. So far as is known, the blood passes from the arteries into the lacunæ and into the perivisceral cavity. From these lacunæ it ultimately finds its way to the branchiæ and heart.

Reverting once more to the heart of the *Crustacea*, Sir Richard Owen, F.R.S., says that "we may trace in the heart of these animals a gradational series of forms, from the elongated median dorsal vessel of *Limulus*, to the short, broad, and compact muscular ventricle in the lobster and the crab. In all the *Crustacea* the heart is situated immediately beneath the skin of the back, above the intestinal tube, and is retained *in situ* by lateral pyramidal muscles.

"In the *Entomostraca*,* and in the lower, elongated, slender, many-jointed species of the Edriophthalmous *Crustacea*, the heart presents its vasiform character. It is broadest and most compact in the crab."

THE POLYZOA.

The perivisceral cavity contains a nutritive fluid. This is kept in constant motion by the action of cilia with which the

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* The *Entomostraca* include the *Phyllapoda, Cladocera, Ostracoda,* and the *Copepoda.*

inner surface of the cavity and the outer surface of the intestine are covered. This movement, which extends into the tube of the common stock, is equivalent to a true circulation of the blood. Consequently, the function of circulation in these animals is comparable to that in the Cœlenterata, for the blood is not, during any part of its course, contained in any system of vessels, but is free in the body cavity.

THE BRACHIOPODA.

The sinuses met with in the *Brachiopoda* are the result of partial limitation of the general cavity of the body, for a special purpose. These sinuses "extend into each lobe of the mantle, and end cæcally at its margins. The lobes of the mantle are probably, together with the ciliated tentacula, the seat of the respiratory function. The sinuses of the pallial lobes of *Lingula* give rise to numerous highly contractile, teat-like processes, or ampullæ. During life the circulating fluid can be seen rapidly coursing into and out of each ampulla in turn."

Between the ectoderm and the lining membrane of the sinus-like "prolongations of the perivisceral cavity in the mantle, and between the endoderm, the ectoderm, and the lining membrane of the perivisceral cavity itself, there is an interspace, broken up into many anastomosing canals," which Prof. Huxley considers, "to represent a large part of the proper blood systems." Dilatations of these canals have been erroneously described as hearts, but they are not contractile. "Although the existence of a direct communication between the perivisceral chamber and the blood canals has not been demonstrated, it is very probable that the perivisceral chamber really forms part of the blood-vascular system."

THE MOLLUSCA.

In the *Mollusca* the circulatory system is more highly differentiated, and "in very many, if not all, the blood cavities communicate directly with the exterior by the organs of Bojanus," or kidneys. The higher *Mollusca* have all of them well-defined hearts, generally with auricles and ventricles (Fig. 44), arteries and veins, though the capillary system is still absent. The hearts of the *Gasteropoda* and *Cephalopoda* have valves and columnæ carnæ; there are also contractile expansions at the base of the vessels conducting the blood to the branchiæ.

We now describe the circulatory system in three orders of the *Mollusca*.

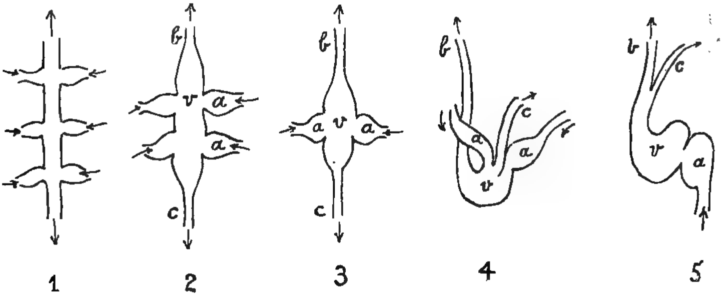

FIG. 44.—DIAGRAM SHOWING THE MODIFICATIONS OF THE HEART IN THE INVERTEBRATA.

1 = part of dorsal trunk of a worm. 2 = heart of *Nautilus*. 3 = heart of a Lamellibranch. 4 = heart of *Octopus*. 5 = heart of a Gasteropod.

v = ventricle. *a* = auricle. *b* = cephalic artery. *c* = abdominal artery.

The arrows indicate the direction of the blood-current.

(1) The *Lamellibranchiata*.—The vascular system consists of a heart, anterior and posterior aortæ, and other blood-vessels and sinuses. In *Anodonta* the heart lies in the middle line of the body, and is surrounded by the pericardium or blood sinus. It consists of a median ventricle, which is perforated by the intestine (see Fig. 18), and of two auricles which are situated on each side of the ventricle. The ventricle gives rise to the anterior and posterior aortæ. The auricles are muscular sacs, and communicate with the ventricle by the auriculo-ventricular openings. These open-

ings are each provided with a pair of valves, which project into the ventricle, and there meet in front of the openings. These valves allow the blood to pass from the auricle to the ventricle, but prevent its return from the ventricle to the auricle. By the contraction of the auricles the blood is forced into the ventricle. After the contraction of the auricles have ceased, the ventricle contracts and forces the blood forwards and backwards through the two aortæ. The blood passes through the ramifications of these vessels into the system of lacunæ or sinuses situated in the mantle and between the viscera. From these lacunæ the blood passes into a large median venous sinus termed the vena cava, which extends between the anterior and posterior adductor muscles. At the base of the branchiæ are two lateral sinuses. The main portion of the blood passes into the renal organ (the organ of Bojanus) and ultimately to the branchiæ, and from thence is returned as arterial blood to the auricular portion of the heart.

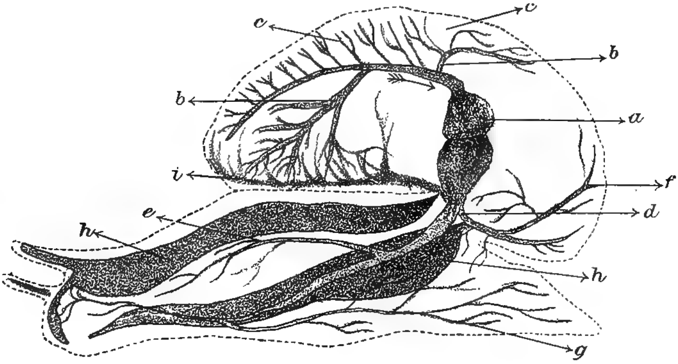

FIG. 45.—CIRCULATORY SYSTEM OF HELIX.

a = heart. *b* = vessels carrying blood from lung to heart. *c* = lung.
d = aorta. *e* = gastric artery. *f* = "hepatic" artery. *g* = pedal artery. *h* = abdominal cavity, supplying the place of a venous sinus.
i = irregular canal communicating with *h*, and carrying blood to lung.

(2) The *Gasteropoda.*—In *Helix* the heart (Fig. 45) is

close to the pulmonary sac. It consists of an auricle and a ventricle. The aorta proceeds from the ventricle, and divides into two branches: one of these passes forward and ramifies in the head and foot, while the other passes backwards and dorsally to the viscera, where it also ramifies. The arterial branches terminate by opening into lacunæ; from these the blood passes through the pulmonary arteries to the lung, and thence through the pulmonary veins, which ultimately join to form a large pulmonary vein which leads into the auricle. The organ of Bojanus, or kidney, "lies close to the pulmonary sac in the course of the current of the returning blood."

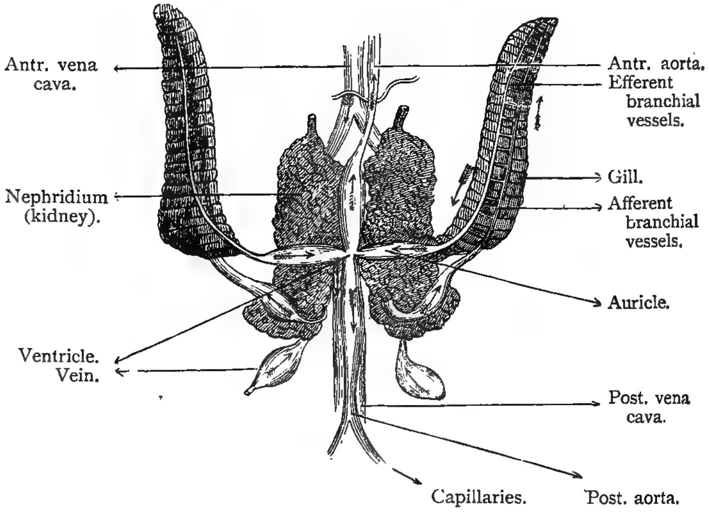

FIG. 46.—BLOOD SYSTEM AND NEPHRIDIA OF SEPIA.

(3) The *Cephalopoda.*—The circulatory system of *Sepia* is seen in Fig. 46. "The heart is placed upon the posterior face of the body, on the hæmal side of the intestine, and receives the blood by branchio-cardiac vessels, which correspond in number with the gills; and, as they are contractile, might be regarded as auricles. The gills themselves have no cilia, and

are, in some cases, if not always, contractile. The arteries end in an extensively developed capillary system, but the venous channels retain, to a greater or less extent, the character of sinuses. The venous blood, on its way back to the heart, is gathered into a large longitudinal sinus—the vena cava—which lies on the posterior face of the body, close to the anterior wall of the branchial chamber, and divides into as many afferent branchial vessels as there are gills. Each of these vessels traverses a chamber, which communicates directly with the mantle cavity, and the wall of the vessel, which comes into contact with the water in this chamber, is sacculated and glandular." In *Loligo media* "the sacculated afferent veins and branchial hearts contract about sixty times a minute. The pulsations of these veins and of the branchial hearts are not synchronous. The branchial veins and the lamellæ of the branchiæ also contract rhythmically," but the branchial arteries do not contract. "The portion of the branchial vein which lies between the base of the gill and the systemic ventricle is very short, and it is hard to say whether it contracts independently or not. Mechanical irritation causes contraction both of the afferent branchial veins and of the branchial hearts." (Huxley.)

In *Eledone cirrhosus* Professor Huxley has "observed regular rhythmical contractions of the vena cava itself, as well as of its divisions, the sacculated afferent branchial veins, of the branchial hearts, and of the branchio-cardiac vessels."

THE TUNICATA.

In the Ascidians the function of circulation differs entirely from other Invertebrates. The peculiarity of this circulation is the *reversal* at regular intervals of the direction of the blood current. The heart is devoid of valves, and contracts with a wave-like movement. If the wave is from below upwards, "the blood passes into an abdominal vessel, thence into transverse ascending canals that lead to the extraordinary network of vessels connected with the respiratory structures, into a dorsal vessel, and thence by a connecting branch to the posterior end of the heart. After a certain period, the wave of contraction through the heart, and the course of the blood, are generally reversed in direction; and the blood now flows from the ventral heart into the dorsal vessel, down through the branching network into the abdominal or ventral vessel, and so to the anterior end of the heart."

The blood consists of a clear plasma containing colourless corpuscles.

In *Appendicularia flabellum*, Professor Huxley states that there are no corpuscles, and "the direction of the pulsations of the heart is not reversed at intervals, as it is in the Ascidians in general. M. Fol,* however, states that, in other *Appendiculariæ* the reversal of the contractions of the heart takes place. . . . . There are no distinct vessels, but the colourless fluid which takes the place of blood makes its way through the interspaces between the ectoderm and endoderm and the various viscera."

Concerning the velocity of the circulation in the *Invertebrata* very little is known; but it may be stated that the blood in these animals is animated by a much slower movement of translation than occurs in the *Vertebrata*.

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* *Etudes sur les Appendiculaires*, 1872.

CHAPTER VIII.

RESPIRATION IN THE INVERTEBRATA.

It is well known that the presence and absorption of oxygen is essential to the life of every tissue, and that one of the products of the action of oxygen on the tissues, &c., is the production of carbonic anhydride, a gas which is inimical to life. Even the lowest members of the animal kingdom require oxygen—without oxygen, no animal life. The *Amœba* and *Paramœcium*, when introduced into a medium containing no oxygen, or containing an excess of carbonic anhydride, very soon die. In all animals there is an interchange between the gases of the organism and the gases of the medium in which they live; and this interchange, which is known as *respiration*, is continuous throughout life.

In the lowest forms no special mechanism is necessary for facilitating the gaseous interchange; for they absorb fluids containing oxygen in solution. In higher forms, canals, along which the air passes, seem to be necessary; and in still higher forms respiration is performed by the movement of the branchiæ, or by tracheæ (air-tubes) and lungs. The absorption or respiration of oxygen is one of the first conditions of nutrition. All organised beings absorb oxygen, and this absorption goes on in all stages of the existence of living matter.

The organs (using the word in its widest sense) of respiration differ considerably in different animals, but they have all the same physiological function to perform—that of supplying oxygen to the tissues and blood; and the elimination of the gaseous products of decay. In fact we may define respiration as "the elimination of the gaseous products of tissue-combustion, and the introduction of the oxygen necessary for that combustion."

The lower forms of the animal kingdom respire directly by changes between the general surface of the body and the medium in which they live; but in the higher forms, respiration is a twofold process: (*a*) internal respiration, or the interchanges between the gases of the blood and the tissues; and (*b*) external respiration, or the interchanges between the gases of the blood and the gases in the air-cells of the lungs. These interchanges, however, are not always confined to the lungs; thus there is a true cutaneous respiration in the skin, an intestinal respiration in the intestines, and most probably interchanges of a like nature take place in other organs; for it may be remarked that many organs of the *Invertebrata* contain various pigments, which have a respiratory function.

The respiratory apparatus is always in intimate relation with the organs of circulation.

THE PROTOZOA.

In most of the *Protozoa*, respiration takes place all over the general surface of the body; but these animals differ somewhat in the mechanism of respiration. In the *Gregarinida* the interchange of gases takes place all over the body. In the majority of the *Infusoria* and *Rhizopoda* there is a differentiation of the function of respiration, for even in these low forms the interchange of oxygen and carbonic anhydride takes place at certain specialised regions (contractile vacuoles), but the air is not brought into direct contact with the circulating fluid. The oxygen or air for respiration is dissolved in water. The contractile vacuoles of these organisms perform several functions, among these being that of respiration. The contractile vacuoles contain liquids, and during contraction send out radiating canals. This system probably communicates with the exterior. By this primitive respiratory organ the working tissues are brought into contact with oxygen dissolved in water.

THE PORIFERA.

In the *Porifera* (*Spongida*) respiration is effected by means of the oxygen dissolved in the water, which permeates through the various canals, and thereby brings it into intimate relation with the whole mass. In the circulation of this water through the ordinary fresh-water sponge (*Spongilla*) there is a fusion of the functions of digestion, circulation, and respiration. "Sponges absorb oxygen and give off carbonic anhydride with great rapidity; and the manner in which they render the water in which they live impure, and injurious to other organisms, suggests the elimination of nitrogenous waste matter." It is possible that the oxygen is retained in the substance of a sponge by certain respiratory pigments—probably a histohæmatin. Sponges are rich in chlorophyll, but this pigment has another function—viz., the formation of fatty matter.*

THE CŒLENTERATA.

In the lower *Cœlenterata* the function of respiration is performed by the general surface of the body. The fluids in these animals are in close relationship to the water in which they live; and consequently the ectodermic lining serves as an organ of respiration. In other words the lower Cœlenterates respire by the skin. In some of the higher orders of this group the respiratory function is performed in the water-vascular tubes along with other functions performed by the same vessels.

But there is no doubt that the chief mode of respiration in

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* MacMunn in *Journal of Physiology*, vol. 9.

the Cœlenterates is by means of the ectodermic lining, for this lining is very largely impregnated with respiratory and other pigments, as shown by Prof. Moseley[*] and Dr. MacMunn.[†]

The respiratory pigments are capable of existing in a state of oxidation and reduction, and no doubt play an important part in the function of respiration.

Professor Moseley discovered a pigment called polyperythrin in various Cœlenterates, and Dr. MacMunn has carefully examined the brown colouring matter of jelly-fishes, and various pigments in the *Actiniæ*.

In *Chrysaora hysocella* a brown pigment is present in "the radiating triangular areas on the upper surface of the umbrella, and in dark patches, thirty-two in number, all round the margin of the disc, also in the tentacles; but in each of these situations it possesses the same properties. It also occurs dotted on the surface of the umbrella between the triangular pigmented areas. Microscopically, it occurs in granules, and is limited to the surface; these granules are yellowish in colour under a high power." Dr. MacMunn could not extract the brown pigment with alcohol, ether, chloroform, alcohol and sulphuric acid, and alcohol and potassium hydroxide. But he obtained an extract by allowing portions of *Chrysaora* to stand, "the sea-water contained in the tissues dissolved the pigment, forming an orange-brown solution, showing a broad dark band at the blue end of the green. When more pigment went into solution, the fluid became a dark brown colour. Boiled in fresh and sea-water the colour went into solution, but showed no bands except the shading at the blue end of the green. A deep layer of this solution only transmitted red and some green. Ammonia and caustic potash precipitated the colouring

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[*] *Quarterly Journal of Microscopical Society*, vol. 17; and *Journal of Physiology*, vols. 7 and 8.

[†] *Quarterly Journal of Microscopical Science*, vol. 30; and *Journal of Marine Biological Association*, 1889.

matter. Hydrochloric acid did not discharge the colour at first, although it became much lighter; strong sulphuric acid and nitric acid discharged it after some time. Absolute alcohol also precipitated the pigment, the fluid becoming flocculent after a while. The colouring matter in the fresh state showed no bands except some shading at the blue end of the green; it also absorbed the violet end of the spectrum."

Dr. MacMunn's investigations on the respiratory pigment of *Chrysaora* confirms those of Dr. J. G. M'Kendrick, F.R.S.,* who has also investigated the pigments from *Cyanea* and *Aurelia* by allowing fragments of these organisms to macerate in sea-water for about thirty-six hours. "In these cases ammonia precipitated the colouring matter from its solutions, and it dissolved in acids." Dr. M'Kendrick states that after death "the body becomes slightly acid, the protoplasm disintegrates, and the colouring matter diffuses out."

When examined by the microspectroscope the fresh pigment from *Cyanea*, as well as an infusion of the organism, gave two bands, one in the orange and the other in the red.

The spectrum of the blue pigment of *Rhizostoma Cuvieri* consists of three bands, one in the red, a dark one at D, and an extremely faint band in the green. There is little doubt that the same colouring matter occurs in *Rhizostoma* as in *Cyanea*. This pigment has been termed cyanein by the late Dr. Krukenberg,† and he compared it with the blue pigment found in *Velella limbosa* by A. and G. De Negri.‡ Cyanein is soluble in water, insoluble in benzene, ether, carbon disulphide, and chloroform. On the addition of alkalies, cyanein is changed into an amethyst colour, while acids colour it red.

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* *Journal of Anatomy and Physiology*, vol. 15, p. 261.

† *Vergl. Physiol. Studien*, zweite Reihe, dritte Abth., 1882, s. 68.

‡ *Gazetta Chimica Italiana*, vol. 7 [1877].

In 1884, Krukenberg stated that cyanein occurs in *Velella*, *Aurelia*, *Cyanea*, and *Rhizostoma*.

Dr. MacMunn* has examined the pigments from the following *Actiniæ*:—*Actinia mesembryanthemum*, *Bunodes crassicornis*, *B. ballii*, *Sagartia bellis*, *S. dianthus*, *S. parasitica*, *S. viduata*, *S. troglodytes*, and *Anthea cereus*.

(*a*) When the solid portions from the ectoderm, endoderm, and tentacles of the red-coloured specimens of *Actinia mesembryanthemum* were examined by the microspectroscope, they gave a band which closely resembled that of reduced hæmoglobin, accompanied by two other bands nearer the violet end of the spectrum. The extreme edges of the shading of the band extend from λ 600 to λ 560, while its darkest part is from λ 580 to λ 563. "These measurements vary according to the colour of the specimen, for in brown specimens the dominant band is nearer the violet, and in some a band is also present before D." The latter spectrum is said to belong to modifications of the same pigment, as the same decomposition products are obtained in both cases. The spectrum of the brown specimens of this species has a close resemblance to the histohæmatins. MacMunn has named this pigment actiniohæmatin.

Actiniohæmatin is soluble in glycerol, but it is insoluble in alcohol, ether, chloroform, carbon disulphide, benzene, &c. This pigment is also extracted (but in a changed condition) by treating with alcohol and potassium hydroxide (either hot or cold). By the latter treatment a reddish solution is *always* obtained, which gives a band at D, generally extending from λ 625 to λ 589, recalling to mind the spectrum of alkaline hæmatin. When ammonium sulphide was added to the alkaline alcoholic extract, the band at D was replaced by two bands which are undistinguishable from the spectrum of hæmochromogen. MacMunn has also observed that all the *red* pigments in the *Actiniæ* gave after this treatment in the

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* *Philosophical Transactions of Royal Society*, 1885 (part ii.), p. 641; and *Quarterly Journal of Microscopical Science*, vol. 30.

solid state (*i.e.*, examined in the compressorium) the spectrum of hæmochromogen. It may be remarked that Professor F. Hoppe-Seyler* found that when solutions of hæmoglobin are treated with potassium or sodium hydroxide in the absence of air, the hæmoglobin is converted into hæmochromogen. In the solid tissues of the *Actinia*, says MacMunn, a similar reaction occurs, but in the solution used to extract the pigment the hæmatin becomes oxidised as it comes out of the tissue, and shows the alkaline hæmatin spectrum, which, however, can be reconverted into hæmochromogen by the addition of ammonium sulphide.

MacMunn could not obtain acid hæmatin, but he did succeed in converting the pigment into hæmatoporphyrin. "By digesting portions of an Actinia in sulphuric acid, and filtering through asbestos, a purple-red solution was obtained, which showed bands like those of acid hæmatoporphyrin, a little rectified spirit being added to the acid solution; but the band nearer the violet is not placed exactly in the same position as the corresponding band of hæmatoporphyrin obtained from hæmoglobin. The first band extended from λ 605 to λ 595, and the second from λ 563 to λ 551, but owing to the presence of biliverdin and proteids these measurements may not be quite reliable; still, they possess a certain value when the results are compared with other cases. If this spectrum be that of a kind of hæmatoporphyrin, it ought to be changeable into alkaline hæmatoporphyrin, and such is the case." From the above remarks there can be no doubt that in *Actinia mesembryanthemum* a pigment is present which can be changed into hæmochromogen and hæmatoporphyrin.

MacMunn has also extracted (by means of alcohol and alcohol and sulphuric acid) the green pigment situated beneath the ectoderm of many specimens of this species of *Actinia*. This pigment gives the reactions of biliverdin ($C_{16}H_{20}N_2O_5$?). "Hence *A. mesembryanthemum* contains in

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* *Zeitschrift für Physiologische Chemie*, vol. 1, p. 138.

its mesoderm and elsewhere a colouring matter undistinguishable from biliverdin" of the *Vertebrata*. As biliverdin is derived from the decomposition of Vertebrate hæmoglobin, its presence in *Actinia* is further proof that these organisms contain pigments closely allied to hæmoglobin.

MacMunn has proved that the hæmatin-yielding pigment of *A. mesembryanthemum* is not the same as Prof. Moseley's actiniochrome, although the latter pigment is present in certain species of the *Actiniæ*. The band of actiniochrome is nearer the red than that of MacMunn's pigment (actiniohæmatin), and the two pigments yield entirely different decomposition products under similar treatment. After a careful examination of the glycerol extracts, MacMunn found that "every specimen of *Actinia mesembryanthemum*, whether its colour was red, reddish-brown, brown, or greenish-brown, gave to the glycerol, after some days' extraction, a certain amount of colouring matter, which in every case could be made to change into hæmochromogen, while actiniochrome never could be changed into it; hence the respective pigments are very different. One is a *respiratory colouring matter* (actiniohæmatin), the other (actiniochrome) is an ornamental one."

The glycerol extract made from the ectoderm of an anemone yielded actiniohæmatin, which, on the addition of potassium or sodium hydroxide and ammonium sulphide, was rapidly changed into hæmochromogen. "It appears that this hæmatin-yielding pigment does not give the same spectrum in brown specimens as in red; but the spectrum of the glycerol extract of red *Actiniæ* has a close resemblance to that of the spectrum of the solid ectoderm and other parts of brown specimens. This does not show that the pigment has been altered by extraction with glycerol, but its molecular condition may be altered. It is well known that the spectrum of a pigment may differ in the solid and liquid state without any necessary change in its composition (Vogel and Kundt)."

(*b*) *Bunodes crassicornis.*—Moseley [*] examined this *Actinia*, and he found in two specimens the tentacula were a rose colour, the colour being due to actiniochrome. MacMunn has more recently examined the pigments of this species of *Bunodes*; and he found that the colour and spectra differ considerably in different cases. The conclusions arrived at are that "in *Bunodes crassicornis* we find actiniohæmatin with tolerable constancy, occasionally actiniochrome and also biliverdin, besides the lutein-like (lipochromes) pigments. In the ectoderm, as well as in the endoderm, and sometimes in the tentacles, actiniohæmatin is present. In none of the specimens were 'yellow cells' present, and by no other solvents except glycerol, and alkaline and acid alcoholic solutions, could any pigments be got into solution."

(*c*) *Bunodes ballii.*—The tentacles and mesenteries of his anemone, when examined by the microspectroscope, gave a number of bands, which showed the presence of a chlorophyll-like pigment. In the *large variety* of this species the tentacles are packed with "yellow cells" [†] lodged in part in their endodermal lining. It appears that these "yellow cells" replace the red pigment of other species, since the latter is present in mere traces. No "yellow cells" are present in the tentacles or elsewhere in the *small variety* of *Bunodes ballii*. The inner tentacles of this variety gave the spectrum of actiniochrome; but no hæmochromogen was produced from these anemones. Still, the fact is interesting, that the pigment of the ectoderm resembles, with regard to the first band of its spectrum, that of *A. mesembryanthemum*; and MacMunn remarks that "it may have been a pigment which is intermediate between actiniochrome and actiniohæmatin. The replacement of this pigment by the colouring matter of the 'yellow cells' in the large variety is of great interest, and teaches that the presence of the colouring matter has

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[*] *Quart. Journ. Micro. Soc.*, vol. 12, p. 143.

[†] Symbiotic algæ.

something to do with the absence of 'yellow cells' in the small variety."

(*d*) *Sagartia dianthus.*—The brown and white specimens both contain a hæmatin-yielding pigment, which is undoubtedly actiniohæmatin.

(*e*) *Sagartia viduata.*—On extracting the ectoderm for twenty-four hours in alcohol and caustic potash a yellow solution was obtained. This gave a chlorophyll-like spectrum, but faint traces of hæmochromogen were detected on the addition of ammonium sulphide.

(*f*) *Sagartia parasitica.*—In this species MacMunn discovered the presence of actiniohæmatin and another pigment, which is different from any other he had previously examined. This latter pigment is peculiar to this species. "In its colour-changes with acids it has a very remote resemblance to the purple pentacrinin of Professor Moseley, also to the colouring matter of *Aplysia*, but differs in spectrum and in some colour-changes." "Yellow cells" are absent in *S. parasitica*; its colouring matter is capable of uniting with oxygen and of giving it up again; consequently it has a respiratory function.

(*g*) *Sagartia troglodytes.*—The solid ectoderm of this species yielded a pigment which is related to hæmochromogen. MacMunn believes that this pigment is a histohæmatin.

(*h*) *Sagartia bellis.*—The tentacles of this species were found packed with "yellow cells." The spectroscopic examination of the tentacles showed a banded spectrum reminding one of chlorophyll, or rather chlorofucin. This spectrum belongs to the mass of "yellow cells" which are embedded in the endodermal linings of the tentacles. The ectoderm and endoderm do not contain hæmatin.

The examination of *solutions* of the tentacles revealed the presence of a small amount of other pigments; but it appears that the presence of the "yellow cells" has something to do with the absence or suppression of respiratory pigments.

(*i*) *Anthea cerus.*—"In some specimens the ectoderm was a pale red, also the base, and the tentacles a pale green tipped with violet. In the violet apices of the tentacles, actiniochrome was detected. The rest of the tentacles gave a spectrum resembling that of chlorophyll." The base in some specimens of this species contained actiniohæmatin. Besides the above-mentioned pigments, there are "yellow cells" present in the body cavity and ectoderm. The "yellow cells" on treatment with Schulze's solution gave the reaction for cellulose. These cells contain starch.

Anthea cereus contains symbiotic unicellular algæ, and MacMunn has proved that the chlorofucin in *Anthea cereus*, *Bunodes ballii*, and *Sagarita bellis*, is without doubt due to the so-called "yellow cells"; and in those anemones possessing "yellow cells" there is more or less suppression of the respiratory pigments found in other *Actiniæ*. The extracts of the "yellow cells," prepared by Sir G. Stokes's fractional method, yielded chlorophyll and chlorofucin, proving that the colouring matters of the algæ are several, for there are present at least one chlorophyll, one chlorofucin, and certain lipochromes, and perhaps other pigments, all of which belong to the "yellow cells."

These "yellow cells" are parasitic algæ and have not a hepatic function as supposed by the late Dr. Krukenberg. In no Invertebrate "liver" are such bodies found.

The Invertebrate *liver*-pigment, or enterochlorophyll, occurs mostly dissolved in oil, or in granules, or diffused through the protoplasm of the lining cells of the "liver" tubes.* The colouring matters of these "yellow cells" belong to the chlorophyll group, and bear no relationship whatever to enterochlorophyll, which is in direct opposition to Krukenberg, who stated that the pigment of the "yellow cells" is a hepatochromate, which is his name for enterochlorophyll.

The function of animal chlorophyll is of use in the respiratory processes of animals.†

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* MacMunn in *Proc. Roy. Soc.* 1885; and *Philos. Trans.* 1886, part i.

† Regnard in *Comptes Rendus*, vol. 101, p. 1293.

(*j*) *Cornynactis viridis.*—MacMunn has examined the red specimens of this little sea anemone. On putting one of these animals into a compressorium and examining it by means of an achromatic condenser and a microspectroscope, a spectrum was obtained whose bands do not correspond with either those of actiniohæmatin or actiniochrome, for they are nearer the violet and differ in other respects. Yet they belong to a pigment which is related to actiniohæmatin, for this pigment can readily be changed into hæmochromogen. No "yellow cells" are present in either the red or green varieties of *C. viridis.* There is no doubt that this anemone contains a respiratory pigment allied to actiniohæmatin.

The important researches of MacMunn and others have shown: (1) That a *respiratory* pigment is largely present in many *Actiniæ.* That it must be respiratory is shown by the fact that one of its decomposition products is capable of existing in a state of oxidation and reduction. That it is closely related to hæmoglobin is proved by the fact that it is capable of being converted into hæmochromogen (reduced hæmatin) and hæmatoporphyrin,* which are undistinguishable from the same products obtained from hæmoglobin. (2) The respiratory pigment in the *Actiniæ* cannot be looked upon as a *carrier* of oxygen, but as a means to *keep* it in combination until it is wanted by the cells for metabolic purposes. "As it is distributed all over the surface of some *Actiniæ,* the whole body of such an animal may, in a physiological as well as in a morphological sense, be considered comparable to a single organ of a higher animal, so far, at least, as *internal*† respiration is concerned."

(3) In every species of *Actiniæ,* even in those almost destitute of colour, the presence of respiratory pigments has been detected. The coloured proteids, which are concerned in tissue-respiration, enable the anemone to abstract oxygen

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* Moseley's polyperythrin is identical with MacMunn's hæmatoporphyrin.

† That is, tissue-respiration.

from the sea-water in which it lives, and to hold the oxygen in its tissues. (4) In animal tissues chlorophyll or allied pigments may be of use in furnishing oxygen to the animal; and in those *Actiniæ* with "yellow cells" the chlorophyll pigment appears to replace (more or less) the respiratory proteid. (5) Throughout the whole animal kingdom, in each tissue and organ there are present pigments which are concerned in the respiration of those tissues and organs; they take the oxygen from the circulating blood, and fix it until it is wanted for metabolic purposes in the cells. MacMunn* calls all these coloured proteids histohæmatins, and the one found in muscle he named myohæmatin. (6) Besides the respiratory pigments found in the *Actiniæ*, there are others which appear to be of use for decorative purposes, and to this class Moseley's actiniochrome belongs. Actiniochrome cannot be changed into anything capable of being oxidised and reduced; in other words, it is not a respiratory pigment. What its use may be it is difficult to say. It may be intended for a protective purpose or as a means of attracting prey.

THE ECHINODERMATA.

The cloacal tubes of the higher *Holothuridea* are most likely of a respiratory function. These tubes, which ramify in the perivisceral cavity, open by two orifices into the cloaca. This cloaca receives the water, and projects it vigorously outwards, on an average three times a minute. Analogous systems exist in many other Echinoderms, and often they are bedecked with cilia.†

The ambulacral vesicles of other Echinoderms constitute internal respiratory organs. Besides these organs, tissue-respiration (by the aid of pigments) is well developed in the Echinoderms.

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* "Researches on Myohæmatin and the Histohæmatins," in *Philosophical Transactions of Royal Society*, 1886, pt. i. p. 267.

† Dugès in his *Physiologie Comparée*, t. 2, p. 355.

MacMunn* has discovered various pigments in the tissues and organs of the Echinoderms; and in most of them the appearances differ in no respect from those seen in *Uraster rubens.*

A portion of the tissue or organ is examined in a compressorium, by means of which any required thickness can be examined: it is illuminated by a strong light condensed upon it by means of a substage achromatic condenser, and is examined by a microspectroscope (see Fig. 32), or by means of a chemical spectroscope.

The generative organs (♂ and ♀) and ova of *Uraster* contain a typical histohæmatin. The spectrum of this pigment gave the following readings:—

1st band	λ 613 to λ 591, or 593.
2nd "	λ 569 " λ 560.
3rd "	λ 556 " λ 548·5.
4th "	λ 537 " λ 516 (about).

A spectroscopic examination of the stomach-wall and the ampullæ of *Uraster* showed the presence of hæmochromogen.

"In the integument of *Uraster rubens,* when it has a brownish tint, the presence of hæmatoporphyrin † can be easily proved, and as the only pigments present in the animal are enterochlorophyll in the radial cæca, histohæmatins in the tissues, and a lipochrome here and there, and as hæmatoporphyrin cannot be obtained from enterochlorophyll or from the lipochromes, it is highly probable it is a metabolite of the histohæmatins, or, what is less likely, that these pigments may be derived from the same radicle."

M. Fœttinger states that he found hæmoglobin in *Ophiactis virens* and MacMunn's researches tend to support Fœttinger's idea of the passage from a histohæmatin to a hæmoglobin.

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* *Philosoph. Trans.*, 1886, pt. i. p. 269; *Quarterly Journ. Micros. Science,* vol. 30, p. 51; *Journal of Physiology*, vol. 7, p. 242.

† This pigment can be isolated by digesting the integument in alcohol and sulphuric acid.

The integument of *Asterias glacialis* does not contain hæmatoporphyrin, but there is present at least one rhodophan-like lipochrome. The radial cæca (so-called liver) contain enterochlorophyll and a lipochrome.

MacMunn has also examined many other species of Echinoderms, and the following table gives a partial summary of the pigments present in various tissues and organs of these animals :—

	Integument.	Ovaries.	Digestive gland.	Radial cæca.
Holothuria nigra .	—	lipochromes	lipochromes	—
Ocnus brunneus .	—	lipochromes	—	—
Asterias glacialis	lipochromes	—	—	entero-chloro-phyll and lipo-chromes.
Asterina gibbosa .	lipochromes	lipochromes	—	”
Goniaster equestris .	”	—	—	”
Solaster papposa .	”	—	—	”
Cribella oculata .	”	lipochromes	—	—

MacMunn says that the *respiratory* proteids "are as important as hæmoglobin, if not more so in some animals, and they have the right of priority in time, as they were developed at an earlier period than hæmoglobin, speaking from a phylogenetic point of view." Even in the lowest of the *Metazoa*—the Sponges—MacMunn * has met with histohæmatins where they are also capable of oxidation and reduction, and are therefore respiratory. "It is not improbable, but indeed likely, that by a process of physiological selection these respiratory proteids may have become more complex, and their molecular instability therefore greater, as the animal body became more elaborated, and a necessity arose for the

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* *Proceedings of Physiological Society*, 1886.

setting apart of respiratory proteids for abstraction of oxygen from the air. In this way hæmoglobin may have arisen, and although it is usually said that the mere colour of hæmoglobin is of no use, yet the fact cannot be denied that *most respiratory proteids are coloured bodies.* The molecular complexity of the histohæmatins is certainly not so great as that of hæmoglobin, and their respiratory capacity is apparently far inferior to that of hæmoglobin, for the histohæmatins do not take up the oxygen in a loose combination, although they certainly do unite with it in a more stable combination. At the same time, one must remember that the myohæmatin or the histohæmatin procurable from dead tissues differs in spectrum, and therefore probably in chemical composition, from that of the living tissues. It is well known that no free oxygen can be obtained from muscle, and if myohæmatin be the body with which it unites, then myohæmatin must certainly have something to do with the storing of oxygen in muscle; and if this be the case in muscle, it must be the case in other tissues, and in the organs in which the histohæmatins are found."

In studying the chromatology of many Invertebrates, MacMunn "has been struck by the fact that while some of their colouring matters can be reduced by such reducing agents as ammonium sulphide, yet by shaking with air, or by passing a stream of oxygen into them, they cannot be re-oxidized; in this point they afford a parallel to the histohæmatins. Krukenberg has noticed the same thing, and he has justly concluded that the respiratory processes of many of these animals is not as simple a matter as it is supposed to be. There can be no doubt that the union of these respiratory colouring matters with oxygen is a much more stable one than is the case with hæmoglobin. It is in the observation of such facts as these that the spectroscope comes to be of value, for if these bodies did not show absorption bands, one could not determine whether they were in the oxidised or reduced state."

THE TRICHOSCOLICES.

The water-vascular systems, which are often ciliated, constitute internal respiratory organs. The water which permeates these tubules contains oxygen. Respiration in many of the organisms belonging to this class is also performed by the external surface of the body; and no doubt internal or tissue respiration takes place by means of various respiratory pigments.

THE ANNELIDA.

In the *Annelida* the principal seat of respiration is the pseudo-hæmal system. For instance, in both the *Hirudinea* and *Oligochæta* this system of vessels is well developed, and has been alluded to in a previous chapter.

The blood which these vessels contain consists of a coloured plasma, and it is stated to possess no nutritive properties. The pigment present in this fluid is hæmoglobin.*

In reality the fluid contained in these vessels has a respiratory function and contains air in solution. The pseudo-hæmal systems are in communication with the external medium. This communication of the respiratory system with the air or water in which the animal lives probably serves the purpose of the gaseous interchanges which are so essential in animal life. There must be a constant accumulation of carbonic anhydride in the respiratory fluid, and therefore a constant diminution of the quantity of oxygen. The oxygen must be restored, the carbonic anhydride excreted. Both these important ends are attained by means of this ever-recurring communication between the water-vascular system and its homologues on the one hand, and the animal's environment on the other. Hence in the lowest as well as in the highest forms of the animal kingdom, cutaneous respiration is an important adjunct to the various organs or devices

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* MacMunn has proved that the integument of *Lumbricus terrestris* contains hæmatoporphyrin (*Journ. of Physiol.*, vol. 7, p. 248).

which are usually called respiratory; and certainly this form of respiration is well developed in *Hirudo.*

In the *Polychæta* there are simple or branched cirri or branchiæ which have ciliated walls and contain blood-vessels. These branchiæ, situated on the dorsal walls, are usually appendages of the parapodia, and have a respiratory function. In the lower Invertebrates the branchiæ are mostly situated externally (*e.g.*, *Arenicola*), so as to float freely in the surrounding water; whilst in the more highly organised, as the Molluscs, these organs are enclosed in a cavity into which the water has free access, and may easily be renewed.

In the *Gephyrea* there appears to be several devices all aiding in the function of respiration.

(*a*) A respiratory function is attributed to the tentacula in these marine vermiform animals.

(*b*) In *Priapulus* and *Sternaspis* there are certain filamentous appendages given off at the posterior end of the body. These are said to be branchiæ.

(*c*) The pseudo-hæmal system is present in most of the *Gephyrea*, and it has a respiratory function.

(*d*) "In *Echiurus*, *Bonellia*, *Thalassema*, a pair of tubular, sometimes branched organs, which are ciliated internally, and communicate by ciliated apertures with the perivisceral cavity, open into the rectum. These appear to represent the water-vessels of the *Rotifera* and the respiratory tubes of the *Holothuriæ.*"

Although the above devices represent the *actual* organs of respiration in the *Annelida*, supplementary respiration, by means of pigments, also occurs in this class of animals.

In *Phyllodoce viridis* there occurs a green pigment which is not chlorophyll.* This pigment is soluble in alcohol and benzene. MacMunn examined a living specimen of this Polychæte *Annelid* in the compressorium, under the microspectroscope, but he could not detect any bands; in fact, he

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* Prof. P. Geddes in *Proc. Roy. Soc. Edin.*, vol. 11, p. 379; and Dr. MacMunn in *Quart. Journ. Micros. Science*, vol. 30, p. 70.

says: "No chlorocruorin, no hæmoglobin, no chlorophyll was present, and no discernible lipochrome. The solid pigment became reddish-brown with sulphuric acid, and red-brown with nitric acid." MacMunn simply names this colouring matter phyllodoce-green, as it is impossible to refer it to any class of animal pigments.

In *Pontobdella,* a pigment, bearing a remote resemblance to chlorophyll, has been extracted from the integument where it occurs in large pigmented cells of a green colour. This worm, belonging to the *Hirudinea,* although it lives on fish-blood, is capable of manufacturing from its food a colouring-matter allied to chlorophyll. This pigment is soluble in alcohol and ether.

Mr. F. E. Beddard, F.R.S.E.,* has examined the glandular cells in the integument of *Æolosoma tenebrarum* and other species of this genus. In the species mentioned these cells are nucleated, and in the centre is a large globule of oily appearance impregnated with a green colouring-matter. Vejdovsky † states that this globule is stained black with osmic acid; but Beddard found that this acid stained the globule a brown colour. Various reactions given in Beddard's paper show that the green colouring-matter of this worm is not chlorophyll. In its behaviour with acids and alkalies it resembles certain pigments described by Prof. Moseley,‡ Dr. MacMunn, and others; and there is little doubt that it has a respiratory function. This pigment is different from bonellein and chlorocruorin, two pigments present in certain Annelids. The blood of *Æolosoma tenebrarum* is colourless, and there are no special respiratory pigments in other parts of the body; therefore, as Beddard justly remarks, "the pigment of the integumental glands may perform the function of respiration."

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* *Proceedings of the Zoological Society,* 1889, p. 51; and *Annals and Magazine of Natural History,* 1889, p. 262.

† *Thierische Organismen der Brunnenwässer von Prag,* p. 61 [1882].

‡ *Quart. Journ. Micros. Science,* vol. 17.

Other species of *Æolosoma* contain various coloured oil-globules, showing the presence of different pigments in each case. These pigments differ considerably in their capacity for oxygenation and deoxygenation—hence the reason of Beddard's remark: "That the orange-brown pigment of *Æolosoma quaternarium* and the bright green pigment of *Æolosoma variegatum* and *Headleyi* may be less perfect as respiratory pigments, and therefore in course of degeneration."

Although chlorophyll is absent in *Phyllodoce*, *Pontobdella*, and *Æolosoma*, certain Annelids contain this pigment.

Chætopterus is one of these animals containing chlorophyll, as shown by Prof. Ray Lankester, whose investigations have been subsequently confirmed by Dr. MacMunn. The alcoholic solution of this pigment possesses a red fluorescence, and gives all the chlorophyll bands, and yields "modified" and "acid" chlorophyll, as well as phyllocyanin, by suitable treatment. There is no doubt that *Chætopterus insignis* contains a true chlorophyll, although it may be remarked that Prof. P. Geddes could not detect any evolution of oxygen on exposing *Chætopterus Valenciennesii* to sunlight; but this is not to be wondered at, since the chlorophyll is shut up within the animal's body (MacMunn).

A large number of the *Annelida* contain hæmoglobin, as shown by Lankester and others: among these may be mentioned the following: *Arenicola, Lumbricus, Terebella, Cirratulus, Nereis,* and *Aphrodite.* In the last-mentioned genus the hæmoglobin is limited to the ventral ganglia. In *Polynöe,* the area round the cerebral ganglion is of a red colour. According to MacMunn this pigment showed a band which somewhat resembled that of reduced hæmoglobin. Many of the *Annelida* are also rich in the pigments known as lipochromes.

There is no doubt that in this class of animals respiration is greatly aided by various respiratory pigments.

THE NEMATOSCOLICES.

Very little is known concerning respiration in the *Nematoidea*, but the investigations of Dr. G. Bunge* have thrown a certain amount of light upon the subject. He has shown that *Ascaris mystax* (infesting the intestine of the cat) and *Ascaris acus* (from the intestine of the pike) will live four or five days in media quite free from oxygen. In the ultimate respiratory processes of these animals there must be a formation of energetic reducing substances (nascent hydrogen and easily oxidisable organic matter), which unite with one atom of the oxygen-molecule, even to a greater extent than in animals which breathe oxygen. These animals possess no respiratory apparatus, but, *à priori*, there may be present in their bodies one or more of the respiratory pigments which retain oxygen within the system; and this retention of oxygen may be for a considerable time.

In order to investigate this important question more fully, Bunge employed larger species of *Ascaris*. The parasite of the horse, *Ascaris megalocephala*, was found unsuitable, as it only lived for two days after removal from the intestine; but *Ascaris lumbricoides* of the pig lived from five to seven days, and it was therefore used in the investigations. In boiled salt solution it gave off abundance of gas, which was collected over mercury. This gas was completely absorbed by potash, and consisted of pure carbonic anhydride. The quantity of gas obtained in this time was from 5 to 10 cc. per gramme of the animal's body-weight. In three experiments a small measured quantity of oxygen was added to this gas artificially, but there was no diminution in its volume after the admixture; thus not only hydrogen, but other reducing substances are absent.

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* *Zeitschrift für Physiologische Chemie*, vol. 8, p. 48; and vol. 14, p. 318.

THE MYRIAPODA.

The respiratory organs of these Arthropods are tracheæ. The tracheæ form a branched series of tubes spreading throughout the body and conveying oxygen to the various organs, tissues, and blood-vessels. The tracheæ communicate with the exterior by openings called stigmata, which are situated on "the lateral or ventral surface of more or fewer of the somites. In *Scutigera* * the stigmata are situated in the median dorsal line of the body."

In this class of animals the function of respiration is of a much higher order than in any other air-breathing animal alluded to in the present chapter. We find in the *Myriapoda* a special set of tubes set apart for respiration and by means of these tubes the air is brought into contact with the blood-vessels distributed over the walls of the tubes. Although these animals breathe principally by means of a tracheæ or air-tubes, they also breathe in lesser degree by their general surface; but this kind of respiration is more marked in those animals whose integument is unprotected by epidermal developments.

The introduction and expulsion of the air in the tracheæ appear to be helped by regular movements of the abdominal walls.

THE INSECTA.

In the *Insecta* the systems of tracheæ or air-tubes are further developed. The ultimate ramifications of these tubes constitute a fine network, analogous in many respects to the capillary networks.

As in the *Myriapoda* these tracheæ communicate externally by means of stigmata. These stigmata are restricted to the somites of the abdominal region of the body; and very frequently these openings are occupied by perforated plates. The perforated plates act as sieves or filters, and thus free the air, as it passes through them, of mechanical impurities.

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* See also Sinclair in *Proc. Roy. Soc.*, 1871; and *Nature*, Dec. 17, 1891, p. 164.

As a general rule, each stigma does not open directly into a tracheal tube, but into an ante-chamber whence the trachea takes its origin. This ante-chamber is frequently provided with a series of little plaits, folds of its lining membrane. These plaits or epiglottides also act as filters.

The principal trunks of the tracheal system have three coats. The internal one (in contact with the air) is a continuation of the integument. The middle one is a spiral coat of chitin, which serves to keep the tube open. The external coat is of connective tissue.

As in the *Myriapoda* the air in the tracheæ is kept in motion by the movements of the abdominal walls. These rhythmical movements are frequent; on an average twenty-five in *Lucanus cervus* (the stag-beetle), eighty in *Apis*,* and from fifty to fifty-five in the *Locusta viridissima* of Linnæus. Notwithstanding the high development of their respiratory apparatus and the activity of their lives, insects resist asphyxia for a long time. The author kept a stag-beetle for six days in an atmosphere containing 60 per cent. of chlorine, with the result that it was still living after the expiration of that time; and many insects resist the action of an atmosphere containing from 40 to 70 per cent. of carbonic anhydride. This may account for the fact that *insects* and other cold-blooded animals were able to withstand an atmosphere so laden with carbonic anhydride as was that of the early ages of the world's history. And if the descendants of the primitive insects are now capable of living in an atmosphere containing only six volumes of carbonic anhydride in 10,000 volumes of air; it is but one of many instances where natural selection (the survival of the fittest) and the direct action of the environment have worked hand in hand together.

Concerning the vitality of insects, it may be remarked that M. Lyonnet states that certain caterpillars revived after being submerged in water for eighteen days.

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* In *Apis* (the bee), Newport observed forty in a state of rest, but they rose to one hundred and twenty with muscular exertion.

Respiration in the aquatic larvæ of certain insects is performed by means of tracheal gills or branchiæ. These branchiæ are delicate folds of the integument, and are richly supplied with minute tracheæ. The oxygen dissolved in water, wherein or whereon these larvæ flit to and fro, passes into the tracheæ. This phase of respiration among the *Insecta* is suggestive of the branchiæ of certain forms of the *Annelida*, into which the vessels of the pseudo-hæmal systems enter.

The larvæ of *Libellula* and *Æschna* present yet another form of respiratory organ. "Although they possess a pair of thoracic stigmata, these appear to have little or no functional importance, but respiration is effected by pumping water into and out of the rectum. The walls of the latter are produced into six double series of lamellæ, in the interior of which tracheæ are abundantly distributed, and which play the same part as the tracheal branchiæ just mentioned. These rectal respiratory organs, in fact, appear to be a complicated form of the so-called 'rectal glands' which are so generally met with in insects."

Besides the systems of tracheal tubes, tissue-respiration is well marked in the *Insecta*, for MacMunn has met with myohæmatin in abundance in these animals; and it is probable that histohæmatin is also present, and both of these pigments have a respiratory function.

THE ARACHNIDA.

In these animals "tracheæ may exist alone, or be accompanied by folded pulmonary sacs, or the latter may exist alone, as in the Scorpion. In this case these lungs* are supplied by blood which is returning from the heart."

"The flow of air into and out of the air cavities is governed by the contractions of muscles of the body, disposed so as to alter its vertical and longitudinal dimen-

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* See also Macleod's paper in *Bull. Acad. Roy. Scien. Belg.*, vol. 3, p. 779.

sions. In the higher forms the entrance and exit of air is regulated by valves placed at the external openings (stigmata) of the tracheæ, and provided with muscles, by which they can be shut." (Huxley.)

In some of the lowest orders of this class there is no higher form of respiration than that by the general surface of the body. In the *Acarina* (represented by *Acarus*), *Araneina* (represented by *Epeira*), and the *Arthrogastra* (represented by *Scorpio*), we have simple tracheal respiration in the first-mentioned order; in the second, respiration is performed by two stigmata opening into tracheæ, and several others opening into pulmonary sacs; and in the third order, all the stigmata open into pulmonary cavities or sacs.

In *Scorpio*, which is the highest of the *Arachnida*, there are no tracheal tubes, the animal breathing wholly by pulmonary sacs. This rudimentary lung consists of a vascular lining membrane extended into several folds, which are in close relationship to the margins of the openings, and thus afford an increase of surface for the contact of blood and air.

Tissue-respiration,* by means of pigments (myohæmatin and probably histohæmatin), also occurs in the *Arachnida*.

THE CRUSTACEA.

These animals breathe by means of branchiæ, which are highly developed in the *Crustacea*.

These organs contain true blood-vessels of a venous nature. The carbonic anhydride from tissue-combustion passes out into the water around, whilst the oxygen dissolved in the water passes into the blood. "The access of fresh water to the branchiæ is secured by their attachment to some of the limbs; and in the higher Crustaceans, one of the appendages, the second maxilla, serves as an accessory organ of respiration. Although especially adapted for aquatic respiration, they

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* MacMunn, in *Philos. Trans. of Royal Society*, 1886, pt. 1, p. 272.

(branchiæ) are converted into air-breathing organs in the land crabs, being protected and kept moist in a large chamber formed by the carapace." These branchiæ are supplied with blood which is returning to the heart.

The gills or branchiæ are composed of either broad lamellæ, or these lamellæ are divided into filaments, giving the gill its plume-like appearance. As already stated, it is essential that the water in contact with the branchiæ should be constantly changed. This change is effected by various devices. Thus, in *Astacus*, *Homarus*, and the higher *Crustacea* the branchiæ are placed in a chamber, which is bounded externally by the branchiostegite, and internally by the lateral walls of the thoracic segments. It is open below and behind, between the bases of the thoracic limbs and the free edge of the branchiostegite. Behind the anterior opening of the chamber (on each side of the body) lies the scaphognathite (a broad fringed organ), which moves continually backwards and forwards, baling out the impure water of the chamber (*i.e.*, the water impregnated with CO_2), and thus compelling fresh or oxygenated water to flow in through the posterior aperture and over the branchiæ.

The number of branchiæ varies considerably in different Crustaceans (*e.g.*, in *Astacus* there are eighteen in each chamber, and in *Nephrops* there are twenty).

The respiratory function in all *Branchiopoda* is performed by the branchial feet; but according to Dr. G. O. Sars,* there is, however, another part of the body in the *Phyllopoda* (*i.e.*, in *Cyclestheria hislopi*) that apparently can lay claim to a true respiratory function. Sars, as well as others, state that the valves of the shell, which receive a considerable quantity of blood, and their inner delicate coating, seem highly calculated to produce an exchange of gases with the water. The necessary renewal of the water is effected by the well-nigh uninterrupted movements of the legs, whereby a continual current is produced within the

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* *Christiania Videnskabs-Selskabs Forhandlinger*, 1887.

shell, bathing not only the legs themselves, but also the inner coating of the valves.

Dr. MacMunn has discovered the presence of histohæmatin, myohæmatin, and enterochlorophyll in the organs and tissues of the following Crustaceans: *Homarus, Cancer, Astacus, Carcinus,* and *Pagarus*; consequently tissue-respiration* is well developed in these animals. No doubt this kind of respiration plays an important part in the land crabs; and, *à priori,* the respiratory pigments should be more largely developed in these animals than in other Crustaceans.

THE ACTIVITY OF RESPIRATION.

We owe to MM. Regnault, Reiset, and Jolyet nearly the whole of our knowledge corncerning the ratio between the carbonic anhydride exhaled and the oxygen absorbed in the *Invertebrata.* The animals employed in these investigations were allowed to remain under a bell-glass for a certain time; and as the oxygen of the air was absorbed, a similar volume of carbonic anhydride was admitted into the apparatus. For an illustration and a description of the apparatus used in these experiments the reader is referred to *Recherches Chimiques sur la Respiration des Animaux des diverses Classes* by Regnault and Reiset, or to the late Dr. A. Würtz's *Traité de Chimie Biologique,* pp. 422, 434, and 440.

The table on p. 234 represents the results obtained by these French savants.

Concerning the figures it may be remarked that among the bivalve *Mollusca* the weight of the shell naturally diminishes the proportion of oxygen absorbed, when this is reported as the gross weight of the animal.

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* See also a recent paper on "The Respiration of Cells in the Interior of Masses of Tissue," by M. H. Devaux, in *Comptes Rendus,* vol. 112 [1891].

		No. of animals.	Weight of animals in grammes.	Temperature: centigrade degrees.	Oxygen absorbed per hour per kilogramme (in grammes).	$\frac{CO_2}{O_2}$ (in grammes).
Crustacea.	*Astacus fluviatilis* . .	8	250	12.5	0.0547	0.86
	Gammarus pulex . .	8	74	12.5	0.1901	0.72
	Falæmon squilla . .	8	395	19	0.1800	0.83
	Cancer pagurus . . .	1	470	16	0.1541	0.84
	Homarus vulgaris . .	1	315	15	0.0979	0.80
	Palinurus quadricornis	1	520	15	0.0636	0.88
Mollusca.	*Octopus vulgaris* . . .	1	2310	15.5	0.0636	0.86
	,, ,, ...	1	2300	16	0.0626	0.65
	Cardium edule . . .	127	1317	15	0.0213	0.84
	Mytilus edulis . .	60	1500	14	0.0176	0.76
	Ostrea edulis . . .	37	1835	13.5	0.0193	0.79
Annelida.	*Hirudo medicinalis* . .	104	235	13.5	0.0331	0.86
	,, ,, 5 days after ingestion of blood	104	235	13	0.0572	0.90
Zoophyte.	*Asteracanthion rubens* .	—	900	19	0.0461	0.79

The next table represents the results of a further series of experiments by the same authorities :

	No. of animals.	Weight of animals in grammes.	CO_2 exhaled per hour (in grammes).	Oxygen absorbed per hour (in grammes).	Oxygen absorbed per hour per kilogramme (in grammes).	Ratio of O in CO_2 to O absorbed (in grammes).
Cockchafer . . .	40	40.3	0.0472	0.0434	1.076	0.791
Silk-worm (larvæ) . .	18	42.5	0.0388	0.0357	0.840	0.798
Silk-worm (imago) .	42	—	0.0478	0.0468	1.170	0.739
Silk-worm (pupæ) . .	25	—	0.00446	0.00508	0.242	0.639
Earthworm . . .	—	112	0.01218	0.01135	0.1013	0.776

Among the results which have been observed by MM. Regnault, Reiset, and Jolyet are (1) that the amount of oxygen contained in the carbonic anhydride exhaled is smaller than that of the oxygen absorbed. (2) The respiration of insects, when these animals are in full activity, has the same energy as that of the higher *Vertebrata;* while the earthworms do not respire more than reptiles. (3) Respiration in the *Invertebrata* diminishes (as a rule) in proportion as the temperature is lowered. This is because these animals are incapable of producing a sufficient internal warmth, and consequently they become gradually colder until the movement when they fall into a state of hibernal sleep, or die. (4) After feeding, most Invertebrates (and particularly the *Insecta*) respire more energetically than at other times. (5) All animals subjected to habitual regimen always expire a little more nitrogen than is contained in the air inspired. (6) In inanition, the absorption of oxygen and the exhalation of carbonic anhydride are greatly diminished. The fewer the functions exercised by an animal, the less carbon it expends.

Dr. Moleschott* has shown that the action of light upon the skin notably augments the intensity of the respiratory phenomena.

In general terms it may be stated that "behind every biological activity there is an oxidation of the anatomical elements. No organ escapes this law, and the nervous centres are as much in subjection to it as the other organic apparatus. Every thought, every volition, every sensation, corresponds to an oxidation of the living substance, as well as every secretion, every movement, &c."

THE POLYZOA.

In this class we have probably the representative of the first stage in the evolution of the respiratory apparatus of

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* *Wiener Medicinische Wochenschrift*, 1885.

the lower *Vertebrata.* In these animals the structure of special interest is the dilated pharynx (see Fig. 17). A constant stream of water enters the mouth and passes into the pharynx, whose walls are richly supplied with blood-vessels, and it is through the walls of the pharynx that absorption takes place. The tentacula serve as an accessory organ of respiration.

In the *Polyzoa* the protrusible parts of the body also absorb oxygen from the surrounding water. MacMunn has examined *Lepralia foliacea* and finds that it contains an abundance of chlorophyll mixed with a lipochrome. The chlorophyll is also accompanied by a second pigment, probably chlorofucin. *Flustra foliacea* also contains a chlorophylloid pigment.

THE BRACHIOPODA.

In these animals the blood is contained in branched sinuses in the perivisceral cavity. In the sinuses of the ciliated tentacle-bearing arms and of the inner wall of the mantle, the blood is purified by being brought into close osmotic relation with the water in which these animals live.

Very little is known concerning the presence of respiratory pigments in the *Brachiopoda.*

THE MOLLUSCA.

The aquatic *Mollusca* have well-developed branchiæ usually enclosed within branchial chambers. These branchiæ are broad and plate-like; and the water in contact with them is changed by means of vibrating cilia. In the *Branchiogasteropoda* the branchiæ are dendritic, instead of plain and plate-like.

The *Cephalopoda* are divided into two distinct orders—the *Dibranchiata* with two gills, and the *Tetrabranchiata* with four gills in the mantle cavity. The water is conducted to the branchial chambers of the *Dibranchiata* (which is the highest of the two orders) by means of the infundibulum whose opening is situated beneath the head.

In the *Pteropoda* "the delicate lining membrane of the pallial cavity serves as the respiratory organ."

The mantle is also "an accessory organ of respiration, being so modified as to direct, or to cause, the flow of currents of water over the branchiæ contained in its cavity."

In the *Pulmogasteropoda* (air-breathers) "the lining wall of the mantle cavity becomes folded and highly vascular, and subserves the aëration of the venous blood, which flows through it on its way to the heart. The lung is here a modification of the integument, and might be termed an external lung. The lungs of the air-breathing *Vertebrata*, on the contrary, are diverticula of the alimentary canal; . . . . and the blood flows from the heart."

The membranous respiratory sac of the *Pulmogasteropoda* is not morphologically a true lung, as it is developed from the integument; but it may be physiologically regarded as a rudimentary lung performing a similar function to the true Vertebrate lung which first appears in *Pisces.**

"Many animals are truly amphibious, combining aquatic and aërial respiratory organs. Thus, among Molluscs, *Ampullaria* and *Onchidium* combine branchiæ with pulmonary organs." (Huxley.)

The Pulmogasteropod lung is the simplest form of lung to be met with in the animal kingdom. It has been compared to "a single so-called air-cell of the Mammalian lung. In each case there is an internal cavity lined by a delicate membrane supplied with impure blood, and having air in contact with its free surface."

Tissue-respiration is wonderfully well developed in the *Mollusca*, for MacMunn has discovered an abundance of respiratory pigments in these animals.

In *Ostræa*, *Unio*, *Anodonta*, *Mytilus*, *Limnæus*, *Paludina*, *Patella*, *Purpura*, *Littorina*, *Helix*, *Limax*, and *Arion*, histo-

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* In *Lepidosiren* (mud-fish) there is a transition from the piscine air-bladder to the Reptilian form of lung. The air-bladder of the fish appears to be chiefly a hydrostatic organ, or rather an accessory one of respiration.

hæmatins have been discovered in various parts of the body; and hæmoglobin occurs in the pharyngeal muscles of the following Molluscs: *Purpura lapillus*, *Littorina littorea*, *Trochus cinerarius*, *Patella vulgata*, *Limnæus stagnalis*, and *Paludina vivipara*.

Myohæmatin is the histohæmatin characteristic of Invertebrate muscle, but in the above-mentioned species this pigment is replaced by hæmoglobin.* This proves that the histohæmatins are connected with hæmoglobin and its derivatives.

Myohæmatin occurs in all the *Pulmogasteropoda* examined by MacMunn. "Myohæmatin is the true intrinsic colouring matter of muscle, and the histohæmatins the intrinsic colouring matters of the tissues and organs; both may be reinforced or replaced at times by hæmoglobin when extra activity of internal respiration is required; probably the same radicle may be made use of for building up all these pigments, for they seem to be related, since the same decomposition product—hæmatoporphyrin—is probably yielded by all of them. The fact that in the lower animals pigments of less complex molecular structure than hæmoglobin and identical with its decomposition products can function like it, forces itself on anyone's attention who studies the pigments of the *Invertebrata*."

MacMunn has extracted hæmatoporphyrin from the integument of *Limax flavus*, *Limax variegatus*, *Arion ater*, and *Solecurtus strigillatus*. With the exception of *Solecurtus*, in all these Molluscs enterohæmatin is found in the so-called liver (pancreas), and histohæmatins in various tissues and organs, and there can be no doubt, as MacMunn states, that here also the hæmatoporphyrin is a metabolite of these pigments.

The so-called livers of the following Molluscs contain enterochlorophylls which are identical with Krukenberg's hepatochromates: *Ostræa*, *Buccinum*, *Fusus*, *Mytilus*, *Cardium*,

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* The blood of *Solen legumen* contains hæmoglobin (Lankester).

Anodonta, *Unio*, *Octopus*, *Paludina*, *Limnæus*, *Patella*, *Helix*, *Purpura*, *Arion*, *Limax*, and *Littorina*.

The enterochlorophyll occurs dissolved in oil globules, also in the granular form, and it is sometimes dissolved in the protoplasm of the secreting cells of the so-called liver. In hibernating snails, these pigments occur in greater abundance in the winter than in the summer time.

In concluding these remarks on the principal colouring matters of the *Mollusca*, we may state that enterohæmatin* occurs in the "livers" of *Helix*, *Limax*, *Arion*, and *Patella*; and MacMunn believes that enterohæmatin is probably the mother-substance of those histohæmatins, which are found in animals in whose "livers" it is built up.

THE TUNICATA.

In the *Pharyngopneustal Series* (*Enteropneustra* and *Tunicata*) a new form of internal aquatic respiratory organ appears. The dilated pharynx of the *Polyzoa* is further developed in these animals, being perforated by lateral openings. These openings are ciliated, and a constant stream of water enters at the mouth or oral aperture, which passes into the pharynx through the openings (branchial clefts), then into the atrial chamber (which is developed round the pharynx), and out of its aperture into the air in which the animal lives. As in the *Polyzoa*, the walls of the pharynx are well supplied with blood-vessels.

The *Tunicata* have been called sea-squirts, for if they are irritated they suddenly contract the muscular walls of the body, and this contraction causes the water contained in the atrial and branchial cavities to squirt out in two jets. It may be remarked that the late Mr. Darwin considered the Tunicate as the representative of the point at which the *Vertebrata* began to work off from primordial forms common to it and to the *Mollusca*.

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* Enterohæmatin is synonymous with hæmochromogen and helico-rubin of Krukenberg.

Drs. MacMunn and Krukenberg have extracted several lipochromes from these animals.

In concluding our account of the function of respiration in the *Invertebrata,* we may summarise the contents of this chapter in the following manner:—(1) There is respiration by the general surface of the body. (2) Respiration by air dissolved in water. In this mode of respiration the respiratory organs are either internal (contractile vacuoles, water-vascular systems, pseudo-hæmal vessels), or external (gills). (3) Respiration of air directly; this mode being performed by three distinct mechanisms, of which the first is the respiration of air (not dissolved in water) by the general surface—*i.e.,* cutaneous respiration. The second is by means of the tracheæ or air-tubes; and the third by pulmonary sacs or rudimentary lungs.*

In addition to the above modes of respiration there is also tissue-respiration by means of various pigments. These pigments are capable of retaining oxygen within the system, and no doubt they play a most important part in the respiration of the *Invertebrata;* and possibly they play a more important part in these animals than in the *Vertebrata,* where the respiratory apparatus becomes highly differentiated into powerful and special organs.

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* Gills first appear in the *Polychæta,* tracheal tubes in the *Myriapoda,* and a rudimentary "lung" first makes its appearance in the *Pulmogasteropoda.*

CHAPTER IX.

SECRETION AND EXCRETION IN THE INVERTEBRATA.

ALL living organisms assimilate and disassimilate incessantly, but the conditions of assimilation become more complex as we ascend in the zoological scale. For the accomplishment of the function of assimilation in the higher forms, auxiliary apparatus, such as those of digestion, circulation, and respiration, are needed. The last three mentioned functions have already been described, but in addition to these there is another, for the waste products of the cells, tissues, food, &c., have to be eliminated from the system. It does not matter how low the organism is in the scale of animal life, there are always waste products formed, and these have to be eliminated, or they act as poisons. The function of elimination of matters hurtful to the animal organism is spoken of as *excretion*. Excretion is partly mechanical—as in the evacuation of the fæces—partly dependent upon the physical process of pressure forcing fluid matters through thin-walled tubes, and partly upon cell development and growth, as in secretion. In the higher animals secretion is performed by five separate mechanisms—the kidneys, the intestines, the lungs or branchiæ, the liver, and the skin. The excretion of carbonic anhydride and other gaseous products by respiration has already been alluded to in the last chapter. The function of excretion by means of a liver does not occur in the *Invertebrata*, as a true liver (similar to that occurring in the *Vertebrata*) is absent in these animals. From these remarks it will be seen that, so far as excretion is concerned the present chapter will be *chiefly* confined to a description of excretion by means of renal or urinary apparatuses.

Besides the waste products there are several useful products of katabolism termed *secretions*—such as saliva, digestive juices, &c. The principal secreting organs* of the *Invertebrata* have already been described in the chapters on digestion; but it may be remarked that in reality the secreting glands are at the same time organs of excretion. All of them take from the blood, or nutritive fluid, water and salts, substances to which they offer a passage without in any respect changing them. In addition, however, they form, at the expense of the sanguineous materials, a special nitrogenous product, the principal agent of these chemical transformations being the epithelial cells. Such a product is a secretion.

When neither the epithelial cells nor the walls of a gland exercise any modifying action on the materials of the blood or nutritive fluid, but simply act as a filter, offering a passage to certain substances and refusing it to others, there is merely excretion.

The excretory organs are never closed, for they always pour externally the humour which they filter. This humour is a dead product—the residuum of nutrition—whose expulsion is necessary to preserve life. The excrementitious humours, of which the urine is a typical example, are solely constituted of water holding in solution certain salts, and crystallisable nitrogenous substances, which, formed in the anatomical elements themselves by disassimilation, pass first of all into the blood or its representative, whence they are extracted and excreted by various mechanisms which in the higher forms are known as glands.

The organs specially concerned in the elimination or excretion of nitrogenous substances are termed kidneys; and in the *Invertebrata* the form of these organs varies

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* Special organs of this nature will be alluded to later in the present chapter.

considerably. In the *Protozoa* they are represented by the contractile vacuoles, which perform other functions besides that of a renal organ.

In the *Porifera* the waste materials of each cell are thrown into the body cavity, and collectively expelled through the exhalent aperture, or osculum; a somewhat similar mode of excretion is observable in the *Cœlenterata.*

The renal organ of the *Echinodermata*, represented by the *Asteridea,* is the five pouches of the pyloric sac (see later in this chapter). Here there is a fusion of digestion and excretion. The water-vascular system, which in other forms performs the functions of excretion and respiration, has a locomotor function in the *Asteridea.*

In the *Cestoidea* and allied orders the water-vascular system opens into the blood system on the one hand, and communicates with the exterior on the other. The water-vascular system is in these animals the representative of an excretory organ.

The segmental organs, or nephridia, of the *Annelida* are true kidneys, and form a medium of communication between the circulatory apparatus and the environment.

In the air-breathing Arthropods, as well as in some *Crustacea* (*Orchestia*), the kidneys are represented by the Malpighian tubules—appendages of the intestine.

The shell glands of the lower *Crustacea* have a similar function to the segmental organs of the *Annelida;* consequently they are renal organs.

The organs of Bojanus in the *Lamellibranchiata* are more or less complex sacs or tubes, joining the blood system on the one hand with the exterior of the body on the other. They resemble the segmental organs of the *Annelida*, and perform a similar function—namely, the elimination of waste nitrogenous matters from the system.

The renal organs in the *Lamellibranchiata* form a paired kidney; in the *Pulmogasteropoda*, represented by *Helix*, the kidney is unpaired, being a single renal sac; but in both of these orders of the *Mollusca* the renal organs communicate by means of an internal opening with the pericardial division of the body cavity.

Finally, in all the *Invertebrata* the blood system is not completely separated from the general cavity of the body, and the general cavity of the body has openings placing it in communication with the exterior medium.

In the *Vertebrata* the urinary organs consist essentially of a number of coiled tubes, and open to the exterior by special openings, which are usually common to the generative organs. "The individual tubules of which the Vertebrate kidney is composed do not open directly to the exterior, as do the segmental organs of the Annelids, but there is present on each side of the body a duct—a kidney duct—which receives the tubules of its own side, and opens posteriorly into the cloaca. They also possess an important structure peculiar to the kidney of the *Vertebrata*, known as the Malpighian body, which consists of a capsular widening of the lumen of each tubule, into which projects a coil of arterial blood-vessels known as the glomerulus."

Besides the excretory or urinary organs, there is another class of secretory apparatus which must be alluded to—we refer to the unicellular and multicellular *integumentary organs.* These are found largely represented in the *Insecta*, and they belong to the category of oil and fat glands, whose function is to lubricate the integument and its special coverings.

"Aggregations of cells whose function is to secrete calcareous matters and pigments* are especially widely present in the integument of the *Mollusca*, and serve for the building up of the beautifully coloured and variously shaped shells of these animals."

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* Dr. MacMunn has shown that whenever hæmochromogen is present in the fluids and organs of the body, it has been produced by excretion; in other words, it is an *excretory* pigment. But there is one exception—namely, in a beetle (*Staphylinus olens*), as its testes seem to contain this substance with hæmoglobin.

But this power of secreting exoskeletons is not confined to the *Mollusca;* even in the *Protozoa* calcareous and siliceous * exoskeletons are secreted by the cells acting in the first instance on the calcium carbonate and silica dissolved in the water in which these animals live. "The hard protective skeletons in all Invertebrate *Metazoa*, except the *Porifera*, the *Actinozoa*, the *Echinodermata*, and the *Tunicata*, are cuticular structures, which may be variously impregnated with calcareous salts formed on the outer surface of the epidermic cells. In the *Porifera*, the calcareous or siliceous deposit takes place within the ectoderm itself, and probably the same process occurs, to a greater or less extent, in the *Actinozoa*. In those *Tunicata* which possess a test it appears to be a structure *sui generis*, consisting of a gelatinous basis excreted by the ectoderm, in which cells detached from the ectoderm divide, multiply, and give rise to a deposit of cellulose."

"In the *Actinozoa* and the *Echinodermata* the hard skeleton is, in the main, though perhaps not wholly, the result of calcification of the elements of the mesoderm. In some Molluscs, portions of the mesoderm are converted into true cartilage, while the enderon of the integument often becomes the seat of calcareous deposit."

Besides the various glands, cells, and devices secreting and excreting calcareous, siliceous, and gelatinous materials, integumentary glands and aggregations of glands may also acquire a relation to the acquisition of food; as, for instance, in the spinning glands of spiders. Finally, mucous glands are very widely present in the integument of animals which live in damp situations (snails, &c.), and in water (Annelids, *Medusæ*, &c.).

At this point we intend to describe in detail the excretory or renal organs, as well as to allude to certain important

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* See also Murray and Irvine's paper in *Proc. Roy. Soc. Edinb.*, vol. 18, p. 229 (1891).

secretory organs as we pass from the lower to the higher forms of the *Invertebrata.*

THE PROTOZOA.

The author* has shown that the contractile or pulsating vacuole of the *Protozoa* performs the function of a true kidney, or, in other words, its secretion is capable of yielding microscopic crystals of uric acid.

Three organisms were used in the author's experiments—namely, *Amœba, Vorticella,* and *Paramœcium.*

(1) *Amœba.*—By observing a number of these organisms under the higher powers of the microscope,† there is seen, within the structure of each, a small cavity or vacuole filled at certain times with a transparent fluid. There is little doubt that the fluid which collects in the vacuole is drawn from the surrounding protoplasmic substance, and is returned to it, or forced out to the exterior on the contraction of the walls of the vacuole.

The author has shown in his paper, "Further Researches on the Physiology of the *Invertebrata,*"‡ that the five pouches of the *Asteridea* also perform the function of kidneys (*i.e.,* the digestive apparatus performs a dual function); and whatever may be the multitudinous functions of the Protozoan contractile vacuoles, one thing is certain, that they excrete periodically a waste nitrogenous substance. This nitrogenous substance was proved to be uric acid.

A number of *Amœbæ* were placed on a microscopic slide and covered by a thin cover-glass. Alcohol was run in between the slide and cover-glass, so as to kill the organisms. It was found that in many cases moderately weak alcohol caused no contraction of the vacuole. The alcohol was followed by nitric acid; the slide gently

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* *Proceedings of Royal Society of Edinburgh,* vol. 16, p. 131.

† Zeiss's E and oc. v; F and oc. iv and v.

‡ *Proceedings of Royal Society of London,* vol. 44, p. 325.

warmed, and finally, ammonia introduced between the slide and cover-glass. In a few minutes prismatic crystals of murexide,* of a beautiful reddish-purple colour, made their appearance. After the addition of alcohol (as already stated), minute flakes were distinctly seen floating in the fluid of certain contractile vacuoles. Bearing in mind the murexide reaction, there is every reason to believe that these flakes were minute crystals of uric acid.

It may be stated that there are times when the fluid of the contractile vacuoles does not contain the least trace of uric acid. These vacuoles perform more than one function, one of these being that of an internal respiratory apparatus (see last chapter); and now we find the same organ performing the function of a kidney. There is little doubt that the contractile vacuole of *Amœba* is the primitive representative of a series of organs which become gradually differentiated in the higher forms of the *Invertebrata.*

(2) *Vorticella.*—The contractile vacuole of *Vorticella* exhibits during life fairly regular diastolic and systolic movements. The fluid which it contains is drawn from the surrounding protoplasmic matter, and is ultimately forced by the contraction of its walls towards the periphery of the bell, and finally ejected into the water in which the organism lives. The contractile vacuole of *Vorticella* performs the function of a true kidney. Its fluid contents yield microscopic crystals of murexide and uric acid when submitted to the same chemico-microscopical reactions as those just described.

(3) *Paramœcium.*—The contractile vacuoles of this organism are situated in the ectosarc almost at each end of the long axis of the body. These cavities are filled with a transparent fluid. During the systole fine radiating canals are produced, which probably communicate with the exterior. The contractile vacuoles of *Paramœcium* are at times the renal

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* The crystals had a green metallic lustre when seen by reflected, and a reddish-purple colour by transmitted light.

organs of this organism. By the same reactions as those described in connection with *Amœba* the fluid of these vacuoles yields crystals of murexide and uric acid. There is little doubt that these vacuoles eliminate the waste nitrogenous products during the systoles which take place periodically.

In these three primitive forms of the animal kingdom there are the rudiments of a true renal system. The contractile vacuoles perform the same function (among others) as the kidney of higher forms, by yielding the same nitrogenous substance which is present in the renal organs of the highest Vertebrates. By the agency of living protoplasm, even these insignificant microscopic cells bring about chemical metamorphoses in albuminoid molecules, with the production of uric acid and possibly other substances. In these lowly creatures there is present the same power of chemical metamorphosis as is present in the more complex cells of the highest Vertebrate. But the contractile vacuoles do not represent solely the renal organs in these forms, for it is by their agency that the mechanisms of respiration and nutrition are performed. The Protozoan cell performs many functions, and in this respect it does not altogether differ from specialised cells of the higher animals. It should be borne in mind that "there is no perceptible relation between the nature of the fluid and of the cell or gland secreting it; and secretions, as pus, for example, are formed by structures where no such secretion previously existed; they alter also without any visible change in the structure of the gland or cell" (Milne Edwards).

THE CŒLENTERATA.

As the means of eliminating the waste products in the *Porifera* and the *Cœlenterata* have already been referred to in this chapter, we now proceed to describe the secretion of carbonate of lime in the *Cœlenterata.*

"The vast organic accumulations known as coral reefs are undoubtedly among the most striking phenomena of tropical oceanic waters. The picturesque beauty of coral atolls and barrier reefs, with their shallow placid lagoons, and their wonderful submarine zoological and botanical gardens, fixed at once the attention of the early voyagers into the seas of equatorial regions of the ocean."

What delight and pleasure a "Captain Nemo," with his submarine boat,* would have in visiting these zoological and botanical gardens, witnessing (among a hundred or more interesting phenomena, not dreamt of in man's philosophy) the *Holothuriæ* and *Scari* feeding upon coral-polypes, &c., and grinding the coral into such a fine mud that it may be more easily re-dissolved in sea water, and thus furnish a new generation of lime-secreting animals with the necessary lime.

It is not our object to describe the theories of Darwin † and Murray ‡ on the origin and formation of coral reefs and islands; but to give the chief points of interest concerning the recent investigations of Dr. J. Murray and Mr. R. Irvine § on the "function of corals and other lime-secreting organisms, and the accumulation of their shells and skeletons on the floor of the great oceans." The conclusions arrived at are the following:—

(*a*) "Coral reefs are developed in greatest perfection in those ocean waters where the temperature is highest and the animal range is least. . . . . Throughout the temperate and polar regions there are no coral reefs. This is all the more remarkable, seeing that organisms belonging to the same orders, families, and even genera as those which build up coral reefs, flourish throughout colder, and even in polar, seas. In these colder seas the representatives of the reef-

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* Jules Verne's *Twenty Thousand Leagues under the Sea.*

† *The Structure and Distribution of Coral Reefs.*

‡ *Proceedings of Royal Society of Edinburgh*, vol. 10, p. 505.

§ *Ibid.*, vol. 17, p. 79.

builders either do not secrete carbonate of lime in their body-walls, or, if they do so, the skeletons are much less massive than in tropical waters." No doubt this difference in the function of lime-secreting is partly due to the direct action of the environment, and partly to natural selection. Mr. Herbert Spencer, in his *Principles of Biology*, has pointed out the influence of the environment on the simplest unicellular organisms, tracing it up to more and more complex organisms, and he has further shown its struggle with atavism, or the principle of heredity, so strongly possessed by all animal and vegetal cells. There is every reason to believe that the direct action of the environment has influenced the protoplasm of the representatives of the coral-polyps living in cold seas, so that it no longer possesses the same power of secreting carbonate of lime.

(*b*) "In descending into deep water in equatorial regions, the amount of carbonate of lime secreted by the animals living on the sea bottom becomes less with increasing depth."

(*c*) "The number of species and individuals of lime-secreting organisms decreases" with the distance from the equator. It appears that these organisms "secrete more lime in regions where there is a uniformly high temperature of the ocean water than in those regions where there are great seasonal fluctuations of temperature, or where there is a uniformly low temperature of the water, as in the polar regions and in the deep sea."

(*d*) "In temperate seas more carbonate of lime is secreted in the warm summer months than during the winter months. Indeed, a high temperature of the sea water is more favourable to abundant secretion of carbonate of lime than high salinity."

(*e*) "The average percentage of carbonate of lime in the *whole of the deposits* covering the floor of the ocean is 36·83, and of this carbonate of lime, it is estimated that fully 90 per cent. is derived from the remains of pelagic organisms that have fallen from the surface waters, the remainder of the carbonate of lime having been secreted by organisms that live on or are attached to the bottom."

(*f*) Sea water collected among coral atolls contained nearly twice as much salts of ammonia as water from oceans where the coral polyp does not live. It appears that the carbonate of ammonia present in sea water arises from the decomposition of animal products, and in the presence of sulphate of lime of sea water becomes carbonate of lime and sulphate of ammonia:

$$(NH_4)_2CO_3 + CaSO_4 = CaCO_3 + (NH_4)_2SO_4.$$

"The sulphate of ammonia is in turn absorbed by the marine flora which form the food of the marine fauna, and is in part resolved into nitrates and free nitrogen."

"The whole of the lime salts in sea water may be changed by the above reaction into carbonate, and may in this way be presented to the coral and shell builders in a form suitable for their requirements. The temperature of the water is of great importance in this reaction. In cold water, of which the great bulk of the ocean consists, the decomposition of nitrogenous organic matter is greatly retarded; whereas in tropical surface waters it proceeds with great rapidity. Here, then, we have probably the explanation of the massive structures formed by lime-secreting organisms in the coral reef regions, which are also the regions of highest and most uniform temperature in the ocean. In the same way we may account for the great extension of lime-secreting pelagic organisms in the tropical surface currents that flow north and south from the equator. Thus the coral reef-builders and pelagic organisms may not only benefit by the decomposition products arising from their own effete matters, but also from the undecomposed nitrogenous matter carried to equatorial regions from the cold water of the deep sea or from the polar regions."

(*g*) As the quantity of carbonate of lime in sea water is exceedingly small, it was supposed that the lime-secreting organisms pumped enormous quantities of sea-water through their bodies so as to be able to separate out a sufficient quantity to form their shells and skeletons.* But there is no doubt that we have a correct explanation in the reactions indicated above which have been so ably investigated by Murray and Irvine. "In higher animals, like hens, the carbonate of lime is secreted from the blood; but in coral polyps, in which there is no true circulatory system, and where the animal is immersed in the sea water, it is most probable that the reaction above referred to—the formation of carbonate of ammonia—is in every way advantageous to these lime-secreting organisms, and facilitates the deposition of carbonate of lime by the protoplasm. In the case of all the lower classes of lime-secreting organisms this change in the constitution of the lime salts may take place within the tissues of the animals." In fact, Murray and Irvine have shown, in their experiments with oysters, that "the excess of carbonate of lime observed in the liquor or diluted lymph was clearly due to the decomposition of the sulphate of lime in the sea water by carbonate of ammonia secreted as such by the protoplasm of the animal."

It may be stated that when sulphate of lime, urea, and water are heated together to about 80° F., carbonate of lime and sulphate of ammonia are formed:—

$$CaSO_4 + CH_4N_2O + 2H_2O = CaCO_3 + (NH_4)_2SO_4.$$

It is possible that the excretions of marine Invertebrates, as well as those of the higher animals, ultimately yield carbonate of lime and sulphate of ammonia due to the action of the sulphate of lime in sea water.

(*h*) Murray and Irvine have also shown that the rate of solution of dead carbonate of lime shells and skeletons by the action of sea water "varies greatly according to the conditions in which these dead remains are exposed to the solvent power of the water." The following table gives a few of their results:—

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* Bischof's *Chemical and Physical Geology*, vol. i, p. 180.

	Temperature (C.)	Exposure in hours.	Amount soluble.	
			In grammes, lime carbonate per litre.	In parts of sea water. One part in
Coral sand	27	12	0.0320	32,000
Harbour mud, Bermuda .	27	12	0·0410	25,000
Isophyllia dipsacea . .	27	12	0.0410	25,000
Millepora ramosa . .	27	12	0.0360	28,000
Madrepora aspera . .	27	12	0.0730	14,000
Montipora foliosa . .	27	12	0.0430	23,000
Goniastrœa multilobata .	10	12	0.0730	14,000
Porites clavaria . . .	11	12	0.0930	11,000
Oculina coronalis . . .	10	96	0.0237	42,600

Their experiments prove that "there is very great diversity as to the amount of carbonate of lime that will pass into solution in sea water from various calcareous structures in a given time." The more dense varieties of coral are less soluble than the porous varieties. "The rate of solution is also much greater when the water is constantly renewed than when the same water remains in contact with the coral, and the solution approaches to saturation."

(*i*) From the investigations and observations of Murray and Irvine "it is evident that a very large quantity of carbonate of lime is in a continual state of flux in the ocean, now existing in the form of shells and corals, but after the death of the animals passing slowly into solution, to go again through the same cycle."

"On the whole, however, the quantity of carbonate of lime that is secreted by animals must exceed what is re-dissolved by the action of sea-water, and at the present time there is a vast accumulation of carbonate of lime going on in the ocean. It has been the same in the past, for with a few insignificant exceptions all the carbonate of lime in the geological series of the rocks has been secreted from sea water, and owes its origin to organisms in the same way as the carbon of the carboniferous formations. The extent of these deposits appears to have increased from the earliest down to the present geological period."

THE ECHINODERMATA.

We have already alluded to the secretion of the protective skeleton in these animals; consequently we proceed to describe the excretory organs of the *Asteridea*, being an important order of the *Echinodermata*.

The author * has shown that the five sacs of the stomach of *Uraster rubens* sometimes act as renal organs. With a quantity of the fluid obtained from a large number of starfishes the following experiments were performed :—

(1) The clear liquid from these sacs was treated with a hot dilute solution of sodium hydroxide. On the addition of pure hydrochloric acid a slight flaky precipitate was obtained, after standing seven and a half hours. These flakes, when examined beneath the microscope ($\frac{1}{6}$ in. obj.) were seen to consist of various crystalline forms, the predominant forms being those of the rhomb. On treating the excretion alone with alcohol, rhombic crystals were deposited which were soluble in water. When treated with nitric acid and then gently heated with ammonia, these crystals yielded reddish-purple murexide crystallised in microscopic prisms.

(2) Another method was used for testing the fluid contents of the sacs of the stomach of *Uraster*. These fluid contents were boiled in distilled water, and evaporated carefully to dryness. The residue obtained was treated with absolute alcohol and filtered. Boiling water was poured upon the residue, and to the aqueous filtrate an excess of acetic acid was added. After standing some hours, crystals of *uric acid* were deposited, and easily recognised by the chemio-microscopical tests mentioned above.

The above-mentioned alcoholic filtrate was tested for urea.

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* See Dr. A. B. Griffiths' paper in *Proceedings of Royal Society*, vol. 44, p. 325.

To do this, the alcoholic solution was diluted with distilled water, and boiled over a water-bath until all the alcohol had vaporised. The warm aqueous solution (A) remaining was now tested for urea in the following manner:—

(*a*) On the addition of mercuric nitrate to a portion of the above solution, no white precipitate was obtained.

(*b*) To another portion of the solution (A), a solution of sodium hypochlorite was added. No bubbles of nitrogen were disengaged.

(*c*) No crystals of urea nitrate were formed in a small quantity of the solution (A) [concentrated by evaporation] after the addition of nitric acid.

(*d*) The distillation of a small quantity of the solution (A) with pure sodium carbonate in a chemically clean Würtz's flask attached to a small Liebig's condenser, failed to produce in the distillate any coloration with Nessler's reagent.

The above tests clearly prove the entire absence of urea in the excretion under examination. No guanin or calcium phosphate could be detected in the excretion, although the author has found the latter compound as an ingredient in the renal excretions of the *Cephalopoda* and the *Lamellibranchiata.**

From these investigations, the isolation of uric acid proves the renal function of the five pouches or sacs of the stomach of the *Asteridea.*† There is no doubt that the stomach of starfishes performs a dual function: it is an excretory organ as well as a digestive gland, and separates the nitrogenous products of the waste of the tissues, &c., from the blood or nutritive fluid in the form of uric acid, which is at certain times to be found in the five pouches of that organ. In the *Invertebrata* there are numerous examples where an organ performs a dual and even a triple function.

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* *Proceedings of Royal Society of Edinburgh*, vol. 14, p. 230.

† See also Durham in *Quart. Journ. Micros. Science*, 1891.

THE ANNELIDA.

(1) The *Hirudinea.*—The author* has examined the nephridia of *Hirudo medicinalis.* These nephridia are in pairs, extending from the second to the eighteenth segments (somites). Each nephridium † consists of a much-convoluted cellular tube. The cells of the tube are perforated by small ducts. The nephridia (segmental organs) open externally on the ventral side of the body.

In *Lumbricus* the nephridium communicates internally by a wide funnel-shaped aperture (which is ciliated) with the perivisceral cavity, but in *Hirudo* it opens internally by a "cauliflower-headed" portion (the analogue of the funnel-shaped aperture in *Lumbricus*) into the perinephrostomial sinus. Each nephridium consists of five principal parts—(*a*) posterior lobe, (*b*) anterior lobe, (*c*) apical lobe, (*d*) the testis lobe, (*e*) the vesicle, with its duct, which opens externally.

The nephridia of *Hirudo* are covered with a pigmented connective tissue. These pigments are no doubt the histohæmatins of Dr. C. A. MacMunn, for he says: "I have found that throughout the whole animal kingdom in each tissue and organ there are present colouring matters." ‡

In examining the physiology of the nephridia or segmental organs of the *Hirudinea,* the author obtained the excretions from a large number of freshly killed leeches. These excretions were examined by the same chemical and microscopical methods used in the examination of the segmental organs of the *Oligochæta* and the renal organs of the *Asteridea.*

The nephridia of *Hirudo* contain uric acid and sodium; and it may be that the uric acid is in combination with sodium as sodium urate.

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* *Proceedings of Royal Society of Edinburgh,* vol. 14, p. 346.

† From νεφρός, a kidney.

‡ *Proc. Birmingham Philosophical Society,* vol. 5, p. 211; *Proc. Roy. Soc.,* 1886; and *Philosoph. Trans.,* 1886.

(2) The *Oligochæta.*—The renal system of *Lumbricus* consists of a large number of coiled tubes (Fig. 47) distributed in pairs, one pair in each somite of the body. Each tube or segmental organ (nephridium) consists of three distinct parts—(*a*) A much-convoluted thin portion, terminating in a funnel-shaped opening; (*b*) a thick-walled glandular portion; (*c*) a thick muscular portion (the outer loop), which opens externally by an aperture near the ventral side of the body. The nephridium as a whole lies on the posterior side of the septum, but the funnel-shaped aperture opens on the anterior surface; that is to say, into the cavity of the segment in front of that in which the main body of the nephridium lies. This is the case in every segment containing these organs. The septa, or mesenteries dividing the body into segments, are richly

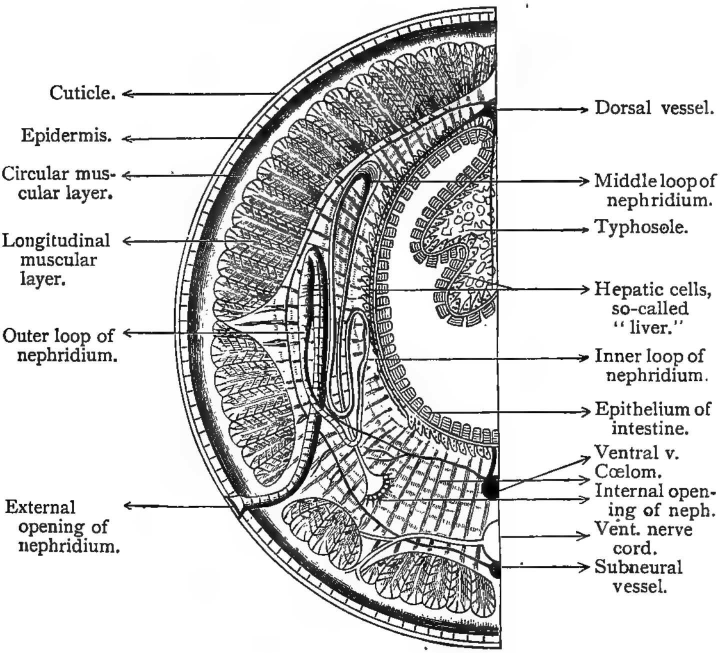

FIG. 47.—NEPHRIDIUM OF LUMBRICUS.

supplied with blood-vessels, many of which are intimately connected with the folds of the nephridia. There is little doubt that the nitrogenous waste matters are absorbed by the glandular portions of these coiled tubes, and ejected by the contractile parts to the exterior.

The author * has isolated uric acid from the excretion of the nephridia or segmental organs of *Lumbricus terrestris.* The contents of these organs do not contain guanin, urea, or calcium phosphate.

The segmental organs in the *Oligochæta* are therefore renal in function, eliminating the nitrogenous waste matters contained in the blood, in the perivisceral cavity. The largest amount of uric acid was found in the excretion contained in the muscular part of the segmental organ (Fig. 47, outer loop of nephridium).

The following table is a summary of the constituents of the nephridia or segmental organs of the *Annelida* :—

	Hirudinea.	*Oligochæta.*	*Polychæta.*
Uric acid	present	present	(?)
Urea	absent	absent	—
Guanin	absent	absent	—
Calcium phosphate .	absent	absent	—
Sodium	present	—	—

The minute structure of the excretory organs in the *Oligochæta,* especially those of *Lumbricus terrestris,* have been worked out by Dr. E. Claparède, and detailed in his "Histologische Untersuchungen über den Regenwurm," † and also by Prof. C. Gegenbaur. ‡

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* *Proceedings of Royal Society of Edinburgh,* vol. 14, p. 233.

† *Zeitschrift für Wissenschaftliche Zoologie,* vol. 19.

‡ *Ibid.,* vol. 4,

THE NEMATOIDEA.

In a paper read before the Royal Society of Edinburgh on July 1, 1889, the author stated the results of his examination of the renal organs of the *Nematoidea.*

The body of the "thread-worms" is elongated, round, and thread-like, tapering (more or less) towards the anterior and posterior ends. The *Nematoidea* are not divided into segments, and they have no segmental organs.

In the species (*Anguillula brevispinus*) selected for investigation the renal organ is a glandular mass situated in front of the gizzard. This organ has a well-developed excretory duct, which opens externally by a tranverse slit (the vascular pore) on the ventral side of the body.

When a section of the glandular organ of *Anguillula* is examined under the microscope, the epithelial lining is seen to consist of nucleated cells, similar to those of the Malpighian tubules of the *Insecta* (see later in this chapter).

The organ contains a clear fluid, which can be made to yield microscopic crystals of uric acid. The author has extracted uric acid from a large number of these organs (obtained by dissection under the microscope) by boiling them in distilled water. The filtrate, tested by the methods already described, yielded uric acid and murexide crystals.

A fresh "glandular organ" was placed upon a microscope slide and crushed; then a drop of dilute acetic acid added, and the whole covered by a cover-glass. On examining with the microscope it was observed that rhombic plates and other crystalline forms had deposited. The cover-glass was slightly raised, and on the addition of a drop of nitric acid, followed by ammonia and gently heating over a spirit lamp, prismatic crystals of murexide were formed.

No urea, guanin, calcium phosphate, &c., could be detected in the excretion of this organ.

These reactions prove that the so-called "glandular organ" of the *Nematoidea* is physiologically a kidney.

THE PROTOTRACHEATA.

This order is represented by the genus *Peripatus*, which contains several species. These animals have the power of "throwing out a web of viscid filaments when handled or otherwise irritated." This viscid matter is secreted by two large ramified tubular glands situated on the sides of the digestive tube, and open externally by the perforations of the oral papillæ. *Peripatus* breathes by means of tracheæ, hence the reason that Prof. Huxley has referred the order to which *Peripatus* belongs to the *Arthropoda*.

From these remarks it will be observed that respiration in *Peripatus* is on the insect-type—*i.e.*, by means of tracheal tubes; but the other excretory organs differ from those of the *Insecta*. In the *Insecta* the renal organs are the Malpighian tubules, but no such appendages to the alimentary canal are present in *Peripatus*.

The kidneys are segmental organs or nephridia, like those of the worms, but of a more highly complex type. There is a pair of these organs in each segment. They open internally into the body cavity, and externally at the base of the limbs.

THE MYRIAPODA.

The intestines of the animals belonging to this class are provided with Malpighian tubules which perform an excretory function; in other words, they are physiologically the kidneys.

THE INSECTA.

Before describing the excretory organs, it is perhaps desirable that we mention certain secretions, and the organs (as far as possible) which give rise to them.

(*a*) The poison which certain insects secrete is a fluid strongly impregnated with formic acid. In many cases this fluid is secreted by a special gland, and poured into a receptacle connected with the sting (*e.g.*, in *Apis* and *Vespa*).

The larva of *Dicranura vinula* possesses a gland which secretes formic acid. The duct of this gland opens in a horizontal slit on the red margin below the true head, and is thus placed in such a position that its contents are ejected in an anterior direction. Disturbance causes the larva to withdraw its head still further, and to inflate the red margin, especially in the region of the gland duct, and at the same time the head is always turned in the direction of the disturbance. Thus the fluid is thrown towards the cause of the irritation, and the terrifying appearance of the larval full-face is also brought to bear upon it (Poulton). The acid ejected by the larva of *D. vinula* is a defensive fluid, and no doubt is a means of protection against enemies.

This defensive fluid is ejected from a transversely placed aperture on the ventral surface of the prothorax, immediately below the head. Mr. E. B. Poulton, F.R.S., Prof. R. Meldola, F.R.S., and Prof. W. R. Dunstan have proved by chemical tests that this fluid secreted by the larva of *D. vinula* is formic acid. "The smell is also quite characteristic, and affords an indication of the large proportion of acid present in the secretion. It is also an interesting fact that the freshly-made and moist cocoon of *D. vinula* is powerfully acid to test-paper."

The secretion consists of a pure aqueous solution of formic acid, containing an average of 33 per cent. of anhydrous acid. A mature larva will eject 0.05 gramme of the secretion, containing 40 per cent. of acid. The rate of secretion is slow; starvation lessens its amount and decreases the quantity of acid; but there is no difference in the nature of the acid when the larva is fed on poplar instead of willow.*

"The larva appears to depend entirely upon *tactile stimuli* for the direction in which to move its terrifying full-face, and towards which to eject the irritant acid secretion. Visual sensations appear to play no part as guides in the assumption of the defensive attitude."

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* See *Report of British Association*, 1887, p. 765.

The larva of *Dicranura furcula* does not eject an irritant secretion, but it possesses an eversible "gland" as a defensive organ. A similar structure is present in the larva of *D. vinula*, but it is unable to evert its prothoracic "gland" voluntarily. This structure is eversible in the larvæ of *Melitæa artemis*, *Orgyia pudibunda*, *Orgyia antiqua*, and *Liparis auriflua;* and there is no doubt that these defensive structures are of constant occurrence in Lepidopterous larvæ.

The power of everting the "gland" in the larva of *D. vinula* has been lost, due to the fact that the "larva has acquired the remarkable power of ejecting the intensely irritant secretion to a considerable distance by forcing it through the narrow chink, with its closely approximated lips, which constitutes the mouth of the duct leading to the sac. Such a formidable means of defence may readily have supplemented the more usual method of eversion, a method which can only give rise to the discharge of vapour into the air, instead of a well-directed stream of fluid, which, if volatile, as it is in these larvæ, of course produces abundance of vapour."

The eversible glands of the larva of *Liparis auriflua* are not often completely everted, but they are very sensitive to tactile impressions, and on "stimulation a clear, transparent secretion appears in the lumen, being probably raised by partial eversion. The secretion is not acid to litmus paper, but it possesses a peculiar and penetrating odour."

The ejection of defensive fluids and vapours are not confined to the anterior parts of insects, for in the Bombardier Beetles, according to Dr. Léon Dufour, a pungent vapour, resembling nitric acid in its properties, is ejected from the anus. *Brachinus displosor* will furnish twelve such discharges, but subsequently explosion with noise is replaced by the emission of a yellowish or brownish fluid, which readily vaporises. These discharges are meant to arrest the onset of larger predacious beetles. *Brachinus crepitans* is sometimes gregarious, and when one individual is disturbed the whole discharge in unison, but after about twenty explosions they only emit a white fluid.

M. F. Pouchet * says:—" L'instinct de la défense est tellement inhérent à la tribu des Bombardiers, qu'au seul coup de canon d'alarme de l'un d'eux, tous les autres crépitent en même temps: c'est un feu roulant sur toute la ligne."

There is something in these insects discharging the fluid *in unison* which seems to point out that they are guided not merely by instinct, but by that which is the equivalent of mind.

The chief enemy of *B. crepitans*, which inhabits Great Britain, is *Calosoma inquisitor* (Fig. 48).

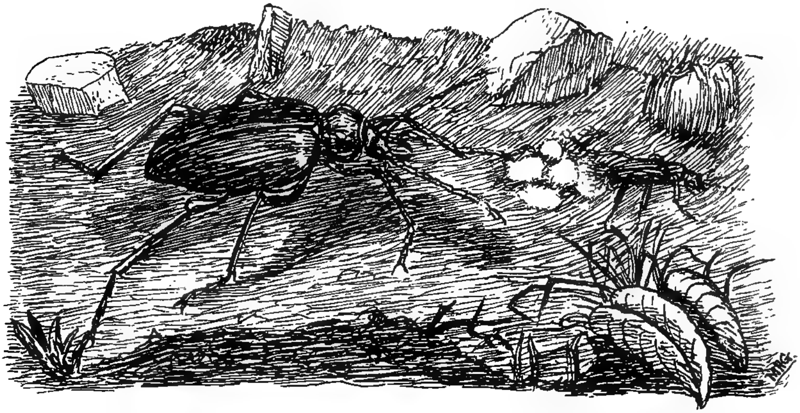

FIG. 48.—BOMBARDIER BEETLE AND ITS ENEMY.
(*After* F. A. POUCHET.)

The secretory glands of the Bugs are situated exterior to the insertion of the posterior legs, and emit fœtid effluvia on seizure.

The ground bettles of the genus *Carabus*, when disturbed, eject a fluid which is caustic if applied to the skin.

In conclusion, it may be remarked that a very large number of insects eject liquids or vapours as a means of

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* *L'Univers*, p. 137.

protecting themselves, more or less, from the attacks of various enemies.*

(*b*) There are two pairs of salivary glands of the larval *Lepidoptera* (see Fig. 7). The posterior or second pair secrete the viscous substance, which hardens on exposure to the atmosphere and forms silk. This silk is the material in which the larvæ or caterpillars invest themselves. The viscous substance from these glands is made into threads and spun into cocoons by means of a slender tubular organ called a spinneret, which is situated on the labium.

Most caterpillars spin silken threads to secure themselves from falling, and many of them, as already stated, spin a cocoon in which to pass the pupal state.

In *Myrmecoles* and the *Hemerobidœ* the silk is furnished by the rectum.

(*c*) The glow-worm, or *Lampyris splendidula*, and many other insects have the power of emitting light. According to Schulze,† the males of the glow-worm have a pair of photogenic organs, "which lie on the sternal aspects of the penultimate and ante-penultimate abdominal somites. Each is a thin, whitish plate, one face of which is in contact with the transparent chitinous cuticula, while the other is in relation with the abdominal nerve-cord and the viscera. The sternal gives out much more light than the tergal face. The photogenic plate is distinguishable into two layers, one occupying its sternal and the other its tergal half. The former is yellowish and transparent, the latter white and opaque, in consequence of the multitude of strongly refracting granules which it contains. Tracheæ and nerves enter the tergal layer, and for the most part traverse it to terminate in the sternal layer, which alone is luminous.

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* For further information on the defensive fluids and the eversible glands of Lepidopterous larvæ, see the papers by Mr. E. B. Poulton, F.R.S., in the *Transactions of Entomological Society of London*, 1885, p. 322; *ibid.*, 1886, p. 156; *ibid.*, 1887, p. 295; *Report of British Association*, 1887, p. 765; and his excellent book, *The Colours of Animals*.

† *Archiv für Mikroskopische Anatomie*, 1855.

Each layer is composed of polygonal nucleated cells. The granules are doubly refractive, contain uric acid, and probably consist of urate of ammonia. Hence the cells of the layer which contain them are termed by Schulze the 'urate cells,' while he calls the others the 'parenchyma cells.' The branches of the tracheæ which ramify among the parenchyma cells end, like those of other parts of the body, in stellate nucleated corpuscles, one process of the corpuscle passing into a ramification of the trachea. Schulze is inclined to think that the other processes end in parenchyma cells. The nerves of the photogenic plates are derived from the last abdominal-ganglion; they branch out between the parenchyma cells into finer and finer branches, which eventually escape observation." (Huxley.)

Lampyris can vary at will the intensity of the phosphoric light. It has been stated that the light is connected with the action of oxygen upon a fatty material secreted by the photogenic organs, and the light so produced is reflected by means of the granules already alluded to.

The function of the Malpighian tubules of insects were not definitely established until a few years ago. Some zoologists stated that they represented the "liver," while others maintained that they were renal in function.

The Malpighian tubules of *Blatta* (*Periplaneta*) have been shown by the author* to contain uric acid and urea.

Dr. C. A. MacMunn† has confirmed the author's investigations, for he has extracted uric acid from the Malpighian tubules of *Periplaneta orientalis*. These tubules were crushed, boiled with distilled water, the extract evaporated to dryness, washed with hot alcohol, and again dissolved in boiling water and filtered. To the filtrate excess of acetic acid was added, and in some hours uric acid crystals of various forms, and giving the murexide test, were formed.

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* *Chemical News*, vol. 52, p. 195.

† *Journal of Physiology*, vol. 7, p. 128.

The author* has also examined the Malpighian tubules of *Libellula depressa* (Figs. 49 and 50), and has proved that they have a renal function.

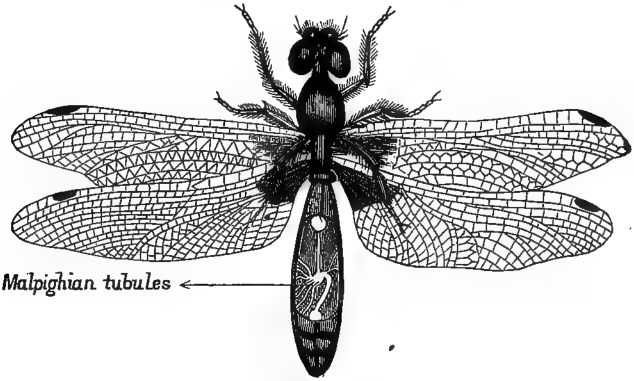

FIG. 49.—MALPIGHIAN TUBULES OF LIBELLULA.

Libellula depressa (the dragon-fly) is a voracious insect, which lives in water, during its earlier stages, where it undergoes an imperfect metamorphosis, the pupa finally creeping out of the water, and changing into the imago. By experimenting with a large number of the larval forms of *Libellula*, the author has extracted (from the larvæ) uric acid crystals, by using similar methods to those already described in this chapter.

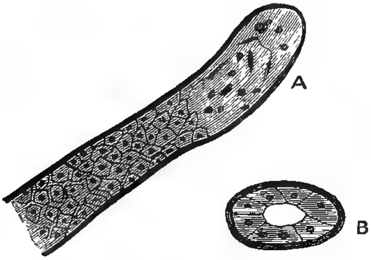

FIG. 50.—MALPIGHIAN TUBULES OF LIBELLULA.

A = Longitudinal section showing the various states of the epithelial lining.
B = Transverse section of tubule. × 230.

In the imago or mature form of the dragon-fly the Malpighian tubules number from sixty to seventy, and are branched. Under the microscope, a Malpighian tubule is

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* *Proc. Roy. Soc. Edinb.*, vol. 15, p. 401.

seen to consist of a connective tissue layer, a delicate "tracheal tube," a basement membrane, and an epithelial layer of comparatively large nucleated cells (Fig. 50). The internal cavity of one of these tubules is very irregular, as is seen by examining various parts of it in a transverse section.

The uric acid contained in these tubules can be extracted by boiling a large number of them in water, filtering, and then evaporating the filtrate to dryness. The residue is treated with alcohol, filtered, and the residue so formed is dissolved in boiling water to which acetic acid is added. After standing for several hours, crystals of uric acid ($C_5H_4N_4O_3$) are deposited. These crystals are readily converted into murexide.

Then, again, if a fresh Malpighian tubule is placed upon a slide under the microscope, and crushed, a drop of dilute acetic acid added, and the whole covered by a cover-glass, rhombic and other crystalline forms are deposited. These crystals are also readily converted into murexide by the action of nitric acid and ammonia.

No other substance besides uric acid could be detected in the Malpighian tubules of *Libellula depressa.*

From the above-mentioned reactions it is evident that the Malpighian tubules of the *Insecta* are physiologically true renal organs.

As already mentioned some zoologists of the older school stated that these appendages of the alimentary canal represented the "liver," and this statement has been recently revived by Dr. B. T. Lowne in his work on *Calliphora.* But the Malpighian tubules of the *Diptera* (including *Calliphora*) readily yield uric acid when the proper tests are skilfully applied; and they do not contain the least trace of biliary acids, glycogen, or even ferments.

The Malpighian tubules of the *Insecta* are undoubtedly true kidneys, although they are developed from the alimentary canal.

THE ARACHNIDA.

(*a*) In the Scorpion the posterior extremity of the abdomen is armed with a sort of hooked claw, which, when the animal is in motion, is always carried over the back in a most threatening attitude. This claw-like organ is the sting, and at its base are situated two poison-glands whose ducts pass into the point of the sting, so that when the animal strikes with its weapon, a small portion of the poison or vemon is instilled into the wound. The sting is a weapon of offence.

(*b*) In the *Araneina* the poison gland is lodged in the cephalo-thorax, and the duct of it opens at the summit of the terminal joint. It will be noticed that in the *Arancina* the poison gland is situated in the anterior part of the body, whereas in the *Arthrogastra* it is in the posterior part.

But "the most characteristic organ of the *Araneina* is the arachnidium, or apparatus by which the fine silky threads which constitute the web, are produced."

In *Epeira diadema* this apparatus contains a thousand glands with separate ducts. These ducts secrete the viscid material which ultimately hardens into silk. "The glands are divisible into five different kinds (aciniform, ampullate, aggregate, tubuliform, and tuberous), and their ducts ultimately enter the six prominent arachnidial mammillæ, which in this species project from the hinder end of the abdomen. The superior and inferior mammillæ are three-jointed; the middle one is two-jointed. Their terminal faces are truncated, forming an area beset with the minute arachnidial papillæ by which the secretion of the glands is poured out."

The Spider usually commences its thread by applying the spinnerets to some fixed object; to this the viscous secretion attaches itself, when the movements of the animal are sufficient to draw out the materials necessary for the continuation of the thread. This power of spinning threads from the secretion of these glands is of the greatest importance to all these animals (*i.e.*, those belonging to the sedentary class), as it not only serves many of them for the construction of dwellings, and of webs for the capture of prey, but is constantly employed in securing them from falls whilst in motion, or in descending in a direct line from an elevated position to some object below them. Many spiders

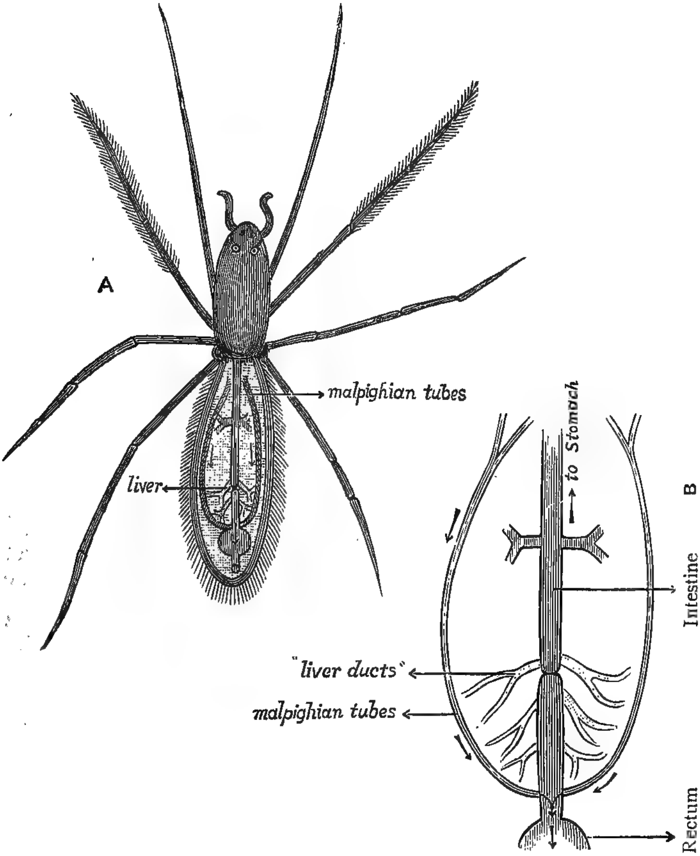

FIG. 51, A AND B.—MALPIGHIAN TUBES OF TEGENARIA.

have the power of emitting this secretion in the form of threads, one end of which floats freely in the air until it meets with some object to which it adheres. By this means spiders often form natural bridges, by means of which they can pass over brooks and rivers, in some cases twenty and even fifty feet wide.

Another purpose to which this secretion is applied by all spiders is the formation of silken cocoons for the reception of the ova, which a few species (*i.e.*, wandering spiders) carry about with them.

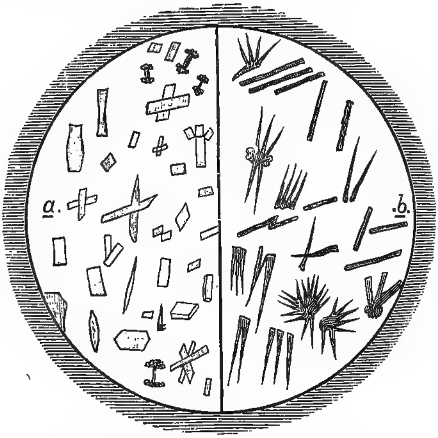

FIG. 52, *a* AND *b*.—CRYSTALS OF URIC ACID AND MUREXIDE.
a = the uric acid crystals. *b* = murexide crystals.

Concerning the excretory apparatus in the *Araneina*, Mr. A. Johnstone, F.G.S., and the author* have examined the Malpighian tubules of *Tegenaria domestica* (Fig. 51, A and B). The intestines of this species form a tube-like body, which dilates into a short rectum, and into this rectum the Malpighian tubules open.

An aqueous extract of a large number of these tubules yielded uric acid (Fig. 52). The secretion is neutral to test papers.

* *Proc. Roy. Soc. Edinb.*, vol. 15, p. 111.

The uric acid was extracted by both of the methods used for testing the pyloric sacs of *Uraster* (see p.) 254.

The uric acid is present as sodium urate, for sodium is easily detected in the secretions of these organs. No doubt some sodium compound is a normal constituent of the blood of *Tegenaria.*

No urea, guanin, or calcium phosphate could be detected in the secretion. But it may be stated that Dr. C. Weinland* has recently extracted crystals of guanin from the excrements of certain spiders. The guanin so extracted is stated to have answered to all the reactions of that substance as described by Capranica.†

There is no doubt that the Malpighian tubules of the *Arachnida* are renal in function.

THE CRUSTACEA.

Among the lower *Crustacea* the renal organ is represented by the so-called shell-gland. It consists of a coiled tube with clear contents. In *Apus* (belonging to the *Phyllopoda*) this gland opens by a duct "on the base of the first pair of thoracic appendages, immediately behind the second maxillæ."

In his paper on *Cyclestheria hislopi* ‡ Dr. G. O. Sars says that the only organ to which an excretory function has been attributed is the so-called shell-gland (see Fig. 11). Its structure is glandular, but of what nature the secretion is, and in what manner performed in this species, has not yet been satisfactorily ascertained. Some naturalists state that this peculiar organ secretes the material of which the shell is built up, but it is far from evident that such is its real function. On examining the organ, Dr. Sars failed to detect in this species any secreting orifice, the whole organ appearing to constitute a convoluted canal or duct recurring in itself.

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* *Zeitschrift für Biologie*, vol. 25, p. 390.

† *Zeitschrift für Physiologische Chemie*, vol. 4, p. 233.

‡ *Christiania Videnskabs-Selskabs Forhandlinger*, 1887, p 43.

But there is no doubt that in other forms of the lower orders of the *Crustacea* the secretion of the shell-gland does contain uric acid, proving the renal function of the organ in question.

In the Decapod *Crustacea*[*] the excretory organs are represented by the so-called green glands. Dr. Rawitz has recently examined the anatomical structure of these glands in *Astacus fluviatilis*, and his results may be summarised as follows:—The gland is uniformly green on the ventral side, but on the dorsal side only at the periphery; elsewhere white, with a round yellow-brown speck in the centre. When examined microscopically the gland is seen to consist of two tubules closely interwoven. The cells of the green part contain a round grass-green drop of protoplasm, and the yellow-brown cells a uniformly yellow-brown coloured nucleus. The tubules anastomose, the yellow-brown cells being the terminal portions of tubules and secretory.[†]

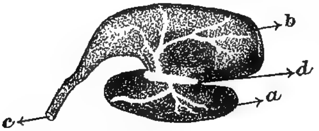

FIG. 53.
GREEN GLAND OF ASTACUS.
a = glandular portion. *b* = sac-like portion. *c* = opening of duct. *d* = nerve with ramifications. × 2 (about).

The author[‡] has made a complete study of the function of the green glands of *Astacus fluviatilis*, and the results of these researches may be stated as follows:—The so-called green glands of the fresh-water crayfish lie in the cavity of the head below the front part of the cardiac division of the stomach (see Fig. 13). The openings of these organs are situated at the base of each antenna. The organ, carefully dissected out of the head of a fresh-killed crayfish, is seen to consist of two principal parts (Fig. 53): a dorsal or upper-

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[*] The *Decapoda* includes the *Brachyura* and the *Macroura*.

[†] See Dr. Rawitz's paper, read before the Berlin Physiological Society on January 28, 1887.

[‡] Dr. Griffiths' paper in *Proceedings of Royal Society of London*, vol. 38 (1885), p. 187.

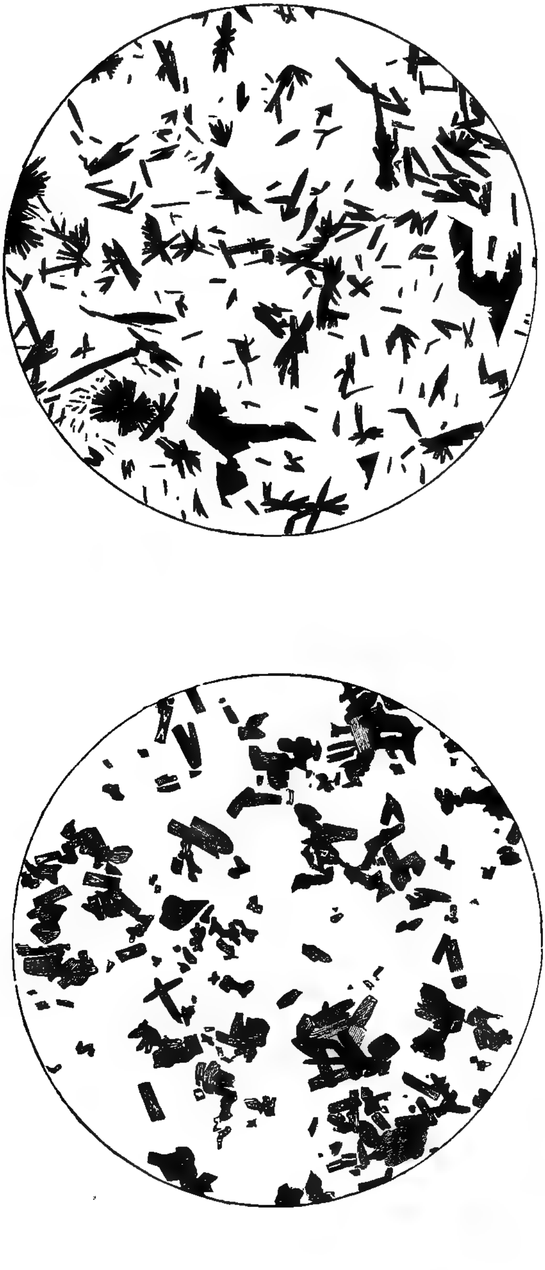

FIG. 54.—URIC ACID CRYSTALS FROM GREEN GLAND OF CRAYFISH.

A = Uric acid. B = Murexide.

most one which is a transparent and delicate sac-like body filled with a clear fluid, and a ventral or an underlying portion of a green colour, glandular in appearance, containing granular cells.

As is well known, these green glands were formerly believed to be the auditory organs of *Astacus;* but in 1848 Drs. Will and Gorup-Besanez* stated that this organ *probably* contained guanin, and from this supposition the green glands have been considered as excretory organs.

The secretion of these glands is acid to litmus paper, and on treating the secretions, obtained from a large number of green glands, with hot dilute sodium hydroxide solution, and then adding hydrochloric acid, a slight flaky precipitate was obtained, and on examining these flakes under the microscope they were seen to consist of small crystals in rhombic plates. On treating the secretion with alcohol these rhombic crystals (Fig. 54 A) were deposited; they were soluble in boiling water.

When these crystals were moistened with dilute nitric acid, alloxanthine ($C_8H_4N_4O_7$) was produced, and on heating this substance with ammonia, reddish-purple murexide (Fig. 54 B) or the "ammonium purpurate" [$C_8H_4(NH_4)N_5O_6$] of Prout was obtained. The murexide so obtained crystallises in prisms, which by reflected light exhibit a splendid green metallic lustre, and by transmitted light are a deep reddish-purple. On running in a solution of potassium hydroxide upon a microscopic slide containing some of the murexide crystals they were dissolved.

It is evident (from the above reactions) that these rhombic crystals are deposits of uric acid ($C_5H_4N_4O_3$) from the secretion of the green gland of the crayfish. These deposits of uric acid crystals were covered more or less with a very thin and superficial coating of some brown colouring matter, probably one of the pigments already described.

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* See *München Gelehrte Anzeigen,* No. 233, 1848.

The secretion of the green gland of *Astacus* contains guanin, which is proved by treating the secretion with boiling hydrochloric acid. A solution is obtained containing flakes of uric acid in suspension, these are filtered off, and the filtrate set aside to cool, when a few crystals (guanin hydrochlorate) separate which are soluble in hot water. On the addition of ammonia to this hot aqueous solution a precipitate is obtained of guanin ($C_5H_5N_5O$), the precipitated guanin being composed of a number of minute microscopic crystals. On running in warm dilute nitric acid (on to the slide), these crystals disappeared, but they where precipitated again on the addition of a drop of silver nitrate in the form of the nitrate of silver compound ($C_5H_5N_5O,AgNO_3$) of guanin.

This investigation proves that the so-called green gland of *Astacus fluviatilis* is a true urinary organ, its secretion containing uric acid and traces of the base guanin. The green gland is, therefore, physiologically the kidney of the animal.*

The nerve, which comes off from the supra-œsophageal ganglion, passes to the neck of this gland (see Figs. 13 and 53), and ramifies over its surface between the outer and inner membranes of which it is composed.

In the Edriophthalmic *Crustacea*, there are occasionally present one or two tubules which open into the posterior part of the alimentary canal. These are renal organs and contain uric acid. They are analogous to the Malpighian tubules of the *Insecta*. In this respect the *Amphipoda* and *Isopoda* differ from other *Crustacea*.

THE BRACHIOPODA.

The shell of these animals is "a cuticular structure secreted by the ectoderm, and consists of a membranous basis, hardened

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* For further details see Dr. Griffiths' papers in *Proceedings of Royal Society*, vol. 38, p. 187; *Chemical News*, vol. 51, p. 121; *Journal of Chemical Society*, 1885, p. 680; *Science Gossip*, 1886, p. 57.

by the deposit of calcareous salts, sometimes containing a large proportion of phosphate of lime (*Lingula*)."

In *Waldheimia* and other Brachiopods, "the perivisceral cavity communicates with the pallial chamber by at least two, and sometimes four, tubular organs, which have been described as hearts, but are now known to have no such nature."

These organs are funnel-shaped, the wide parts of which open into the perivisceral cavity. The narrower parts of these organs pass through the anterior wall of the visceral chamber, and terminate in small openings in the pallial cavity.

According to Dr. Morse, the ova pass through these organs in *Terebratulina septentrionalis*. The so-called pseudo-hearts have a double function, being renal organs and genital ducts. They are the homologues of the organs of Bojanus of the *Mollusca*, and of the segmental organs of worms.

THE MOLLUSCA.

The excretion of carbonate of lime is an important function in a large number of Molluscs.

In *Anodonta*, which is taken as a typical example of the *Lamellibranchiata*, the shell is a "cuticular excretion from the surface of the mantle," and consists of variously disposed lamellæ of organic matter impregnated and hardened by the deposition of calcareous salts (chiefly carbonate of lime, mineralised as arragonite). The shell has no cellular structure; "but from the disposition of its lamellæ, and from the manner in which the calcareous deposit takes place in them, it may present varieties of structure which have been distinguished as nacreus, prismatic, and epidermic" (Fig. 55).

In the young Lamellibranch shell there is a much larger percentage of calcium phosphate present than in the adult shell: the calcium phosphate being gradually replaced by calcium carbonate as the animal arrives at maturity.

The ligament which unites the valves together is an uncalcified chitinous material. This material is continuous with the horny cuticle which spreads over the external surface of the valves, and is reflected over the ventral edges into the mantle or pallium.

The pearly or nacreus layer has a laminated texture, and is secreted by the mantle. The production of pearls (*e.g.*, in *Meleagrina margaritifera*, the "pearl oyster") is as follows: A grain of sand, or other hard substance, gets in between the pallium and the shell. Consequently the external surface of the pallium becomes irritated, and the laminated mother-of-pearl layer (nacreus layer) is secreted by the pallium, during the remainder of the animal's life, around this irritant nucleus.*

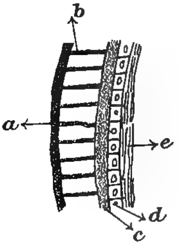

FIG. 55.
SECTION OF SHELL OF GAPER.

a = cuticula. *b* = prismatic layer.
c = nacreus layer. *d* = epithelium.
e = mantle.

The exoskeletons of the *Brachyura* and *Macroura* have a similar structure to the Lamellibranch shells;† and it has been shown that the particular combinations of lime requisite for the formation of these shells, &c., are calcium chloride, calcium carbonate, or calcium phosphate. The sulphate of lime present in sea water cannot be utilised for shell formation unless it is first converted into one of the above forms. The researches of Irvine and Woodhead‡ prove that " shell formation in the crab is somewhat different from egg-shell formation in the hen, and occupies an intermediate position between

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* According to Dr. G. Harley, F.R.S. (*Proc. Roy. Soc.*, 1888) pearls have the following composition :—

Calcium carbonate	91.72
Organic matter (animal)	5.94
Water	2.23
	99.89

† See Vitzou's paper in *Archiv de Biologie*, tome 10, p. 659.

‡ *Proc. Roy. Soc. Edin.*, vol. 15, p. 308 ; vol. 16, p. 324.

such egg-shell formation and bone formation, as the carbonate of lime is deposited in the chitinous portion of growing epithelial cells in the crab shell."

"In the secreting layer of the mantle of certain Molluscs the lime in the epithelial cells is principally phosphate, whilst the fluid bathing its outer surface and the shells themselves contain the lime, principally in the form of a carbonate. If there is a definite interval between the secreting surface and the area of deposition, or if much chitin or other tissue is developed between the actively secreting cells and the tissue in which the lime is deposited, there is always a greater tendency to the formation and deposition of carbonate of lime."

Phosphates of the alkalies and alkaline earths occur in the blood or nutritive fluid, and the latter acts as a carrier of lime, &c., to every part of the body where carbonic anhydride may be given off; thus carbonate of lime is formed, and the phosphoric acid re-enters the circulation.

As already stated, the embryonic and young shells of the *Lamellibranchiata* are richer in phosphate of lime than the shells of the fully-grown animal. No doubt as greater activity goes on a larger amount of carbonic anhydride is produced, and by this means more carbonate of lime is deposited than phosphate of lime.

When alkaline phosphates, associated with lime and albumin, preponderate in the blood, the lime so separated is in the form of phosphate, as in bone formation; when these are partially replaced by an excess of alkaline carbonates, as in the majority of marine animals, the lime is secreted as carbonate.

The corals have a secreting layer of cells which, according to Irvine and Woodhead, produce chitin—chitin infiltrated with calcium carbonate, and almost pure calcium carbonate, with a small quantity of cementing organic material.

The carbonate of lime is formed by the ammonium carbonate produced by the decomposition of the effete products of animals, as urea, &c., decomposing the calcium sulphate in the sea water with the formation of calcium carbonate.

In the blood of the lime-secreting Invertebrates there are phosphates of lime and soda, along with alkaline chlorides, carbonates, and sulphates associated with albuminous matter, carbonic anhydride and oxygen being also present in varying quantities. This blood is alkaline, which is due to the presence of alkaline phosphates and carbonates.

Dr. Schmidt found that the blood of *Anodonta cygnea* was slightly alkaline; and on evaporation it yielded crystals of calcium carbonate resembling gaylussite. "These could not have been present originally in the alkaline fluid, and it is probable that they were produced by the formation of ammonium carbonate from the decomposition of urea* and nitrogenous organic matter."

The membrane which secretes chitin also brings lime to the surface, and in performing its protoplasmic function carbonic anhydride is set free; this readily forms calcium carbonate after decomposing certain lime salts. "But it must be noted that the chitin is directly in contact with the upper secreting cells, in fact, the younger layers of chitin still form the upper or older portion of the cell." Irvine and Woodhead "maintain that the direct contact allows of the dialysis into the chitin of a portion of the phosphate of lime before it is completely transformed into the carbonate. As the carbonate of lime is formed the free phosphoric acid is apparently reabsorbed and utilised afresh. In proof of this fact, and as bearing on the whole question of lime secretion, we refer to the investigations of Schmidt, who, in speaking of *Unio*, *Anodonta*, and *Helix*, describes the structure of the secreting membrane of the mantle as a layer of hexagonal cells on which is a structureless transparent membrane in which the lime is deposited, and ascribes to it the function of decomposing the blood, of secreting a compound of albumin with phosphate of

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* Urea and uric acid are present in the excreta of *Anodonta*, see the author's paper in the *Chemical News*, vol. 51, p. 241.

lime next the shell, which is decomposable even by the carbonic anhydride of the air or of the water, but of retaining the phosphoric acid and returning it to the organs which require it for the process of cell formation. In proof of this he gives the following analysis of the ash of the secreting layer of the mantle:

	I.	II.
Calcium phosphate	14·85	14·91
Calcium carbonate, sodium phosphate, sodium chloride, and calcium sulphate	2.71	3.45

showing how large a proportion of the lime salts must, in this secreting layer, be in the form of phosphates. As further proof he gives analysis of the mucus which is found between the shell and the mantle, in which he finds much albuminate (basic) of lime, a small proportion of carbonic anhydride, but not a trace of phosphate. In the delicate membrane in which the lime is deposited we have an analogous membrane to that of egg-shell membrane (of birds), separated from the secreting layer of cells by a fluid containing albumin, carbonic anhydride, and lime salts, in whatever way combined, and deposited in the structureless membrane. According to analysis of the ash, the lime salts present are in the following proportion:

	Anadonta.		*Helix.*
Calcium carbonate	99.45	...	99.06
Calcium phosphate	0.55	...	0.94

So that Schmidt was able to trace the transition stages through the excess of phosphate in the mantle, the albuminate in the intermediate bathing mucus, and the carbonate in the shell."

Irvine and Woodhead believe that the carbonic anhydride in this case was the result of metabolic processes going on in the mantle, and that the carbonate of lime formed was gradually passed on in this condition from the lime-mucous solution (if present in that condition) into the membrane again by dialysis.

"As the process of shell-formation must necessarily go on slowly, it is not at all astonishing that such a small proportion of carbonic anhydride should be found in the mucous material. It is used up as it is formed in laying down the carbonate of lime of the shell.

"As regards the proportion of the lime salts and chitin, Schmidt found that the amount of earthy phosphate increases in proportion to the quantity of chitinous tissue present in the basement structure:

	Crayfish.		Squilla.		Lobster.
Chitin . . .	46.73	...	62.84	...	22.94
Lime salts . .	53.27	...	37.17	...	77.06
	100.00	...	100.00	...	100.00
Calcium phosphate	13.17	...	47.52	...	12.06
Calcium carbonate	86.83	...	52.48	...	87.94
	100.00	...	100.00	...	100.00

"He argued from this that the calcium (lime) phosphate is in intimate relation with cell-formation." But Irvine and Woodhead think that as the chitin becomes older and thicker the cellular layer becomes less active, less carbonate is formed, and that there is thus a more direct passage outwards of the phosphate. In their papers already mentioned, Irvine and Woodhead give the following analyses as showing the comparative amount of calcareous and organic matter in the common edible crab:

Water, blood, salts, &c.	6,646	grains
Flesh (gave 14.56 of ash containing 4.94 lime phosphate) .	295	"
Outer calcareous structure	2,956	"
Inner calcareous structure	103	"
	10,000	"

The calcareous structure consisted of:

	Total.	Chitin.	Lime carbonate.	Lime phosphate.	Percentage.
Carapace . .	817	150.32	656.80	9.87	OUTER. Chitin . 20.00 $CaCO_3$. 78.80 $Ca_3P_2O_8$. 1.20 100.00
Chelæ . .	1184	236.80	933.00	14.20	
Ambulatory limbs	736	147.20	579.97	8.83	
Abdominal segments .	156 63	31.20 12.60	122.93 49.64	1.87 0.76	
Outer structure weight .	2956	587.12	2342.34	35.53	
Inner structure weight .	103	35.00	66.98	1.02	INNER. Chitin . 34.00 $CaCO_3$. 65.00 $Ca_3P_2O_8$. 1.00 100.00
Teeth (mandibles) weighed . 17 grains. Stomachical teeth (horny matter) weighed . . . 27 „					

The nutritive fluid (blood) of an edible crab weighing about 8000 grains contained:—

Calcium phosphate	11.10 grains
Phosphoric acid	15.78 „

Having alluded to the secretion of the shells and exoskeletons in the *Mollusca* and *Crustacea*, we now proceed to describe the organ of Bojanus in *Anodonta cygnea* and other *Lamellibranchiata*. The function of this organ has been investigated by Mr. Harold Follows, F.C.S., and the author.* It is a paired, elongated, oval, glandular sac with folded walls. It is situated beneath and behind the pericardium, and in front of the posterior adductor muscle (see Fig. 18). This organ is composed of a yellowish or brownish spongy tissue, which is covered with a closely ciliated cellular layer. Its secretion is acid to litmus paper, and it contains uric acid, urea, and calcium phosphate. The presence of these compounds were proved by the methods already described in this chapter.

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* *Chemical News*, vol. 51, p. 241; *Journal of Chemical Society*, 1885, p. 921; *Proceedings of Royal Society of Edinburgh*, vol. 14, p. 233.

Mr. Follows and the author also examined the blood (of *Anodonta*) contained in the vena cava before it enters the organ of Bojanus, and it was proved that the blood contains uric acid and urea. After leaving the vena cava the blood passes into the organ of Bojanus and thence to the branchiæ. The blood in the branchiæ does not contain uric acid or urea.

The investigation proves—(*a*) that the organ of Bojanus is physiologically the kidney of the animal, eliminating the nitrogenous waste matters (in the form of uric acid and urea) contained in the impure blood as it is brought to this organ by the vena cava; (*b*) that after the blood has passed through the organ of Bojanus, it is freed from urea and uric acid.

The secretion of the organ of Bojanus in *Mya arenaria* (see Fig. 18) contains uric acid, urea, and calcium phosphate.

Drs. Will and Gorup-Besanez* stated that they found guanin in the organ of Bojanus of the fresh-water mussel, but subsequently Voit could not detect the least trace of this base in the organ in question. Mr. Follows and the author entirely agree with the conclusions of Voit, for we also could not detect guanin in the organ of Bojanus in *Anodonta cygnea*, although it may be remarked that guanin is present in the green glands of *Astacus* and *Homarus*.†

The organ of Bojanus appears to be well-developed in the majority of the *Lamellibranchiata*, but in *Ostrea* and *Teredo* it seems to be present in only a very rudimentary form.‡

The nephridia of *Helix aspersa* and *Limax flavus* contain uric acid, and were proved by MacMunn § to have a renal function.

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* *Ann. der Chem. und Pharm.*, vol. 59, p. 117; and *München Gelehrte Anzeigen*, 1848.

† See Dr. Griffiths' papers in *Proc. Roy. Soc. of London*, vol. 38, p. 187; and *Proc. Roy. Soc. of Edinburgh*, vol. 14, p. 233.

‡ See the papers of Lacaze-Duthiers in *Annales des Sciences Naturelles*, 1854–1861.

§ *Journal of Physiology*, vol. 7, p. 128.

The author has confirmed MacMunn's investigations, and he has also proved the renal function of the nephridia in *Limax maximus*, *Helix pomatia*, *Limax variegatus*, *Arion ater*, and other Gasteropods. They contain, in addition to uric acid, urea and calcium phosphate. Many of these organs also contain some of the histohæmatins; and in the case of "*Arion ater* the nephridium showed a spectrum resembling that of myohæmatin, and this spectrum is remarkable for its resemblance to that of the kidney of Vertebrates." (MacMunn.)

The *Gasteropoda* are provided with numerous glands which secrete mucus. The epiphragm of *Helix* is secreted by mucous glands, but it becomes hardened and strengthened by the deposition of calcareous matters. This epiphragm (perforated) is secreted before hybernation (*i.e.*, the winter sleep), and closes the shell-opening when the animal is retracted. The epiphragm is cast off in the spring when the animal awakes.

The secretion of the mucous glands of slugs is of value to the animals as a means of protection against the attacks of enemies. The mucus secreted is often pigmented, and it gives a polished appearance to the pigments which resemble certain metallic hues; such pigments are spoken of as protective colours.

Having referred to certain secretions of the *Pulmogasteropoda*, we have now to consider those of the *Branchiogasteropoda*.

The author* has investigated the nephridia of *Patella vulgata*. These organs consist of two parts—left and right lobes. The left nephridium is very small in comparison to the right. The anatomy and histology of these organs have been fully described by Professor E. Ray Lankester, F.R.S.,† J. T. Cunningham,‡ and Harvey Gibson.§

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* *Proceedings of Royal Society*, vol. 42, p. 392.

† *Annals and Magazine of Natural History*, vols. 20 (1867), and 7 (1881).

‡ *Quarterly Journal of Microscopical Science*, vol. 22, p. 369.

§ *Transactions of Royal Society of Edinburgh*, vol. 32, p. 617.

After dissecting the nephridia from the bodies of a large number of fresh limpets, the secretions of the left nephridia were examined separately from those of the right nephridia.

Both secretions were examined chemically by two separate methods as follows:

(*a*) The clear liquid from the nephridia was treated with a hot dilute solution of sodium hydroxide. On the addition of HCl a slight flaky precipitate was obtained after standing for some time. These flakes when examined microscopically were seen to consist of small rhombic plates and other forms. On treating the secretion alone with alcohol, rhombic crystals were deposited, which were soluble in water. When these crystals were treated with nitric acid and then gently heated with ammonia, reddish-purple murexide was obtained.

(*b*) The second method for testing the secretion of the nephridia of *Patella* was as follows: The secretion was boiled in distilled water, and then evaporated carefully to dryness. The residue so obtained was treated with absolute alcohol and filtered. Boiling water was poured upon the residue, and to the aqueous filtrate an excess of pure acetic acid was added. After standing about seven hours, crystals of uric acid ($C_5H_4N_4O_3$) were deposited, and readily recognised by the chemico-microscopical tests mentioned above.

The secretions of both the left and right nephridia yield uric acid. It has been suggested by Professor R. J. Harvey Gibson (in his masterly memoir on the "Anatomy and Physiology of *Patella vulgata*"*) that the secretions of the two nephridia may be chemically distinct. The author could not extract or detect (after a most searching investigation) the presence of any other substance besides uric acid in the secretion of either nephridium. The isolation of uric acid proves the renal function of the nephridia of *Patella vulgata.*

The nephridia of the *Cephalopoda* have also been examined

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* *Transactions of Royal Society of Edinburgh*, vol. 32, p. 601.

by the author.* Taking *Sepia officinalis* as a type of the *Cephalopoda*, it was proved that the nephridia of the animal are true renal organs. The venous blood, as it passes from the vena cava, is distributed by a number of afferent branchial vessels which communicate with the sacculated and glandular nephridia; it then passes into the branchiæ, and hence it is sent back to the heart.

The secretion of the nephridia contains uric acid and calcium phosphate, but urea, guanin, calcium carbonate, and magnesium carbonate are absent.

Uric acid is also present in the blood of the vena cava before it enters the nephridia, but the blood after passing into the branchiæ contains no uric acid.

The nephridia of the *Cephalopoda* are true renal organs, eliminating the nitrogenous waste matters in the form of uric acid, contained in the impure blood as it is brought to these organs by the vena cava.

As already stated no urea could be detected in the nephridia of *Sepia*, and the same remark applies to those of *Octopus*. The muscular tissues of these animals do not yield urea; but it may be remarked that the muscular tissues of certain Lamellibranchs do contain this base. For instance, 100 grammes each of the adductor muscles and foot of *Mya arenaria* (large individuals) were chopped into small fragments and were allowed to remain in contact with alcohol for twelve hours. The alcohol was then squeezed out and evaporated on a water-bath. The residue obtained was dissolved in water, placed in the receiver of a mercury pump, and treated with sodium hypobromite. By this method the following results were obtained:—

	I.	II.	III.
Adductor muscles	42.6	56.2	56.8
Foot	48.9	52.0	58.6

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* *Proc. Roy. Soc. Edin.*, vol. 14, p. 230.

These results are expressed in milligrammes of urea per 100 grammes of muscular tissue.*

It is most probable that the formation of urea takes place in the muscles. It is certainly present in the blood of *Mya* and *Anodonta.* Milne-Edwards states that "it is probable that in all cases the secreted matter exists in the blood already formed. It was thought, for example, that the urea found in urine must be formed by and in the kidneys, since it could not be detected by chemical analysis in the blood; but if these organs be destroyed in a living animal, or removed, urea will, after a certain time, be formed in the blood, thus clearly proving that the kidneys do not form it."

In the higher animals an abundant alimentation gives rise to a greater excretion of uric acid and urates. On the contrary, in abstinence the uric acid and its salts disappear, but urea is excreted in greater quantity. This applies not only to Vertebrates but also to many Invertebrates. Urea is a product of more or less complete oxidation of organic substances, and is formed, as already stated, in muscular tissues, by the disintegration of the anatomical elements. Uric acid, on the other hand, is the result of an incomplete oxidation, and is produced for the most part in the bood or its equivalent, when such fluid is surcharged with peptones which the tissues are unable to assimilate. Secretion and excretion can be traced back to the phenomena of nutrition—that is to say, to the molecular acts effected in the midst of glandular cells, which means that it can be accomplished without the intervention of the nervous system. Such is the case with the lowest Invertebrates; but in the higher forms, possessing a more or less complete nervous system, secretion and excretion are largely influenced by nerves. It may be probable that if the commissural cords connecting the supra-œsophageal with the sub-œsophageal ganglion were severed nervous stimulus would not be supplied to the green glands of

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* See also Smith's new method for estimating urea in the *Pharm. Journ. Trans.* [3], vol. 21, p. 294.

Astacus, and consequently the secretion of urine would be most probably influenced. At any rate, this is a question for research. In the *Vertebrata* there is no doubt that the nervous centres do greatly modify the secretions. Forty-six years ago, Schiff demonstrated that lesions of the cerebral peduncles rendered the urine albuminous and acid. Claude Bernard* proved that punctures of the roof of the fourth cerebral ventricle gave rise to the formation of glucose sugar in the urine. Lesions of the isthmus and of the lower part of the cervical marrow can prevent the urinary excretion, or in other words, produce anuria.

There is no doubt that in the *Invertebrata* the nerves play an important part in the phenomena of secretion, and even in the lower orders, where there are no traces of nervous elements, the protoplasm of the cells, being irritable, is capable of bringing into play the phenomena which we have been discussing in the present chapter. Experimental evidence shows that the *Amœba*, for instance, excretes, digests, and respires; but so far at least as present microscopic expedients reach, this organism appears to be simply a small mass of protoplasm, nevertheless it has the power of adjusting its low organisation to the environment. "In the organism lies the principle of life; in the environment are the conditions of life. Without the fulfilment of these conditions, which are wholly supplied by environment, there can be no life."

The wonderful adaptations of each organism, and of each part of every organism to its environment, inspire us with a sense of the boundless resource and skill of Nature in perfecting her arrangements for each single life. The causes of these adaptations are to be sought in the numberless structural modifications brought about by means of natural selection and by the *direct* action of the environment.

As already stated, not only an organism as a whole, but each organ is also capable of undergoing modification. Hence

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* *Leçons de Physiologie Opératoire.*

the reason that there are strange facts to confront in determining the nature of an organ. For instance, the Malpighian tubules of the *Insecta* are diverticula of the alimentary canal, consequently they have been described as livers, and morphologically they ought to have the function of a liver. But when physiology, aided by chemical methods, steps in, we find that these organs have solely a renal function. Is it possible that the Malpighian tubules had originally the function of a liver? This is improbable, but it is well known that an organ may lose its original function, and yet persist because it is of use for some other purpose: one of these predominate at one time, another at another, and the organ undergo structural modification in consequence.*

The variety of modifications or forms of the renal organs in the *Invertebrata* may be illustrated by the table on pp. 290–1.

The table on p. 292 is a summary of the constituents (present and absent) in the renal organs of the higher *Invertebrata.*

In the lower *Invertebrata* the kidney performs other functions besides that of a renal organ; but in the higher forms a special organ is set apart for that function, and it resembles in many respects the Vertebrate kidney.

On this point Prof. Huxley says: "In the *Vertebrata*, the renal apparatus is constructed on the same principle [as the renal organs of the *Mollusca*] . . . . The Vertebrate kidney is an extreme modification of an organ, the primitive type of which is to be found in the organ of Bojanus in the Mollusc, and in the segmental organ of the Annelid; and, to go still lower, in the water-vascular system of the Turbellarian. And this, in its lowest form, is so similar to the more complex conditions of the contractile vacuole of a Protozoon, that it is hardly straining analogy too far to regard the latter as the primary form of uropoietic as well as of internal respiratory apparatus."

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* In the higher animals, for example, we have the formation of a lung from a swimming bladder, and of the ear passage from a gill cleft.

THE INVERTEBRATE KIDNEY.

(*Compiled from the Author's researches.*)

Classes, Orders, &c.		Kidney represented by—	Products present in Secretion.
Protozoa . .	(*a*) Protoplasta .	Contractile vacuoles*	Uric acid.
	(*b*) Infusoria .		
Porifera or Spongida		Contractile vacuoles*	(?)
Cœlenterata		Water-vascular system* . .	(?)
Echinodermata	(*a*) Asteridea . .	The five pouches of the stomach (stomach has a dual function) . .	Uric acid.
Annelida .	(*a*) Hirudinea . .	Cellular tubes (nephridia)	Uric acid (as sodium urate).
	(*b*) Oligochæta . .	„ „ (segmental organs) . .	Uric acid.
	(*c*) Polychæta . .	„ („) . .	(?)
Nematoscolices	(*a*) Nematoidea .	"Glandular organs" . . .	Uric acid.
Arthropoda .	(*a*) Prototracheata . .	Segmental organs	Uric acid.
	(*b*) Orthoptera . . .	Cellular tubules (Malpighian tubes) . .	Uric acid
	(*c*) Neuroptera . .	„ „ („ „) . .	Uric acid.

* These perform other functions as well as that of a renal organ.

Arthropoda	(*d*) Coleoptera	Cellular tubules (Malpighian tubes)	Uric acid.
	(*e*) Araneina	„ , („ „)	Uric acid (as sodium urate), guanin.
	(*f*) Edriophthalmia	„ „ (, „)	Uric acid.
	(*g*) Brachyura	Cellular glands	Uric acid and guanin.
	(*h*) Macroura	„ ("green glands")	„ „
Brachiopoda	(*a*) Clistenterata	Pseudo-hearts (tubular organs)	(?)
Mollusca	(*a*) Lamellibranchiata	Cellular "organs of Bojanus"	Uric acid, urea, calcium phosphate.
	(*b*) Gasteropoda		
	(1) Pulmogasteropoda	Cellular gland (nephridium)	Uric acid, urea, calcium phosphate.
	(2) Branchiogasteropoda	, „ (,)	Uric acid.
	(*c*) Cephalopoda		
	(1) Dibranchiata	Pair of sacculated and glandular organs (nephridia)	Uric acid, calcium phosphate.
	(2) Tetrabranchiata	Pair of sacculated and glandular organs (nephridia)	Uric acid (?).

+ = Present. – = Absent.

	Cephalopoda.	Gasteropoda.	Lamellibranchiata.	Crustacea.	Arachnida.	Insecta.	Nematoidea.	Oligochæta.	Hirudinea.
Uric acid . .	+	+	+	+	+	+	+	+	+
Urea . . .	–	+*	+	–	–	+		–	–
Guanin . . .	–		–	+	+†			–	–
Calcium phosphate .	+	+*	+	–	–			–	–
Sodium . . .	?		?	?	+			–	+

* Absent in the *Branchiogasteropoda*.

† That is, according to Weinland (*Zeitschrift für Biologie*, vol. 25, p. 390).

NOTE.—Since this work was placed in the hands of the printers, two papers have appeared on excretion in the *Invertebrata*. (1) Mr. S. F. Harmer (*Quart. Journ. Micros. Science*, 1891) has shown that excretion in the marine *Polyzoa* is carried on by free mesodermic cells, and to some extent by the connective tissue and by the walls of the alimentary canal. (2) Mr. H. E. Durham (*Quart. Journ. Micros. Science*, 1891) believes that the "wandering cells" in the *Echinodermata*, etc., have an excretory function.

CHAPTER X.

THE NERVOUS SYSTEMS OF THE INVERTEBRATA.

NERVOUS tissue consists of two distinct structural parts: (*a*) nerve-cells and (*b*) nerve-fibres. The nerve-cells are usually found in aggregates, termed ganglia or nerve-centres; and ganglia are united to ganglia by nerve-cords or bundles, which consist of many delicate nerve-fibres. The latter act as the conductors of nervous force; in fact, "the characteristic function of nerve-fibres is that of conducting stimuli to a distance. The function of nerve-cells is different, viz., that of accumulating nervous energy, and, at fitting times, of discharging this energy into the attached nerve-fibres. The nervous energy, when thus discharged, acts as a stimulus to the nerve-fibre; so that if a muscle is attached to the end of a fibre, it contracts on receiving this stimulus. When nerve-cells are collected into ganglia, they often appear to discharge their energy spontaneously; so that in all but the very lowest animals, whenever we see apparently spontaneous action, we infer that ganglia are probably present." There is another important point, viz., the difference between muscles and nerves under the influence of a stimulus. "A stimulus applied to a *nerveless* muscle can only course through the muscle by giving rise to a visible wave of contraction, which spreads in all directions from the seat of disturbance as from a centre. A nerve, on the other hand, conducts the stimulus without sensibly moving or undergoing any change of shape. Therefore muscle-fibres convey a *visible* wave of contraction, and nerve-fibres convey an *invisible*, or molecular, wave of stimulation. Nerve-fibres, then, are functionally distinguished from muscle-fibres—and also from protoplasm—by displaying the property of conducting invisible, or molecular, waves of stimulation from one part of an organism to another, so establishing physiological continuity between such parts, without the necessary passage of waves of contraction." (Romanes.)

Nerve-fibres may be functionally divided into five groups —motor, sensory, vascular, secretory, and inhibitory. When a nerve-fibre is stimulated from some nerve-centre, it may give rise to the contraction of a muscle or a blood-vessel, increased secretion from a gland, or a diminution or arrest of some other kind of nervous action.

In all these cases, "the nervous influence travels outwards from a ganglion or nerve-centre towards the periphery, thus presenting an analogy to ordinary motor nerves." Perhaps the best classification of *nerve-fibres*, from a physiological point of view, is the following;

Centrifugal (motor) nerve-fibres.
- (*a*) *Motor* (efferent), excite contraction of muscles.
- (*b*) *Vascular* (vaso-motor), excite contraction of blood-vessels.
- (*c*) *Secretory*, excite secretion.
- (*d*) *Inhibitory*, affect other nerve-centres so as to moderate or destroy their action.
- (*e*) *Connecting*, which connect motor-cells in nerve-centres.

Centripetal (sensory) nerve-fibres.
- (*a*) *Sensory*
  - (1) *General*, "convey to nerve-centres in brain influences which cause sensations of a vague character (not permanent)."
  - (2) *Special*, "convey to nerve-centres in brain influences which cause visual, auditory, gustatory, olfactory, or tactile sensations."
- (*b*) *Afferent*, "convey to nerve-centres influences which cause no sensation, and which may or may not be followed by further nervous activity."
- (*c*) *Connecting*, "which connect sensory cells in nervous centres."

The centrifugal nerve-fibres convey influences outwards from a nerve-centre; while the centripetal nerve-fibres convey influences inwards towards a nerve-centre. It should be borne in mind that the different nerve-fibres merely act as conductors, the effects depend upon the arrangements or apparatuses at the end of the fibres.

It is the totality of the properties which nerve-cells and nerve-fibres are capable of giving rise to, which constitutes innervation.

When nerve-centres or ganglia are excited the activity or energy produced is not the same in each case. Some produce the sensations of light, sound, pain, &c.; others are the cause of secretion or locomotion; others are associated with psychical states; while a fourth exerts an influence over other nerve-centres. These nerve-centres may be classified as follows: (*a*) "*Receptive centres*, to which influences arrive which may excite sensations or some kind of activity not associated with consciousness. (*b*) *Discharging centres*, whence emanate influences which, according to structures at the other ends of the nerves connected with them, may cause movements (muscles), secretion (glands), or contractions of vessels. (*c*) *Psychical centres*, connected with sensation, in the sense of conscious perception, feeling, volition, intellectual acts, and will. (*d*) *Inhibitory* centres, which inhibit, restrain, or even arrest the action of other centres."

In the majority of cases there are terminal organs at the commencement of sensory, and the terminations of motor nerves. Such organs are seen in the rods and cones of the retina and the terminal plates of muscle; but in some few cases nerve-fibres may terminate in loops towards the periphery of the body or in the interior of organs.

We now proceed to describe the nervous systems in the *Invertebrata.*

THE PROTOZOA.

In none of these animals has any trace of a nervous system been discovered; nevertheless, as nervous elements are nothing more than the products of the differentiation of protoplasm, it is logical to assume that certain parts of the protoplasmic cells of the *Protozoa*, are the means of conveying nervous energy. If no nervous system is anatomically differentiated, there is every reason to believe that the protoplasm contains a "diffused nervous system" (Gruber).

In these organisms innervation is rudimentary; and the nervous function devolves upon the protoplasm, which is the cause of the phenomena of contraction, secretion, &c., and according to M. Binet, of certain psychical acts.

Certainly no definite nerve-tracts have been discovered in these animals; "but any one who has attentively watched the ways of a *Colpoda*, or still more of a *Vorticella*, will probably hesitate to deny that they possess some apparatus by which external agencies give rise to localised and co-ordinated movements. And when we reflect that the essential elements of the highest nervous system—the fibrils into which the axis fibres break up—are filaments of the extremest tenuity devoid of any definite structural or other characters, and that the nervous system of animals only becomes conspicuous by the gathering together of these filaments into nerve-fibres and nerves, it will be obvious that there are as strong morphological, as there are physiological, grounds for suspecting that a nervous system may exist very low down in the animal scale, and possibly even in plants." (Huxley.)

THE PORIFERA.

No differentiated nervous system has been discovered, but there is little doubt that nervous function is traceable in the protoplasm of these animals.

The nervous system of the horny sponges has been recently examined by Dr. R. von Ledenfeld.* He gives an account of *Euspongia anfractuosa*, which differs in some particulars from *Euspongia officinalis* (the bath sponge). The fine membrane which extends from the tips of the horny

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* *Sitzungsberichte der Kgl. Preussischen Akademie der Wissenschaften in Berlin*, 1885, p. 1015.

fibres consists of parallel spindle-shaped cells, which are set perpendicularly to the outer surface of the sponge; they end in extraordinarily fine tips. The protoplasm contains small, but highly and doubly refractive, granules embedded in a single refractive substance. The granules are so arranged as to give the appearance of a kind of transverse striation. These are muscle-fibres.

If the investigations of Ledenfeld are correct, we have in these animals the beginning of a true nervous system.

THE CŒLENTERATA.

Kleinenberg has shown that in *Hydra* the cells of the ectoderm terminate internally in delicate processes from which fine longitudinal filaments are produced. These filaments form a layer between the ectoderm and endoderm. According to Kleinenberg, these filaments are the representatives of both muscle and nerve; in fact, he regards them as neuro-muscular elements in an undifferentiated state. But Prof. Huxley believes that Kleinenberg's fibres "are solely internuncial in function, and therefore the primary form of nerve. The prolongations of the ectodermal cells have indeed a strangely close resemblance to those of the cells of the olfactory and other sense-organs in the *Vertebrata;* and it seems probable that they are the channels by which impulses affecting any of the cells of the ectoderm are conveyed to other cells and excite their contraction."

Dr. G. J. Romanes, F.R.S.,* has shown that in the *Medusæ* we find phenomena similar to nervous transmission sent along definite tracks, or sometimes diffused from one part of the body to the other, without any histological trace of differentiated nerve-fibre. As in the *Protozoa,* we have in these animals the early stages of the evolution of a nervous system.

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* *Philosophical Transactions of Royal Society,* 1875, p. 269; *ibid.* 1877, p. 659; *ibid.* 1879, p. 161; and his book, *Jellyfish, Starfish and Sea Urchins.*

Prof. E. Haeckel[*] has described the nervous system of the *Geryonidæ*. It forms a circle all round the margin of the nectocalyx (umbrella), "following the course of the radial (nutrient) tubes throughout their entire length, and proceeding also to the tentacles and marginal bodies." There is a ganglion at the base of each tentacle from which the above-mentioned nerves take their origin. These ganglia contain fusiform and nucleated cells of high refractive power. "The nerves that emanate from the ganglia are composed of a delicate and transparent tissue, in which no cellular elements can be distinguished, but which is longitudinally striated in a manner very suggestive of fibrillation. Treatment with acetic acid, however, brings out distinct nuclei in the case of the nerves that are situated in the marginal vesicles, while in those that accompany the radial canals, ganglion-cells are sometimes met with." Haeckel's researches have been confirmed by Allman, Claus, Harting, Romanes, and others.

According to Drs. O. and R. Hertwig,[†] the nervous system of the naked-eyed *Medusæ* consists of two parts, a central and a peripheral. "The central part is localised in the margin of the swimming-bell, and there forms a nerve-ring, which is divided by the insertion of the veil into an upper and a lower nerve-ring. . . . . In all species the upper nerve-ring lies entirely in the ectoderm. Its principal mass is composed of nerve-fibres of wonderful tenuity, among which are to be found sparsely scattered ganglion-cells. . . . . The fibres which emanate from them are very delicate, and, becoming mixed with others, do not admit of being further traced."

"Beneath the upper nerve-ring lies the lower nerve-ring. It is inserted between the muscle-tissue of the veil and umbrella, in the midst of a broad strand wherein muscle-fibres are entirely absent." The lower nerve-ring belongs

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[*] *Beiträge zur Naturgeschichte der Hydromedusen*, 1865.

[†] *Das Nervensystem und die Sinnesorgane der Medusen.*

to the ectoderm, and consists also of nerve-fibres and ganglion-cells. In these respects there is no difference between the lower and upper nerve-rings; but it may be remarked that a difference is distinguishable between the two. In the former there are many nerve-fibres of considerable thickness, whereas in the latter the nerve-fibres are exceedingly slender, and there are few ganglion-cells. "The two nerve-rings are separated from one another by a very thin membrane, which, in some species at all events, is bored through by strands of nerve-fibres which serve to connect the two nerve-rings with one another."

"The peripheral nervous system is also situated in the ectoderm, and springs from the central nervous system, not by any observable nerve-trunks, but directly as a nervous plexus composed both of cells and fibres. Such a nervous plexus admits of being detected in the sub-umbrella of all *Medusæ*, and in some species may be traced also into the tentacles."

This nerve-plexus is situated between the muscle-fibres and the epithelium. "There are also described peculiar tissue elements, such as, in the umbrella, nerve-fibres which probably stand in connection with epithelium-cells; nerve-cells which pass into muscle-fibres, similar to those which Kleinenberg has called neuro-muscular cells; and in the tentacles neuro-muscular cells joined with cells of special sensation. No nervous elements could be detected in the convex surface of the umbrella, and it is doubtful whether they occur in the veil." (Romanes.)

The nervous system of the covered-eyed differs from that of the naked-eyed *Medusæ*. In the former the central nervous system consists of separate centres unconnected with commissural cords. There are eight, twelve, or sixteen (but generally eight) of these nerve-centres situated in the margin of the umbrella. They consist of cells of special sensation and a thick layer of delicate nerve-fibres. These nerve-fibres are merely prolongations of epithelial cells, as true ganglion-cells are entirely absent.

Professor E. A. Schäfer, F.R.S.,* has shown the presence of "an intricate plexus of cells and fibres overspreading the sub-umbrella tissue" of *Aurelia aurita.* Dr. Claus has also described the presence of numerous ganglion-cells in the sub-umbrella of *Chrysaora.*

It appears that as far as the nervous system is concerned, the naked-eyed are more highly developed than the covered-eyed *Medusæ.*

It is now our intention to briefly allude to the important researches of Dr. G. J. Romanes,† which have been made from the stand-point of experimental physiology. He has studied—(*a*) the effects of excising the entire margins of the nectocalyces of both the naked-eyed and the covered-eyed *Medusæ;* (*b*) the effects of excising certain portions of the margins of the nectocalyces; (*c*) the effects upon the manubrium of excising the margin of a nectocalyx (swimming organ); and he has arrived at the following conclusions:—

"With a single exception to hundreds of observations upon six widely divergent genera of naked-eyed *Medusæ*, I find it to be uniformly true that the removal of the extreme periphery of the animal causes instantaneous, complete, and permanent paralysis of the locomotor system. In the genus *Sarsia*, my observations point very decidedly to the conclusion that the principal locomotor centres are the marginal bodies, but that, nevertheless every microscopical portion of the intertentacular spaces of the margin is likewise endowed with the property of originating locomotor impulses.

"In the covered-eyed division of the *Medusæ*, I find that the *principal* seat of spontaneity is the margin, but that the latter is not, as in the naked-eyed *Medusæ*, the *exclusive* seat of spontaneity. Although in the vast majority of cases I have found that excision of the margin impairs or destroys the spontaneity of the animal for a time, I have also found that the paralysis so produced is very seldom of a permanent

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* *Philosophical Transactions*, 1878.

† *Ibid.* 1875, p. 279.

nature. After a variable period occasional contractions are usually given, or, in some cases, the contractions may be resumed with but little apparent detriment. Considerable differences, however, in these respects are manifested in different species, and also by different individuals of the same species. Hence, in comparing the covered-eyed group as a whole with the naked-eyed group as a whole, I should say that the former resembles the latter in that its representatives usually have their main supply of locomotor centres situated in their margins, but that it differs from the latter in that its representatives usually have a greater or less supply of their locomotor centres scattered through the general contractile tissue of their organs. But although the locomotor centres of a covered-eyed *Medusa* are thus, generally speaking, more diffused than are those of a naked-eyed *Medusa*, *if we consider the organism as a whole*, the locomotor centres in the *margin* of a covered-eyed *Medusa* are *less* diffused than are those in the *margin* of a naked-eyed *Medusa*. In no case does the excision of the margin of a swimming organ produce any effect upon the movements of the manubrium."

Romanes has proved the effects of various stimuli upon the *Medusæ*. After the removal of the locomotor centres (ganglia) all these animals invariably respond to stimulation, but the degrees of irritability in responding to stimuli differ considerably in different species.

The covered-eyed, and a few of the naked-eyed *Medusæ* respond with one or more contractions to the action of light. In the case of *Sarsia tubulosa*, a flash of light causes it to respond; in fact, light acts as a stimulus. It has been observed that the marginal bodies of *Sarsia* are organs of special sense, adapted to respond to luminous stimulation; in other words, they perform the *function of sight*—in fact, the marginal bodies are rudimentary eyes.

Romanes has shown that when these marginal bodies are excised, the mutilated animals did not seek the light, "but swam hither and thither without paying it any regard." *Sarsia tubulosa* and *Tiaropsis polydiademata* are probably the only two naked-eyed *Medusæ* sensitive to light. But the action of light on *Sarsia* and *Tiaropsis* differs considerably. In the case of the latter, sunlight causes it to go into a kind of tonic spasm—the whole of the nectocalyx being drawn together. The period of latency* in *Sarsia* is instantaneous with all stimulations (mechanical, electrical, luminous, &c.); but in *Tiaropsis* the period of latency is not instantaneous with luminous stimulation, for a little more than a second elapses after the first occurrence of the stimulus. With all other stimulations, in *Tiaropsis*, the period of latency is instantaneous. Romanes has shown "that the enormously long period of latent excitation in response to luminous stimuli was not, properly speaking, a period of latent excitation at all; but that it represented the time during which a certain summation of stimulating influence was taking place in the ganglia, which required somewhat more than a second to accumulate, and which then caused the ganglia to originate an abnormally powerful discharge." The ganglionic matter of *Tiaropsis* represents, according to Romanes, the most rudimentary type of visual organ.

All the excitable parts of the *Medusæ* are highly sensitive to electrical stimulation, but the most sensitive parts are those which correspond with the distribution of the main nerve-trunks. The external or convex surface of the nectocalyx, and the whole of the "gelatinous substance to which the neuro-muscular sheet is attached," are insensitive to stimulation.

The extreme sensitiveness of the tissues to electrical stimulation suggested to Romanes the idea of ascertaining whether there is any localization of *definite excitable tracts* in these animals. In the case of *Sarsia*, "the apex of the swimming-bell is much the least excitable portion of the animal; and

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* The time which elapses between the application of a stimulus and the response to that stimulus.

from this point downwards to the margin there is a beautiful and uninterrupted progression of excitability, the latter being greatest of all when the electrodes are placed upon the string of cells described by Agassiz as nerve-cells." In regard to "the marginal tract of excitable tissue, the degree of excitability differs slightly in different parts." In other parts of the nectocalyx there is "a marked difference between the excitability of this organ when the electrodes are placed upon any one of the four radiating canals (and so upon the ascending nerve-chains described by Agassiz), and when the electrodes are placed upon the tissue between any of the canals. The ratio is generally about 9 centims. to 6½ centims."

Concerning the action of electrical stimulation the following conclusions have been arrived at by Romanes :—

(1) "The excitable tissues of the *Medusæ*, in their behaviour towards electrical stimulation, conform in all respects to the rules which are followed by the excitable tissues of other animals. Thus closure of the constant current acts as a much stronger stimulus than does opening of the same, while the reverse is true of the induction-shock.

(2) "Different species of the *Medusæ* manifest different degrees of sensitiveness to electrical stimulation, though in all cases the degree of sensitiveness is wonderfully high.

(3) "When the constant current is passing in a portion of the strip of a severed margin, the nectocalyx sometimes manifests uneasy motions during the time the current is passing. It is possible, however, that these motions may be merely due to accidental variations in the intensity of the current.

(4) "When the intrapolar portion of the severed margin of *Staurophora laciniata* happens to be spontaneously contracting prior to the passage of the constant current, the moment this current is thrown in, these spontaneous contractions often cease, and are then seldom resumed until the current again is broken, when they are almost sure to recommence.

This effect may be produced a great number of times in succession.

(5) "Exhaustion of the excitable tissue of the nectocalyx may be easily shown by the ordinary methods. Exhausted tissue is much less sensitive to stimulation than is fresh tissue. Moreover, so far as the eye can judge, the contraction is slower, and the period of latent stimulation prolonged.

(6) "The tetanus produced by faradaic electricity is not of the nature of an apparently single prolonged contraction (except, of course, such among the naked-eyed *Medusæ* as respond to all kinds of stimuli in this way), but that of a number of contractions rapidly succeeding one another—as in the heart under similar excitation."

Romanes, in his important papers (*loc. cit.*), has shown the amount of section which the neuro-muscular tissues of the *Medusæ* will endure without suffering loss of their physiological continuity; and this is in the highest degree astonishing. He has also investigated the rate of transmission of stimuli; as well as the regeneration of excitable tissues in these animals (*i.e.*, after injury). It may be remarked that if the contractile sheet, which lines the nectocalyx is completely severed throughout its whole diameter, it again reunites, or heals up, in from four to eight hours after the operation.

The nervous system of the naked-eyed *Medusæ* is more highly developed than it is in the covered-eyed *Medusæ;* and Romanes has demonstrated the occurrence of reflex action in the *Medusæ.* This reflex action occurs "only between the marginal ganglia (in *Sarsia*) and the point of the bell from which the manubrium is suspended—it being only the pull which is exerted upon this point when the manubrium contracts and acts as a stimulus to the marginal ganglia."

Romanes has brought much *physiological* evidence to bear on the distribution of nerves in *Sarsia* and it may be stated that his researches prove "that nervous connections unite the tentacles with one another and also with the manubrium; or perhaps more precisely, that each marginal body acts as a co-ordinating centre between nerves proceeding from it in four directions—*viz.*, to the attached tentacle, to the margin on either side, and to the manubrium."

"The nervous connections between the tentacles and the manubrium are of a more general character than those between the tentacles themselves; that is to say, severing the main radial nerve-trunks produces no appreciable effect upon the sympathy between the tentacles and the manubrium.

"The nervous connections between the whole excitable surface of the nectocalyx and the manubrium are likewise of this general character, so that, whether or not the radial nerve-trunks are divided, the manubrium will respond to irritation applied anywhere over the internal surface of the nectocalyx. The manubrium, however, shows itself more sensitive to stimuli applied at some parts of this surface than it is to stimuli applied at other parts, although in different specimens there is no constancy as to the position occupied by these excitable tracts."

Romanes has examined the distribution of nerves in *Tiaropsis* (especially *T. indicans**), *Staurophora*, *Aurelia*, and other *Medusæ*. In all these forms *primitive* nerves are well developed. By the word "nerves" is meant certain physiologically differentiated tracts of tissue, which either stimulation or section prove to perform the function of conveying impressions to a distance.

Romanes has also studied the subjects of co-ordination and natural and artificial rhythm in the *Medusæ;* but it is not our object to detail these important investigations, as a full account of them will be found in the *Philosophical Transactions of the Royal Society*, to which our readers are referred. Nevertheless, the following may be taken as a general summary of the results :—

(1) That in the covered-eyed *Medusæ* the lithocysts are

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* This species was first described by Romanes; see *Journ. Linn. Soc.* (*Zool.*), vol. 12, p. 524.

the exclusive seats of spontaneity, so far as the " p movements " are concerned.

(2) The rate of the natural rhythm has a tendency an inverse ratio to the size of the individual, though, be remarked, that size is not the only factor in deter such rate.

(3) The cutting off the manubrium (polyprite) or a of the nectocalyx (swimming-bell), causes, first accel of the rhythm, and then a progressive decline to a point below the original rate. The rate then r stationary at this point, but may again be made temp to rise and permanently to fall by removing another of the nectocalyx. "In these experiments the r besides becoming permanently slowed, is also often re permanently irregular. Again, paring down the cont tissues from around a single lithocyst* has the effect, the tissue is greatly reduced, of giving rise to enor long periods of inactivity. During such period, ho stimulation may initiate a bout of rhythmical contra to be followed by another prolonged pause. These fac to show that the apparently automatic action of the lit is really due to a constant stimulation supplied by parts of the organism."

(4) "Temperature exerts a profound influence on t of rhythm. This influence may be best observed moderate limits of variation; for water below 20° C. su spontaneity and even irritability, while water above permanently slows the rhythm after having temp quickened it. But water between 50° and 60° C. perma quickens the rhythm during the time that the *Medusæ,* have been removed from colder water, are exposed influence. In very cold water the loss of spontanei gradual though rapid process, as is also its return in w water. After having been frozen solid, *Aurelia* will r

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* The marginal bodies in the covered-eyed *Medusæ* occur in the little bags of crystals; hence they have been termed lithocysts.

on being thawed out, but the original rate of rhythm was not observed fully to return."

(5) Oxygen accelerates the rhythm, while carbonic anhydride retards it, and in strong doses destroys both spontaneity and irritability. Deficient aëration of the water in which the *Medusæ* are living, causes irregularity of their rhythm, as well as the occurrence of pauses; until at last spontaneity altogether ceases; but on now removing the animals to fresh sea-water, their recovery is surprisingly sudden.

(6) As regards stimulation, Romanes has shown that a few drops of hot water allowed to run over the excitable tissues of these animals cause a responsive contraction. Single mechanical or chemical stimuli applied to paralyse the nectocalyces of covered-eyed *Medusæ* frequently produces in response a small series of rhythmical contractions.

(7) Light acts as a powerful stimulus to some species of *Medusæ;* and it may be stated that the stimulus has been proved to be light *per se*, and not the sudden transition from darkness to light.

(8) The period of latent stimulation in the case of *Aurelia aurita* is greatly modified by certain conditions. Of these, temperature exerts the greatest influence, but the most important influence, from a physiological point of view, is that of the summation of stimuli. At the bottom of a "staircase" the latent period is $\frac{5}{8}$ of a second, while at the top of a "staircase" it is only $\frac{3}{8}$ of a second. Summation of stimuli also greatly increases the amplitude of the contractions; so that it both develops in the tissue a state of expectancy and arouses it into a state of increased activity.

(9) The excitable tissues of *Aurelia* may be thrown into tetanus by means of strong faradaic stimulation; and Romanes has proved that the the tetanus is due to the summation of contractions.

(10) Reflex action occurs in various species of *Medusæ.* In *Sarsia* definite nervous connections of constant occurrence

have been shown to exist between the tentacula, but not between the tentacula and polypite. Section of the neuromuscular sheet proves that in the case of this genus physiological harmony may, as a rule, be easily destroyed, although it occasionally happens that such is not the case.

(11) Romanes has shown that the essentially nervous function of maintaining *excitational continuity* is able to persist in these primitive nervous tissues after they have been subjected to the severest forms of section. This fact "cannot be explained by Kleinenberg's theory of double-function cells; for sometimes contractile waves will become blocked by section before the tentacular waves, and sometimes *vice versâ*. We seem, therefore, driven upon the theory of a nerve-plexus, whose constituent elements are capable of vicarious action in almost any degree."

(12) Contractile waves in *Aurelia* travel at the rate of 18 inches per second, if the temperature of the water is normal; but the rate is greatly modified by temperature, straining, anæsthetics, and various foreign substances. Stimulus-waves only travel at the rate of 9 inches per second, if the stimulus which starts such a wave is not strong enough at the same time to start a contractile wave; but if the stimulus is strong enough to start both waves, they both travel at about the same rate.

(13) There appears to be no further co-ordination among the lithocysts of the covered-eyed *Medusæ* than such as arises from contractile waves coursing rapidly from one of the number, and, as it passes the others, causing them successively to discharge; but, in the case of the naked-eyed *Medusæ*, true co-ordination has been proved to occur between the marginal ganglia, and the tracts through which it is effected have been proved to be the marginal nerves. Slightly cutting the margin of a naked-eyed *Medusa* exerts a very deleterious influence upon the vigour of the animal; and violent nervous shock, while it always suspends both spontaneity and irritability, will sometimes also destroy

co-ordination for a considerable time after spontaneity returns.

(14) Romanes has ascertained the effects of the following poisons—chloroform, amylic nitrite, caffein, strychnia, morphia, curare, veratrium, digitalin, atropin, nicotin, alcohol, and potassium cyanide—upon the *Medusæ*.* He has shown that there is a wonderful degree of resemblance between the actions of the above-mentioned poisons on the *Medusæ* and on the higher animals. This is a most important discovery, especially "when we remember that in these nerve-poisons we possess so many tests wherewith to ascertain whether nerve-tissue, where it first appears upon the scene of life, presents the same fundamental properties as it does in the higher animals." In fact the primitive nervous tissues of the *Medusæ* adhere to the rules of toxicology that are followed by nervous tissues in general. "In one respect, indeed, there is a conspicuous and uniform deviation from these rules; for it has been observed that in the case of every poison mentioned, more or less complete recovery takes place when

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* Fresh water acts as a deadly poison to the *Medusæ;* and brine acts as an anæsthetic. The fresh-water *Medusa* (*Limnocodium Sorbii*) is even more intolerant of sea water than are the marine species of fresh water; and brine acts as a poison to the fresh-water form. "We have thus a curious set of cross relations. It would appear that a much less profound physiological change would be required to transmute a sea-water jellyfish to a jellyfish adapted to inhabit brine, than would be required to enable it to inhabit fresh water. Yet the latter is the direction in which the modification has taken place, and taken place so completely that the sea water is now more poisonous to the modified species than is the fresh water to the unmodified. There can be no doubt that the modification was gradual—probably brought about by the ancestors of the fresh water *Medusa* penetrating higher and higher through the brackish waters of estuaries into the fresh water of rivers—and it would be hard to point to a more remarkable case of profound physiological modification in adaptation to changed conditions of life. If an animal so exceedingly intolerant of fresh water as is a marine jellyfish, may yet have all its tissue changed so as to adapt them to thrive in fresh water, and even die after an exposure of one minute to their ancestral element, assuredly we can see no reason why any animal in earth or sea or anywhere else may not in time become fitted to change its element." (Romanes.)

the influence of the poison has been removed, even though this has acted to the extent of totally suspending irritability. In other words, there is no poison in the above list, which has the property, when applied to the *Medusæ*, of destroying life till long after it has destroyed all signs of irritability." As an explanation of this peculiarity it should be borne in mind "that in the *Medusæ* there are no nervous centres of such vital importance to the organism that any temporary suspension of their functions is followed by immediate death. Therefore, in these animals, the various central nerve-poisons are at liberty, so to speak, to exert their full influence on all the excitable tissues without having the course of their action interrupted by premature death of the organism, which in higher animals necessarily follows the early attack of the poison on a vital nerve-centre." Then, again, the mode of administering the poisons to the *Medusæ* was different from that which is generally used when administering them to the higher animals.

(15) Romanes' researches prove that the phenomena of muscular tonus, as they occur in *Sarsia*, tend more in favour of the exhaustion, than of the resistance, theory of ganglionic action. "The exhaustion theory supposes that the rhythm is largely due to the periodic process of exhaustion and recovery on the part of the responding tissues."

Besides the researches on the nervous systems of the *Medusæ*, Dr. Eimer * has investigated the nervous system of the *Ctenophora*. In these animals the mesoderm contains numberless fibrils, varying in diameter from $\frac{1}{30000}$ to $\frac{1}{12500}$ of an inch. "These fibrils present numerous minute varicosities, and, at intervals, larger swellings which contain nuclei, each with a large and refracting nucleolus. These fibrils take a straight course, branch dichotomously, and end in still finer filaments, which also divide, but become no smaller. They terminate partly in ganglionic cells, partly in muscular fibres, partly in the cells of the ectoderm and endoderm. Many of

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* *Zoologische Studien auf Capri*, 1873.

the nerve fibrils take a longitudinal course beneath the centre of each series of paddles, and these are accompanied by ganglionic cells, which become particularly abundant towards the aboral end of each series. The eight bands meet in a central tract at the aboral pole of the body; but Eimer doubts the nervous nature of the cellular mass, which lies beneath the lithocyst, and supports the eye spots."

Professor Huxley says that "the nervous system of the Ctenophoran is, therefore, just such as would arise in *Hydra*, if the development of a thick mesoderm gave rise to the separation and elongation of Kleinenberg's fibres; and if special bands of such fibres, developed in relation with the chief organs of locomotion, united in a central tract directly connected with the higher sensory organs. We have here, in short, virtual, though incompletely differentiated brain and nerves."

In the *Actinozoa*, there is a plexus of fusiform ganglionic cells connected by nerve-fibres at the base of the body; and at the base of the tentacula of the *Actiniæ*, near the pigment-cells (eyes ?) isolated nerve-cells have been discovered.

THE ECHINODERMATA.

Among these animals the nervous system consists of a number of ganglia, connected by commissural cords, so as to form a ring, from which nerve-fibres pass to various parts of the body.

"The internal nervous system of *Echinus* consists of five radial trunks, which may be traced from the ocular plates along the ambulacral areas, external to the radial canals to the oral floor, where they bifurcate and unite with each other, so as to form a pentagonal nerve-ring. This ring lies between the œsophagus and the tips of the teeth, which project from the lantern. Small branches leave the ring and supply the œsophagus, and lateral branches arise from the several trunks to escape with the pedicels through the apertures of the pore plates. Each trunk lies in a sinus (Fig. 56, *c*) situated between the lining membrane of the shell (Fig. 56, *d*) and the ambulacral radial canal (Fig. 56, *e*); the lateral branches, which accompany the first series of pedicels through the oral floor are large and deeply pigmented; the other branches within the auricles are small; those external to the auricles

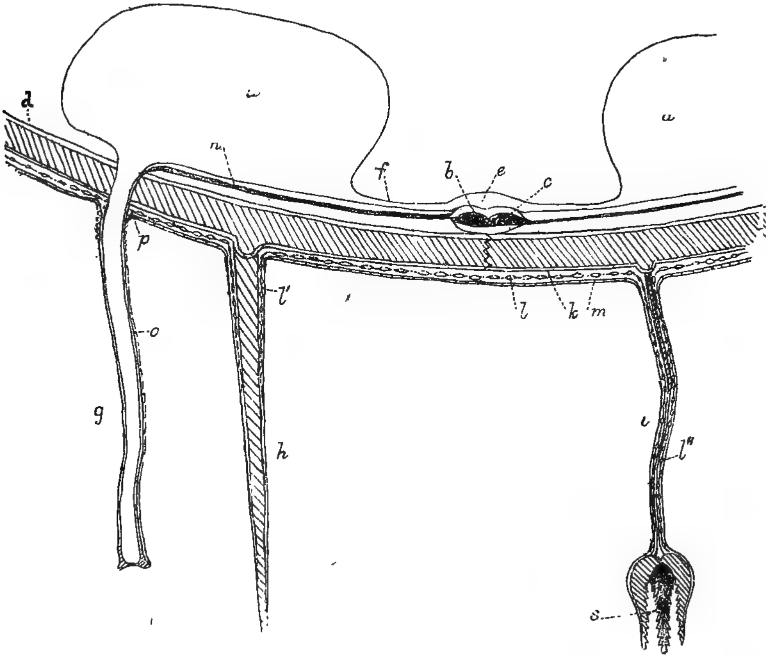

FIG. 56.—DIAGRAM SHOWING PORTIONS OF AMBULACRAL AND NERVOUS SYSTEMS OF ECHINUS.

(*After* ROMANES *and* EWART.)

a = ampullæ. *b* = radial nerve. *c* = neural radial sinus. *d* = lining membrane of shell. *e* = radial ambulacral canal. *f* = lateral branch of radial canal. *g* = pedicel. *h* = spine. *i* = pedicellaria. *k* = layer of fibres external to shell. *l* = subepidermic nerve-plexus. *l'* = plexus extending over base of spine. *l''* = plexus extending over pedicellaria towards base of mandibles. *m* = epidermis. *n* = lateral branch from nerve-trunk. *o* = continuation of lateral branch. *p* = portion of lateral branch. *r* = ambulacral plate.

gradually increase in size until the equator is reached, and from the equator to the ocular plates they again diminish." The nerve-trunk is enveloped by a fibrous sheath containing pigmented cells. The nerve-trunk consists of delicate fibres, and of fusiform cells (Fig. 57). The cells are nucleated.

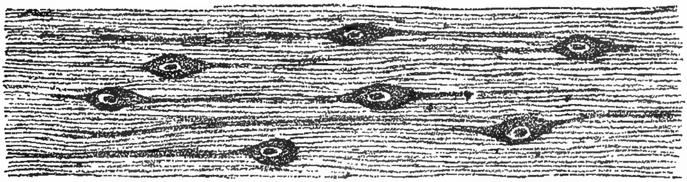

FIG. 57.—STRUCTURE OF A NERVE-TRUNK OF ECHINUS.
(*After* ROMANES *and* EWART.)

"The lateral branches of the nerve-trunk escape along with, and are partly distributed to, the pedicels; the remainder breaks up into delicate filaments, which radiate from the base of the pedicel under the surface epithelium (Fig. 56, *l*). When one of the large branches is traced through the oral floor after sending a branch to the foot, it breaks up into delicate fibres, some of which run towards the bases of the adjacent spines and pedicellariæ, while others run inwards a short distance towards the oral aperture."

There is also an external plexus situated under the surface epithelium, and extending from the shell to the spines and pedicellariæ. "The fibres (Fig. 58) of this plexus closely resemble those of the lateral branches of the trunk; but generally they are smaller in size, and have a distinct connexion with nerve-cells. The cells consist of an oval nucleus and of a layer of protoplasm, which is generally seen to project in two, or sometimes in three, directions—the several processes often uniting with similar processes from adjacent cells, so as to form a fibro-cellular chain or network."

Romanes and Ewart * have succeeded in tracing the plexus over the surface of the shell between the spines and pedi-

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* *Philosophical Transactions*, 1881, pt. iii. p. 836.

cellariæ; and from the surface of the shell to the capsular muscles at the bases of the spines (Fig. 59).

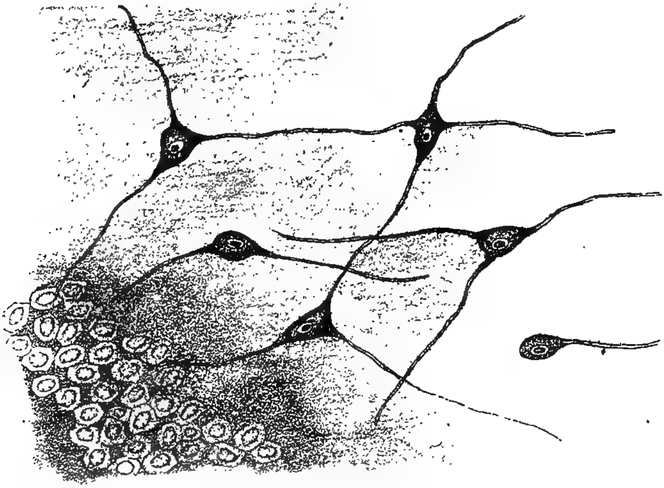

FIG. 58.—EXTERNAL NERVE-PLEXUS OF ECHINUS.
(*After* ROMANES *and* EWART.)

"In the case of the pedicellariæ, the plexus on reaching the stem runs along between the calcareous axis and the surface epithelium, to reach and extend over and between the muscular and connective tissue-fibres between the calcareous

FIG. 59.—NERVE-CELLS LYING AMONG MUSCULAR FIBRES AT THE BASE OF A SPINE IN ECHINUS.
(*After* ROMANES *and* EWART.)

axis and the bases of the mandibles (Fig. 56, *l''*, and Fig. 60). The plexus, now in the form of exceedingly delicate fibres connecting small bipolar cells, reaches the special muscles of the mandibles. . . . . Although this plexus is especially related to the muscular fibres—lying over and dipping in between them—it is also related to the surface epithelium, and delicate fibres often extend from it to end under or between the epithelial cells."

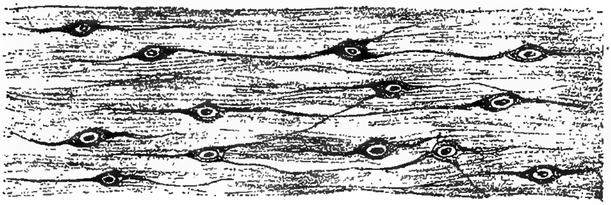

FIG. 60.—NERVE-PLEXUS LYING OVER MUSCULAR FIBRES NEAR BASE OF MANDIBLES OF PEDICELLARIA.

(*After* ROMANES *and* EWART.)

Romanes and Ewart have shown that the *Echinodermata* respond to all kinds of stimulation. The period of latency varies considerably in different species, and in different parts of the same animal.

"The external nerve-plexus supplies innervation to three sets of organs—the pedicels, the spines, and the pedicellariæ; for when any part of the external surface of *Echinus* is touched, all the pedicels, spines, and pedicellariæ within reach of the point that is touched immediately approximate and close in upon the point, so holding fast to whatever body may be used as the instrument of stimulation. In executing this combined movement the pedicellariæ are the most active, the spines somewhat slower, and the pedicels very much slower. If the shape of the stimulating body admits of it, the forceps of the pedicellariæ seize the body and hold it till the spines and pedicels come up to assist."

The function of the pedicellariæ is to aid locomotion by grasping hold of sea-weeds, &c., when an *Echinus* is climbing perpendicular or inclined surfaces of rock.

Starfishes (with the exception of Brittle-stars) and *Echini* are attracted by light, but when their eye-spots are removed, they no longer are so. Romanes and Ewart have demonstrated that severing the ray-nerve destroys all physiological continuity between the pedicels on either side of the division. Severing the nerve at the origin of each ray, or severing the nerve-ring (Fig. 61) between each ray, has the effect of totally destroying all co-ordination among the rays; "therefore the animal can no longer crawl away from injuries, and when inverted it forms no definite plan for righting itself—each ray acting for itself without reference to the others, there is, as a result, a promiscuous distribution of spirals and doublings, which as often as not are acting in antagonism to one another. This division of the nerves, although so com-

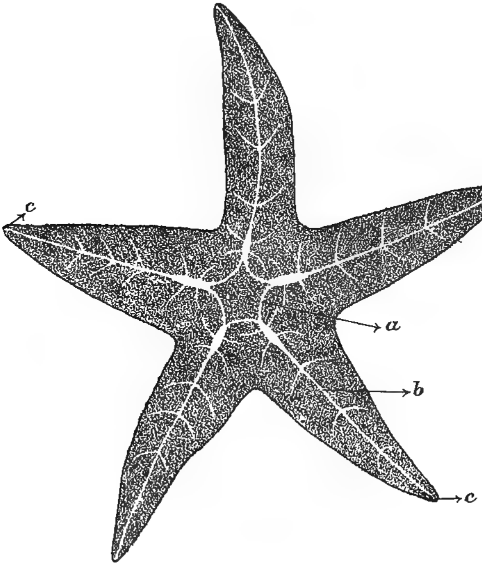

FIG. 61.—NERVOUS SYSTEM OF STARFISH.
a = nerve-ring. *b* = ambulacral nerve. *c* = eyes.

pletely destroying physiological continuity in the rows of pedicels and muscular system of the rays, does not destroy, or perceptibly impair, physiological continuity in the external nerve-plexus; for however much the nerve-ring and nerve-trunks may be injured, stimulation of the dorsal surface of the animal throws all the pedicels and muscular system of the rays into active movement. This fact proves that the pedicels and muscles are all held in nervous connexion with one another by the external plexus, without reference to the integrity of the main trunks."

The function of the spines and pedicellariæ in *Echinus* are dependent upon the external nerve-plexus; for if the latter is injured they have not the power of localising and closing, round a seat of stimulation. But "other nervous connexions, upon which another function of the spines depends, are not in the smallest degree impaired by such injury. This other function is that which brings about the general co-ordinated action of all the spines for the purposes of locomotion. That this function is not impaired by injury of the external plexus is proved by severely stimulating an area within a closed line of injury on the surface of the shell; all the spines over the whole surface of the animal then manifest their bristling movements, and by their co-ordinated action move the animal in a straight line of escape from the source of irritation."

It will be apparent from the above remarks that there is a local reflex function of the spines and pedicellariæ, which is entirely dependent upon the external nerve-plexus. There is also the universal reflex function of the spines, which consists in their general co-ordinated action for the purposes of locomotion, and which is entirely independent of the external nerve-plexus.

The nerves which give rise to the universal reflex function are distributed over the internal surface of the shell—that is they form an internal nerve-plexus.

The internal nerve-plexus of *Echinus* has been recently discovered by Dr. J .C. Ewart, of Edinburgh University. He has found that this "internal plexus spreads all over the inside of the shell, and is everywhere in communication with the external plexus by means of fibres, which pass between the sides of the hexagonal plates of which the shell of the animal is composed."

The nerve-centres in *Echinus* are to be found in the nerve-ring, for as soon as the latter was removed, the animal lost, completely and permanently, all power of co-ordination among its spines—*i.e.*, the function of locomotion was entirely lost. Although locomotion was destroyed, the spines were not entirely paralysed or motionless, for they still retained the power of closing round a seat of irritation on the external surface of the shell. This is due to the fact that all the spines and pedicellariæ are connected with the external plexus, and when it is irritated, all the spines and pedicellariæ in the vicinity move over to the seat of irritation. "On the other hand, it is the internal plexus which serves to unite all the spines to the nerve-centre which surrounds the mouth, and which alone is competent to co-ordinate the action of all the spines for the purposes of locomotion."

Dr. Romanes* has shown experimentally that the ambulacral feet of *Echinus* are co-ordinated by the nerve-centre, quite as much as are the spines. The nervous system of *Echinus* consists of the following parts (Table, p. 319).

Dr. L. Fredericq† has also investigated the nervous system of *Echinus*. He finds that the pentagonal nerve-ring and its five radial nerve-trunks are contained in as many sheaths, which are expansions of the lining membrane of the shell. The lateral branches of these nerves are also contained in a similar sheath; the latter pass out of the ambulacral pores in company with the pedicels, which they serve to enervate, a delicate nerve running along the whole length of each pedicel to terminate at its distal end in a tactile organ. The

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* See *Jellyfish, Starfish, and Sea-Urchins*, pp. 307–317.

† *Archiv. de Zool. Experi. et Générale*, tome 5, pp. 429–440.

Nervous System.	Situation.	Function.
External nerve-plexus.	External to shell.	Unites feet, spines, and pedicellariæ together, so that they all move over to a seat of irritation in that plexus.
Internal nerve-plexus.	Over internal surface of shell and is in communication with external plexus.	Brings feet, spines, and pedicellariæ into relation with co-ordinating nerve-centre.
Nerve-centre.	Mainly round mouth.	Presides over co-ordinated action of spines and feet. It gives rise to nerve-trunks.

pentagonal nerve-ring sends off, in addition to the ambulacral trunks, the nerve-cords to the intestine.

The physiological experiments of Fredericq (see p. 436 of his paper, *loc. cit.*) are almost entirely in accordance with those of Romanes and Ewart.

Dr. H. Prouho* has investigated the nature of the external nerve-plexus in *Echinus acutus;* and Dr. O. Hamann† has found and traced nerves in the various pedicellariæ of the *Echinidea*, and he finds that from the main nerves branches are given off to sense organs and glandular sacs. All the pedicellariæ are tactile organs, as the nerve-terminations indicate; the trifoliate ones seem to remove sand, *Protozoa*, &c. The large pedicellariæ serve to keep off layers of living bodies—*e.g.*, worms, and therefore act as weapons, as well as for organs of attachment when the animal is moving about. There is no doubt that the latter function is the most important; in other words, the pedicellariæ aid locomotion.

In *Echinus microtuberculatus* the gemmiform gland-bearing pedicellariæ hold fast sea-weeds, &c., when the animal is at

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* *Comptes Rendus*, tome 102, p. 444.

† *Sitzungsberichte Jenaisch. Gesell. für Med. und Naturwiss.* 1886.

rest; these help to hide it, and the secretion from the glands is therefore of the greatest service.

It will be noticed that the nervous system of the *Echinodermata* is much more highly developed than that of the *Cœlenterata*.

THE TRICHOSCOLICES.

According to De Quatrefages the nervous system of the *Turbellaria* consists of two ganglia situated in the anterior end of the body, from which, in addition to other branches, a longitudinal nerve-cord extends backwards on each side of the body. As a general rule, the lateral trunks exhibit ganglionic masses, and from these ganglia nerves are given off. These "may become approximated on the ventral side of the body, thereby showing a tendency to the formation of the double ganglionated chain characteristic of higher worms."

In the *Rotifera*, the nervous system consists of a large ganglion situated on one side of the body near the trochal disc. This ganglion, sometimes divided into two portions, gives off nervous filaments.

The nervous system of the *Cestoidea* consists of two longitudinal lateral nerve-trunks, which run down the body externally to the main canals of the excretory system. In the so-called head of the animal, where they are swollen (ganglia), they are united by a transverse commissure.

Dr. G. Joseph * has recently examined the nervous system of the *Cestoidea*. The results arrived at are—(*a*) That the two cerebral ganglia are in many cases (*Tœnia transversalis, T. rophalocera*) connected, not by a single dorsal commissure, but by two, separated by a matrix and muscle-processes; (*b*) that each cerebral ganglion is triple, consisting of a median and two smaller (dorsal and ventral) ganglia separated by muscle-processes, as is best seen in *Tœnia crassicollis;* (*c*) that in the bladder-worm, before evagination of the hooks, the

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* *Biologisches Centralblatt*, vol. 6, p. 733.

central system exhibits six equatorial ganglionic masses, which afterwards form a nerve-ring by the growth of bipolar processes.

The Annelida.

The nervous system of the *Gephyrea* surrounds the œsophagus, and from it a simple or ganglionated nerve-cord proceeds backwards in the ventral median line. This nerve-cord gives off branches. The nerve-ring surrounding the œsophagus usually has a ganglionic mass. This mass is connected with rudimentary eyes.

The nervous system of the *Hirudinea*, and of *Hirudo* in particular, is highly developed. It consists of large supra-œsophageal ganglia, which send off five pairs of nerves to the five pairs of eyes. These ganglia are connected with a sub-œsophageal ganglion by a circum-œsophageal nerve-ring. They also communicate with the buccal ganglia situated over and in front of the mouth. From the sub-œsophageal ganglion two longitudinal, ventral, and ganglionated cords proceed along the median line of the ventral aspect of the body.

The ganglia of the two ventral longitudinal cords are united together in pairs by transverse commissures. Each pair of ganglia sends off, to the right and left, two nerves. There are twenty-three pairs of ganglia on the ventral cords, in addition to the sub-œsophageal ganglion, which is composed of three or four pairs which have coalesced, and the caudal ganglion, which lies in the region of the posterior sucker, and is composed of seven coalesced ganglia.

There is also a system of visceral nerves, consisting of a nerve, which proceeds from the supra-œsophageal ganglia, and runs above the ventral ganglionated nerve-chain, giving off along its course branches to the cæca of the stomach.

The nervous system of the *Oligochæta*, as represented by *Lumbricus*, consists of two cerebral ganglia situated on the dorsal side of the pharynx in the third segment. These ganglia are connected by two nerves, which embrace the pharynx, with the sub-œsophageal ganglia. The latter ganglia are the first of the ventral ganglionated nerve-cord. This ventral nerve has a double ganglionic enlargement in every segment posterior to the third. A large nerve, which divides and sub-divides, proceeds forward from each of the cerebral ganglia.

Four or five nerves run backward from the upper part of each half of the circum-pharyngeal ring, and are distributed in the muscular walls of the pharynx. Nerves are also given off from the lower portion of this ring to the muscles of the fourth segment. Two pairs of nerves from each bilateral ganglionic enlargement of the ventral cord, proceed to the viscera and muscles of each segment. Two nerves, one from each side, pass off from the ventral nerve at a point nearly half-way between the double ganglionic masses. These supply the posterior sides of the mesenteric septa.

When examined under high power the nerve-rods of *Lumbricus* are seen to contain a large number of nerve-cells along with the nerve-fibres. This is a characteristic feature of *Lumbricus* and *Peripatus*. In *Hirudo* the nerve-

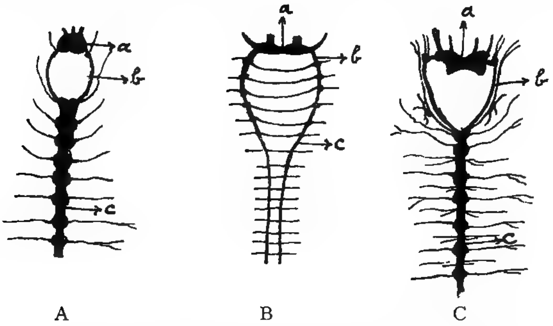

FIG. 62.—NERVOUS SYSTEMS OF POLYCHÆTA.

A = *Polynöe squamata.* B = *Sabella flabellata.* C = *Nereis regia.*

a = cerebral ganglia. *b* = œsophageal commissures.
c = longitudinal commissures of ventral ganglia.

cells are confined to the ganglia; in this respect the nerves of the leech are like those of *Astacus* and the spinal cord of the *Vertebrata.*

"The nervous system of the *Polychæta* usually consists of a chain of ganglia—one pair for each somite—connected together by longitudinal and transverse commissures, which diverge between the cerebral ganglia and the succeeding pair, to allow of the passage of the œsophagus. The most important differences presented by the nervous systems of the *Polychæta* result from the varying length of the transverse commissures. In *Vermilia, Serpula, Sabella,* these commissures are very long, so that two distinct and distant series of ganglia appear to run through the body, while, in *Nepthys,* the two series of ganglia are fused into a single cord enlarged at intervals. . . . In most *Polychæta* a very extensive series of visceral nerves supplies the alimentary canal."

THE NEMATOSCOLICES.

In the *Nematoidea* the nervous system consists of a nerve-ring surrounding the œsophagus. From this ring proceed six nerves in an anterior, and two in a posterior direction. Two of the anterior nerves proceed in the lateral lines—that is, one in each—and four in the interspaces between the lateral and median lines. The posterior nerves proceed to the tip of the tail—one in the dorsal, and the other in the ventral median line of the body. Near to the nerve-ring, in front and behind it, arranged in dorsal, ventral, and lateral groups, lie certain ganglia. These are respectively known as dorsal or supra-œsophageal, ventral or sub-œsophageal, and lateral ganglia. In addition to these, there are groups of ganglia in the median and lateral lines, in the posterior part of the body; these are known as caudal ganglia.

In the *Acanthocephala,* represented by *Echinorhyncus,* the nervous system consists of a simple ganglion, which is situated at the base of the proboscis. Nerves are given off from this ganglion to the proboscis, and through the retinacla to the muscular wall of the body.

THE CHÆTOGNATHA.

This class contains only one genus—*Sagitta.* The nervous system consists of a cerebral ganglion (brain) on which the eyes are placed, and a ventral ganglion situated near the middle of the body. These two ganglia are united by commissures. Near the mouth there are a pair of subœsophageal ganglia, which are united to each other, and to the cerebral ganglion by commissures which embrace the œsophagus.

THE PROTOTRACHEATA.

The nervous system of *Peripatus* consists of two large supra-œsophageal ganglia, and two imperfectly-ganglionated, widely-separated nerve-trunks, which proceed to the posterior part of the body. From these two trunks many lateral nerves pass outwards and inwards; and, according to Grube,* the latter act as commissures between the two nerve-trunks.

THE MYRIAPODA.

The nervous system of these animals forms a ventral chain, with a pair of ganglionic enlargements for each segment of the body. The anterior pair is united by commissures with the cerebral ganglia. The ventral chain gives off on each side a number of lateral nerves. The nervous system of the *Myriapoda* has been compared to that of the larvæ of the *Insecta.* The cerebral ganglia furnish nerves to certain sense organs, such as the eyes.

The ganglia are constituted of cells, and the cords of nerve-fibres.

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* *Archiv für Anatomie,* 1853.

THE INSECTA.

In these animals there is always a well-developed cerebral ganglion or brain connected by nerve-trunks with a series of ventral ganglia. One of the reasons of the great development of the brain is assuredly the greater perfection and the more important office of the organs of the special senses in the *Insecta.* According to Gegenbaur, many *Diptera, Hymenoptera, Lepidoptera,* and the large-eyed *Libellulæ,* have powerful cerebral ganglia. The cerebral ganglion or brain of the ants, of bees, and of the spinning spiders (among the *Arachnida*), is remarkable for its size, and even for its conformation. Though *Apis* is a much smaller insect than *Melolontha,* it possesses a cerebral ganglion more highly developed, and relatively three times larger, if we take into consideration the difference of size. The cerebral ganglion of the ant is proportionally larger still. Besides, the surface of these ganglia or brains is mammillated; and there are convolutions. According to M. Dujardin,* the brain of *Apis* has a very singular form. "We perceive a disc with stellated striæ surmounting like a hood the superior ganglion; and from certain experiments of M. Faivre,† the cerebral ganglion has, like the cerebral hemispheres of the Vertebrates, the property of being insensible to punctures and lacerations."

The nervous system of the *Insecta* (speaking in general terms) consists of a cerebral ganglion connected to a ganglionated nerve-trunk or trunks, which passes backwards along the ventral surface of the animal. Lateral nerves are given off from these ganglia to the organs of sense, limbs, viscera, &c. Fig. 63 represents the nervous systems of various insects; and numbers 4 and 5 of the same figure represent the nervous system of *Periplaneta.*

The nervous system of *Periplaneta* consists of supra-œsophageal ganglia (brain), which are connected by short,

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* *Annales des Sciences Naturelles,* 1850.

† *Ibid.* 4 s., tomes 8 et 9.

thick commissures with the sub-œsophageal ganglion, which corresponds to several pairs of ganglia fused together. This

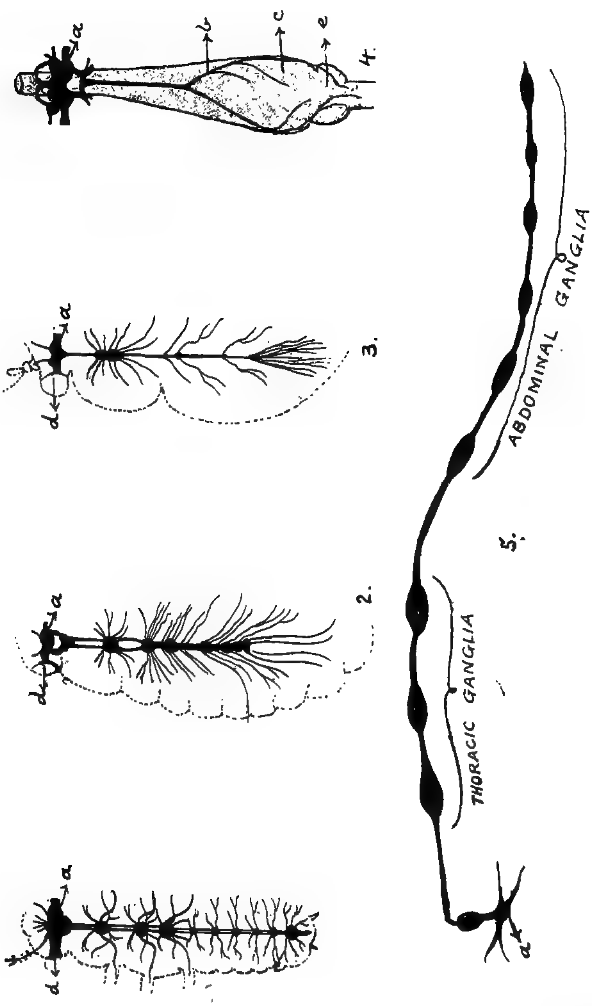

FIG. 63.—NERVOUS SYSTEMS OF THE INSECTA.

1 = *Formica*. 2 = *Dytiscus* (*Coleoptera*) 3 = *Musca* (*Diptera*). 4 = the brain and visceral nerves of *Periplaneta*. 5 = *Periplaneta* (*Orthoptera*).

a = brain. *b* = visceral nerves. *c* = crop. *d* = eye. *e* = gizzard.

sub-œsophageal ganglion leads into a ventral ganglionated chain, which has three pairs of coalesced ganglia in the thorax, and six pairs of closely connected and smaller ganglia in the abdomen. The brain gives off nerves to the sense organs (eyes, antennæ), the sub-œsophageal ganglion supplies the mouth, and the other ganglia the rest of the body. The visceral nervous system is well developed in the *Insecta*. (Fig. 63, 4).

In the *Insecta*, "the nervous system varies very much in the extent to which its component ganglia are united together. In most *Orthoptera* and *Neuroptera*, and in many *Coleoptera*, the thoracic and abdominal ganglia remain distinct and are united by double commissures as in *Blatta* (*Periplaneta*). In the *Lepidoptera*, the thoracic ganglia have coalesced into two masses united by double commissures; while in the abdomen there are five ganglia, with single or partially separated commissural cords. The concentration goes furthest in some *Diptera* and in the *Strepsiptera*, in which the thoracic and abdominal ganglia are fused into a common mass." In many insects there are respiratory nerves, whose branches are distributed to the muscles of the stigmata. The inner ends of these nerves form a plexus, which is situated "over the interval between two of the ganglia of the central nervous cord, and they are connected by longitudinal cords with one another, and with these ganglia."

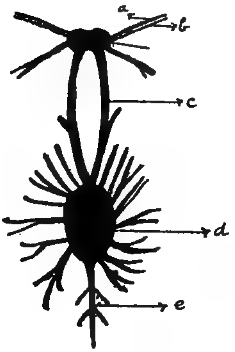

FIG. 64.

NERVOUS SYSTEM OF CRAB.

a = optic nerve. *b* = antennary nerve. *c* = circum-œsophageal nerve. *d* = fused thoracic ganglia. *e* = nerve-cord of abdomen.

THE ARACHNIDA.

In the *Arthrogastra*, there is a bilobed cerebral ganglion or brain connected by commissures with the sub-œsophageal ganglion: from this passes a nerve-trunk (consisting of two closely-applied commissural cords) to the three ganglia situated in the region of the twelfth to the fourteenth somites of the body. The abdomen contains four ganglia, from the last of which leads two nerves terminating in the extremity of the body. The cerebral ganglion, as in the *Insecta*, gives off nerves to the eyes and other sense organs; while branches from the sub-œsophageal ganglion are distributed to the maxillæ and following somites.

The visceral nervous system is well developed in these animals.

In the *Araneina*, the nervous system is more concentrated than in the last-mentioned order. It consists of cerebral and sub-œsophageal ganglia with branch-nerves, which proceed to the organs of sense and other parts of the body. In fact it will be observed that in the *Araneina* the ganglia are concentrated round the œsophagus. The same arrangement occurs in the *Acarina*.

THE CRUSTACEA.

As a representative of the lower *Crustacea* we describe the nervous system of *Cyclestheria hislopi*, belonging to the *Phyllopoda*. The nervous system of this animal has been recently worked out by Dr. G. O. Sars.* The cerebral ganglion or brain (see Fig. 11) is located within the pre-oral part of the head, posterior to the compound eye and immediately below the anterior part of the alimentary canal. It is rather large and of a somewhat irregular form, but very difficult to examine minutely on account of its being to a great extent concealed by the scape of the antennæ. From the upper part of this ganglion, and somewhat in front, the strong optic nerves originate. These nerves are not united, but quite separate throughout their whole length, each giving rise, at the end, to a ganglion, lying at a short distance posterior to the eye and sending off to this organ numerous

* *Christiania Videnskabs-Selskabs Forhandlinger*, 1887.

fine nerve-fibres. The anterior corner of the cerebral ganglion is exserted to a narrow point, applied against the posterior angle of the ocellus. The antennular nerves, apparently originating from the posterior part of the cerebral ganglion, may be easily traced as a delicate stem running along the axis of the antennulæ and dividing at their extremity into a number of nerve-fibres, which end with numerous ganglionic cells, filling up the dilated terminal part of these organs at the base of the sensory filaments. The nerves of the antennæ do not seem to arise from the cerebral ganglion itself, but from the strong commissures encompassing the œsophagus. The closer structure of these nerves, and the mode by which they innervate the several parts of the antennæ, Dr. Sars has not succeeded in tracing out.

The ventral nervous system, and especially its anterior part, is very difficult to examine. By carefully dissecting the trunk, and spreading it out in a ventral aspect after the intestine had been removed, Dr. Sars has succeeded in partly tracing out the double nerve-cord, which seems to agree in structure precisely with that in other known *Phyllopoda*, exhibiting the peculiar ladder-like appearance characteristic of those animals.

In the *Cirripedia*, "the nervous system consists of a pair of cerebral ganglia situated in front of the œsophagus, and connected by long commissures with the anterior of five pairs of thoracic ganglia, whence nerves are given off to the limbs. In the middle line, the cerebral ganglion gives off two slender nerves, which run parallel with one another in front of the stomach and enlarge into two ganglia, when they are continued to a double mass of pigment, representing the eyes. From the outer angles of the cerebral ganglion arise the large nerves, which proceed into the peduncle and supply the sac. These appear to correspond with the antennary and frontal nerves of other *Crustacea;* and Mr. Darwin describes an extensive system of splanchnic nerves."*

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* Huxley's *Invertebrata*, p. 295.

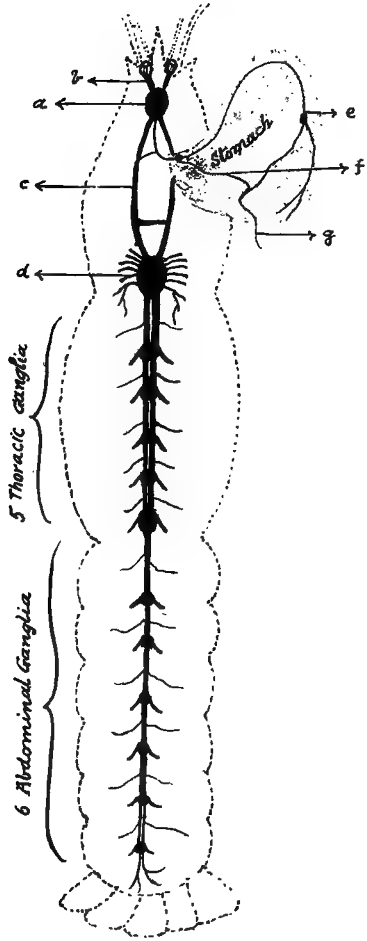

FIG. 65.
NERVOUS SYSTEM OF ASTACUS.
a = brain. b = optic nerve. c = "collar."
d = sub-œsophageal ganglion.
e = visceral nerve. f = posterio-lateral nerve. g = "hepatic" nerve.
The stomach is turned on one side to show its nerves.

In some *Crustacea*, such as the shore-crab (*Carcinus mœnas*), there is a large cerebral ganglion which gives off nerves to the eyes and antennæ; while the ventral chain of ganglia (of other forms) is fused into one mass (Fig. 64). From this mass radiate the nerve-cords. The nerve-cords connecting the cerebral ganglion with the nervous mass form the œsophageal ring or collar. There is in *Carcinus* a degree of concentration of the ganglionic cells, greater, in some respects, than in the Vertebrates themselves.

The nervous system of *Astacus fluviatilis* (Fig. 65, and see also Fig. 13) consists of thirteen ganglia joined together by means of commissures. These ganglia are divided as follows: one cerebral, one sub-œsophageal, five thoracic, and six abdominal ganglia. The cerebral ganglion or brain gives off nerves to the eyes; to the auditory organs; to the antennæ; to the carapace in front of the cervical suture; to the green glands; to the visceral nervous system; and to the sub-œsophageal ganglion. The latter nerves form the œsophageal collar. The sub-œsophageal ganglion supplies the somites, from the fourth to the ninth, and their appendages, and gives off also delicate nerves to the œsophagus. The five anterior abdominal ganglia supply the muscles and the appendages with nerves; while the sixth and last abdominal ganglion sends nervous branches to the telson (tail). The sixth abdominal ganglion also sends out two nerves, which unite into one common trunk, and from which nerve-fibres are given off to the intestine. The genital organs are supplied with nerves from the third, fourth, and fifth thoracic ganglia.

"The size of the ganglia is in direct ratio with the development of the segments and their appendages, to which they belong" (Von Siebold).

The physiology of the nerves of the *Macroura* (under stimulation) have been investigated by Drs. L. Fredericq and G. Vandevelde.* They experimented upon the nerves of the flexor muscles of the chelæ of *Homarus*. The nerves of *Homarus* when dissected out of the body very rapidly lose their excitability. When a nerve is submitted to section the excitability disappears progressively from the surface of the section to the extremity of the periphery. Concerning *Homarus*, Fredericq and Vandevelde state: "Ainsi, sur une pince séparée du corps de l'animal, il arrive un moment où l'excitation électrique du nerf près de la surface de section ne produit plus de contraction musculaire, alors que la même excitation appliquée sur un point plus rapproché du muscle y provoque de violentes secousses."

These experimenters have shown that the nerves of *Homarus* present the same distribution of electric tensions, and the same negative variation, as those of the frog (*Rana*).

They have also ascertained the rate of transmission of motor nervous influx in the nerve connected with the flexor muscle of the dactylopodite. In these experiments they had recourse to the graphic method employed by Helmholtz. By

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* *Bulletins de l'Académie Royale de Belgique*, 2 série, t. 47 [1879].

exciting the nerve at a point near the muscle, and notin moment of excitation and the moment of contraction, (able to ascertain the time which, elapses between th(phenomena: the same experiment is then repeated on a of the nerve further from the muscle. The difference i time observed in these two experiments—that is to sa;

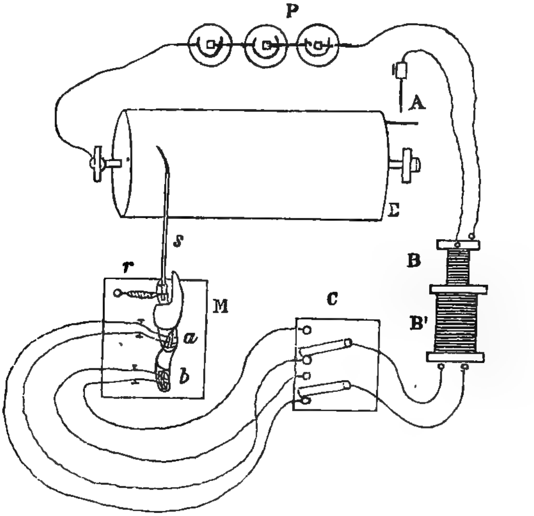

FIG. 66.—APPARATUS FOR STUDYING THE TRANSMISSION OF MOT(EXCITATION IN THE NERVE OF THE CHELA.

M = myograph carrying claw of *Homarus*. *s* = style attached to the opodite. *r* = elastic spring which holds the dactylopodite. *a* = electrodes. *b* = another pair of electrodes. C = commutator. P = l E = registration cylinder. BB' = the two coils. A = steel needles for the circuit at each revolution of the cylinder.

lapse of time between the second contraction and the fi gives the time employed by the motor excitation to ru distance between the two excited points. Knowing distance, one can calculate the rate of transmission.

Fredericq and Vandevelde exposed the nerve (in a lobster) which leads to the claw by two openings. A

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* The style used was that of Dr. Marey, the distinguished Profe Experimental Physiology in the College of France.

was attached to the dactylopodite of the chela (Fig. 66), and all firmly fixed, by the aid of bands, upon the horizontal plate of the myograph. The dactylopodite was held by means of a horizontal elastic spring; the object being to keep it away from the other portion of the claw. A pair of platinum electrodes were applied upon each of the two portions of the exposed nerves. The four wires from these electrodes were fastened to the wires of the induction coil by means of a commutator, which allowed the changing of the electric shock into one or other of the pairs of electrodes, and of exciting the nerve in its nearest or furthest point from the muscle. Fig. 66 shows the arrangement of the apparatus used in these experiments.

After ascertaining that the muscle reacts sufficiently to the excitation of the nerve, and that the point of the style marks properly on the smoked paper of the registration cylinder, Fredericq and Vandevelde arranged the commutator in such a manner that the induction shock could not act upon the nerve, and then allowed the cylinder to turn until it attained its normal velocity. The point of the style traces upon the paper a horizontal line, an absciss of which the turns are reproduced exactly. The cylinder continuing its revolutions, the commutator was so arranged as to excite the point *b* of the nerve at the moment when the two points of the needles which close the circuit touch each other. The muscle contracted, and the style gave a graphic tracing (a curve) of the contraction. In a similar manner the commutator was arranged so as to excite the point *a;* this gave a second curve, situated a little in front of the first. The distance from the beginning of the two curves compared to the length of the nerve enabled the experimenters to determine the rate with which the excitation was transmitted. They then marked on the cylinder the part where the nerve was excited. For this purpose, the commutator was closed in such a manner as to permit excitation, when contact was made, between the two needles. At this moment a contraction was produced, which inscribes itself as a simple line raised above the absciss whilst the cylinder was at rest. In these experiments, it had been previously ascertained that the cylinder had a uniform rate of rotation in inscribing by the aid of the "signal Marcel-Desprèz" the interruptions of an electric current produced by a tuning-fork of 100 vibrations per second. It was also ascertained that the contact between the two steel points always took place at the same moment of the rotation of the cylinder. Fig. 67 is an example of a graphic tracing obtained with *Homarus*.

The nerve was excited at A. The curve CD represents the curve inscribed by the muscle when the nerve was excited at the point *a* (Fig. 66). The curve EF was obtained by exciting the nerve at *b* (Fig. 66). The distance between the starting points of the two curves represents about 100th of a second.

Fredericq and Vandevelde measured the distance of the two excited points of the nerve, putting the points of the compass at each pair of electrodes, with those of the wire which were turned to the side of the muscle. This distance = 56 millimetres. The rate of transmission was consequently 100 × 0·56 = 5·6 metres per second. The following results were obtained in these experiments:—

A lobster (♀) weighing 559 grammes (without blood); the right chela being used; and the length of the nerve was 59 mm.

Experiments			
A,	interval in hundredths of a second . .	0.9 or	6.49 m. per second.
B,	,, ,, ,, . .	0.8 ,,	6.8 ,,
C,	,, ,, ,, . .	1.0 ,,	5.9 ,,
D,	,, ,, ,, . .	0.8 ,,	6.8 ,,

A lobster (♂) weighing 487 grammes (without blood); the left chela being used; and the length of the nerve was 56 mm.

Experiments			
E,	interval in hundredths of a second . .	1.1 or	5.04 m. per second.
F,	,, ,, ,, . .	1.1 ,,	5.04 ,,
G,	,, ,, ,, . .	1.0 ,,	5.60 ,,
H,	,, ,, ,, . .	0.9 ,,	6.16 ,,

The mean of these eight determinations is 5·95 metres, or in round figures 6 metres, per second.

The motor nervous excitation is transmitted, then, with infinitely more slowness in the lobster than in the frog or man.

In Fig. 67 the distance AC, which separates the beginning of the curve CD from the point A, corresponds to about 500ths of a second. This duration represents the sum of the two periods: 1st, the time which is lost from the excitation produced at the point *a* to run the length of the nerve as far as the termination of it in the muscle; and 2nd, the time of latent excitation of the muscle. The latter is known and determined, among other things, upon the same muscle. It suffices to obtain a graphic tracing of the muscular contractions by directly placing the exciting electrodes upon the flexor muscle of the dactylopodite. This time was found to be 1.500ths of a second, and that it did not exceed 200ths of a second. There remained, then, at least 5 − 2 = 300ths of a second, which represented the necessary time for the motor excitation to travel from the point *a* along the nerve to the interior of the muscle. The length of this portion of the nerve could not be directly determined; but it was very probably less than 500ths in these experiments, and did not certainly reach 1000th. That gave a velocity of 1.66 m. per second in the first hypothesis, and 3.33 m. in the second. From these

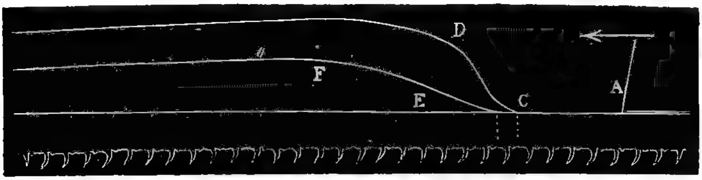

Fig. 67.—A Graphic Tracing for Determining the Rate of Transmission of Motor Excitation.

A = moment of excitation of nerve. CD = curve of contraction obtained by the excitation of the nerve at *a* (Fig. 63). EF = curve of contraction obtained by the excitation of the nerve at *b* (Fig. 63). (Hundredths of a second.)

investigations it is evident, that the rate of transmission of the motor nervous influx in its passage from nerve to muscle finds in the last nervous ramifications considerable delay.

The following conclusions have been arrived at by Fredericq and Vandevelde:—

(1) There appears to be a complete identity in the properties of the muscles of *Homarus* and those of *Rana.*

(2) The motor nerves of *Homarus* present, from a *physiological point of view,* great points of resemblance to those of *Rana.* The most characteristic difference consists in the slowness with which the motor excitation travels the length of the motor nerves. In *Homarus* it is 6 metres, and in *Rana* 27 metres per second. The slow rate of transmission of the motor excitation proves in *Homarus* a considerable slackening in the muscular terminations of the motor nerves.

The difference in the rate of transmission may be due to the difference in the composition of the nervous matter of the two animals. The following table represents the chemical composition* of the nerves of *Homarus* and *Rana* respectively:—

	Homarus.		*Rana.*	
	I.	II.	I.	II.
Albuminoids	20.61	21.00	29.20	30.00
Lecithine	7.79	8.11	9.92	9.90
Cholestrine and fats	58.34	57.67	47.13	46.44
Cerebrine	8.26	8.03	9.78	9.75
Insoluble substances (in ether)	4.10	4.26	3.50	3.46
Salts	0.90	0.92	0.47	0.45
	100.00	99.99	100.00	100.00

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* Dr. A. B. Griffiths' analyses.

The composition of the *ashes* of the nervous matter in each case is represented in the following table:—

	Homarus.	*Rana.*
Potash	33.00	36.24
Soda	11.98	10.87
Magnesia	1.87	1.30
Lime	0.99	0.81
Iron oxide	0.16	0.21
Phosphoric acid (combined)	41.51	40.32
Phosphoric acid (free)	6.81	7.92
Sulphuric acid	0.90	0.72
Chlorine	1.96	1.21
Silica	0.82	0.40
	100.00	100.00

The first table gives the chemical composition of the nervous matter in a *dry* state; the following table gives the composition of the nervous matter with its accompanying water:—

	Homarus.	*Rana.*
Water	70.21	66.42
Solids	29.79	33.58
	100.00	100.00

The last two tables represent the averages of six analyses in each case.

The difference in the composition of the nervous matter of the two animals, may possibly account for the difference in the rates of transmission as observed by Fredericq and Vandevelde.

THE POLYZOA.

The nervous system of these animals is very simple, and consists of a ganglion, situated between the mouth and the anus (see Fig. 17), which gives off many nerve-fibres to the tentacula and the alimentary canal.

THE BRACHIOPODA.

The nervous system of the *Clistenterata* consists of a ganglion on the ventral side of the oral aperture. From this ganglion proceeds a commissure, which surrounds the œsophagus, and bears two small ganglia. "The latter probably answer to the cerebral, the former to the pedal, ganglia of the *Lamellibranchiata*. Immediately behind the pedal mass, from which two large nerves to the dorsal or anterior lobe of the mantle are given off, are two elongated ganglia, connected by a commissure of their own, which possibly correspond with the parieto-splanchnic ganglia of the higher Molluscs. The nerves to the ventral lobe of the mantle, and those to the peduncle arise from these ganglia."

The nervous system of the *Tretenterata* has not been so thoroughly worked out as that of the *Clistenterata;* but in *Lingula*, Sir Richard Owen, F.R.S., has shown that the visceral nerves are more developed than those of *Terebratula*, which belongs to the latter order. "Filaments to the muscles are also more distinct: a pair, which come off from the sub-œsophageal ganglion, diverge as they pass backwards along the visceral chamber, then converge to their insertion in the anterior muscles; a second pair, also from the sub-œsophageal ganglia, run more parallel as they pass along the ventral aspect of the anterior muscles to go to the posterior muscles.

Lingula has also the pallial and brachial systems of nerves as well developed as in *Terebratula*."*

THE MOLLUSCA.

In the *Mollusca* there are usually at least three ganglia with radiating nerves—one in the head, one in the foot, and one posterior and above the alimentary canal.

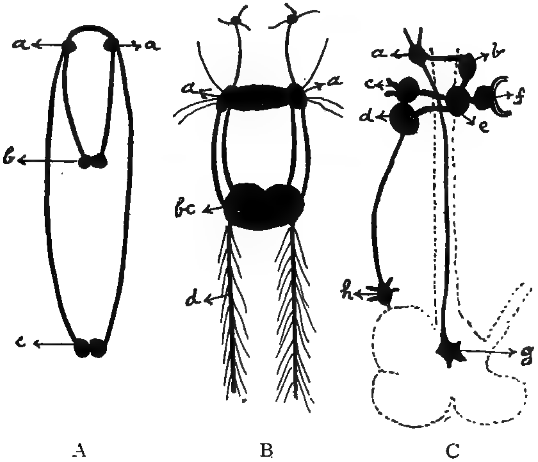

FIG. 68.—NERVOUS SYSTEMS OF THE MOLLUSCA.

A = diagram of nervous system of *Anodonta*. *a* = cerebral ganglia. *b* = pedal ganglia. *c* = parieto-splanchnic ganglia.

B = nervous system of *Limax*. *a* = cerebral ganglia. *bc* = pedal parieto-splanchnic ganglia. *d* = nerves to foot.

C = nervous system of *Sepia*. *a* = posterior buccal ganglion. *b* = anterior buccal ganglion. *c* = pedal ganglion. *d* = parieto-splanchnic ganglion. *e* = cerebral ganglion. *f* = optic nerve and ganglion. *g* = splanchnic ganglion. *h* = ganglion stellatum.

As an example of the *Lamellibranchiata*, we describe the nervous system of *Anodonta*. There are three pairs of ganglia. (*a*) The cerebral ganglia, which are united by a commissure, are situated at the sides of the mouth. They send

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* Owen's *Comparative Anatomy and Physiology of the Invertebrate Animals*, p. 492 (2nd ed.).

off nerves to the anterior portion of the pallium; to the anterior adductor muscle; to the labial palps, &c.; and to the branchiæ. (*b*) The pedal ganglia are situated in the foot, or in the corresponding part of the body when the foot is absent, as is the case in some of the *Lamellibranchiata*. These ganglia are fused together on the median line of the body, and are connected by commissures with the cerebral ganglia. The pedal ganglia send off nerves to the foot.(*c*) The parieto-splanchnic or visceral ganglia lie on the ventral side of the posterior adductor muscle. They are united with the cerebral ganglia by commissures (Fig. 68 A), which traverse the organ of Bojanus (kidney). These ganglia send off nerves to the branchiæ; to the posterior and middle parts of the pallium; to the posterior adductor muscle; to the heart; to the siphons —as in *Mya;* and to the viscera generally.

In the *Gasteropoda*, represented by *Helix*, the nervous system consists of the following parts: (*a*) The cerebral or supra-œsophageal ganglia, lie on the dorsal side of the œsophagus, and are joined close together by a transverse nervous band (Fig. 68 B). Each ganglion sends off a commissure to the pedal ganglia, which are situated close together on the ventral side of the œsophagus. Commissures also join the cerebral ganglia with the so-called parieto-splanchnic ganglia (a group of paired ganglia), which come into close relationship with the pedal ganglia; in fact, they are fused together with the latter ganglia. The cerebral ganglia supply nerves to the eyes, tentacula, &c., and also give off a pair of nerves—one on either side of the œsophagus—to the buccal ganglia. (*b*) The pedal ganglia are closely united. (*c*) As already stated, the parieto-splanchnic ganglia are fused with the pedal ganglia. They send off nerves to the nephridia, heart "lung," sexual and olfactory organs, and pallium. (*d*) The small paired buccal ganglia are situated above and below the buccal mass. These regulate the movements, &c., of the mouth; and they have been regarded by some investigators as sympathetic in function.

In the *Cephalopoda*, the nervous system consists of a cerebral or supra-œsophageal, pedal and parieto-splanchnic ganglia situated around the œsophagus, and connected by commissures. "In addition to these, buccal, visceral, branchial, and pallial ganglia may be developed on the nerves which supply the buccal mass, the alimentary canal, heart, branchiæ, and mantle."

In the *Dibranchiata* (Fig. 68 C), the cerebral ganglia send off nerves to the eyes, &c., and to the buccal ganglia; in the *Tetrabranchiata*, the same ganglia supply nerves to the eyes, &c., and to the buccal mass. The pedal ganglia, in the *Dibranchiata*, supply the arms, funnel, and they are connected with the auditory nerves. In the *Tetrabranchiata*, the pedal ganglia supply the branchiæ and the funnel. In both sub-orders of the *Cephalopoda*, the parieto-splanchnic ganglia supply the branchiæ, but in the *Dibranchiata* they also send nerves to the pallium and sexual organs. In the last-mentioned sub-order, "each parieto-splanchnic ganglion gives off a nerve, which runs along the shell-muscles to the anterior wall of the mantle, and there enters a large ganglion—the ganglion stellatum." The anterior and posterior buccal ganglia give off nerves to the œsophagus and stomach. The nervous system of the *Cephalopoda* is characterised by its great concentration and high development.

Notwithstanding the apparent irregularity of its general arrangements, the nervous system of the *Mollusca* is modelled upon the same plan as that of the *Arthropoda*. In the *Mollusca*, we still find the œsophageal ring, giving off from its central portion a ganglionic peripheral nervous system, distributing itself to the various organs, but without symmetry, as, however, the general conformation of the body demands. The cerebral or super-œsophageal ganglia are very small in the *Lamellibranchiata*; but are not exceptionally so, as these animals have no head provided with sense-organs.

The cerebral ganglion is, however, very large in the *Cephalopoda*, due to the highly developed sense-organs.

The cerebral or supra-œsophageal ganglion of the *Mollusca* appears to have special functions. According to M. Vulpian,* if this ganglion in *Helix* is removed, the animal survives the operation four or five weeks, but remains completely motionless. On the other hand, the removal of the sub-œsophageal ganglion kills the animal in twenty-four hours. Mechanical or electrical stimulation of the supra-œsophageal ganglion of the *Mollusca* produces little or no effect; but with the sub-œsophageal ganglion, both kinds of stimulation cause vigorous muscular agitation. Electrical stimulation often causes the heart to stop, in the state of diastole. Exactly the same phenomenon occurs when electrical stimulation is applied to the pneumogastric nerves in the *Vertebrata*.†

These facts would seem to confirm the theory of the German school of evolutionists, who connect the genealogy of the *Vertebrata* with the *Mollusca;* but this theory has had its day, and the latest embryological researches explain the origin of the Vertebrate brain and spinal cord as the outcome of the nervous system of the *Arthropoda*. The nervous system of the acranial Vertebrates can be considered as a coalescent ganglionic nervous system. The central nervous system of *Amphioxus* (one of the acranial Vertebrates) is a spinal cord with a series of ganglionic enlargements, each of which corresponds with the origin of a pair of nerves. An enlargement, which is comparable to the central ganglion of the *Arthropoda*, terminates (anteriorly) the spinal cord of the acranial *Vertebrata*. It does not perceptibly differ from the others, but gives off five pairs of nerves, among which are the optic and auditory nerves. The great difference between the *Arthropoda* and the *Vertebrata* is the complete absence in the latter of an œsophageal nervous ring; and that the nerve-cord has a dorsal aspect in the *Vertebrata*,

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* *Leçons sur la Physiologie Générale et Comparée du Système Nerveux*, pp. 757–761.

† From these investigations it is difficult to decide whether the supra- or the sub-œsophageal ganglion represents the brain in the *Mollusca*.

whereas it is situated ventrally in the *Arthropoda.* Nevertheless there is a certain amount of homology between the spinal cord of the cranial and acranial *Vertebrata* on the one hand, and the ganglionic chain of the *Arthropoda* on the other. In both the *Vertebrata* and the higher *Invertebrata,* there is a special nervous network, which supplies the alimentary canal, the respiratory and urino-genital organs, and the circulatory system. In both of these sub-kingdoms this system has its origin, or at least its roots, in the great nervous centres.

In concluding these remarks, it may be stated that on the whole, every nervous system, whether Invertebrate or Vertebrate, resolves itself into a number of cells, and into a number of fibres, which connect the cells or terminate therein. The parts of the system where the cells accumulate in great number are the nervous centres. The parts are almost wholly composed of fibres from the nervous cords, and if we look at the animal kingdom as a whole, we see that where the cellular centres are the more voluminous and the less numerous, the higher the animal is in the zoological scale. In fact, the mammal has been said to be "a sort of summary of the entire kingdom. In him are combined all the tissues, all the apparatus scattered through the entire series: he has a special nervous system, but he possesses, nevertheless, a portion of the ganglionic system of the Invertebrates, and in him, as in them, this ganglionic system is constituted essentially of fibres," derived in the first instance from a protoplasmic basis.

THE TUNICATA.

The nervous system of these animals consists of an elongated cerebral ganglion situated on the dorsal side of the pharynx. Nerves are given off from this ganglion to the entrance of the pharyngeal sac, &c.; nerves are also sent out laterally and posteriorly. In the Ascidian larva the nervous system is composed of a cerebral ganglion, which has at first the form of a cord containing a cavity. This ganglion is constricted into three parts, and is connected with ganglia in the tail. The first or anterior part of this ganglion gives off nerves to the margin of the pharyngeal aperture. The middle portion of this ganglion has on it the auditory vesicle, the optic organ, and a stalked ciliated olfactory organ. The optic and auditory organs degenerate just before the adult condition is reached. The third or posterior portion of the ganglion is continued into a long nerve, which at the base of the tail forms a ganglionic enlargement. This ganglion gives rise to a nervous cord, which passes into the tail, where it forms a number of small ganglia. Just before the animal reaches maturity, the tail aborts, the muscles and notochordal sheath degenerate, and the notochordal axis contracts. The nervous system and sense-organs also degenerate, and the cavity in the nerve-cord and cerebral ganglion disappears.

In concluding the chapter it may be stated that Prof. E. Ray Lankester* states that "the structure and life-history of the Ascidians may be best explained on the hypothesis that they are instances of *degeneration;* that they are the modified descendents of animals of higher, that is, more elaborate structure, and, in fact, are *degenerate Vertebrata,* standing in the same relation to fishes, frogs, and men, as do the barnacles to shrimps, crabs and lobsters."†

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* *Degeneration,* p. 41.

† For further information relative to the above subject see the papers of Dr. A. Giard in the *Archives de Zoologie Expérimentale,* t. i (1872); *Association Française pour l'Avancement des Sciences,* t. 3 (1874): *Revue Scientifique* du 11 juillet 1874; *Revue des Sciences Naturelles,* septembre 1874; et *Comptes Rendus,* 1874–5; and also Dr. W. A. Herdman's papers in the *Challenger Reports.*

CHAPTER XI.

THE ORGANS OF SPECIAL SENSE, ETC., IN THE INVERTEBRATA.

As we have already seen, all nerves have not the power of transmitting sensations to the brain or its equivalent; some, on the contrary, are clearly nerves of motion, whether acted on by will or excited by other means. Some nerves, as the optic, transmit only the impressions received from colours—*i.e.*, due to the action of light; to other stimulants this nerve is insensible. The olfactory nerve is sensible to various odours, but it is insensible to the action of light or sound. To these modifications of the sensibility of nervous elements are due the phenomena of special senses. The senses of touch, taste, smell, hearing, and seeing, are so many distinct faculties putting the animal kingdom in relation with the various qualities of the external world.

The apparatus or mechanism of the sensibility is not composed only of the different parts of the nervous system, whose use we have already alluded to; for the sense-nerves do not terminate freely in the exterior, so as to receive directly the contact of the producing agents of sensations, but terminate in various mechanisms destined to collect the excitation, and to prepare it in such a way as to assure its action. These mechanisms are the sense-organs, and it is essentially by the intermedium of these organs that the sensations reach the brain or its equivalent; but it may be remarked that they are not indispensable for the exercise of all the special senses; the tactile sensibility may be called into play everywhere, where nerves exist adapted to conduct the ordinary sensations, and it is only by the senses of taste, smell, hearing, and sight, that this intermediate organ between the nerve and the external world is a necessary condition.

We now proceed to describe the sense-organs in the principal divisions of the *Invertebrata*.

The Protozoa.

As these organisms are destitute of any true nervous system, it would be consistent, on *à priori* grounds, to assume that they have no special sense-organs. But would it be consistent to assume that these lowly organisms do not digest, respire, and excrete, because there are present no special organs set apart for the functions of digestion, respiration, and excretion? Certainly not, and there is every reason to believe that one or more of the special senses are represented in the *Protozoa*.

Tactile sensibility is generally distributed over the whole surface of the body; frequently, however, it is concentrated on processes and appendages of it. This is more or less true in the whole animal kingdom. In the *Protozoa*, the whole surface of the body is exceedingly sensitive; but it may be stated that the protoplasmic expansions called pseudopodia have been regarded as fulfilling the function of organs of touch as well as of locomotion. In other forms (*e.g.*, *Paramœcium*, see Fig. 3) the vibrating cilia are considered by Dr. Stein to be organs of touch; and the long rigid bristle in *Cryptochilum*, according to M. Maupas, has a similar function, its principal use being "to advise the animal of the approach of other *Infusoria*."

In touch, sensibility is brought into play by simple shock, or contact of bodies: it is spoken of as the least perfect of the senses, and is also the one which offers the least variety in the different animal classes, compared among themselves.

Of all the sense-organs, the eye is the one which is first differentiated; and a large number of the lowest organisms possess an ocular spot, which is a differentiated organ having the function of sight.

In the *Protozoa*, this organ is chiefly found in the group of Monads or *Flagellata,* and is generally coloured red. Klebs has studied the structure of these ocular spots in the Euglenæ. When one of these organisms is treated with a solution of sodium chloride (1 to 100), the contractile vesicle, which is in close proximity to the ocular spot, dilates enormously, and consequently causes the same thing to occur in the ocular spot itself. By this means Klebs observed that the spot "is a small discoid or triangular mass, of jagged and irregular outline (see Fig. 1); it is formed of two parts: for a base it has a small mass of reticulated protoplasm, and in the meshes of the protoplasm there are small drops of an oily substance coloured red."

"What is the physiological significance of these spots? Ehrenberg considered them as eyes; hence the name *Euglena* (word for word, pretty eye), which he had given to a species of the *Flagellata* provided with ocular spots. This interpretation had been questioned by all the authors of his time, and especially by Dujardin." At the present day, however, many distinguished French naturalists hold the same opinion as Ehrenberg—viz., that the so-called ocular spots of the *Protozoa* are true visual organs. According to M. Pouchet, the ocular spot of *Glenodinium polyphemus* (one of the *Peridineæ*) has without doubt the function of an eye. It always occupies a fixed and definite position in the cell, and it is composed of two parts—a crystalline humour and a choroid. "The crystalline humour is a strongly refractive, hyalin, club-shaped body, rounded at its free end, which is always directed forwards, while the other end is immersed in the mass of pigment which represents the choroid. The latter is clearly determined; it forms a sort of hemispherical cap, enveloping the posterior extremity of the crystalline humour. In fact, the visual organ of this organism is composed of exactly the same parts as the eye of a Metazoon, with one exception, the absence of the nerve-element."

The ocular spots of other *Flagellata* had been previously investigated by Künstler, Claparède, and Lachman, and they found crystalline humours and pigmented capsules (a choroid); but what their true function was, they did not know, as no nerve-apparatus fitted to perceive the impressions received was, in the least, demonstrable in these organisms. On the other hand, certain French savants state that "the coexistence of a pigment and of a crystalline humour amply suffices to characterize a visual organ. As to the nerve-apparatus susceptible of perceiving impressions, it is replaced by the protoplasm, which, as is well known, is sensitive to light." It has also been stated, by some observers, that the red pigment in the ocular spots of the *Protozoa* exhibits similar reactions to the pigment, which is present in the rods of the retina of the *Vertebrata*. But it should be borne in mind that pigment is not indispensable for the sensation of light, because there are many eyes of complicated structure from which pigment may be altogether absent. Therefore the only reasons which those observers, who state that a visual organ is present in certain *Protozoa*, have for such an assertion is, that the ocular spot has a definite position, and it possesses a crystalline humour. Are these facts sufficient to speak of it as an eye? The Rev. W. H. Dallinger, F.R.S., and Dr. J. Drysdale,* who examined the ocular spots in various Monads, failed to discover the function of these bodies after a most searching inquiry.

In concluding this account of the sense-organs in the *Protozoa*, it may be stated that the vesicles of Müller in *Loxodes rostrum* (one of the *Ciliata*) have been considered as possessing an auditory function.

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* *The Monthly Microscopical Journal*, vol. 11, p. 8

THE PORIFERA OR SPONGIDA.

In these animals the sense-organs are not further differentiated than those of the *Protozoa*.

THE CŒLENTERATA.

The sense of touch in these animals is believed to be chiefly located in the tentacula, which surround the mouth, but in *Hydra*, as well as in other forms, every cell is sensitive to touch.

The small pits in connection with nerves, and provided with an epithelial lining of hair-bearing sense cells, in the *Medusæ*, are regarded as the simplest olfactory organ. They are situated round the margin of the bell; in fact in all the *Medusæ* the sense-organs are marginal. The small pigmented spots are undoubtedly eyes; and according to some writers, otolithic sacs or simple auditory organs are also situated on the edge of the bell.

The rudimentary eyes of the *Medusæ* are much better developed than those which are supposed to exist in the *Protozoa*; for in certain species, nerves penetrate manifestly into the capsule (Gegenbaur). But the exact function of the ocular spots in these animals was not understood until Dr. G. J. Romanes, F.R.S.,* investigated their nature from a physiological standpoint. His mode of investigating this subject was to put two or three hundred *Sarsiæ* into a large bell-jar, and then to completely shut out the daylight from the room in which the jar was placed. By means of a dark lantern and a concentrating lens, he cast a beam of light through the water in which the *Sarsiæ* were swimming. "From all parts of the bell-jar they crowded into the path of the beam, and were most numerous at that side of the jar which was nearest to the light. Indeed, close against the glass they formed an almost solid mass, which followed the light wherever it was moved. The individuals composing

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* *Philosophical Transactions*, 1875, p. 295; *ibid.*, 1879, p. 189.

this mass dashed themselves against the glass nearest the light with a vigour and determination closely resembling the behaviour of moths under similar circumstances. There can thus be no doubt about *Sarsia* possessing a visual sense."

To prove that the ocular spots of these animals are really eyes, Dr. Romanes experimented in a like manner with a dozen vigorous specimens; nine of which had previously had their ocular spots removed, while three specimens were left intact. The difference in the behaviour of the mutilated and the unmutilated individuals was very marked. The three unmutilated individuals sought the light as before, while the nine blind or mutilated individuals swam hither and thither without paying it any regard.

It was suggested by Professor L. Agassiz, that it was the heat, or ultra-red rays of the spectrum, which was the real cause of the above phenomenon, but Dr. Romanes has shown that when a heated piece of iron ("just ceasing to be red") was placed against the bell-jar containing the specimens of *Sarsia*, not one of the organisms approached the heated metal.

These investigations prove that in *Sarsia* the faculty of appreciating luminous (but not heat) rays is present, and that this faculty is lodged exclusively in the ocular spots.

Dr. Romanes has also shown that the lithocysts of the covered-eyed *Medusæ* resemble, in function, the marginal bodies of the naked-eyed *Medusæ*—that is, they are rudimentary or incipient organs of vision. The lithocysts are stimulated by the approach of a candle or the access of daylight, but if the lithocysts are removed, the approach of a luminous object produces no stimulating effect.

The ocular spots in the *Actinozoa*, and especially in *Actinia mesembryanthemum*, have been investigated by Schneider, Rötteken, Duncan, and MacMunn. These coloured bodies are situated in the oral disc outside the tentacula; and they are diverticula of the body wall. Beneath the surface "lies a layer of strongly refracting spherules, followed by another layer of no less strongly refracting cones. Subjacent to these, Professor P. M. Duncan, F.R.S.,* finds ganglionic cells and nerve-plexuses. It would seem, therefore, that these bodies are rudimentary eyes."

The colouring matter of the blue ocular spot of the above-mentioned species of *Actinia* has been spectroscopically investigated by MacMunn,† and these investigations have led him to believe that it is possible that this pigment is capable of absorbing certain rays of light, so as to enable the animal to distinguish light from darkness.

THE ECHINODERMATA.

The sense of touch is well developed in the *Echinodermata*, and seems to have its seat in the ambulacral feet, pedicellariæ, and tentacula situated in the neighbourhood of the buccal orifice. Romanes and Ewart state that "all the *Echinodermata* seek to escape from injury. Thus, for instance, if a starfish or sea-urchin is advancing continuously in one direction, and if it be pricked or cut in any part of an excitable surface facing the direction of advance, the animal immediately reverses that direction." There is no doubt that the sense of touch is present in these animals.

The sense of smell also appears to be developed to a certain extent in starfishes. If several of these animals (contained in a tank) are advancing in the direction of a luminous portion of the water,‡ they immediately retract their steps, if a small quantity of bromine or sulphuretted hydrogen water is gently poured into the luminous portion of the water. This fact appears to support the idea of a sense of smell in the *Asteridea*.

According to Leydig § certain *Echinodermata* appear to be provided with auditory vesicles, in which float powerfully

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* *Proceedings of Royal Society*, 1873.

† *Philosophical Transactions*, 1885, pt. 2, p. 660.

‡ The water was illuminated by means of a small incandescent lamp.

§ *Histologie Comparée*, p. 316.

refracting homogeneous granules. These vesicles receive nerves, and sometimes even rest on the central ganglia of the nervous system.

The eyes or ocular spots in the *Asteridea* are five in number, and they are situated at the end of each ray. These organs are spheroidal, pedunculated, and pigmented prominences; being expansions of the ectoderm, and continuous with the ambulacral or radial nerve (see Fig. 61). Each eye contains a number of clear oval bodies surrounded by a pigment. These are said to represent the crystalline cones of a compound eye.

In the *Echinidea* the five ocular spots are situated on a similar number of small plates, which form the apex of each ambulacral segment. The ocular along with the five genital plates surround the anus.

The true function of the ocular spots in the *Echinodermata* have been ascertained by Drs. Romanes and Ewart.* The *Asteridea* and *Echinidea* (but not the *Ophiuridea*) crawl towards, and remain in, the light; but when their ocular spots are removed they no longer do so. On the other hand, if only one of the five ocular spots were left intact, the animal crawled towards the light as before. It may also be stated that when their ocular spots are left intact, these animals can distinguish light of very feeble intensity.

THE TRICHOSCOLICES.

In the *Turbellaria* the organs of touch are distributed over the whole surface of the body, but the cilia are the chief tactile organs. Some of these animals have auditory sacs provided with otoliths; and most of them possess eyes. Many *Planariæ* have first of all in the embryonic state pigmented spots in the place where, at a later period, eyes with crystalline cones are developed.

In the *Rotifera*, the tactile organs are cutaneous, and have

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* *Philosophical Transactions*, 1881, pt. 3, pp. 856, 873, 877.

the form of papillæ or prominences covered with hairs, or of tubular prolongations of the skin. In some of these animals there is a sac filled with calcareous granules attached to the ganglion. This sac is most likely an auditory organ.

One or more ocular spots are sometimes situated on the ganglion in the *Rotifera*.

In some of the *Trematoda*, ocular spots have been observed, but no other sense-organs.

THE ANNELIDA.

In these animals the sense-organs are variously distributed. The organs of touch are cutaneous, and they have the form of bristles (setæ), &c., in connection with sensitive fibres. According to Leydig, these tactile organs are sometimes, in the *Hirudinea*, grouped in large numbers at the bottom of cup-shaped depressions. In *Hirudo*, there are about sixty of the cup-shaped depressions in the head, and others in the posterior part of the body. They are in connection with the terminations of nerves given off to those in the head from the supra-œsophageal ganglia, and to those posteriorly situated, from the caudal ganglion. These organs are also of an olfactory function (Leydig).

In the *Gephyrea* rudimentary or incipient eyes are sometimes connected with the cerebral ganglion. Simple eyes are usually present on the anterior segment in the *Hirudinea*. These are supplied by nerves from the supra-œsophageal ganglia.

In *Hirudo* the eyes are situated on the dorsal surface of the first three segments.

In *Lumbricus* (one of the *Oligochæta*) no eyes or other special sense-organs are present. Although devoid of sense-organs, *Lumbricus* "possesses a generalised sensitiveness, due to the plentiful distribution of nerve-fibres through the body, and which, in many respects, takes the place of a series of specialised organs, corresponding to the senses of touch, taste, sight, hearing, and smell. Its sensitiveness to touch and its dislike to sunlight are well known; and, though not possessed of organs of sight or smell, it is able easily to find its way to stores of food, and to retreat from sources of danger into a burrow" (Gibson).

In *Alciope* (one of the *Polychæta*) the eyes are large and well developed.

As already stated the visual organs in the *Annelida* are usually situated in the anterior part of the body; but in "the remarkable genus *Polyophthalmus*, De Quatrefages discovered, besides the ordinary cephalic eyes, a double series of additional visual organs, one pair being allotted to each somite. In *Branchiomma*, eyes are situated at the ends of the branchial plumes. Ehrenberg has described two caudal eyes in *Amphicora*, and De Quatrefages has shown that similarly placed eyes exist in three other species of *Polychæta*, two of which are closely allied to *Amphicora*, while the other is an errant form, related to *Lumbrinereis*. Auditory sacs, containing many otoliths, have been observed upon each side of the œsophageal ring in *Arenicola*, and similar organs have been noticed in other *Tubicola*; but hitherto their existence has not been certainly determined in the *Errantia*" (Huxley).

THE NEMATOSCOLICES.

In the *Nematoidea*, the papillæ and hairs situated chiefly in the region of the mouth are organs of touch.

In non-parasitic Nematodes (*e.g.*, *Enoplus*) pigmented ocular spots are present on the œsophageal nervous ring.

THE CHÆTOGNATHA.

The eyes in *Sagitta* are situated on the supra-œsophageal or cerebral ganglion.

THE MYRIAPODA.

Concerning the sense of touch in these animals, there are on the antennæ and other appendages, filiform prolongations —these transmit the effects of mechanical pressure, &c., to the nerves attached to these organs.

Although some species of the *Myriapoda* are blind, the majority have eyes; and these organs are either simple or compound eyes. Prof. H. Grenacher has recently investigated the eyes in this Arthropod class. He distinguishes those of (1) *Scolopendridæ*, (2) *Lithobius*, (3) *Julus*, (4) *Glomeris*, and (5) *Scutigera*; all except the last are stemmata. *Scutigera* has compound eyes of a very anomalous type, in no wise resembling those of the *Insecta* and *Crustacea*. The eyes of the *Chilopoda* are more polymorphic and more complex than those of the *Chilognatha* (*Diplopoda*). Physiologically, the simple eyes of at least some of the *Myriapoda* must be very unlike the ordinary stemmata of spiders or insects. These are true eyes. In the *Myriapoda*, on the other hand, each stemma has its retinal elements, or their representatives so disposed in regard to the axis of the cornea-lens, and therefore to the incident rays of light, that it seems very doubtful whether such eyes can do more than distinguish between degrees of light and darkness.

The sense of smell appears to be feebly developed in the *Myriapoda*.

THE INSECTA.

"The sense of touch appears to be seated in the *Insecta* in very different parts of the body. It is chiefly located in the palpi of the mouth, which, for this purpose, are usually terminated by a soft surface. The antennæ also serve as tactile organs, but in a very variable manner, according to their forms, the degree of their development, and the habits of the species. These organs receive, each, directly from the cerebral ganglion, a nerve; these nerves perceive the slightest disturbances occurring in the antennal integuments, which are solid and often provided with hairs and bristles. Among those *Insecta* in which these organs are very long, filiform, and movable in various directions, they serve, like the vibrissæ of many *Mammalia*, to announce the presence of external bodies. With very many other *Insecta*, they are very movable, and are distinctly used as tactile organs, like the fingers of the human hand. It is also by means of these organs that insects perceive the various conditions of the atmosphere, especially the temperature, and thereby regulate their movements and actions. With those *Insecta*, where the parts of the mouth are modified into organs of suction, it is quite evident that the extremity of the proboscis is the seat of a very delicate sense of touch. Also with those female insects having an ovipositor, which is used to deposit their eggs in holes of various depth, the apex of this organ must be endowed with the same power."*

The extremities of the limbs in many *Insecta* are also tactile organs. Besides these special devices, the skin of the *Insecta* is sensitive to touch. In spite of the chitinous covering, these animals feel strongly the contact of external objects at any point of their own bodies. This is due to the sensitiveness of the underlying membrane.

The sense of taste is confined to the mouth and pharynx. This sense is, as a general rule, connected with the tactile sensation of the buccal cavity, and also with the olfactory sensation.

In the *Insecta*, as well as in other *Arthropoda*, a specific sensory epithelium is present at the entrance to the buccal cavity: this is stated to possess a gustatory function.

In the *Insecta* the cuticular appendages of the antennæ, in which the ganglionated extremities of nerves occur, are considered to be olfactory fibres. Dr. G. Hauser† has recently examined the olfactory organs of the *Insecta*. In all the

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* Siebold's *Anatomy of the Invertebrata* (American edition), p. 414.

† *Zeitschrift für Wissenschaftliche Zoologie*, vol. 34, p. 367.

Orthoptera, *Diptera*, *Lepidoptera*, *Neuroptera*, *Hymenoptera*, and *Coleoptera*, a strong nerve arising from the cerebral ganglion passes into the antennæ, and there is a sensory terminal organ, formed by cells developed from the hypodermis, with which the nerve-fibres are connected. The function of this organ was ascertained by extirpating the antennæ, and the insects which turned away from carbolic acid, turpentine, &c., before the antennæ were cut off, now showed no repugnance at all in the presence of these compounds. It was also found that when the antennæ were removed the insects did not rush to food.

The author has entirely confirmed Hauser's investigations; and there is no doubt that in the antennæ of these animals, there resides the sense of olfaction; but it should be borne in mind that the antennæ are also tactile organs—*i.e.*, they have a dual function.

The sense of hearing is somewhat well developed in the *Insecta*.* "The only organs which can safely be regarded as auditory in insects, are those which occur in grasshoppers (*Acrididæ*), crickets (*Achetidæ*), and locusts (*Locustidæ*), and which were first accurately described by Von Siebold. They have since been studied by Leydig, Hensen, Ranke, and Oscar Schmidt, but it must be confessed that much obscurity still hangs over their minute structure. In the *Acrididæ*, the chitinous cuticula of the metathorax presents on each side, above the articulation of the last pair of legs, a thin tympaniform membranous space surrounded by a raised rim. On its inner face, the cuticular layer of the tympaniform membrane is produced into two processes, one of which is a slender stem ending in a hollow triangular dilatation. A large tracheal vesicle lies over the tympanic membrane, and between its wall and the latter, a nerve derived from the metathoracic

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* The weevils (*Sitona crinita* and *Sitona lineata*), which feed upon the leaves of beans and peas, are very sensitive to sound, and if approached they usually drop from the leaves to the ground. (See Dr. Griffiths' *The Diseases of Crops*, p. 26.)

ganglion, passes to the region occupied by the processes, and there enlarges into a ganglion, the outer face of which, beset with numerous glassy rods arranged side by side, is in contact with the tympaniform membrane. A nerve arising from the ganglion passes along the groove to the 'stem,' and ends in a ganglion in its dilatation. From this ganglion certain fine filaments proceed. In the *Achetidæ* and *Locustidæ*, the tibiæ of the fore-legs present similar tympaniform membranes, which are easily seen in the common cricket, but, in other forms, become hidden by the development over them of folds of the cuticle of the adjacent region of the limb. Two spacious tracheal sacs occupy the greater part of the cavity of the tibia, and a large nerve ends in a ganglion in the remaining space. Upon this ganglion a series of peculiar short rod-like bodies are set."

For a tolerably full *résumé* concerning the auditory organ in the *Insecta* the reader is referred to Mr. A. H. Swinton's *Insect Variety: Its Propagation and Distribution*, pp. 230–252.

As a general rule, the *Insecta* have a pair of compound eyes, which are sessile and are situated upon the sides of the head. The compound eye is literally an agglomeration of simple eyes, having each a cornea, a vitreous humour of conical form, a pigmented layer, and a nervous filament. In some insects a compound eye contains upwards of twenty-five thousand of these simple eyes. All the small corneæ are hexagonal, and unite together so as to form a kind of common cornea, whose surface presents a vast number of facets. The retina of such eyes has a hemispherical form, the convex surface being directed outwards, and consists of large compound nerve-rods and retinulæ, which are separated from each other by pigmented sheaths. In front of these rods are placed the strongly refractile crystalline cones, and in front of these again the lens-shaped corneal facets. The compound eye is enclosed by a firm chitinous layer, which following the sheath of the entering optic nerve surrounds the soft parts, and reaches as far as the cornea.*

Almost all the *Insecta* have a pair of these compound eyes; but they are sometimes replaced by simple eyes, and at other times both kinds are present. In a few cases there are neither compound nor simple eyes; among these are certain species of *Ptilium*, that live under the bark of trees; the *Nycteribia*, which is parasitic on the skin of certain animals; the *Anophthalmus*,† which lives in dark caves; and the *Claviger*, which dwells in the nests of ants. The larvæ of the *Diptera* and *Hymenoptera*, and most of the apodal larvæ of the *Coleoptera* are also blind.

The second form of eye occurring in the *Insecta* is the simple eye, ocellus, or stemma. It contains the following parts:—sclerotica, cornea, lens, vitreous humour, and choroid; and it is of globular form. "But the lens appears to be always a mere thickening of the cuticle, which constitutes the cornea, and the so-called vitreous humour is partially or wholly made up of crystalline cones, analogous to those which are found in the compound eye. In this respect the ocellus of the insect resembles the simple eye in the *Arachnida* and *Crustacea*."

The larvæ of the *Lepidoptera*, *Neuroptera*, *Coleoptera*, and some *Hymenoptera* and *Diptera* have only ocelli. Two or three of these ocelli remain, but with superadded compound eyes, in the majority of the winged orders except the *Coleoptera*, in which only compound eyes are present in the perfect state. Simple eyes are present in the following *Insecta:—Pediculidæ*, *Coccidæ*, *Poduridæ*, *Nirmidæ*, and the larvæ of the *Phryganidæ*, *Hemerobidæ*, *Myrmeleonidæ*, and *Raphididæ*.

The sense of sight must be keen in the *Insecta*, but their mode of vision is essentially different from that of the higher *Vertebrata*. On this point, Professor C. Lloyd Morgan‡ says: "Remember their compound eyes, with mosaic vision, coarser

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* Claus' *Lehrbuch der Zoologie*. † See Darwin's *Origin of Species*, p. 111.
‡ *Animal Life and Intelligence* (1891).

by far than our retinal vision, and their ocelli of problematical value, and the complete absence of muscular adjustments in either one or the other. Can we conceive that, with organs so different, anything like a similar perceptual world can be elaborated in the insect mind? I, for one, cannot. Admitting, therefore, that their perceptions may be fairly surmised to be analogous, that their world is the result of construction, I do not see how we can for one moment suppose that the perceptual world they construct can in any accurate sense be said to resemble ours."

"The sounds produced by insects are, in a great proportion of cases, effected by the friction of the hard parts of the integument one against the other. . . . Landois, however, found that the thorax of a bluebottle fly continued to buzz after the separation of the head, the wings, the legs, and the abdomen. . . . The acoustic apparatus, in fact, lies in the immediate neighbourhood of the thoracic stigmata. . . . The vocal organ of the fly appears to be a modification of the occlusor apparatus of the stigmata, just as the organ of voice of mammals is a modification of the occlusor apparatus of their respiratory opening."

In *Apis* the voice organs are three-fold, the vibrating wings, the vibrating rings of the abdomen, and the true vocal apparatus in the breathing aperture or spiracle; the first two produce the buzz; while the hum—surly, cheerful, or colloquially significant—is due to the vocal membrane. Some of the bee's notes have been interpreted. "Huumm" is the cry of contentment;* "wuh-wuh-wuh" glorifies the incessant accouchements of the queen; "shu-u-u" is the frolic note of young bees at play; "ssss" means the muster of a swarm; "brrr" the slaughter or expulsion of the drones; the "tu-tu-tu" of newly-hatched young queens is answered by the "qua-qua-qua" of the queens still imprisoned in their cells.

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* The poet Byron says in *Don Juan* (c. i. v. 123)—"Sweet the *hum* of bees."

THE ARACHNIDA.

The palpi are the principal seat of the sense of touch, being in connection with nerves arising from the cerebral ganglion. The feet are also very sensitive tactile organs.

The eyes are always simple, like the ocelli of the *Insecta;* and there are usually from two to twelve* in number. Auditory organs have not been discovered in the *Arachnida*, but we have many proofs of the existence of this sense in these animals, and it would even appear that some of them are sensible "to the charms of music." The parasitic *Acarina,* and allied groups, are entirely devoid of organs of vision.

THE CRUSTACEA.

The sense of touch is well developed in these animals. Its principal seat is in the antennæ, which also contain nerves from the supra-œsophageal ganglion. Often the mouth organs have one or more pairs of tactile appendages; and no doubt the limbs, especially the anterior ones, are also the means of giving rise to tactile impressions.

In the lower *Crustacea,* Dr. G. O. Sars has shown that the principal seat of the sensation of touch is in the antennæ. The antennulæ have no such function.

The olfactory organ is situated in the antennulæ. In *Astacus,* this organ is situated in the delicate setæ of the endopodite of each antennule (Fig. 69, A); these setæ are provided with nerves. A similar arrangement occurs in many *Crustacea* besides the *Decapoda.* If the antennulæ of *Astacus* are removed, the animal will approach a small cup containing bromine placed at the bottom of the tank in which the animal lives. On the other hand, if the antennulæ are left intact, the animal will not approach the cup. Other obnoxious liquids of high density give rise to similar results.

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* *Scorpionidæ* (Von Siebold)

This proves that the sense of smell is developed in *Astacus* and that the olfactory organs are the antennulæ.

Auditory organs have been observed in the higher *Crustacea*, especially in the *Decapoda*. In *Astacus* (Fig. 69, D), there is an auditory sac lodged in the basal joint of each antennule. The upper face of the basal joint has a small oval aperture, the outer lip of which is invested by hairs directed inwards. This aperture leads into a wide delicate sac, which contains a fluid in which minute sandy particles (otoliths) are suspended. A ridge, formed of the posterior and inferior wall of the sac, projects into its interior. Each side of this ridge is covered with a series of delicate setæ (auditory setæ), which project into the fluid. An auditory nerve, which enters the sacs, breaks up into fine fibrils that are distributed to the setæ. A fibril passes through the base right up to the summit of each seta, where it terminates in a peculiar rod-like body. The sonorous waves, transmitted through the water in which *Astacus* lives to the fluid and sandy contents of the auditory sac, are taken up by the delicate nerve-endings and conveyed through the auditory nerve to the brain or supra-œsophageal ganglion.

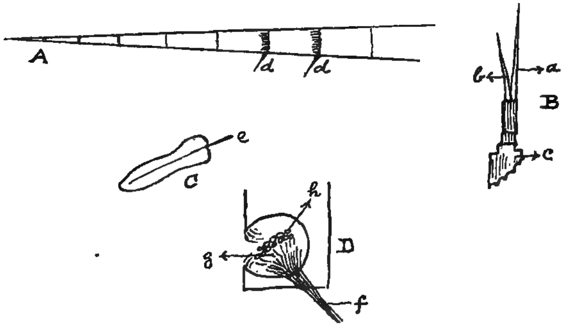

FIG. 69.—THE OLFACTORY AND AUDITORY ORGANS OF ASTACUS.

A = Antennule, with setæ at *d*. C = *d* enlarged, showing olfactory nerve (*e*). B = Antennule complete: *a* = exopodite; *b* = endopodite; *c* = protopodite. D = auditory organ: *f* = nerve; *g* = auditory hairs (setæ); *h* = otoliths.

In *Astacus*, *Homarus*, and other *Decapoda*, it may be remarked that both the olfactory and auditory organs are lodged in the antennulæ.

The eyes of the *Crustacea* are formed on a plan very similar to those of the *Insecta.* Sometimes they are simple; but generally they are compound eyes, and in all the higher *Crustacea* they are carried on movable peduncles, an arrangement not met with in any of the other classes of the *Arthropoda.*

"The *Cirripedia*, the *Penellina*, and the *Lernæodea* alone are without an organ of vision; and even here this deficiency occurs only during the last phases of their retrograde metamorphosis, when these animals remain fixed to foreign bodies.* There is, moreover, in the other orders, here and there a genus, which contains blind individuals: such is the case with the females of certain parasitic *Isopoda;*† and the same remark applies to some subterranean *Myriapoda.*"‡

The eyes of *Astacus* and other *Decapoda* are two in number—one seated at the extremity of each of the ophthalmic peduncles, the cuticle of which is continuous with the transparent cornea. The corneal membrane is divided into numerous minute square facets, each of which corresponds

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* The adult *Cirripedia*, notwithstanding the absence of eyes, are very sensitive to light (Von Siebold).

† *Bopyrus, Jone, Phryxus* (*i.e.*, the ♀).

‡ *Polydesmus*, *Cryptops*, *Geophilus*, and *Blaniulus.* The blindness of these and other animals is generally attributed to the effects of disuse. Concerning the blind cave-crabs, Darwin in the *Origin of Species* (p. 110) says: "In some of the crabs the foot-stalk for the eye remains, though the eye is gone. . . . . As it is difficult to imagine that eyes, though useless, could be in any way injurious to animals living in darkness, their loss may be attributed to disuse." On the other hand, Mr. W. P. Ball says: "The cave-crabs which have lost their disused eyes, but *not the disused eye-stalks*, appear to illustrate the effects of natural selection rather than of disuse. The loss of the exposed, sensitive, and worse-than-useless eye, would be a decided gain, while the disused eye-stalk, being no particular detriment to the crab, would be but slightly affected by natural selection, though open to the cumulative effects of disuse." (See Ball's book: *The Effects of Use and Disuse*, p. 17.)

with the base of a crystalline cone. Each cone passes inwardly into a nerve-rod, and then thickens into a striated spindle-shaped body. The inner extremities of the striated spindles become narrow again, and then pass into the optic nerve (Fig. 70).

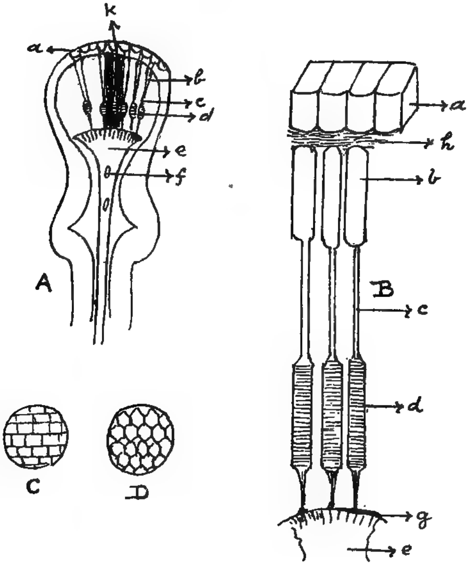

FIG. 70.—THE EYE OF THE DECAPODA.

A = Eye of *Astacus*. B = Eye of *Homarus*. *a* = cornea. *b* = crystalline cones. *c* = nerve rods. *d* = striated bodies. *e* = optic nerve. *f* = lenticular bodies. *g* = fenestrated membrane. *h* = layer not present in *Astacus*. *k* = pigment cells between cones. C = cornea of *Decapoda*. D = cornea of *Insecta*.

There are certain species of crayfishes which are blind; among these may be mentioned *Cambarus setosus* (Faxon), which lives in the caves of south-western Missouri, and *Cambarus pellucidus*, the well-known species from the Mammoth Cave. Mr. G. H. Parker* has recently examined the question of degeneration of these organs. He states that

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* *Bulletin of the Museum of Comparative Anatomy at Harvard College*, vol. 20 (1890).

not only has the finer structure of the retina been affected, but the shape of the optic stalks has been altered. The optic stalks are not only proportionally smaller than those of crayfishes possessing functional eyes, but they have in these two cases characteristically different shapes. In crayfishes with fully developed eyes, the stalk is terminated distally by a hemispherical enlargement; in the blind crayfishes it ends as a blunt cone. In both forms of crayfishes the optic ganglion and nerve were present, the latter terminating in some way undiscoverable in the hypodermis of the retinal region. In *C. setosus* this region is represented only by undifferentiated hypodermis, composed of somewhat crowded cells, while in *C. pellucidus* it has the form of a lenticular thickening of the hypodermis, in which there exists multinuclear granulated bodies; these are shown to be degenerated clusters of cone-cells.

THE MOLLUSCA.

The sense of touch, according to Gegenbaur, is chiefly confined to certain cutaneous cells with setiform prolongations, disseminated where the body is not covered with hard pieces. These cells are provided with nerves, which offer here and there ganglionic expansions. In the *Lamellibranchiata*, there are frequently tentacula around the branchial and anal openings of the pallium, and the orifice of the siphon. These and similar devices receive nerves from those of the pallium. The tentacula and the ciliated labial palps are the tactile organs of the *Lamellibranchiata*.

In the *Gasteropoda*, represented by *Helix*, all the parts of the body (excepting the shell) are capable of feeling when touched. The tentacula, the edges of the lips, and the lobes of the pallium and foot, however, have the sense of touch developed in a specially high degree.

In the *Cephalopoda*, the sense of touch is well developed. It is situated in the arms, the fringed labial membranes, and in the whole of the cutaneous covering.

In the *Mollusca* there appears to be special organs of taste, in the form of a specific sensory epithelium at the entrance of the buccal cavity.

In the *Cephalopoda*, "the fleshy point of the tongue is undoubtedly a gustatory organ. It is concealed in the anterior angle of the lower jaw, and its rounded surface is covered with numerous soft villosities, which very probably serve as gustatory papillæ."

The olfactory organ of the *Branchiogasteropoda* has been examined by Dr. J. W. Spengel.* He finds that in *Trochus*, *Turbo*, and *Vermetus*, the so-called "rudimentary gill," or colour gland of T. Williams, is an olfactory organ. This organ consists of a large mass of nervous matter, invested by a layer of epithelium, into which nerve-fibres distinctly pass. Spengel has also proved that the ciliated organs of Gegenbaur in the *Pteropoda* have an olfactory function.

Dr. D. Sochaczewer † has also examined the olfactory organs in the *Pulmogasteropoda*. In these animals, the tentacula, the organ of Semper, and the pedal gland have each been considered to have the function of an olfactory organ. Sochaczewer has tried the following experiments: (*a*) Having cut off the tentacula of *Helix pomatia*, the wound was allowed to heal. The snails were then placed on a flat plate, the edge of which was smeared with turpentine. Both the mutilated and unmutilated specimens turned away from the edges. This shows that the tentacula are not the seat of the olfactory organ. (*b*) The organ of Semper is small in *Helix*, *Arion*, and *Limnæus*; but is well developed in *Limax*. Here it has the form of four or five glandular lobate processes, which are set at the sides of the mouth. This organ is supplied with four nerve-fibres. The two median are muscular in character, while the lateral branches are the proper labiales, which give off, one on either side, a fine nerve-branch to the glandular branches of Semper's organ. The cells of

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* *Zeitschrift für Wiss. Zoologie*, vol. 35, p. 333.

† *Ibid.* p. 30.

the constituent lobes resemble the glandular cells of the salivary glands; in other words, this organ has not an olfactory function. (*c*) The pedal or foot gland is looked upon by Sochaczewer as an olfactory organ. It is well supplied with nerves; but experiments are difficult to try in such an organ.

The olfactory organs of the *Cephalopoda* are situated near the eyes. They are either depressions or papillæ of the integument. The nerves which supply these organs arise from the optic ganglion of the œsophageal nerve-ring.

The auditory organs (Fig. 71) of the *Lamellibranchiata* consist of a pair of vesicles or sacs. These vesicles are filled with a fluid (endolymph) containing otoliths; and they are attached by short nerves to the pedal ganglia. In the *Mollusca* generally, a delicate sensory epithelium marks the percipient portion of the inner wall of the auditory sac.

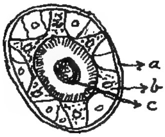

FIG. 71.

THE AUDITORY ORGAN OF CYCLAS

a = capsule or sac. *b* = ciliated epithelial cells. *c* = otolith.

The auditory organs of the *Gasteropoda*, as represented by *Helix*, are in pairs, close to and connected with the pedal ganglia. Each auditory organ or otocyst consists of an internally ciliated vesicle or sac containing a fluid and otoliths; an auditory canal which may communicate with the exterior; and an auditory nerve from the cerebral ganglia.

A pair of auditory vesicles are always present in the *Pteropoda*.

In the *Dibranchiata*, the auditory organs are situated in the cavities of the cephalic cartilage. The internal walls of the auditory vesicles in the *Octopoda* are smooth; but in the *Loligina* they are raised into papillæ.

In the *Tetrabranchiata*, represented by *Nautilus*, the auditory organs are attached to the pedal ganglia, and are not situated in the cranial cartilage. In both orders, the auditory nerve gives rise to nerve-filaments within the sac; and in the *Dibranchiata* there is a single, irregular, white otolith of a crystalline texture ($CaCO_3$). On the other hand the auditory sac of the *Tetrabranchiata* contains many otoliths.*

In the *Mollusca*, organs of sight are met with in various degrees of development. They are absent in the fixed *Mollusca*. Certain of these, which in the state of mobile larvæ had eyes, lose them by degeneration when they have become immobile. Certain species of the *Lamellibranchiata* have as eyes sometimes only pigmented spots, and sometimes brilliant organs, disseminated on the edge of the pallium.

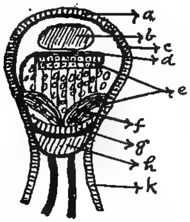

FIG. 72.—THE EYE OF PECTEN.

a = cornea.
b = lens.
c = sclerotica.
d = optic nerve (2).
e = retina.
f = optic nerve (1).
g = pigment layer.
h = vitreous humour.
k = eye-stalk.

In *Pecten*, there are a large number of simple emerald-green coloured eyes situated round the edge of the pallium. Each eye (Fig. 72) consists of a cornea, lens, sclerotica, retina, choroid, and vitreous humour. The eye is pedunculated, and it has a double optic nerve.

The table on p. 369 gives the colour, &c., of the eyes of various *Lamellibranchiata*.

The *Scaphopoda* and *Polyplacophora* have no eyes.

In the *Pulmogasteropoda* (*e.g.*, *Helix*) there are a pair of simple eyes situated on the summits of the large tentacula. The eye of *Helix* consists of the following parts: sclerotica, choroid, lens, cornea, vitreous humour, and an optic nerve which expands into an outer and inner retina. The eye in these animals is much more highly developed than the simple

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* Dr. J. D. Macdonald in *Proc. Roy. Soc.*, 1855.

eyes of other *Invertebrata.* Highly-developed simple eyes are also present in the *Branchiogasteropoda.*

	COLOUR.	REMARKS.
Pholas	yellowish-brown	non-pedunculated.
Pecten	green	pedunculated.
Venus	yellowish-brown	non-pedunculated.
Mactra	reddish-blue	non-pedunculated.
Arca	reddish-brown	non-pedunculated.
Solen	yellowish-brown	non-pedunculated.
Pinna	brownish-yellow	short peduncles.
Pectunculus	reddish-brown	non-pedunculated.
Tellina	reddish-yellow	pedunculated.
Anomia	brown	non-pedunculated.
Lima	green	pedunculated.
Spondylus	green	pedunculated.
Plicatula	green	pedunculated.
Ostrea	brown	short peduncles.

In the *Pteropoda* the visual organ is either absent or it is rudimentary.

In the *Cephalopoda* the organs of vision are large and highly developed; in fact, the eyes of the typical Dibranchiate *Cephalopoda* are more highly organised than those of any other Invertebrate animal. A pair of eyes are situated in the orbital cavities at the sides of the head in all the *Dibranchiata.* The eye (Fig. 73) is more or less of globular form and consists of the following parts: cornea, tapetum, ciliary body, crystalline lens, vitreous humour, sclerotica, retina, white glandular body, and the optic ganglion* and nerve.

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* A great part of the eyeball is occupied by the optic ganglion.

In the *Tetrabranchiata*, as represented by *Nautilus* and its allies, the eye has no cornea, lens or vitreous humour. It is a mere cup or cavity lined by the retina.

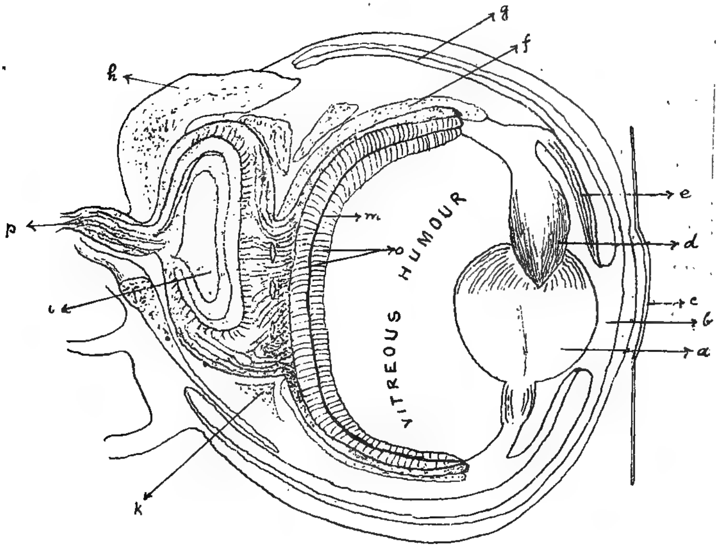

FIG. 73.—EYE OF SEPIA. (*After* GEGENBAUR.)

a = lens. *b* = anterior chamber. *c* = cornea. *d* = ciliary body. *e* = cartilage of iris. *f* = sclerotica. *g* = tapetum. *h* = cephalic cartilage. *i* = optic ganglion. *k* = white glandular body. *m* = pigment layer. *o* = outer and inner layers of retina. *p* = optic nerve.

In *Onychoteuthis*, *Ommastrephes*, and allied genera, the crystalline lens is exposed to the sea water; this is due to the entire absence of the cornea.

The eye of the *Dibranchiata* has been stated to resemble the Vertebrate eye, but this resemblance is merely superficial. In fact, "the rods and cones of the Vertebrate eye exactly correspond with the crystalline cones, &c., of the Arthropod eye; and the reversal of the ends, which are turned towards the light in the *Vertebrata*, is a necessary result of the extraordinary change of position which the retinal surface undergoes in them." The above is an additional fact substantiating the theory, that the *Vertebrata* have been developed from the *Arthropoda* rather than from the *Mollusca.* (See Chapter X.).

In this chapter we have seen that many of the lower animals have tolerably well-developed organs of sense, and as such organs are the means of awakening consciousness, it is reasonable to conclude that, on the whole, every nervous system, however little developed, in the *Invertebrata* as well as the *Vertebrata*, may be traced to a conscious cellular part, in continuous relation with two nervous systems, the one afferent, through which sensory excitation is conveyed, the other efferent, by which motor incitation is transmitted. The mode of action of such a mechanism is evidently reflex action, and, in fact, there is not a central nervous act, from the *Protozoa* to the highest *Vertebrata*, which cannot be traced to reflex nervous acts. First of all, the reflex action is absolutely unconscious; but in a later phase the nervous cell becomes conscious of vibration of its molecules; it experiences the sensations of touch, taste, smell, &c., more or less varied according as the organ or organs are more or less differentiated. At the same time it has impressions of pain, but in the lower animals these impressions are only momentary—there is no memory. Later still, however, this faculty becomes manifested; which is followed by the co-ordination of impressions, sensations, &c., in other words—understanding, intelligence, or reason, comes into play. But behind all this labyrinth of psychical phenomena there are simply reflex acts, transformed sensations and impressions. It has often been stated that animal "intelligence" is merely due to instinct and not to reason; that instinctive actions are not the result of experience or of previously acquired knowledge through the senses, whilst those of reason can be readily traced to these sources. Many acts of the *Insecta* and the *Arachnida*, for example, such as slave-making, cell-making, web-making, &c., are described as due to instinct; but there are many actions among these Invertebrates which appear to come under the head of reason. Among these may be mentioned the following: (*a*) Certain moths formerly entered the hives of the working-bee, and thereby caused great damage to the comb, &c. To prevent this nuisance the bee built a barrier, which now prevents the entrance of the larger intruders, yet at the same time allows the entrance of the rightful owner. (*b*) On the authority of an American naturalist, a pastrycook in Chicago found his shop invaded by a colony of ants, who feasted nightly on the delicacies deposited on a certain shelf. After cudgelling his brains for some time in order to discover a plan for stopping the depredations of the active insects, he resolved to lay a streak of treacle around the tray containing the coveted food. In due time the ants came forth in their hundreds, and were led towards the feast by their chief. On reaching the line scouts were then sent out to survey, and eventually "the word of command" was passed around, and instantly the main body of the ants made for a part of the wall, where the plaster had been broken by a nail. Here each snatched up a tiny piece of mortar and returned to the spot indicated, where their burdens were deposited upon the molasses. By this means, and after an infinite amount of labour, a bridge was formed, and the triumphant army marched forward to partake of the fruits of victory, the pastrycook meanwhile standing by filled with wonder. (*c*) The dens or burrows of the trap-door spiders having been entered by large predacious insects, these spiders constructed smaller lateral burrows, provided with trap-doors, into which they can now retreat in case the dens are forcibly entered. In this way these spiders protect themselves against enemies. (*d*) The modes of building webs across various streams; the strengthening of webs by buttress-like devices, when they are constructed in gorge-like and windy situations: these facts, combined with the power of the spider to adapt itself to every possible circumstance, seem to point out that the spider (as well as many other Invertebrates) is not guided merely by "blind instinct," but by that which is the equivalent of mind, and which is capable of developing with every generation—*i.e.*, according to the Darwinian law.

But it is not our intention to go fully into the subject of animal intelligence as displayed in various groups of the *Invertebrata;* such information the reader will obtain by consulting special treatises devoted to this fascinating subject.*

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* Morgan's *Animal Life and Intelligence;* Romanes' *Animal Intelligence;* and Lubbock *On the Senses, Instincts, and Intelligence of Animals, with special reference to Insects.*

CHAPTER XII.

MOVEMENTS AND LOCOMOTION IN THE INVERTEBRATA.

In this chapter we give an account of locomotion and other movements in the *Invertebrata.*

There is scarcely any species in the animal kingdom, which is not more or less endowed with the power of movement or motility; but it is not essentially a property inherent in organised matter; for many histological elements are destitute of it, and when an animal is only differentiated in a small degree, motility is the attribute and the function of a special tissue, at least in its most perfect mode.

In the lowest animals, where there is no differentiation of parts, the whole body is constituted of a substance which is contractile and which changes its form perpetually—emitting and retracting pseudopodia unceasingly. The pseudopodia are the first organs of motion; but they are simply expansions of the substance of the body—viz., the sarcode. The first effort of differentiation appears to be the formation of cilia and flagella. In this case these expansions are no longer transitory; for they have a fixed and definite form. They are persistent organs, constituting the principal organs of locomotion in the *Infusoria.* As we ascend in the zoological scale muscles become differentiated; and by the alternate shortening and lengthening of these muscles, movements of the body are brought about. Muscles are present in all but the simplest animals—*i.e.*, in all animals higher than the *Protozoa* and *Porifera.*

THE PROTOZOA.

In these animals a distinct muscular tissue has not been demonstrated, but the sarcode of their bodies is contractile. It may be mentioned, however, that the contractile stalk or peduncle of *Vorticella* contains a differentiated, longitudinal muscular fibre, which is capable of contracting so as to give the stalk the form of a spiral.

The organs of locomotion in the *Protozoa* are the pseudopodia, flagella, and cilia.

In the *Amœba* it is by means of pseudopodia that the animal moves; "it emits them in the direction in which it is going, then it retracts them, while other parts of the mass are in their turn elongated. The whole body moves by creeping. This organism in moving has the aspect of a drop of oil moving along. To explain the mechanism of this movement, it must be supposed that the extended pseudopodium seizes some point of support with its free end, then, in contracting, draws the entire mass of the body up to this."

According to M. Rouget the retraction of the pseudopodia is the analogue of muscular rigidity, the emission of these organs being due to internal pressure; and that the hyaline substance of the pseudopodia is a kind of hernia of the ectosarc, "resulting from a diminution of the elastic resistance at the point where each pseudopodium appears, with an increase of elasticity in those parts of the ectosarc where pseudopodia are not produced. When the elastic tension of these parts diminishes, and returns to its original state the pseudopodium re-enters into the mass." M. Rouget further states that in *Amœba terricola*, the most external portion of the ectosarc shows "striæ of a granular appearance which may be identical with the striæ or contractile fibrils of the ectosarc of the ciliated *Infusoria—Stentor*, *Spirostomum*, *Paramœcium*, &c."

The *Gregarina* moves in a worm-like, gliding, fashion, but very slowly. This movement, which only occurs occasionally, is due to the contractile nature of its body.

The Flagellate *Infusoria* are provided with flagella; these are appendages which have a dual function, being organs of locomotion as well as of prehension. "The *Protozoon* with its flagellum executes the most varied movements, moving first in one direction, then in another, and in different planes; sometimes the animal curves about entirely; but most frequently, when it uses the flagellum as an organ of prehension, it extends the whole length of the organ; the basal part remaining completely immovable and rigid, while the free end alone executes movements destined to drive food to the mouth, which is generally situated at the base of the flagellum." In certain genera of the *Flagellata* (among these the *Peridineœ*), there are organisms which have the power of throwing off their flagella before entering into a dormant state; and they can as readily regenerate these important organs. (Bütschli.)

"In *Anthophysa*, there are two motor organs—the one a stout and comparatively stiff flagellum, which moves by occasional jerks, and the other a very delicate cilium, which is in constant vibratory motion."

Drs. Dallinger and Drysdale* (who have so thoroughly worked out the life-history of several species of Monads or *Flagellata*) state that in some of these organisms there is a peculiar structure, which is intimately connected with the bases of the flagella, this appears to be muscular and is the probable cause of movement in the flagella. They also state, "that in every instance where there was only one flagellum, or where the two arise and move from the same point, their insertion in the body-sarcode was always in front; so that the flagellum or flagella had a pulling motion like that of the paddle of an ancient coracle; never the pushing motion from the stern like the sculling or rowing of a modern boat. This

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* *Monthly Microscopical Journal*, 1874, p. 264; and 1875, p. 190.

evidently arises from the complete flexibility of the flagella, by which a propelling motion plainly could not be applied."

The diameter of the flagellum of some forms is only 0.00000488526 or the $\frac{1}{204700}$th of an inch.*

In the *Ciliata*, the outer surface of the body is provided with vibratile cilia. These are organs of locomotion, touch, and prehension; and they may also aid in the function of respiration by causing a renewal of the water, which furnishes the necessary air for the function of respiration.

The cilia of these animals are homogeneous structures continuous with the ectosarc.

The *Ciliata* are divided as follows—

	CILIA.
Holotricha	They are of equal length and distributed all over the body.
Heterotricha	They are of unequal length, but cover the whole surface of the body.
Hypotricha	They are situated only on the ventral side of the body.
Peritricha	They form a zone round the anterior part of the body.

As already stated certain *Infusoria* have a portion of the protoplasm differentiated, so as to suggest a body comparable to the muscular fibres of the higher animals. This filament, or myophane, occurs in the peduncle of the *Vorticellæ;* and it is by this means that the stalk or peduncle is capable of forming a spiral, when the animal is disturbed.

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* See the paper by the Rev. W. H. Dallinger, F.R.S., in the *Transactions of the Royal Microscopical Society*, 1878, p. 174.

THE PORIFERA OR SPONGIDA.

Movements in these animals are caused by the contractile material of the body-substance and of the flagella; the latter being used to aid respiration, &c. The embryos of certain *Porifera* are richly ciliated, and thereby become free-swimming larvæ.

THE CŒLENTERATA.

The movements of *Hydra* are performed partly by true muscular fibres, and partly also by the contractions of the body-wall. The tentacula are used for locomotion as well as for prehension. In the *Actiniæ*, locomotion is brought about by the contractions of the disc of the foot.

Dr. G. J. Romanes* has made a thorough examination of the locomotor system of the *Medusæ*, from the standpoint of experimental physiology. As these researches would fill a volume in themselves, we must refer the reader desirous of information on the subject to the original memoirs mentioned in the foot-note. However, "it is known to every one that the *Medusæ* are naturally locomotive animals, the various species swimming more or less rapidly by means of an alternate contraction and dilatation of the entire swimming-organ. It may not be so generally known that these swimming-movements, although ordinarily rhythmical, are, at any rate in the case of some species, to a limited extent voluntary—using the latter term in the same sense as it is applicable to invertebrated animals in general. For instance, if *Sarsia* or *Aurelia*, &c., be *gently* irritated, the swimming-motions immediately become accelerated, and the acceleration persists for some time after the irritation has been withdrawn; but to secure this result, the irritation must not be of such a character as an inanimate object might supply. Again, individuals belonging to some discophorous species of the

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* See *Philosophical Transactions of the Royal Society*, 1875, p. 269; 1877, p. 659; 1879, p. 161.

naked-eyed *Medusæ* exhibit peculiar movements on being alarmed; but I am not sure whether these are, as is most probable, purely involuntary, or performed with the view of affording protection to the more vital parts of the animal. Possibly the object may be to decrease the buoyancy of the nectocalyx, and so escape from the source of injury by sinking in the water. At any rate, these peculiar movements consist of a sudden folding together of the entire nectocalyx, consequent on an abnormally strong contraction of the swimming-muscles; and this contraction, besides being of unusual strength, is also of unusual duration. Thus the last idea of this movement will perhaps be gained by regarding it as a sort of spasm. The time during which this spasmodic contraction lasts is pretty uniform in different individuals of the same species; but it varies in different species from three to six seconds or more. In all cases the disappearance of the spasm is comparatively gradual, the nectocalyx re-expanding in a slow and graceful manner, instead of with the rapid motion characteristic of ordinary swimming. These movements only occur when the animal is being injured, or threatened with injury." (Romanes.)

Romanes has shown that the lithocysts are the exclusive seats of spontaneity, so far as the so-called "primary movements" are concerned; and he has failed to detect the slightest evidence of spontaneity on the part of the contractile zones, as asserted by Dr. Eimer.

The tentacula of the *Medusæ* are prehensile organs capable of seizing upon and destroying animals of far more complicated structure than themselves.

THE ECHINODERMATA.

In these animals the muscular system is well developed; its fibres are flat and without transverse striæ.

The natural movements of the *Echinodermata* have been studied by Drs. Romanes and Ewart;* and they have shown that the ambulacral system is instrumental in the locomotion of all these animals, except the *Ophiuridea.*

The *Asteridea.*—(*a*) The common starfish (*Uraster rubens*) crawls upon a flat horizontal surface at the rate of two inches per minute. "The animal usually crawls in a determinate direction, and, while crawling, the ambulacral feet at the end of each ray are protruded forwards as feelers; this is particularly the case with the terminal feet on the ray, or rays, facing the direction of advance. When in the course of their advance, these tentacular feet happen to come into contact with a solid body, the animal may either continue its direction of advance unchanged, or may deflect that direction towards the solid body." *Uraster rubens* has the power of ascending perpendicular surfaces, and also of attaching itself to solid bodies. The ambulacral feet are so strong in holding on to a perpendicular surface, that the feet of one or two rays are sufficient to support the animal when its body is distended in a horizontal position (Fig. 74). If *Uraster* is turned over on its dorsal surface upon the flat floor of a tank, it does not occupy more than half a minute in righting itself. This is done by a number of the ambulacral feet of three rays getting a firm hold of the floor of the tank; this being done, the animal turns a complete somersault—the disc and inactive rays being thrown over the active ones with considerable rapidity.

(*b*) The sun-stars (*Solaster*) move about in a similar manner to *Uraster;* but the method of righting themselves is slightly different from that just described.

(*c*) *Astropecten aurantiacus.*—Romanes and Ewart state that the ordinary locomotor movements of this species are highly peculiar. The general form of the animal resembles *Uraster*, although its disc is proportionally larger, and the whole animal smaller. Its ambulacral feet are pointed tubes, about a quarter of an inch long, and unprovided with any

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* *Philosophical Transactions*, 1881, p. 829.

sucker at the tip. "When the animal is not walking, these feet are nevertheless in a constant state of movement, and their movements are then of a peculiar writhing, almost

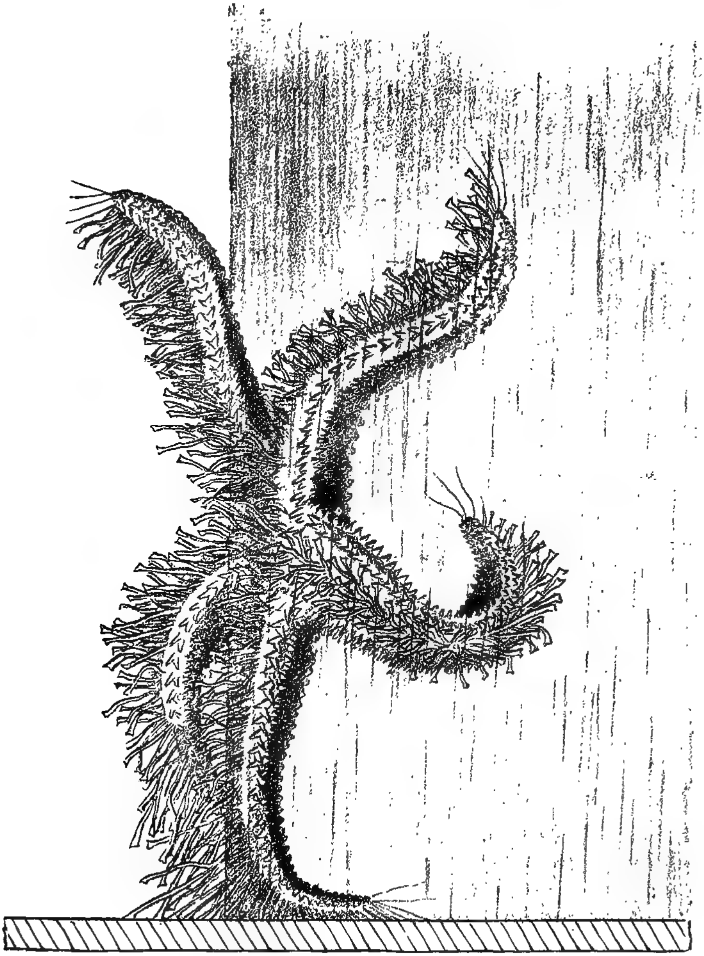

FIG. 74.—URASTER HOLDING ON TO A PERPENDICULAR SURFACE. (*After* ROMANES *and* EWART.)

vermiform character—twisting about in various directions, and frequently coiling round each other. When fully protruded, however, they are perfectly straight and stiff." A number of these feet are continually being retracted, while others are being protruded, and this state of affairs goes on alternately.*

These animals can crawl up perpendicular surfaces, but are very soon tired. This is due to the absence of any differentiated structures in the form of sucking discs.

The mode of locomotion of *Astropecten* is peculiar. Upon a dry, flat surface, it "points all the feet of all the rays in the direction of advance, and then simultaneously distends them with fluid; they thus become so many pillars of support, which raise the animal as high above the flat surface as their own perpendicular length. The fluid is then suddenly withdrawn, and *Astropecten* falls forward flat with a jerk. This manœuvre being again and again repeated at intervals of about a quarter of a minute, the animal progresses in a uniform direction at the rate of about an inch per minute. In this mode of progression, all the feet of all the rays are co-ordinated in their action for determining one definite direction of advance—those in the ray facing that direction acting forwards, or centrifugally, those in the hinder rays backwards, or centripetally, and those in the lateral rays sideways."

When *Astropecten* is walking along a flat horizontal surface under water, its mode of locomotion is the same as the above, only the motion is very rapid. "It appears, however, as if the feet, besides being used as walking poles in the manner just described, are also used to sweep backwards along the floor of the tank, and so to assist in propelling the animal forwards after the manner of cilia. Therefore, while walking in water, *Astropecten* is kept stilt-high above the surface on which it is walking, by some of its feet, while others of its feet are engaged in these sweeping movements."

Astropecten has a rapid rate of movement, being between one and two feet per minute. When placed upon its back, it has the power of righting itself very rapidly.

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* The feet usually remain extended for a quarter to half a minute, but very suddenly collapse.

(*d*) The *Ophiuridea.*—In the brittle-stars the ambulacral feet are only rudimentary, although exceedingly active; they are devoid of suckers; and their mode of protrusion and retraction is exactly like that of *Astropecten*, but more rapid in action. These animals are much the most actively locomotive of all the starfishes; "and the reason is, that having discarded the method of crawling by the ambulacral system, which is common to nearly all the other Echinoderms, they have adopted instead a completely new, and a much more effectual

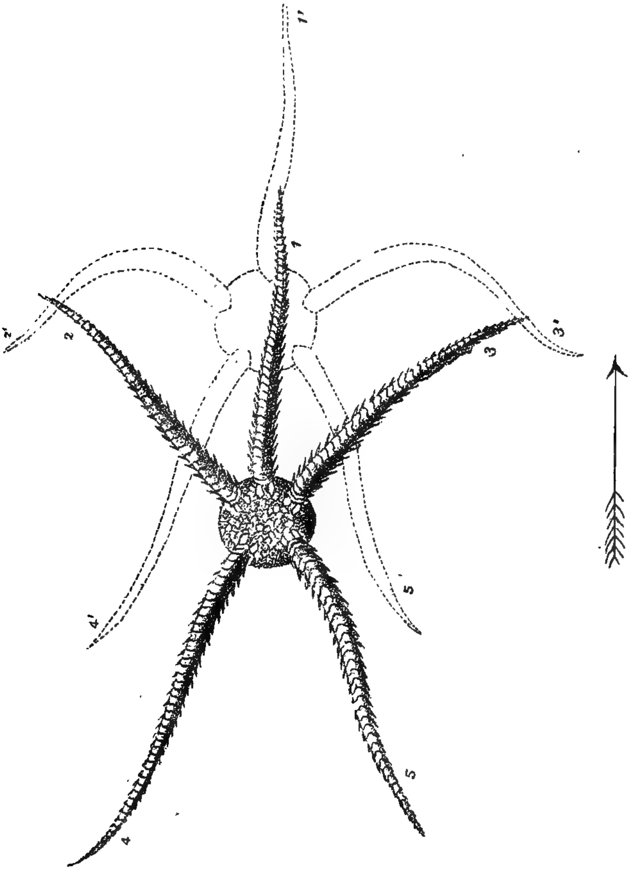

Fig. 75.—Locomotion of Ophiura. (*After* Romanes *and* Ewart.)

method. The muscular system of the rays is very per developed, enabling these long and snake-like appenda perform with energy and quickness a great variety of s like writhings. As the movement of all the arms is co nated, the animal is able by these writhings to shuffle along flat horizontal surfaces at a considerable speed. when it desires to move still more rapidly, it adopts ar plan. If the animal is advancing in the direction c arrow (Fig. 75), one of its rays, 1, is pointed straight i direction; the two adjacent rays, 2 and 3, are throw wards as far as possible, and then, by a strong contr downwards upon the floor of the tank, these two rays elevate the disc, and, while keeping the disc so ele throw themselves violently backwards into the for crescents, as represented in 2′ and 3′. The result c movement is to propel the animal forwards—ray 1 pushed into the position 1′, while rays 4 and 5 are dr along into the position 4′ and 5′. As soon as the rays 2 have assumed the position 2′ and 3′, they are again, w an instant's delay, protruded straight, to be again ins thrown into the form of the curves 2′ and 3′. Thu animal advances by a series of leaps and bounds, whicl between 1½ and 2 inches in length, and which follo another with so much rapidity, that a lively *Ophiur* easily travel at the rate of 6 feet per minute. While travelling, the ray, 1, is usually kept straight pointe partly uplifted—doubtless in order to act as a feeler sometimes the animal varies its method of progression, to use two pairs of arms for the propelling movement in this case the remaining arm is, of course, dragged b and so rendered useless as a feeler. *Ophiura* is able any pair, or pairs, of its arms as propellers indifferentl in all cases it so uses them by resting their outer, or thirds upon the tank floor, and at each leap raising remaining two-thirds, together with the anterior part disc, off the floor; at the end of each leap, howeve whole animal (except, perhaps, the elevated feeler-ray) lies flat upon the floor." (Romanes and Ewart.)

Ophiura when placed on its back has the power of righting itself; but it is unable to ascend perpendicular surfaces owing to the rudimentary condition of its ambulacral apparatus.

(*e*) The *Echinidea.*—Unlike the rapid movements of the starfishes, the *Echini* have a slow rate of locomotion. Along a horizontal surface it is six inches per minute, while up a perpendicular surface it is only a quarter of an inch per minute. The ambulacral feet or pedicels have a greater power of anchorage than the same appendages of the starfishes. In *Echinus* the pedicels are also used as feelers. When a perpendicular surface is reached, the animal may either ascend it or crawl along for an indefinite distance, feeling it all the way with its pedicels. When an *Echinus* is inverted upon its aboral pole, it has the power of righting itself, although it is a much more difficult task than is the case with the starfishes. This is due to the formation of its body—for it is a rigid, non-muscular, and globular mass, whose only motive power available for conducting the evolution is that which is supplied by relatively feeble pedicels.

The spines and lantern* are also used in locomotion. When the animal is taken out of the water and placed upon a table, Romanes and Ewart observed that it began to walk in some definite direction—*i.e.*, in a straight line, and in doing so the only organs used for the purposes of locomotion are the spines and the lantern, the ambulacral feet under these circumstances not being protruded at all. The rate of locomotion is very slow—viz., about one inch per minute. The so-called "Aristotle's lantern" is capable of being protruded and retracted; and these movements are perfectly rhythmical, at the rate of three or four revolutions per minute. The pedicellariæ of *Echinus* assist in locomotion. It is by means

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* "Aristotle's lantern," or dental apparatus, in *Echinus* is worked by thirty muscles.

of these small forceps or grasping organs, that the animal is capable of "climbing perpendicular or inclined surfaces of rock, covered with waving sea-weeds." In the *Asteridea* and the *Holothuridea*, the pedicellariæ are only rudimentary—changed habits of life on the part of these animals have caused the inherited appendages to dwindle from disuse. For instance, "the *Ophiuridea* never climb sea-weed covered rocks at all, and those starfishes which do so have their ambulacral feet restricted to the ventral surface; it would therefore be useless for these animals to have well-developed pedicellariæ, adapted to hold sea-weeds steady in the manner which may be of so much use to the globular *Echinus*, who throws out on all sides feet feeling for attachments."

Spatangus (one of the *Echinidea*) crawls about somewhat slower than *Echinus*; and it is incapable of climbing perpendicular surfaces. When placed upon its back it has even a greater difficulty in righting itself than *Echinus*. It rights itself entirely by its long and mobile spines.

(*f*) The *Holothuridea*.—These animals "crawl slowly, and indulge in prolonged periods of quiescence. They are, however, able to climb perpendicular surfaces."

THE TRICHOSCOLICES.

The *Turbellaria*.—Although the parenchyma of these animals is contractile, they have only a very feebly-developed muscular system. The muscular fibres appear to be unstriated. The *Turbellaria* are divided into (*a*) the *Rhabdocœla* and (*b*) the *Dendrocœla*. The smaller species of the first-mentioned sub-order swim by means of their ciliated epithelium; whereas the larger species appear "to float from place to place by means of their epithelium." The *Dendrocœla*, on the other hand, crawl along somewhat in the manner of the *Gasteropoda*. Sometimes the tentacle-like processes (situated at the anterior end of the body) are used as oars when these animals move upon the surface of the water. According to

Martens,* *Planaria lichenoides* moves by means of the protruded lobes of its muscular pharynx.

The *Rotifera.*—The muscular system of these animals is composed of unstriated fibres. The most characteristic apparatus is the so-called "wheel." By its agency these animals swim freely about, or, when at rest, create certain water currents. The "wheel" or trochal disc and its appendages vary in different genera. The edge of this disc is generally ciliated, but in some forms (*e.g.*, *Stephanoceros*) it is produced into ciliated tentacula. Besides being organs of locomotion, the appendages of the trochal disc are indirectly prehensile organs.

The *Trematoda* and *Cestoidea.*—The movements of the body are due to sucking-cups and cavities (*i.e.*, suctorial organs), horny hooks and spines.

THE ANNELIDA.

Muscular tissues are highly developed in the *Annelida.* In *Hirudo,* the muscular system into which the integument is continued, forming a dermo-muscular tube, consists externally of a circular muscular layer, and internally of a longitudinal muscular layer. Both these layers are traversed by radial muscle-fibres, which run from the interior of the body to the surface. At the lateral edges of the body, the radial muscles pass directly from the dorsal to the ventral surface. Certain muscle-fibres run obliquely. In *Hirudo,* locomotion is chiefly effected by means of the suckers, which contain both circular and radiating muscle-fibres. The posterior sucker is attached to something, then the animal stretches itself forward to its fullest extent and fixes its anterior sucker. After releasing the posterior sucker the body is powerfully contracted. The posterior sucker now attaches itself close to the anterior sucker, which is then loosened and thrust forward as before. *Hirudo* can also

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* *Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg,* tome 2.

swim, though its motion in water is rather slow. "Whilst swimming, the body becomes flattened by the contraction of the vertical muscle-fibres, which pass from the dorsal to the ventral surface; and then by perpendicular quick serpentine undulations, it progresses like a wavy ribbon."

The muscle-fibres are developed, as in the higher animals, out of nucleated, spindle-shaped, muscle-cells. The fibres are not transversely striated, but they are enveloped in a structureless sheath.

In the *Oligochæta*, represented by *Lumbricus*, the muscular system is somewhat similar to that already described. Beneath the cuticle and hypodermis there is an external layer of circular muscle-fibres and an internal one of longitudinal muscle-fibres; there are also radiating and obliquely intertwisted fibres. On the ventral surface of each somite (in *Lumbricus*) four pairs of minute pits occur, from each of which projects a long hook-like seta or bristle. The setæ or bristles can be projected or retracted at will, and they aid locomotion in a somewhat similar manner to the suckers of *Hirudo*. Both these devices are the means of anchorage, while the subcutaneous muscles produce the vermicular motions of the body.

The *Polychæta*, or marine worms, are usually provided with parapodia (rudimentary limbs), having numerous chitinous setæ embedded in them. In the body-wall the circular and longitudinal muscle-fibres are well developed. The sub-order *Errantia* contains the free-swimming *Polychæta*. The head of these animals contains tentacula, and generally cirri, and the anterior portion of the pharynx is like a proboscis, being eversible. The parapodia are well developed in the *Errantia*.

The *Tubicola*, or sedentary *Polychæta*, have no cirri, and the parapodia are only slightly developed. None have a proboscis or eversible pharynx. The *Tubicola* are not free and actively locomotive animals like the *Errantia*. They live in tubes, which they construct either by gluing together sand and pieces of shells, or "by secreting a chitinous or calcified shelly substance."

Locomotion in the *Annelida* is aided by means of aciculi and setæ. These are used as fulcra when they creep, or as oars when they swim.

THE NEMATOSCOLICES.

The general movements of the body in the *Nematoïdea* are due to a subcutaneous circular muscle-layer; and its longitudinal and transverse muscles are quite distinct from each other. In most of the *Nematoidea* the longitudinal muscles form four large bands—two on the ventral and two on the dorsal surface. These animals are devoid of limbs, though they may sometimes be provided with setiform spines or papillæ.

THE MYRIAPODA.

Great advance is observed in the mode of locomotion in the *Arthropoda*. There is no longer any contractile envelope like the *Annelida* and their allies, for here the muscular fibres are all grouped into distinct masses or individual muscles, which are inserted into such and such a limb or part of the body by means of tendons. In the *Arthropoda* all the muscles are transversely striated.

Locomotion in the *Myriapoda* is produced by means of the limbs. Almost all the segments bear at least a pair of articulated limbs terminated by claws.

The *Chilopoda* (centipedes) usually live in the earth or under stones; they run with considerable swiftness in pursuit of their prey, and can even progress backwards by the aid of their tail-like posterior limbs, which at other times are dragged helplessly behind them.

The *Diplopoda* or *Chilognatha* (millipedes) possess two pairs of limbs on each segment except the posterior segment, which is devoid of these organs. The movements of these animals, notwithstanding their immense number of limbs, are always very slow, and they generally try to escape danger by rolling themselves up into a ball.

THE INSECTA.

In this class the thorax always bears the organs of locomotion, which, in *most* insects, consist of six ambulatory limbs and four wings. The form of these organs is very various, but their general anatomy is always similar. The centre of the ventral surface of the thorax is occupied by a narrow piece termed the sternum, which frequently projects as a ridge externally, and generally gives off an internal process for the insertion of muscles. On each side of this are the sockets for the legs, of which each segment of the thorax bears a pair. The first joint or coxa of the legs is sometimes immovably attached to the thorax, sometimes articulated with it by a sort of ball-and-socket joint. The next four joints are termed respectively—the trochanter, femur, tibia, and tarsus. The tarsus or foot sometimes consists of one, but generally of from three to six joints. The terminal or sixth tarsal joint is furnished with two curved and pointed claws or ungues, often toothed, and in many cases accompanied by a pair of soft membranous organs or pulvilli, which are very distinct in *Musca* (house fly). These adhere, like suckers, to any object against which they may be applied, and thus enable their possessors to walk securely even in a reversed position.

The ambulatory limbs and their various joints undergo very many modifications in the different orders and groups of the *Insecta;* always, however, in exact coincidence with the habits of the individuals—in leaping or jumping insects, such as *Eupteryx,** *Locusta,* and *Gryllus,* the posterior limbs are much lengthened and the femora very thick, forming powerful jumping organs. In *Mantis,* the anterior limbs are so much

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* See Dr. Griffiths' *The Diseases of Crops,* p. 51 (Bell & Sons).

three. When the tripod which is moving has come to the developed as to give the insect a praying attitude—these limbs are used as prehensile organs. The anterior limbs of *Gryllotalpa* (the mole cricket) are modified to suit this insect to its burrowing habits. In those insects which swim, such as *Dytiscus*, the tarsi are generally flattened, ciliated, and disposed like oars. In fact, *Dytiscus* possesses organs of natation, of burrowing, of reptation, and of flight. This Coleopterous insect is, in a sense, comparable to the great epic poet's fiend in the nature of its various movements, and also the different elements in which it is capable of living:—

> "Through strait, rough, dense, or rare,
> With head, hands, wings, or feet, pursues its way,
> And swims, or sinks, or wades, or creeps, or flies." *

These wonderful modifications of a general plan are certainly strong points in the theory of natural selection. "It may metaphorically be said that natural selection is daily and hourly scrutinising, throughout the world, the slightest variations; rejecting those that are bad, preserving and adding up all that are good; silently and insensibly working, whenever and wherever opportunity offers, at *the improvement of each organic being in relation to its organic and inorganic conditions of life*. We see nothing of these slow changes in progress, until the hand of time has marked the lapse of ages, and then so imperfect is our view into long-past geological ages, that we see only that the forms of life are now different from what they formerly were." †

Mr. H. H. Dixon, of Trinity College, Dublin, has recently made some observations on the locomotion of various insects, and he finds that in the case of those which move quickly, the best method for observation is instantaneous photography. Instantaneous photographs of moving flies show that they move the front and hind legs of one side almost simultaneously with the middle leg of the other, while they stand on the other

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* Milton's *Paradise Lost.*

† Darwin's *Origin of Species* (6th ed.), p. 65.

ground, the other tripod is raised, and so on. Dixon's observations show, however, that while no leg of one tripod ever moves simultaneously with any leg of the other, yet there is a succession in the movements of the legs of each tripod. The hind leg on one side is first moved, then the middle on the other, and when the hind leg has been moved forward and almost reached the ground, the front leg of that side is raised. The middle leg and the front leg of the opposite sides come to the ground almost simultaneously. It is usually just when the hind leg is reaching the ground, and the front leg is being raised, that the tripod on which the fly is resting thrusts the body forward. After the movement of each tripod there appears to be a short pause, during which all six legs are on the ground together.

Dixon has also observed the tripodic walk in earwigs, water scorpions, aphides, and some beetles. In the case of some slowly moving beetles and aphides, which can be observed without photographic means, quite irregular movements have been observed. By cooling aphides, they can be made to move very slowly. In this condition one was observed to move its legs in slow succession in the following order:—(*a*) Right hind, (*b*) right middle, (*c*) right front, (*d*) left hind, (*e*) left middle, (*f*) left front. This walk was continued for some time, occasionally interrupted by the following order, or some other quite irregular walk:—(*a*) Right hind, (*b*) right middle, (*c*) left hind, (*d*) left middle, (*e*) left front, (*f*) right front.

In caterpillars the legs forming a pair seem to move simultaneously; the motion begins at the posterior end of the body, and proceeds regularly forward till the most anterior pair of legs are moved.*

According to Darwin,† *Papilio feronia*, of Brazil (one of the

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* Mr. Dixon kindly sent the author several photographs illustrating the above movements, but unfortunately they cannot be reproduced as woodcuts.

† *Journal of Researches* (chap. ii.).

Lepidoptera), uses "*its legs for running*," this being an exceptional habit among butterflies.

The wings of insects are appendages attached to the mesothorax and metathorax. They are composed of a double membrane, supported internally by a variable number of nervures. These serve to keep the wings extended. There are never more than two pairs of wings, sometimes only one, and they vary in form. When they really serve for flight they are thin, translucent, and covered with microscopic scales as in the *Lepidoptera;* but the anterior wings often become hard and opaque, and becoming useless as organs of flight, form elytra—*i.e.*, protecting sheaths, for the posterior pair of wings: such an arrangement occurs in the *Coleoptera.* Although the wings of insects are usually four in number, the posterior pair is frequently absent, and, in fact, the *Diptera* is characterised by the possession of only one pair of wings. In these insects a pair of small knobbed filaments, situated on the sides of the thorax behind the wings, and which are called halteres, have been regarded as the representatives of the posterior wings.

In almost every order of the *Insecta* there are genera, species and individuals, as certain female aphides, which are apterous or wingless.

"The movements of the wings are produced by two extensor and several smaller flexor muscles,* which arise from the middle and posterior thoracic segments, and are inserted on the tendinous process at the base of each wing. The size of these muscles is proportionate to the size of the wings and their mode of use in flight. They are, consequently, all equally developed when the four wings participate equally

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* Dr. Allen Thomson has measured the diameters of the muscular fibres in the *Insecta* with the following results :—

Greatest diameter	$\frac{1}{200}$	inch.
Least ,,	$\frac{1}{755}$	,,
Average ,,	$\frac{1}{420}$	,,
Distance of transverse striæ	$\frac{1}{9500}$	,,

in the act of flying, as is the case with the *Lepidoptera*, *Hymenoptera*, the majority of the *Neuroptera*, the *Libelludidæ*, *Perlidæ*, and finally, the *Cicadidæ*, and the *Aphididæ*. The muscles of the anterior wings are comparatively smaller than those of the posterior, when the first are not used, properly speaking, except to cover the latter, as is the case with the *Coleoptera*, the Bugs, and many of the *Orthoptera*." (Von Siebold.)

There are also certain accessory organs which aid in the phenomenon of flight. Prof. Huxley says that "the air-sacs doubtless assist flight by the diminution of the specific gravity of the insect, which follows upon their distention."

Concerning the phenomenon of flight Sir Richard Owen has justly remarked that "in no part of the animal kingdom is the mechanism for flight so perfect, so apt to that end, as in the class of insects. The swallow cannot match the dragon-fly in its aërial course; this insect has been seen to outstrip and elude its swift pursuer of the feathered class: nay, it can do more in the air than any bird—it can fly backwards and sidelong, to right or left, as well as forwards and alter its course on the instant without turning." *

THE ARACHNIDA.

In the *Arachnida* the organs of locomotion are all fixed to the cephalo-thorax, and consist of eight pairs of limbs, strongly resembling those of the *Insecta*; and almost always terminated by two hooks. The length of these organs is generally considerable, and they easily break; but, as in the *Crustacea*, the stump, after having cicatrised, reproduces a new limb, which increases by little and little, and ends by becoming similar to that of which the animal had been deprived.

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* The flight of the bee exceeds twelve miles an hour, and it will go four miles in search of food. Its wings, braced together in flight by a row of hooklets, bear it forward and backward, upward, downward, or suddenly arrested course, by a beautiful mechanical adaptation. (See Cowan's *Honey Bee.*) For a full exposition of the flight of insects the reader is referred to the work of Chabrier in *Mém. du Muséum*, tomes 6-8

The *Arachnida* are entirely devoid of wings, and the organs of locomotion are never inserted on the abdomen.

The *Araneina* may be conveniently divided into two groups —the wandering and the sedentary spiders. In the former group belong the swift-runner, the side-walker, and the vaulting or leaping spiders. All the wandering spiders trust to their swiftness of movement in securing their food; and some of them can run in any direction.

THE CRUSTACEA.

In the lower *Crustacea*, represented, for example, by the *Phyllopoda*, Dr. G. O. Sars states that there are two modes of locomotion. In the case of *Cyclestheria hislopi*, one of these is accomplished when the animal is freely suspended in the water; in the other it takes place while it is at the bottom of the water; in the former case, it is a swimming motion; in the latter, a creeping or more generally a burrowing, motion. The swimming motion is performed exclusively by the aid of the antennæ, the repeated strokes of which propel the animal through the water. During this motion, the antennæ, together with the anterior part of the head, remain exserted from the front part of the shell, being moved laterally to a greater or less extent. The locomotion effected by this means is not very rapid, nor abrupt or jerking, but a perfectly even run through the water, whereby the animal as a rule turns the dorsal part uppermost. Not rarely, however, this attitude becomes changed, and the animal is often observed to revolve several times before breaking off the motion and sinking to the bottom. On the whole, the swimming motion appears to be effected with considerable effort, especially when the individuals are carrying a young brood; and hence this motion is never continued for any length of time, but takes place at intervals, the animal being more frequently found resting on the bottom or affixed to some submerged object.

The creeping or burrowing mode of locomotion, which takes place while the animal is on the bottom, is effected partly by the antennæ, but more especially by the flexion and powerful extension of the trunk, the caudal plate being thus exserted from the shell inferiorly and moved rapidly behind, as it strikes against the bottom. This mode of locomotion has sometimes a distinctly jerking character. Often, by repeated strokes of the tail, the shell will be turned round several times in succession, and may thus get rather deeply buried in the loose muddy deposit at the bottom of the water.

Dr. Sars, in his important paper (*loc. cit.*, p. 33), also describes the movements of the shell, head, trunk, tail, eye, antennulæ, antennæ, &c., but it is not our object to refer to these separate movements.

In the higher *Crustacea* the organs of locomotion or limbs are connected in pairs with the different thoracic segments; there are frequently seven pairs, as in the *Isopoda* (*e.g.*, *Oniscus*), the prawns, and the *Talitri* (sand-hoppers); but in other *Crustacea*—*e.g.*, the crabs, crayfishes, and lobsters—there are only five pairs of limbs. The structures of these appendages differ considerably: in some forms they are wholly foliaceous, membranous, and exclusively adapted for swimming; in others they have the form of small flexed columns, articulated, and disposed only for walking; in others, still, besides remaining adapted for this mode of locomotion, they become suited to act as so many small spades wherewith to dig the earth, and in that case they are enlarged and lamellated towards the extremity; and still, finally, in others they terminate in forceps, and become prehensile organs, performing at the same time the function of locomotion. In the swimming *Crustacea*, such as *Astacus*, *Homarus*, *Palæmon*, &c., the abdomen terminates in a tail-fin, which is the principal organ of locomotion; but in those individuals which walk more than they swim, the tail-fin is, as a rule, very small, and folded under the thorax: in the crabs, for example, this portion of the body is reduced almost to nothing, and constitutes then a movable apron placed on the lower surface of the body between the limbs.

In *Astacus* the ambulatory limbs are composed of seven separate joints: the basal joint being the coxopodite which is followed in succession by the following joints:—the basipodite, ischiopodite, meropodite, carpopodite, propodite, and dactylopodite.

THE MOLLUSCA.

The movements in these animals are, as a rule, executed by means of a muscular organ, termed the foot, which varies greatly in its form, in accordance with the habits of the animal. The foot consists of a mass of muscular fibres, running in various directions, by the contraction of which its movements are effected. In many of the *Mollusca*, the foot forms a flat disc, which adheres to any substance to which it may be applied, and thus, by the alternate contraction and dilatation of its different parts, enables the animal to crawl slowly along. In other forms, the foot is bent upon itself, so that its sudden extension causes the animal to perform a considerable leap (*e.g.*, *Cardium* and *Trigonia*). This organ is also the means by which the burrowing species bury themselves in the sand or mud; and in those species which bore in the solid rock, the foot is also called into requisition; its surface in these cases being covered with minute silicious particles, which assist greatly in the enlargement of its owner's ony dwelling.

But although most *Mollusca* possess a greater or less power of locomotion, others are confined to a single spot, during all but the earliest period of their existence, when they are free-swimming organisms. In the non-locomotive *Mollusca* the foot is either wholly undeveloped (*e.g.*, *Ostrea*), or serves merely to support a glandular organ, from which a chitinous or shelly substance is secreted, which serves to attach the animal to submarine objects. This modification occurs in *Mytilus*, *Pinna*, &c.*

In the *Pteropoda* the function of swimming is performed by the flapping epipodia, which are muscular expansions, but it may be remarked that in these *Mollusca* "the rest of the foot is always small, and often rudimentary, in correspondence with the small size of the neural face of the body."

The locomotive organs of the *Cephalopoda* are the tentacula, which are arranged round the head, and furnished on their inner surface with numerous sucking-cups, which enable the animal to take a firm grasp of any object. By means of the tentacula † the *Cephalopoda* creep along the bottom of the sea with the head downwards. These animals also swim rapidly by the expulsion of the water from the branchial chamber.

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* For an account of the movements of various parts of certain bivalve Molluscs, see the papers by D. M'Alpine in the *Proc. Roy. Soc. Edinb.*, vol. 15, p. 173; vol. 16, p. 725.

† The tentacula are also prehensile organs.

CHAPTER XIII.

REPRODUCTION AND DEVELOPMENT IN THE INVERTEBRATA.

EVERY living organism possesses the power of reproducing its kind. The process by which this reproduction or procreation is maintained may be either asexual or sexual; and some scientists* assert a third mode of "reproduction"—viz., by spontaneous generation, abiogenesis, or heterogenesis, *i.e.*, the origin of living organisms *de novo*, without parents. It is not our object to discuss the arguments for and against the theory of spontaneous generation, suffice it to say that the researches of Pasteur, Tyndall, Dallinger, and others, point out that "no definite instance of life originating *de novo* has been proved," and their experiments appear to negative its possibility.† Yet, it has been stated that the facts adduced against the theory "do not appear to invalidate the possibility

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* See Dr. Bastian's *Beginnings of Life* (1872); Bennett's *Physiology*, p. 421; Pouchet's *Nouvelles Expériences sur la Géneration Spontanée et sur la Résistance Vitale*, p. 110; and also the works of Prof. P. Mantegazza and MM. Bernard, Pennetier, Joly, and Musset.

† Concerning the controversy on spontaneous generation, Prof. Huxley states that biogenesis (life from previous life) has been "victorious along the whole line;" but at the same time he remarks "that with organic chemistry, molecular physics, and physiology yet in their infancy, and every day making prodigious strides, it would be the height of presumption for any man to say that the conditions under which matter assumes the qualities called vital, may not some day be artificially brought together." And further the great biologist remarks, "that as a matter not of proof but of probability, if it were given me to look beyond the abyss of geologically recorded time, to the still more remote period when the earth was passing through chemical and physical conditions, which it can never see again, I should expect to be a witness of the evolution of living protoplasm from non-living matter."

of abiogenesis occurring in certain conditions, and it is unphilosophical to assert the impossibility of its occurrence now or in some past time. The intimate relations known to exist between physical, chemical, and vital phenomena, depending on the laws of the conservation and transmutation of energy, and the theory of evolutional development, indicate the probability of abiogenesis, and it is one of the problems of biological science to ascertain the conditions in which this may occur."

"In the domain of science any logical and necessary deduction or induction ought to be admitted, though it may shock old ideas and shatter old dogmas. The same religious and metaphysical prejudices, which have been so deeply disquieted by the doctrine of evolution are still more alarmed and annoyed by the idea of spontaneous generation. But this may be changed as time rolls on, as has been the case with the Darwinian theory. . . . . Not many years ago the majority of naturalists believed in the immutability of all organised beings, and, as every epoch had its special fauna and flora, it was necessary to recognise, as did the immortal Cuvier, a series of successive creations. When God, irreverently compared to the machinist of an opera, whistled once, an implacable cataclysm annihilated all the living world; when He whistled a second time, but creatively, a new fauna and a new flora rose to life. Thus had things to go on at every geological epoch. From the trilobite to the mammoth every species had thus to be formed by 'magical crystallisation.' Assuredly there was here *spontaneous generation* of the most astonishing kind, but it shocked no one, because it was in more or less tacit accordance with metaphysical and religious ideas." But all this is now changed, for the majority of, if not all, naturalists firmly believe in the doctrine of evolution, or the mutability of organised beings, as revealed by the genius of Darwin.

Although spontaneous generation is, at the present time, "not proven," we mention the fact that it is still looked upon by some scientists as one of the "modes of reproduction."

ASEXUAL REPRODUCTION includes the processes of gemmation, fission, endogenous cell formation; and a variety of asexual reproduction is known by the name of parthenogenesis.

(*a*) *Gemmation.*—In this mode of reproduction a small portion of the body enlarges and gradually increases in size. When fully developed this bud may either become detached from the parent and develop into a free organism (like the parent), or it may remain permanently attached to it, giving rise to a colony.

(*b*) *Fission.*—This mode of reproduction, common in the lower animals (and of special importance in the formation of new cells), consists simply of a division of the animal into two or more parts. Each part then grows and ultimately assumes the same form as the parent; and possesses the same power of reproducing its kind. Should the division, however, remain permanently *incomplete*, colonies of the animal will be produced.

(*c*) *Endogenous cell formation.*—This mode of asexual reproduction or agamogenesis occurs in the *Protozoa*. The animal becomes encysted—*i.e.*, it surrounds itself with a covering or cell-wall. After this, the nucleus becomes constricted and ultimately may be divided into many portions. The protoplasm then divides in a similar manner, and there may result two, four, eight, &c., cells, in each of which there is at least one nucleus.* These cells finally rupture the parent-cell and are set free.

(*d*) *Parthenogenesis.*—As already stated parthenogenesis is a variety of asexual reproduction. In this case the whole development of the embryo is effected without the succour of fecundation. Parthenogenesis is the production of young, apparently without any previous congress with the male

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* Such a process is termed segmentation, and may be seen in the early stages of the development of the embryo of higher forms.

organism; and it is illustrated by the development of various forms of *Medusæ*, *Tænia*, and of *Aphides*.

SEXUAL REPRODUCTION.—This mode of reproduction, or gamogenesis, is the result of the fusion of two distinct elements—a male element, or spermatozoon, and a female element or ovum. These are differentiated cells, produced in special organs, of the parent or parents, and by their coalescence a series of changes take place, which ultimately give rise to a new organism. These elements (♂ and ♀) may be produced in the same individual (as in many *Annelida* and *Mollusca*): such a condition is termed hermaphroditism; but in the majority of the *Invertebrata* the male and female organs are on different individuals, in other words, the sexes are completely separate.

Prof. Huxley states that it is probable that hermaphroditism "was the primitive condition of the sexual apparatus, and that unisexuality is the result of the abortion of the organs of the sex, in males and females respectively."

Although some Invertebrates have both sexual organs on the same individual, these organs are often so arranged that self-fertilisation is almost impossible. As already stated certain *Mollusca* and *Annelida* are hermaphrodites, but these all pair. Darwin* states that he had "not found a single terrestrial animal which can fertilise itself. This remarkable fact, which offers so strong a contrast to terrestrial plants, is intelligible on the view of an occasional cross being indispensable; for owing to the nature of the fertilising element there are no means, analogous to the action of insects and of the wind with plants, by which an occasional cross could be effected with terrestrial animals without the concurrence of two individuals. Of aquatic animals, there are many self-fertilising hermaphrodites; but here the currents of water offer an obvious means for an occasional cross." Darwin also remarks that he failed "to discover a single hermaphrodite animal with the organs of reproduction so perfectly enclosed

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* *Origin of Species* (6th ed.), p. 79.

that access from without, and the occasional influence of a distinct individual, can be shown to be physically impossible." Darwin concludes, from a large number of observations and facts that "an occasional intercross between distinct individuals is a very general, if not universal, law of nature."

The male element or spermatozoon varies in form and size in different animals, but consists of a head and filiform appendage or appendages.* The spermatozoa move by vibrations in a fluid called the semen, where they exist in large numbers.

The female element or ovum is a nucleated cell developed in the ovary. In all animals the ovum is nearly identical. It consists of a vitelline membrane, a protoplasmic contents or vitellus, a germinal vesicle (nucleus), and a germinal spot (nucleolus).

As already stated it is the union of these two elements which give rise to offspring. Fecundation is brought about by various methods in the animal kingdom. But as far as the *Invertebrata* are concerned, these methods will be described more in detail later in this chapter. Suffice it to say that in the majority of the unisexual *Invertebrata* copulation or the union of the sexes takes place. In animals higher in the zoological scale—for instance in fishes, the male discharges the semen over the spawn or ova of the female, for there is no act of copulation. In many of the *Amphibia* and *Reptilia*, the male clings to the back of the female, and then discharges the seminal fluid or semen over the ova as they pass through the uro-genital aperture.

In the *Aves* and *Mammalia*, and also in many of the *Invertebrata*, the semen is introduced by the penis into the genital organs of the female.

By any one of the above acts the ovum becomes fertilised: a series of changes occur which result in a more or less complete segmentation. If this segmentation or division is complete—*i.e.*, involves the whole vitellus—it is called

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* In *Astacus* there are many appendages.

holoblastic. Holoblastic segmentation occurs in the *Mammalia*, Batrachians, the lower *Crustacea*, *Vermes*, &c.; but if the segmentation is incomplete or involves only a portion of the vitellus, so that the remaining portion may be utilised as nourishment during the early stages of the development of the embryo, it is termed meroblastic. Meroblastic segmentation occurs in the ova of *Aves*, *Amphibia*, *Cephalopoda*, the higher *Crustacea*, and the *Insecta*.

The detailed description of the changes which occur in the ovum after fecundation belongs to embryology, consequently it is beyond the province of this volume, which treats of the *functions* of animals after birth. Nevertheless, we shall allude, in passing, to the broad outlines of the development of the fecundated ovum.*

Besides the above-mentioned mode of sexual reproduction (viz., that of the fusion of two *different* elements), there is another mode termed conjugation, or the union of two *similar* protoplasmic masses. These may be derived from different parts of the same individual, or from two individuals of the same species. The union of these similar masses ultimately results in the development of a new organism. This mode of reproduction occurs in some *Protozoa*.

THE PROTOZOA.

The mode of reproduction in the *Monera* and *Protoplasta* is either by fission or by endogenous cell formation. In the former the cell divides into two portions, each portion gives rise to a perfect organism. In the latter mode of reproduction a cyst is formed, and within this the protoplasm of the original cell divides into a number of segments which ultimately rupture the parent cell and escape as separate individuals.

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* For further details on the subject of embryology the reader is referred to Balfour's *Treatise on Comparative Embryology;* and Foster and Balfour's *Practical Embryology*.

In the *Gregarinæ* reproduction occurs by endogenous division of the encysted body. Sometimes two full grown organisms come together, adhere, and then surround themselves with a cyst. The result in each case is the formation of segments, which become spindle-shaped cells, called pseudo-navicellæ. These grow and finally rupture the cyst, and thereby are set free. The pseudo-navicellæ are surrounded by cell-walls, but these burst, and the protoplasmic contents of each escapes as a moner-like cell resembling *Protamœba*. The moner now becomes differentiated into ectosarc and endosarc, and the young *Gregarina* is now amœbiform. In this stage of the development two arm-like projections appear: one of these lengthens and separates, forming a perfect *Gregarina*. The other elongates and absorbs the rest of the mass and also becomes a perfect *Gregarina*. This elongating stage has been termed by Van Beneden, the pseudo-filaria phase. Afterwards the body becomes shorter and broader, and a nucleus appears, the animal then passes into the adult form.

The *Infusoria* propagate by fission, endogenous division, gemmation, and conjugation.

In the *Infusoria flagellata* multiplication by longitudinal fission occurs in several genera. For instance, in *Codosiga*, the flagellum is first retracted and then fission takes place; in *Anthophysa* the cell becomes encysted before the division occurs.

Drs. Dallinger and Drysdale have investigated the life-cycle of many genera and species of the *Infusoria flagellata*. Many of these forms multiply by—

(*a*) Fission (with or without encystment).

(*b*) Conjugation.

In the case of conjugation, the body which is formed becomes encysted for a time, but ultimately the contents of the cyst divide into either large or small bodies, which are destined to assume the parental form.

The complete life-history of *Amphipleura pellucida* is described by Drs. Dallinger and Drysdale[*] as follows—"development from a germ or sporule of extreme minuteness, and on the attainment of maturity multiplication by fission,[†] constantly and for an indefinite time; but the vital power is at intervals renewed by the blending of the genetic elements, effected by the union of two, when both are in an amœboid condition, from which a still sac results, in which germs or sporules are formed, which eventually escape, and again originate the life-cycle."

Drs. Dallinger and Drysdale have shown that the investigations of Bastian, Gros, and others, on heterogenesis and the transformation of living forms, are erroneous. They state that as far as their researches on the Monads go, they are bound to say that not the slightest countenance is given to the doctrine of heterogenesis. "On the contrary, the life-cycle of a Monad is as rigidly circumscribed within defined limits as that of a mollusc or a bird. There is no indication of any unusual or more intense methods of specific mutation than those resulting from the secular processes involved in the Darwinian law, which is held to furnish the only legitimate theory of the origin of the species."

The *Infusoria tentaculifera* multiply by (1) longitudinal fission, (2) "the development of ciliated embryos in the interior of the body. These embryos result from the separation of a portion of the endoplast, and its conversion into a globular or oval germ, which, in some species, is wholly covered with vibratile cilia, while in others, the cilia are confined to a zone around the middle of the embryo. The germ makes its escape by bursting through the body wall of its parent." This free swimming organism rapidly assumes the adult form. (3) Conjugation takes place in these organisms, which

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[*] *Transactions of Royal Microscopical Society*, 1875, p. 195.

[†] In the case of *Tetramitus rostratus*, fission proceeds for from six to eight hours; and in that of *Dallingeria Drysdali* there are from seven to eight acts of fission in an hour, for the first four hours, and about five per hour during the next two hours, after which acts are performed at longer intervals.

is followed by endogenous division. (4) Gemmation, as in *Vorticella.*

The *Infusoria ciliata* multiply by division or by conjugation. The first mode of reproduction is effected by a constriction of the adult cell in a transverse direction. The cell ultimately becomes divided into two portions which separate; each portion finally developing into separate organisms.

Paramœcium bursaria conjugates in pairs when the anterior ends of two individuals unite and remain united for five or six days. According to Balbiani,* the nucleolus and nucleus of each organism, at this period of their life-histories, become converted into sexual organs. The nucleolus ♂ is converted into an oval body which acquires a striated structure; ultimately it divides into two or four parts. These parts again divide, giving rise to capsules containing rods which are pointed at one end. These rods represent the spermatozoa of higher forms. The nucleus ♀ gives rise to bodies analogous to ovules. The result of conjugation is the formation of cells which escape as young *Paramœcia.* During the act of conjugation the two organisms, as already stated, are always united together at their anterior ends; in other words at the apertures which form the mouth. "It has been thought that this aperture must play the part of a sexual orifice through which the two organisms in copulation effect the exchange of reproductive matter; it has also been suggested, moreover, that a special sexual orifice is present close to the mouth; but these questions of structure are still doubtful."

Balbiani's investigations have been confirmed by Claparède, Lachmann, Kölliker, Stein, Bütschli, Grüber, and others.

It should be borne in mind that in these low organisms the nucleus of the cell is the all-important agent in producing many physiological functions—without it, the above mode of reproduction cannot take place. In fact, it has been stated that "the nucleus plays the primordial *rôle* in the cell; if, to use an old comparison of Aristotle's, we compare the proto-

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* *Journal de la Physiologie,* tome 1 (1858)

plasm to the clay, we must compare the nucleus to the potter that fashions it. The nucleus comprehends all the physiological properties, the totality of which goes to constitute life."

Concerning the first mode of reproduction—viz., that of transverse fission, Balbiani states, that in forty-two days *Paramœcium* can produce 1,384,116 young, that is to say that a single individual organism measuring 0.2 mm. long, grows 277 metres in bulk.*

THE PORIFERA.

Reproduction takes place asexually—by fission and by gemmation; and sexually—by the production of spermatozoa and ova. The needle-shaped spermatozoa lie in small pockets lined with cells until required. The ova, derived from the cells of the mesoderm, are naked amœboid cells with a germinal vesicle and spot. They are fertilised before leaving the parent. The impregnated ovum divides into two, four, eight, and more cells, and thereby passes into the morula condition. The cells of the morula subsequently become separated into two layers—an epiblast and a hypoblast. These layers give rise respectively to the ectoderm and endoderm of the young animal. The embryo sponge is a free swimming larva, and in such a condition it is stated to be in the planula stage of its life-history. After a time the ciliated cellular portion or hypoblast of the free swimming embryo invaginates, and the dark granular cells or epiblast grow over it. The latter form the ectoderm and the mesoderm is also derived from them. The invaginated cells (ciliated) give rise to the endoderm of the gastric cavity. This constitutes the gastrula stage in the development of the *Porifera*. After a time the young sponge becomes more or less cylindrical, and an osculum and inhalent pores are produced; and calcareous spicules appear in the mesoderm.

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* For further information on the reproduction in the *Infusoria*, see Mantegazza's *Ricerche sulla generazione degli Infusorii, e descrizione di alcune nuove specie* (1852); and W. Saville Kent's *Manual of Infusoria*.

THE CŒLENTERATA.

The modes of reproduction in *Hydra* are by gemmation, fission, and sexual reproduction.

Gemmation is the most common mode of multiplication. The buds may remain attached, or may become separated from the parent; and consequently lead an independent life. The bud of *Hydra* "consists always of a simple fold of the wall of the stomach and the skin, so that the stomach of the young individual is in direct communication with that of the parent, and the chyme (nutritive fluid) can pass freely from one to the other." When the foot of this new being has acquired a proper development, it is completely detached at its inferior extremity.

In regard to the second mode of reproduction—by natural fission—it may be stated that it is comparatively rare. Fission takes place longitudinally or transversely, and each part repairs itself, and ultimately develops into a new *Hydra* identical with the parent. In some forms of the *Cœlenterata* the fission may or may not be complete. "When it is complete the cells of the corallum are definitely limited, as in *Astræa*, *Favia*, and *Caryophyllia*, but when incomplete, the cells are branched, lobulated, and of irregular contour, as in *Agaricia*, *Mœandrina*, *Monticularia*, &c."

Sexual reproduction takes place in *Hydra*; but the animal is hermaphrodite. In the summer, testes are developed at the base of the tentacula; and one or more ovaries at the base of the column near the disc. The testis is simply a mass of inner ectodermal cells, by the division of whose nuclei, spermatozoa are formed. A spermatozoon consists of a small oval head and a long filament. This filament by its rapid movements enables the spermatozoon (when liberated) to swim about in the water; and in this medium it retains its fertilising properties for many days.*

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* The retention of the fertilising properties of spermatozoa after expulsion from the body, varies in different animals. In trout the property is

The ovary in *Hydra* is a small group of ectodermal or interstitial cells. One cell, however, lying in the centre of the group is larger and clearer than the rest; from this central cell the naked amœboid ovule is produced.

In *Hydra*, as already stated, the sexes are united in the same individual; but in other *Cœlenterata* they are distinct; "with the colonial polyps the sexes are separate, and each colony may be composed of individuals which are androgynous, or of one sex alone. Some species are sexless, and remain so; but they produce by gemmation individuals of a particular character, which have sexual organs."

In *Hydra* when gemmation takes place there is ultimately a complete separation of the buds, but in some *Cœlenterata*, there is gemmation without separation of the young; this occurs, for example, among the *Coralligena*.

Concerning the development of *Hydra*, the following is an outline of the process: After the ovule or egg-cell escapes from the ovary it is fecundated by spermatozoa, which are discharged from the testes into the surrounding water. There is no act of copulation. As the result of fecundation the naked egg-cell acquires a cell-wall, and segmentation of its mass follows; that is, a morula or blastosphere is formed. After this a chitinous shell is elaborated which envelopes the embryo. The embryonic cells fuse together, giving the embryo the appearance of an unsegmented egg-cell. In the centre of this mass a small cavity (the beginning of the body cavity) is produced. This gradually widens and lengthens so that the embryo becomes a closed sac. After several weeks the above-mentioned shell is ruptured, and the hollow germ escapes enveloped in a thin membrane. The protoplasmic

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lost in a few minutes. Spermatozoa in the seminal reservoir of the female bee retain their powers for several years. In mammals the seminal elements retain their powers of fertilisation for some time in the genital passages of the female; in the female rabbit Balbiani found them twenty-four hours after coition; and Drs. E. van Beneden, Benecke, Eimer, and Fries have observed spermatozoa in the uterus of bats for several months.

mass which surrounds the body or somatic cavity differentiates or divides into an ectoderm and endoderm. During all this embryological development, the embryo has been growing in length. At one end of the elongating embryo, a mouth is formed by rupture of the tissues. "It first appears as a star-shaped cleft which gradually becomes more or less round. The tentacula next appear simultaneously. The animal then bursts the thin membrane, comes out of it, and starts life on its own account as a perfect *Hydra*. There is no metamorphosis in the development of *Hydra* (no invagination, and no ciliated planula as in many other Hydroids). The young *Hydra* passes into the adult condition by continuous growth."

In the *Medusæ* the sexes are separate; the females have yellowish-coloured ovaries, while the males possess rose-coloured genital glands. The ova undergo their embryonic development in the oval tentacula. The embryonic development of these animals presents the following phases:—(*a*) egg; (*b*) morula (blastosphere); (*c*) gastrula (by invagination); (*d*) planula (ciliated larva), this stage is formed by the closing of the gastrula mouth and the "ciliating" of the ectodermal cells; (*e*) next appears the hydra-form or scyphistoma, which is produced by the planula becoming fixed and developing tentacula and a mouth at the free end. During the scyphistoma stage there is at first multiplication by gemmation, but afterwards fission occurs, and the animal then reaches the strobila stage; (*f*) the detached segments of the strobila swim away in the ephyra form; (*g*) the ephyra form after some weeks is converted into the adult animal (in this case, *Aurelia*). In the development of *Aurelia* it will be observed there is an alternation of generations; the asexual generation being represented by scyphistoma and strobila.

In the *Actiniæ* the sexes are united. The testes and ovaries form closely convoluted tubules and the generative products are discharged into the somatic or digestive cavity.

The embryo arises from the fecundated ovum without any metamorphosis. The ovum (Fig. 76, *f*) undergoes segmentation within the ovary, and the embryo is born alive as a ciliated larva, possessing a somatic or digestive cavity. and a mouth. After this two mesenteric tissues are produced which divide the internal chamber into two unequal parts. Two new mesenteries subsequently arise in the larger or anterior chamber. A third pair are next developed in the posterior chamber, and then a fourth pair in the lateral spaces. Next the tentacula are developed; and afterwards four new mesenteries appear, these are situated one on either side of the two primary mesenteries, so that in all twelve somatic cavities are formed which ultimately become of equal size.

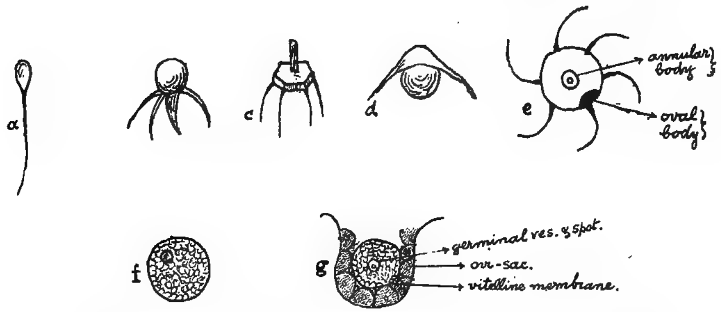

FIG. 76.—SPERMATOZOA AND OVA OF CERTAIN INVERTEBRATES.

a = Lumbricus. *b* = Pagurus. *c* = Pisa. *d* = Grapsus. *e* = Astacus (♂). *f* = Actinia. *g* = Astacus (♀).

The *Actinæ* are also reproduced by gemmation or budding.

For fuller details the reader is referred to special books and memoirs on the subject.*

THE ECHINODERMATA.

These animals propagate by sexual organs, and the sexes are distinct; hermaphroditism is very rare. The ova are

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* See also Prof. A. Giard's paper in *Comptes Rendus de l'Académie des Sciences*, 1877.

covered by a delicate chorion, and contain a variously coloured vitellus with germinal vesicle and spot; the ova also contain a little albumin. The spermatozoa are nearly always composed of a round or oval body and a delicate hair-like filament. "With a few exceptions, the embryo leaves the egg as a bilaterally symmetrical larva, provided with ciliated bands, and otherwise similar to a worm-larva, which may be termed an *Echinopædium.* The conversion of the *Echinopædium* into an Echinoderm is effected by the development of an enterocœle, and its conversion into the peritoneal cavity and the ambulacral system of vessels and nerves; and by the metamorphosis of the mesoderm into radially disposed antimeres, the result of which is the more or less complete obliteration of the primitive bilateral symmetry of the animal." (Huxley.)

The external appearances of the sexual organs in the *Echinodermata* are somewhat similar, but at the period of procreation they frequently differ in colour. They are composed of either simple or branched tubules with or without excretory ducts. In the latter case, the contents of the organ, male or female as the case may be, are discharged by rupture into the body cavity, from whence they pass out through the respiratory openings.

The *Echinodermata* are devoid of copulatory organs; the ova being fecundated by the spermatozoa in the water in which these animals live.

In the *Holothuridea,* there is only one testis and ovary in male and female respectively. Both are composed of a tuft of highly-branched tubules, which unite to form a common duct, which opens externally near the mouth. The early stages in the development of *Holothuria* are like those of the *Asteridea,* which will be described later in this chapter. The free-swimming larva is called an *Auricularia.* The larva is transparent, vermiform, and has four or five bands of cilia; and while still growing, the young Holothurian begins to bud out by the side of the larval stomach. The larva or *Auricularia* is gradually absorbed by the developing

Holothurian; and the adult form of the animal is attained without any further changes.

Although the sexes are distinct, there is one exception among the *Holothuridea*, and that is the genus *Synapta.* These animals are hermaphrodites. According to De Quatrefages,* the testes and ovaries are united so as to form one organ. This organ consists of branched tubules and secretes both spermatozoa and ova; its excretory duct opens near the oral end of the body.

In the *Asteridea*, the sexes are separate. The genital organs are very similar in appearance, but the colour of the ova is either yellow or red and the seminal fluid is white. The ova are fecundated in the water. There are five pairs of genital glands, one pair lying in each ray. They are sacculated or racemose organs, whose ducts open externally by a narrow orifice on the dorsal side of the body. Dr. G. O. Sars has shown that in *Brisinga endecacnemos* the genital organs consist of many distinct glands forming two well-marked series, which are situated one on each side of the middle line of the central half of each ray.

Concerning the development of *Asterias* (a typical example of the *Asteridea*), the following may be taken as an outline of what occurs:--(*a*) The ovum, after fecundation, becomes totally and equally segmented—thus forming the morula stage. (*b*) The segmented ovum gives rise to a spheroidal embryo consisting of an external ciliated cellular wall and an internal gelatinous substance. (*c*) A depression of the external wall now makes its appearance, and gives rise to the first rudiment of the alimentary canal. The opening of this depression ultimately becomes the anus. This is the gastrula stage.. (*d*) The ciliated embryo lengthens and four surfaces can now be distinguished. There is a continuous band of cilia which has a locomotory function. The alimentary canal, which in this stage acquires a mouth, becomes modified into three portions—œsophagus, stomach, and intestine.

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* *Annales des Sciences Naturelles*, tome 17, p. 66.

Before the formation of the mouth, two lobe-like bodies are formed from the upper part of the alimentary canal. These lobes ultimately separate and form two distinct cavities. These develop into two water-tubes which elongate until they surround the alimentary canal, extending on the other side of it beyond the mouth where they join, giving rise to a **Y**-shaped canal. (*e*) The ventral ridge containing the band of cilia becomes prolongated into processes of various shapes. These processes are arranged with close regard to bilateral symmetry (*Bipinnaria* and *Brachiolaria*, or bilateral larval stage). (*f*) At this point the body of the future starfish begins to develop from the larva. "On one of the branches of the united water-tubes the feet or tentacula are produced as a series of lobes, while on the opposite branch of the water-vascular canal many small calcareous rods are elaborated. These rods afterwards form a regular network, and indicate the dorsal side of the young *Asterias*." (*g*) At this stage the larva *Brachiolaria* shrinks and drops to the bottom of the water, where it fixes itself by means of its short arms. (*h*) That portion of the larva which is more developed into the true starfish form than the remaining portion, now absorbs the latter and acquires a conical and disc-like form, with a crenulated edge. In this stage the organism remains for two or three years. Then the rays or arms lengthen and the mature form is assumed.

According to Greef,* parthenogenesis appear to occur in *Uraster rubens*.

In the *Ophiuridea*, the sexes are distinct,† and the genital organs consist of lobular, pedunculated sacs, which are situated, in pairs, in the inter-radial spaces of the disc. These organs pour their secretions into the peritoneal cavity; the latter, however, is in communication with the external medium by narrow apertures situated inter-radially on its margins. The ova are fecundated in the water, and in that

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* *Marburg Sitzungsberichte*, 1871.

† *Ophiolepis squamata* is hermaphrodite.

medium the embryos are developed; but in the case of *Ophiolepis ciliata*, the embryo is developed within the body cavity of the parent. The early stages of the embryological development of most *Ophiuridea* are similar to those of other *Echinodermata;* nevertheless, in some forms the embryo passes directly into the adult condition without first becoming an *Echinopædium.* "Where an *Echinopædium* stage exists, the larva is a *Pluteus.* The dorsal wall of the body of the embryo exhibits a medium conical outgrowth; along the course of the ciliated band symmetrically disposed processes are developed; and these outgrowths are supported by a calcareous skeleton, which is also bilaterally symmetrical."

In the *Echinidea** there are five unpaired ovaries or testes, which are situated inter-radially. As a rule, they project far into the body cavity, and are composed of ramified tubules. The ducts of the genital glands open externally by five apertures in the genital plates which surround the apical pole. The early stages in the embryological development of *Echinus* are similar to those of the starfish. The free-swimming larva, however, assumes the *Pluteus* form, and in this respect it is similar to the *Ophiuridea.* The *Pluteus* form has eight long slender arms, which are supported by calcareous rods extending from the body. The adult form of *Echinus* is developed within the body of the larva, the alimentary canal and dorsal sac (the commencement of the ambulacral system) alone persisting. The larval body is gradually absorbed by the developing and growing *Echinus,* the spines and pedicels of the latter increasing in size and number until the animal assumes the adult form.

It may be remarked that Professor A. Giard † has shown that at certain times the genital glands of the *Echinidea* secrete small crystalline concretions of a brownish colour. These concretions consist of calcium phosphate, which is

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* The sexes are distinct.

† *Comptes Rendus de l'Académie des Sciences,* 1877.

destined to furnish the vitellus and spermatozoa with phosphorus—an element which is present in large quantities in the genital products.*

In the *Crinoidea*, the sexes are distinct; and the tubular genital organs are situated under the perisoma of the pinnulæ. In *Antedon* the ovaries open externally on the pinnulæ, and the ova are discharged by the dehiscence of the integument of the pinnula; but before leaving the female *Antedon* the ova remain attached to the opening of the integument for a few days; during that time they are fecundated. "The testis develops no special aperture, but the spermatozoa appear to be discharged by the dehiscence of the integument." The development of the embryo *Antedon* is as follows: After the ovum is impregnated it undergoes total segmentation—*i.e.*, a morula is formed. It then passes into a gastrula stage, hatching as a barrel-shaped larva with four bands of cilia. This larva passes through a metamorphosis, and ultimately becomes a fixed pentacrinus-like form —*i.e.*, *Antedon* is stalked when young. After some time, however, it separates from its stalk and moves about independently.

Professor Huxley says that "on comparing the facts of structure and development, which have now been ascertained in the five existing groups of the *Echinodermata*, it is obvious that they are modifications of one fundamental plan. The segmented vitellus gives rise to a ciliated morula, and this, by a process of invagination, is converted into a gastrula, the blastopore of which usually becomes the anus. A mouth and gullet are added, as new formations, by invagination of the epiblast. The embryo normally becomes a free *Echinopædium*, which has a complete alimentary canal, and is bilaterally symmetrical. The cilia of its ectoderm dispose themselves in one or more bands, which surround the body; and, while retaining a bilateral symmetry, become variously modified. In the *Holothuridea*, *Asteridea*, and *Crinoidea*,

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* Similar concretions are found in the renal organs of many Invertebrates.

the larva is vermiform, and has no skeleton; in the *Echinidea* and the *Ophiuridea* it becomes pluteiform, and develops a special spicular skeleton."

THE TRICHOSCOLICES.

The *Turbellaria* multiply by two methods, (*a*) transverse fission; (*b*) by sexual organs. In the smaller *Rhabdocœla*, the first mode of reproduction is the rule, for no genital organs are present. These animals are both monœcious and diœcious; and the "genital and copulatory organs of both sexes are situated upon one and the same individual so that they are capable of self-impregnation; but there is generally a reciprocal copulation."[*]

In the higher *Turbellaria* the female genital organs consist of the following parts: a germarium which develops ova; a vitellarian gland in which the vitellus or food yolk is formed; an oviduct; a uterus and vagina; and a spermatheca—the function of which is to store the semen after the act of coition. The male genital organs consist of a testis, vas deferens, and penis; the latter "is often eversible and covered with spines." The impregnated ova are enclosed within a hard shell. In some genera the hard shell is only formed on the winter ova, while the summer ova are only covered by a soft vitelline membrane. The rhabdocœlous ovum undergoes complete segmentation and the embryo passes directly into the adult form.

In the marine *Planariæ*, there is no vitellarium, and in some of these animals the embryo after leaving the ovum differs considerably from the adult. The *Planariæ* are hermaphrodites, but *Planaria dioica* is unisexual. The *Proctucha* are nearly always hermaphrodites, and the ova and spermatozoa are discharged externally by the dehiscence of the integument.

Nemertes is diœcious, and the genital organs (♂ and ♀) have the same structure, being sacs filled with spermatozoa

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[*] Coition has been observed in *Planaria*, *Mesostomum*, &c.

or ova according to the sex of the animal containing them. The genital organs are situated in the lateral part of the body between the pouch-like diverticula of the intestine. They are arranged in pairs along the body and open externally by paired apertures. The development of *Nemertes* occurs with metamorphosis. The following are the stages through which the embryo passes: (*a*) Before hatching—egg, morula, and planula. (*b*) After hatching—a ciliated larva or *Pilidium* is formed; and the adult condition is attained by direct growth, or by budding out from the *Pilidium*.

In the *Rotifera* the sexes are distinct, and the male animals are much smaller than the females. The genital apparatus of the male consists of a testis, in which the spermatozoa are produced and stored; the testis opens by a duct situated near the posterior end of the body, usually on a muscular protruberance or penis. The male *Rotifera* are short-lived, and are only born into the world to impregnate the ova of the females. The genital apparatus of the female consists of a round sac-like ovarium or ovary, filled with ova in various stages of development, and a short oviduct which opens into the cloaca. The female produces both summer and winter eggs. According to Prof. Huxley the winter eggs are produced parthenogenetically—*i.e.*, without previous impregnation. In fact, he says in regard to *Lacinularia* that the winter eggs appear to be "segregated portions of the ovarium." On the other hand, Cohn believes that it is the summer eggs which are produced parthenogenetically, while the winter eggs are impregnated. The egg undergoes complete and irregular segmentation; then a two-layered embryo is formed. An involution of the epiblast occurs, giving rise to the primitive mouth, which remains permanently open. The trochal disc grows out of the walls surrounding the epiblastic depression; and the nerve-ganglion is also produced from the epiblast. At the bottom of the primitive depression, the true mouth is formed; while the œsophagus and the remaining portion of the alimentary canal are developed from the hypoblast.

The *Trematoda* are nearly always hermaphrodites; and the genital apparatus consists of the following parts: the ovary, vitellarium, oviduct, uterus, vagina, common genital vestibule, testis, vasa deferentia (internal and external), and the penis and its sac. The ovum, as it passes into the oviduct, is devoid of a vitelline membrane, and the vitellus or yolk is clear; but after fecundation, which takes place in the oviduct, a shell is developed and the accessory yolk is added by the action of the vitellarium. The oviduct, which is ciliated internally, communicates with a duct which proceeds from the testis; it also receives the vitellarian duct. The oviduct then passes into the uterus, which terminates by the vagina and common genital vestibule in close proximity to the male organs. The oval-shaped testis, situated posteriorly to the ovary, does not contain spermatozoa, but simply a granular mass. The external vas deferens comes into contact with the ovary, and then passes, after several bends, into the anterior part of the body, terminating in the penis, which occupies, in common with the uterus, the genital vestibule.

In the case of *Aspidogaster* (the above being an account of its reproductive organs), the embryo assumes the adult form without any metamorphosis; but in other species, the development is either direct* or accomplished by a complicated metamorphosis,† accompanied by alternation of generations.

The ova of *Aspidogaster*, as they pass down the oviduct, are impregnated, "either by the spermatozoa conveyed by the internal vas deferens, or by those received by the vagina, when copulation with another individual, or possibly self-impregnation, occurs."

As already stated, nearly all the *Trematoda* are hermaphrodites, but among those that are diœcious is the parasitic *Bilharzia*, which lives in the blood-vessels of man. The female *Bilharzia* is much smaller than the male; and a

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* *Polystomum, Gyrodactylus.*

† *Distoma, Monostomum.*

curious mode of pairing occurs—for the male, not content to unite with the female, retains the latter in a gynæcophore or canal; but it may be stated that very little is known concerning the reproduction and development of this Trematode.

So far we have seen that the *Trematoda* only multiply sexually; but some of these animals also multiply by conjugation and by a kind of gemmation. For instance, in the genus *Diporpa*, two individuals (devoid of sexual organs) conjugate, and the result is a double-bodied *Diplozoon paradoxum*, which ultimately develops sexual organs.

In the case of *Gyrodactylus*, a kind of internal gemmation occurs.

The *Cestoidea* are hermaphrodites in the mature condition, but in the earlier stages of their growth they are devoid of sexual organs (*i.e.*, in the cystic form). Some, like *Caryophyllœus*, have only a single set of hermaphrodite organs; and *Ligula* is an unsegmented form with many sets of these organs. The Tape-worms are segmented animals, and in each proglottis or segment there are male and female organs. The male organ consists of innumerable pear-shaped vesicles or testes, scattered in the parenchyma of the body. The vasa efferentia open into the common duct—the vas deferens; the latter lies in the cirrus sheath. By the contraction of the cirrus sheath, the vas deferens ("cirrus") can be forced through the vagina.* In this case the vas deferens acts as a copulatory organ or penis.

The female organ consists of the following parts: An ovary leading into a single oviduct, which has an enlarged portion or pouch, termed the receptaculum seminis. Branching out from the oviduct are the vitellaria or yolk glands, whose efferent tubes ultimately coalesce with the oviduct forming a common duct. At the point where the ducts of the vitellaria unite with the oviduct, the shell gland is

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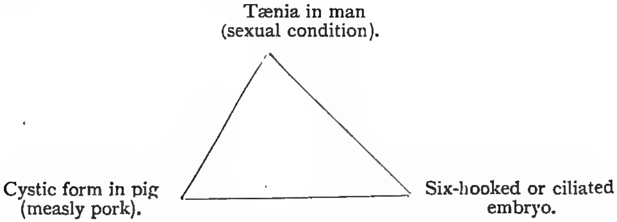
* The vagina and vas deferens open into a cloaca or genital vestibule, which is situated on the lateral margin of the proglottis.

attached. This gland secretes a substance which becomes the investment of the ova. The terminal portion of the oviduct passes into the uterus. The vagina is usually a long canal, and at its inner end is the receptaculum seminis. The small ova are either oval or round. They are formed by three glands—the ovary, vitellarium, and shell gland.*

As already stated, the Tape-worms are composed of many segments or proglottides, and at the end of the body the segments become detached. In this condition they retain their vitality for some time. The uterus of the proglottis contains very many ova; and the embryo (ciliated or hooked) is developed in a similar manner to that of the *Trematoda*.

The Tape-worms live a portion of their life in one animal (cystic condition), and the other portion in an entirely different one (cestoid condition). For instance, the following diagram illustrates the life-history of *Tænia solium*, which infests man:—



"The Tape-worms are rarely met with in both the cystic and cestoid conditions in the same animal; but the cystic form is found in some creature which serves as prey to the animal in which the cestoid form occurs."

THE ANNELIDA.

The *Myzostomea* are small unsegmented worms, parasitic on *Comatula* (*Antedon*). These animals are hermaphrodites. The two oviducts open into the cloaca; and the male organ

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* The ovary forms the nucleus, the vitellarium the yolk, and the shell gland the external covering of the egg.

opens externally by separate ducts—the vasa deferentia—on each side of the ventral surface of the body.

The *Gephyrea* are also unsegmented worms, but they are diœcious (*i.e.*, the sexes are distinct), and the spermatozoa and ova are developed from the epithelial cells, which line the walls of the perivisceral cavity, or they are developed in simple cæcal glands. The earlier stages in the development of these animals are similar to those of the *Oligochæta* and *Polychæta.* The adult state is attained from the embryonic condition by a metamorphosis. In the genus *Bonellia,* the males, which are minute, rudimentary, and Planarian-like, live in the uterus of the female.*

The *Hirudinea* are hermaphrodites.† The male organs of *Hirudo* consist of nine pairs of testes, situated in successive segments. The first pair are in the segment behind that which contains the eversible penis; and the others are in the following eight segments, a little in front of the nephridia or segmental organs. From each testis a duct passes into the vas deferens (situated laterally), which, in front of the anterior pair of testes, becomes much coiled, forming the vesicular seminalis. The latter opens into a duct, which passes forward to the ventral median line, and, along with the same duct of the vas deferens of the other side of the body, opens into the prostate gland. A duct proceeds from the prostate gland, which forms a sheath of the eversible penis, and opens in the twenty-fourth segment. The spermatozoa are enclosed in a case, called a spermatophore. The female organs are situated in the segment behind that which contains the penis. They consist of two small ovaries provided with oviducts; the latter open into the uterus, which is surrounded by an albumin gland. The uterus proceeds into a vagina, which opens by a small orifice situated between the twenty-ninth and thirtieth segments. It will be noticed that the external orifices of the genital organs are unpaired.

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* This is different from *Bilharzia* (one of the *Trematoda*), for the male retains the female within its own body.

† Except *Histriobdella* and *Malacobdella*, which are diœcious.

The impregnation of the ova takes place within the body; and the ova, when laid, are enclosed in a cocoon which is secreted by the integument. Although these animals are hermaphrodites, copulation between two separate individuals takes place. "The female copulatory organs are upon the ventral surface of the anterior part of the body, and behind the male organs—so that two individuals, by placing together their anterior ventral surfaces in an inverse position, can be mutually impregnated." (Von Siebold.)

The ovum of *Hirudo* passes through a metamorphosis, the mesoblast undergoing division into segments, which ultimately give rise to the characteristic structure of this and other segmented animals.

The *Oligochæta* are hermaphrodites; and the genital organs are situated (like *Hirudo*) in the anterior part of the body. In the fresh-water *Oligochæta* (*Nais* and *Tubifex*), these organs have no genital ducts, but the ova and spermatozoa are conveyed outwards by the nephridia, which are situated in those segments of the body containing the genital glands. "In *Nais* and *Chætogaster*, agamic multiplication occurs by the development of posterior segments of the body into zooids, which may remain associated in chains for some time, but eventually become detached and assume the parental form."

In *Lumbricus*, the testes are two pairs of white sacs situated on the posterior sides of the septa, separating the ninth and tenth, and the tenth and eleventh segments. The spermatozoa are not fully developed on leaving the testes, and they are known in this condition as spermospores. The spermospores are further developed by a process of budding, which takes place in the vesiculæ seminales (two pairs of reservoirs). The fully developed spermatozoa (Fig. 76 *a*) are conveyed outwards by four ducts—the vasa deferentia; but the two vasa deferentia on either side of the body unite, forming one duct, which opens on the ventral side of the fifteenth segment. The female genital organs consist of a pair of small ovaries

($\frac{1}{16}$ in. long), situated in the thirteenth segment. The ova when fully developed rupture the walls of the ovaries, and pass into the body cavity. Ultimately the ova find their way into the oviducts, which are quite distinct from the ovaries. The pair of oviducts are small, funnel-shaped, ciliated tubes; the funnel-shaped portion opens internally in the thirteenth segment, whereas the opposite end opens externally by a small aperture on the ventral side of the fourteenth segment.

Although *Lumbricus* is hermaphrodite, copulation takes place between two separate individuals, the impregnating seminal fluid being stored in four small spherical sacs or spermathecæ, which open externally between the ninth and tenth, and the tenth and eleventh segments. The ova are impregnated externally by the seminal fluid from the spermathecæ. Groups of these ova become surrounded by mucous and chitinous secretions termed cocoons. These cocoons sometimes contain forty or fifty ova, an albuminous substance, and packets of spermatozoa. In the development of the *Oligochæta*, the segmentation of the ovum is total and nearly regular, giving rise to a flattened ciliated blastosphere. The latter invaginates, and a gastrula is formed; and between the epiblast and hypoblast in this stage of the development a mesoblast is formed. "On the ventral side of the embryo, the mesoblast divides into a row of quadrate masses, which are symmetrically arranged on each side of what becomes the median line of the adult body. This series of symmetrically placed quadrate masses resembles the protovertebræ of the embryo of a Vertebrate animal." After this "a cavity forms in the interior of each quadrate mesoblastic mass, making it into a kind of sac. The adjacent anterior and posterior walls of the row of sacs unite, and this union gives rise to the dissepiments of the somites, while the cavities become the body cavity or perivisceral chambers." (Johnstone.) The epiblast now thickens inwardly, along the median line, ultimately giving rise to the ganglionic nervous system.* The nephridia or segmental organs begin as outgrowths from the posterior face of each septum; and finally the adult form is attained just before the hatching of the egg.

The *Polychæta* are diœcious and rarely hermaphrodite.† Some of these animals multiply by fission and gemmation. In *Syllis*, transverse fission takes place; while in *Myrianida* gemmation occurs giving rise to zooids. In some other Polychætous forms reproduction is produced by a combination of fission and gemmation.

The genital organs of the *Polychæta* are very simple in structure, and the genital products ultimately float about in the perivisceral cavity, probably passing outwards through the apertures at the bases of the parapodia. In some *Polychæta*, the nephridia act as genital ducts. The ova of these animals undergo a somewhat similar metamorphosis to those of the *Oligochæta* and *Hirudinea*; "but the embryos of the *Polychæta* differ from those of the *Oligochæta* and *Hirudinea* in being ciliated."

THE NEMATOSCOLICES.

The *Nematoidea* are nearly all diœcious, unsegmented worms.‡ These animals and their genital products are possessed of great vitality. According to M. Devaine, the ova of *Ascaris lumbricoides* § are capable of withstanding the action of a solution of chromic acid (2 per cent.) for five years; and Mr. W. Carruthers, F.R.S., states that vitality was restored in some Nematodes, after they had been in the botanical department of the British Museum for more than thirty years.‖

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* The nervous system, almost throughout the animal kingdom, has an epiblastic origin.

† *Protula* is hermaphrodite.

‡ *Pelodytes* is hermaphrodite; and *Ascaris nigrovenosa*, which at first produces spermatozoa, afterwards only produces ova.

§ The *ἕλμινς στρογγύλος* of Hippocrates.

‖ See Dr. Griffiths' *Diseases of Crops*, pp. 18 and 119.

As a rule, the male organ consists of a single cæcal tube opening on the ventral side into the cloaca or the posterior end of the intestine. The spermatozoa,* which are amœboid in shape, are developed from the blind end of the cæcal tube, whose remaining portion has the function of a vas deferens. One or two, sometimes long, chitinous spicula are developed in the cloacal region of the male. These spicula are used by the male during copulation—the object being to distend the vulva of the female, in order to allow the seminal fluid to pass freely into the vagina and uterus. The spermatozoa undergo further changes in the female organs of reproduction, but ultimately fuse with the ova.

The female organ consists of a single or double tube, which is blind at one end. The blind end of this tube contains internally a protoplasmic substance or rhachis, from which the ova are developed; this portion of the tube is, therefore, physiologically the ovary of other forms. The tube then becomes differentiated into an oviduct, and later into a uterus. The ova are free in the oviduct, and they are impregnated in the uterus, where they become surrounded by a hard shell. The uterus then passes into the vagina, which opens on the ventral surface, usually near the centre of the body.

The vitellus of the fecundated ovum becomes segmented, and gives rise to a single row of cells, which ultimately become indented on one side—*i.e.*, the ovum forms a kind of invaginated gastrula.† The body wall and the alimentary canal are developed from two layers of cells, which are produced by the invagination of the above-mentioned single layer. At this point the embryo rapidly assumes the adult form; and is found rolled up within the shell. After hatching, the young Nematode casts its cuticle, which is shed a second time when it acquires its sexual organs—*i.e.*, there is a period

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* In the *Nematoidea,* the spermatozoa retain the character of cells.

† The ova of *Ascaris dentata* and *Oxyuris ambigua* are unsegmented after fecundation.

in which the *Nematoidea* are sexless worms. In the genera *Mermis* and *Gordius*, the anterior ends of the embryos are provided with spines—the spines being used to pierce holes in the bodies of insects, in which these Nematodes live a portion of their life-history. According to Sir John Lubbock, the male of *Sphærularia* becomes permanently fixed to the female. Many of the Nematodes are only parasitic in the sexless stage of their existence; but some are free in the larval or sexless stage; and some again are parasitic both in the sexless and sexual condition.

In the *Acanthocephala*—represented by *Echinorhynchus*—the genital organs are attached to the posterior end of the proboscis sheath by the ligamentum suspensorium, which traverses the body cavity. The sexes are distinct. The female organ consists of a tubular ovary; a uterine bell—the mouth of which opens into the body cavity, while the upper portion leads into the uterus; the uterus then passes into the vagina, which opens externally at the posterior end of the body. The ova, discharged from the ovary into the body cavity, are ultimately taken up by the mouth of the uterine bell, which is continually expanding and contracting, and thence the ova pass into the uterus. The male organ consists of two oval testes provided with vasa deferentia, which proceed to the posterior end of the body. At this point the vasa deferentia fuse together, forming a bulb-like structure, called the ductus ejaculatorius, which is usually provided with six or eight glandular sacs. The ductus ejaculatorius is furnished with a long penis placed in the centre of the bottom of a bell-shaped bursa situated at the posterior end of the body. The development of the fecundated ovum commences with an irregular and a complete segmentation. This gives rise to an embryo, which is enclosed in the membranes. The embryo, at this stage, is provided anteriorly with small spines. The ova (containing the embryo) are usually "swallowed" by various *Amphipoda*, *Isopoda*, and *Insecta* (larvæ); in this stage the membranes are dissolved by the secretions of the alimentary canal, and the embryos becoming free, bore their way through the walls of the intestine of their host. While in the alimentary canal of the host, the embryo loses its spines, and develops into an elongated larva. In this condition, the skin gives rise to the muscular body wall, the dermal vessels, and the lemnisci of the adult; all the other organs are developed from the "embryonic nucleus," which makes its appearance early during the embryonic development—*i.e.*, before the ovum is "swallowed" by one of the above-mentioned Invertebrates. Finally, the embryo finds its way into the alimentary canal of one of the *Vertebrata* (*e.g.*, fishes, aquatic birds, pigs, &c.), and while there, it develops sexual organs.

THE CHÆTOGNATHA.

This group contains only one genus—*Sagitta*. These animals are hermaphrodites; and the male and female organs are situated at the sides of the posterior end of the body. There are two tubular ovaries, the ducts of which open externally on each side of the anus. The tubular testes, situated behind the ovaries in the caudal region of the body, open by short ducts at the sides of the tail. The fecundated ovum becomes completely segmented, giving rise to a blastosphere. By invagination, the hemispherical, two-layered, cup-shaped gastrula is formed. The primitive opening now closes, and a permanent mouth is formed at the opposite end. At this point the embryo has an oval shape, but it finally elongates and acquires the adult form before leaving the egg.

THE ONYCHOPHORA.

Professor H. N. Moseley* has shown that in *Peripatus* the sexes are distinct. The testes are egg-shaped; and they are provided with coiled vasa deferentia, which ultimately unite, forming a common duct. This duct opens on the ventral

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* *Philosophical Transactions of the Royal Society*, 1874.

side of the rectum. Like the testes, the ovary is situated in the posterior end of the body. It is a small, single, bilobed organ provided with two long oviducts, which unite before passing into a short vagina. The vagina opens externally on the ventral side of the rectum. The oviducts are provided with uterine dilatations, and in these the ova are developed, *Peripatus* being a viviparous animal. For details concerning the development of *Peripatus*, the reader is referred to Moseley's original paper, already cited.

THE MYRIAPODA.

The *Myriapoda* are diœcious. The testes, in the *Chilopoda*, assume various forms; but in most of these animals, the testes are said to be "fusiform acini united by delicate ducts with a median vas deferens; and two, or four, pairs of accessory glands are connected with the opening of the male apparatus." According to Favre,* the testis, in *Lithobius*, is a single tube connected with the vas deferentia, the latter being situated on each side of the rectum. A vesicula seminalis opens into each vas deferens.

In the *Chilognatha* (*Diplopoda*), the tubular testes are situated between the alimentary canal and the nervous system. The testes are provided with lateral tubules, the former being connected with the latter by transverse ducts. There are two penes connected with the bases of the seventh pair of legs. In *Scolopendra* (centipede), *Geophilus*, and *Cryptops*, the spermatozoa are enclosed in spermatophores.

In both the *Chilopoda* and *Chilognatha*, the ovary is a long single tube. It is situated above the alimentary canal in the *Chilopoda*, and between the alimentary canal and the nervous system in the *Chilognatha*. The female organ in each order is provided with double vaginæ, which open beneath the anus in the *Chilopoda*, and behind the bases of the second pair of legs in the *Chilognatha*. Two spermathecæ are generally present in the *Myriapoda*.

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* *Annales des Sciences Naturelles*, 1855.

"The *Chilognatha* copulate. In *Glomeris* and *Polyxenus*, the genital apertures of the two sexes are brought together during copulation; but in *Julus*, the penes of the male are charged with the spermatic fluid before copulation takes place, and it is by their agency that the female is impregnated. The *Chilopoda* have not been observed to copulate, indeed the female shows a tendency to destroy the males, as among the *Araneina*. The male *Geophilus** spins webs, like those of spiders, across the passages which he frequents, and deposits a spermatophore in the centre of each."

The development of the embryo of the *Myriapoda* has been worked out by Metschnikoff,† whose papers the reader is referred to for important information.

THE INSECTA.

The *Insecta* multiply by means of genital organs, and the sexes are distinct. According to M. Lacaze-Duthiers, ‡ the copulatory organs in these animals present wide and manifold variations. Among the colonies of ants, bees, and wasps, besides the males and females, there are large numbers of neuter individuals. The sexual organs of the *Insecta* are developed chiefly during the pupal stage; but the rudiments of these organs exist in the larvæ—*e.g.*, the female genital organs exist in the larvæ of *Apis*, and it is due to an increase in the quantity of nourishment that the larvæ become females or queens.

Among the *Aphidæ*, parthenogenesis occurs; for many successive generations of females are born viviparously without copulation with the males.

As a typical example of the genital organs in the *Insecta*, we describe in detail those of *Periplaneta* (the cockroach). The male organ consists of numerous short testicular sacs attached to a short vas deferens. It is situated above the

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* Belonging to the *Chilopoda*.

† *Zeitschrift für Wissenschaftliche Zoologie*, 1874–5.

‡ *Annales des Sciences Naturelles*, tomes 12, 14, 17, 18, and 19.

posterior abdominal ganglion. The anterior end of the vas deferens is dilated; and this duct in the adult male always contains spermatozoa. The spermatozoa appear to be formed in the testis or mushroom-shaped gland of the young, and then accumulate in the vas deferens, for in the adult cockroach the testis atrophies.

The two ovaries, each of which consists of eight tubules, are situated in the posterior part of the abdomen. The ovarian tubes or the contracted portion of the ovaries pass into two short oviducts. The two oviducts unite in the middle line of the body, and open externally by a very short but wide vagina. Behind the union of the oviducts with the vagina, there is the spermatheca or seminal receptacle; and behind the latter are two much-branched tubular colleterial glands which secrete the chitinous substance of the egg-cases. There are sixteen eggs enclosed in each case. "The female carries the egg-case about for a week or more, before depositing it. The young leave the eggs as minute active insects, colourless, except for the large dark eyes." *Periplaneta* does not pass through any pupal stage; but undergoes seven ecdyses or moultings of the skin; and attains its mature condition during the fifth year.

The penes or male copulatory organs in the *Insecta* are often very complex in structure. "Kraepelin,* who has examined the development of these parts in the Drone, and the modifications found in hermaphrodite Bees, is led to the conclusion that they are developed from the eighth and ninth somites of the abdomen, and therefore are the homologues of the parts of the sting in the female. In the male *Blatta* (*Periplaneta*), however, it is obvious that the male copulatory apparatus belongs to a more posterior somite than that upon which the female gonapophyses are developed."

In most *Insecta*, the vitellus of the ovum undergoes only partial segmentation; but in some *Poduridæ* segmentation is complete. During the development of the embryo, there are

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* *Zeitschrift für Wiss. Zoologie*, 1873.

certain parts * which are comparable to the amnion of the *Vertebrata*. This amniotic investment is not, however, universal among the *Insecta*, although it is present in the *Orthoptera* (*Libellula*), *Diptera*, *Lepidoptera*, *Hymenoptera*, *Coleoptera*, and *Hemiptera*.

As material agents in the propagation of the *Insecta*, the following may be mentioned: their odours, colours, dances, and music. For instance, (1) in some *Lepidoptera*† there are two glands, situated near the opening of the vagina, which secrete an odorous substance that excites copulation; and one could give many examples where odours play an important part in the amours of various insects. (2) Female *Libellulæ* and flies with bright metallic colours may often be noticed reposing on plants in the sunshine, "attracting ever and anon the attention of some passing male, who, staying his course, remains for a while, as seized with an ecstasy, suspended over their charms like a hawk marking his quarry, and seeming as if dazed by the glow of pigment beneath him. This is very characteristic of the *Libellulæ* and *Syriphidæ*." In other insects it is the males which have the gorgeous colours. (3) The aërial dances of certain *Diptera*, *Lepidoptera*, *Neuroptera*, &c., are said to be means favouring copulation. The males of some *Neuroptera* dance and collect, and when joined by their attracted females they pair. (4) Stridulation or instrumental music is a characteristic phenomenon in many insects. "The musical organs sexually common in most beetles, butterflies, and moths, as in a grasshopper genus, assume generally masculine differentiation in the *Orthoptera*, indicating dermal alteration and induration; they are either duplicate, paired, and similarly situate as regards the bodies' median line, or their development is single, as the alar organ of leaf-crickets, or quasi unique, as in the family of bugs, and the longicorn beetles. Reciprocating stimulatory friction of articulate parts to

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* The lamina of the sternal band.

† *Argynnis, Zygnæna, Melitæa.*

express emotion postulates adaptive acquisition, consequent on assumed integumental tendency under attrition to determine a smooth undulatory surface, and propagation by hereditary transmission; a rudimentary structure of this description exists in the Stag Beetle at the inferior and posterior extremity of the head; and whenever a number or group of insects is capable of music, we may establish a degradation of the organs almost invariably in mute individuals of the opposite sex, or in other members of the genus or family. Practically, the microscope establishes the essential constituent, the file (lima), to be a dermal or skin excrescence, with a systematic exaggeration or coalescence of external callosities, wrinkles, tubercles, or a protrusion of the spiral thread of the wing-veins or other tracheal organ. Theoretically, this active or passive source of sonorous vibration is a variously-placed more or less *f*-shaped tumour, provided with denticulations more or less regular, which are vibrated and sounded diagonally over a narrow raised callosity or ridge, on the chitinous integument or modified alar vein. These latter, constituting the passive or active clasping organ, assume the function of a violin bow or plectrum." Many of the musical sounds emitted by insects are said to express fear, anger, and "the more complex emotions of love and rivalry, causing, at certain seasons, the music to assume the character of a stimulus to reproduction and migration."

"The action of stridulation with the majority of beetles and one of the bee group is a more or less rapid protrusion and contraction of the abdominal segments, a respiratory movement which we shall show results from tracheal disposition in the *Insecta*. In some moths and grasshoppers, music is implicated with a bladdery inflation of the skin; but in other insects it is not directly dependent on respiration. With some the action is a sharp nid-nodding, performed by the elevator and depressor muscles of the prothorax or head. Many butterflies and the crickets produce their music by wing friction, resulting from a rapid movement of the extensor and deflexor muscles; and the grasshoppers to the same end employ the subtile elevator and depressor muscles of their agile leaping legs."

The following table gives the orders of the *Insecta* which possess the power of emitting musical sounds:—

	Sexes, &c.
Certain genera of the *Coleoptera* . .	both sexes stridulate
" " " *Orthoptera* . .	male stridulates, the female is mute
" " " *Hemiptera* (*Heteroptera*) .	both sexes stridulate
" " " *Hemiptera** (*Homoptera*) .	vocal music
" " " *Hymenoptera* . .	both sexes stridulate
" " " *Lepidoptera* . .	both sexes stridulate
" " " *Diptera* (?) . .	male stridulates (?)

Many sounds emitted by insects are certainly not musical to the human ear; nevertheless, as the latter is only capable of appreciating sonorous vibrations within narrow limits, the sounds produced by the *Insecta* may be musical to them; at any rate these sounds have their uses, or the organs which produce them would not be so well developed as they are in the *Insecta*. If many of us are incapable of appreciating *insect* music, the ancients, and especially the Greeks, appear to have regarded it with feelings of great satisfaction; and the *Cicada* is often referred to by certain Greek poets. Anacreon, for instance, has devoted an ode to singing the happiness of this insect. An element of this happiness, according to Zenachus, is, that the *Cicadæ* † "all have voiceless wives," an opinion which will probably find supporters in the present day.

Besides stridulation, many insects produce sounds by means of their wings (wing-beating), and stigmata, spiracles,

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* Various *Cicadæ*.

† For a full description of these insects, see Buckton's *Monograph of the British Cicadæ or Tettigidæ*.

or "breathing-slits." These sounds are said to give rise to various emotions—fear, anger, and love; consequently the musical sounds produced by "wing-beating" and the "vocal organs" are material agents in the reproduction of many *Insecta;* for it should be borne in mind that those females which are mute always "alight near"* the musical males, and many insects (of either sex) know the particular notes of their kind.†

From what has been said in the last few pages, it will be seen that odours, colours, dances, and music are important agents in bringing about *sexual* reproduction in many orders and genera of the *Insecta.*

We now consider the subject of parthenogenesis or virginal reproduction, which occurs in certain insects. In *Chermes abietis* and *Coccus hesperidum,* the females produce ova which give rise only to females, for no males have been discovered. In the *Aphidæ* both sexes are developed in the autumn; these copulate, when the females lay eggs, which are hatched in the following spring. But instead of producing individuals of both sexes, these eggs give rise only to female insects, which produce living young without any congress with the male; the brood thus brought forth again produces living young in the same manner, and this goes on throughout the whole summer, without the appearance of a single male insect. In the autumn again, male and female individuals are produced, the latter lay eggs which are to continue the species until the following summer. The production of parthenogenetic females has no definite limit, but is regulated to a certain extent by temperature and food supply. To retain the parthenogenetic function, the *Aphidæ* require warmth and a plentiful supply of food; for on the failure of either of these conditions the parthenogenetic females give rise to both males and females. The genital organ of a

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* Darwin's *Descent of Man,* vol. I, chap. 10.

† For further information, see Swinton's *Insect Variety,* pp. 102–229; and Von Siebold's *Invertebrata,* p. 406.

parthenogenetic or viviparous female is different from the oviparous form; for in the former the spermathecæ and colleterial glands are entirely absent, whereas these organs are present in the latter.*

"The unimpregnated, apterous, caterpillar-like females of the Lepidopterous genera *Psyche* and *Solenobia*, lay eggs out of which only females issue. The males occur but rarely and locally, and, from the impregnated eggs, males and females issue in about equal numbers." Among ants, wasps, and humble-bees, the ovaries of the neuters often contain ova; and in the two last-mentioned insects these ova give rise to young (sex ?).

In *Polistes gallica* the so-called neuters (♀) lay ova, which develop only male insects; and the unimpregnated females of *Nematus ventricosus* lay ova which give rise to males.†

Parthenogenesis among hive-bees is an established fact; the young unwedded queen-bee lays ova profusely, but all of them give rise to males or drones. The impregnated ova, however, give rise to females, which become either queens or neuters, according to the supply of food given to them. If a queen-bee dies, the inmates of the hive feed a selected female larva on "chyle-food," elaborated in the so-called chyle-stomach of the nurses, until it assumes the pupal change, from which it emerges a perfect female. The future worker or neuter is weaned on the fourth day, and fed henceforth on honey and digested pollen, with the result that its ovaries are rudimentary and sterile, while its further genital structure renders it incapable of mating. The fecundation of the queen-bee takes place within a few days of her quitting the cell, and lasts for life; the millions of spermatozoa dis-

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* See Prof. Huxley's paper in *Transactions of the Linnean Society*, 1857; Balbiani's paper in *Annales des Sciences Naturelles*, 1869–72; and Von Siebold's *Anatomy of the Invertebrata.*

† Parthenogenetic females which produce male young are termed arrentokous, while those which produce female young are termed thelytokous.

charged by the males are retained in the spermatheca of the queen-bee, and they only escape one by one to fertilise each ovum as it is laid.

Insects in their most complete character pass through four stages of existence—the ovum, the larva, the pupa, and the imago. In none of these, except the larval stage, does the insect increase in size. Some insects (*Aptera*) pass only three stages—the ovum, the "younger stage," and the imago; and in others the perfect state or imago, is attained without passing through more than two. The ova of insects are usually deposited externally (this deposition in many cases being assisted by an ovipositor), but in some few cases they are hatched in the body of the parent. In the larval stage, the insect moults several times, and after each ecdysis attaining a sudden and rapid increase in size. The larva does not always take the form of a grub or maggot; for in the *Aptera*, *Hemiptera*, and *Orthoptera*, it assumes a good deal of the appearance of the perfect insect. In this imperfect metamorphosis it changes its skin as the maggots do, and it does not assume a different form for the pupal stage. In the *Diptera*, *Hymenoptera*, *Neuroptera*, *Lepidoptera*, and *Coleoptera*, the larvæ, on their last change of skin, assume the pupal stage, in which they remain dormant until the last change takes place, when they come out as perfect insects. In some cases the pupæ remain on or in the earth; while in others, cocoons or cases are made by the larvæ in which they pass the pupal stage.

In concluding our remarks concerning the modes of reproduction and development in the *Insecta*, it may be stated that a very full account of the genital organs and their countless modifications in the various orders, genera, &c., are given in Von Siebold's *Anatomy of the Invertebrata*,* to which the reader is referred.

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* This is one of the best books on the subject ever written, and is still indispensable to the biologist.

THE ARACHNIDA.

In the *Pentastomida*, the ovary of the female is a large sac-like organ, with oviducts which pass off from its anterior end. The oviducts terminate in an aperture situated near the anus. The ova are developed in the ovary. The testis of the male is situated on the ventral side of the intestine. It is provided with two vasa deferentia, which pass in an anterior direction, and terminate in two dilatations, which contain long, chitinous penes (*i.e.*, a penis in each dilatation). These animals are parasitic, and the parasitism is almost similar to that of the *Cestoidea*—*e.g.*, *Pentastomum denticulatum*, which is sexless, inhabits the liver of rabbits and hares; but in the sexual state this parasite, known as *Pentastomum tænioides*, infests the nasal cavities of wolves and dogs.

In the *Arctisca* or *Tardigrada*, the sexes are not distinct, for these microscopic animals are hermaphrodites. The ovary is a sac-like organ, situated on the posterior half of the digestive canal, and opens into the cloaca, which is a dilatation of the rectum. The ova of *Emydium*, *Milnesium*, and *Macrobiotus ursellus* are invested by a chorion, and they are deposited in an ephippium, which is in reality the cuticle of the parent. The vitellus undergoes complete segmentation, but there is no metamorphosis.*

The *Pycnogonida* are diœcious, and "the testes and ovaria are lodged in the legs and open upon their basal joints. The embryo emerges from the egg as a larva provided with a rostrum, and with three pairs of appendages, which represent the short anterior three pairs in the adult. (A. Dohrn.) The four pairs of great limbs of the adult are produced by outgrowths from a subsequent posterior elongation of the body."

In the *Acarina*, the sexes are distinct. The male organs are formed on distinct types. The testes of *Ixodes*, for

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* See Kaufmann's paper in *Zeitschrift für Wiss. Zoologie*, 1851.

instance, consist of a group of five pairs of follicles which unite in the abdomen. There are two vasa deferentia which terminate in the base of the so-called chin-like process. The male introduces this process, together with the cheliceræ, into the vagina of the female during copulation. In *Trombidium*, the testis consists of twenty follicles attached to a vas deferens which opens between the posterior legs. Although there are twenty follicles comprising the testis of *Trombidium*, that of *Gamasus* has only two; but each of these has its own vas deferens. Many *Acarina* (*e.g.*, *Oribates*, *Bdella*, *Gamasus*) possess a penis, which is situated in a similar position to that of the vulva of the females. As accessory organs of reproduction, some of the legs are used by the males to retain the females during coition. The female organ consists of a pair of ovaries, whose ducts open in a common vulva situated, as a rule, in the middle of the abdomen on the ventral side of the body. In *Gamasus* and *Ixodes*, the genital aperture is situated on the thorax. The two oviducts of *Ixodes ricinus* open into a pyriform uterus, whose neck, according to Von Siebold, communicates laterally with a large cæcum coming from the vulva. The cæcum is a receptacle for the spermatic fluid during copulation; which, after the act, flows into the uterus and oviducts. This cæcum is also in connection with two small glands, filled with transparent cells, which secrete a substance for enveloping the ova.

The oviduct of many *Acarina* opens into a protractile ovipositor—an organ used in depositing the ova under the epidermis of animals or plants. Most of the *Acarina* are oviparous, but the *Oribatidæ* are viviparous. (Dujardin.) There is no metamorphosis in these animals, except in *Hydrachna* and *Trombidium*. In the latter genus, "the hexapod larvæ are attached to flies, grasshoppers, plant-lice, and various other terrestrial insects."

In the *Araneina* the sexes are distinct. The testis of the male consists of two long cæca situated between the so-called "hepatic" lobes; and from them lead two vasa deferentia which terminate in an aperture situated at the base of the abdomen. There is no penis, for these animals use their palpi * to introduce the spermatophores into the vulva of the female. The female organ consists of two ovaries, situated (in the female) in the same position as the testis in the male. They open by two oviducts into a vagina situated between the pulmonary sacs; and the vagina opens externally "after having previously received the excretory ducts of the two contiguous receptacula seminis. The females surround their eggs in groups, with a web." The *Araneina* † are oviparous and, according to Claparède, there is no metamorphosis.

As already stated, the male spider applies his palpi containing spermatophores to the genital apertures of the female; this is due to the fact that the female spider is prone to slay and devour the male. "The young and inexperienced male, always the smallest and weakest of the sexes, has been known to fall a victim, and pay the forfeit of his life for his too rash proposals. The more practised suitor advances with many precautions, carefully feels about with his long legs, his outstretched palpi being much agitated; he announcès his approach by vibrating the outer border of the web of the female, who answers the signal, and indicates acquiescence by raising her fore-feet from the web, when the male rapidly approaches; his palpi are extended to their utmost, and a drop of clear liquid exudes from the tip of each clavate end, where it remains attached, the tips themselves immediately coming in contact with a transverse fleshy kind of teat or tubercle protruded by the female from the base of the under side of the abdomen. After consummation, the male is sometimes obliged to save himself by a precipitate retreat: for the ordinary savage instincts of the female, '*etiam in*

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* The palpi take up the spermatophores from the genital aperture.

† Concerning the development of the *Araneina*, see Kamakichi Kishinouye's paper in *Journal of College of Science, Imperial University of Japan* (Teikoku Daigaku), vol. 4.

amoribus sæva,' are apt to return, and she has been known to sacrifice and devour her too long tarrying or dallying spouse." *

In the *Arthrogastra* the sexes are distinct. There are three (?) ovaries consisting of many tubules united by transverse anastomoses; and two oviducts which unite in a short vagina opening near the base of the abdomen. According to Meckel, the oviducts dilate into a receptaculum seminis before uniting with the vagina. The testes terminate in two vasa deferentia, which unite before opening at the genital aperture, the latter being situated at the base of the abdomen. Just before the vasa deferentia unite, they receive two long and two short cæca; these organs have the function of vesiculæ seminales. There is a rudimentary penis, in the form of a small papilla which projects out of the genital aperture.† Unlike the *Araneina*, the palpi of the *Arthrogastra* take no part in coition. The *Arthrogastra* are viviparous, the embryo being developed in the ovaries; and in *Scorpio* there is only a partial segmentation of the vitellus, but in *Chelifer* and *Obisium* the segmentation is complete. In the *Arthrogastra* there is no metamorphosis.‡

THE CRUSTACEA.

Among the *Crustacea* there are hermaphrodite as well as diœcious animals.

In the *Ostracoda*, the ovaries are situated in "the valves of the carapace, and terminate in oviducts, which open by distinct apertures in front of the caudal appendage. Immediately anterior to them are the openings of two horny

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* Sir Richard Owen's *Comparative Anatomy and Physiology of the Invertebrate Animals* (2nd ed.), p. 462.

† Like the genital organs of the *Araneina*, those of the *Arthrogastra* are situated between the so-called "hepatic" lobes.

‡ Concerning the group of marine spiders (*Pycnogonidea*), see *Den Norske Nordhavs-Expedition* [xx] by Dr. G. O. Sars; and Dr. T. H. Morgan's *Embryology and Phylogeny of the Pycnogonids* (1891). These animals do not belong to the *Arachnida* or to the *Crustacea*; but they, along with the *Arachnida* and *Crustacea*, have come down the stream of evolution in parallel lines.

canals, called vaginæ by Zenker, each of which is continued into a long convoluted transparent tube, and eventually terminates in a large vesicle, the spermatheca, in which the spermatozoa of the male are received. In the males, the antennæ, the second maxillæ, or some of the thoracic limbs, are modified in such a manner as to enable them to seize and hold the females. The testes are elongated cæca in *Cypris*, globular vesicles in *Cythere*, and communicate with a long vas deferens, which opens into the copulatory apparatus." (Huxley.) The development of *Cypris* (taken as a type of the *Ostracoda*) consists of a complicated metamorphosis, but begins with a Nauplius larva, which is furnished with a bivalve shell.

In the *Branchiopoda* the sexes are distinct, and sexual reproduction occurs; but in *Apus*, *Daphnia*, and other genera, parthenogenesis occurs, along with sexual reproduction. In *Limnadia gigas* no males are known to exist.

The *Cirripedia* are, as a rule, hermaphrodites. The ovaries are situated in the peduncle; and the oviducts pass into the body and open on the basal joint of the first pair of cirri. The testis consists of numerous ramified follicles, which are united to two long vasa deferentia; the latter unite, and then pass into the penis. The penis is situated in, and opens at, the extremity of the tail. The tail can be used as a copulatory organ, being brought into contact with the aperture of the oviducts. Self-impregnation may take place in the *Cirripedia*. It was Goodsir * who first proved that all these animals were not hermaphrodites, for in *Balanus balænoides* the sexes are distinct. Darwin † proved that *Scalpellum* and *Ibla* are both diœcious and hermaphrodite *Cirripedia*. The males of *Ibla* lie within the sac of the female; as these males are supernumeraries, Darwin termed them complemental males.

After impregnation the segmentation of the vitellus is

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* *Edinburgh New Philosophical Journal*, 1843.

† *Nature*, 1873, p. 431.

complete, "and the embryo attains to its earliest larval condition within the egg." *

In the *Amphipoda* and *Isopoda*, the male organ consists of a testis, which opens on the first abdominal somite. There are either one or two pairs of penes. The female organ consists of two ovarian tubes; and the ducts open on the ventral side of "the antepenultimate thoracic somite or on the bases of the limbs of this somite." The ova, after being laid, are deposited in an incubating pouch or chamber, situated "beneath the thorax, enclosed by the oostegites of the thoracic appendages." No true metamorphosis takes place, except in the young of certain parasitic forms. The vitellus in some forms undergoes complete segmentation, whereas in others it is only partial.

In the *Stomapoda* the sexes are distinct. The testes of the male consist of ramified glands, from which pass off two vasa deferentia, which terminate in penes projecting at the base of the last pair of feet. The ovaries consist also of ramified glands, situated in the lateral portions of the posterior abdominal segments. These glands are united in a long tube, which envelopes the alimentary canal. "The portion of the ovary, contained in the three segments to which are attached the ambulatory feet, sends towards the ventral surface three branches, which join, upon the median line beneath the abdominal cord, with those of the opposite side, and form, in the middle of each of these three segments, a round sinus. These sinuses are connected by longitudinal anastomoses, and the anterior one is prolonged into a common papillary vulva, situated in the middle of the first abdominal segment, beneath a horny process." (Von Siebold.)

The genital organs of the *Anomoura* and *Brachyura*, differ so little in structure from those of the *Macroura*, that we describe only those of the latter order, with the addition of a few general remarks on the first two mentioned orders.

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* For further information see Claus' *Grundzünge der Zoologie;* and Darwin's *Monograph of the Cirripedia*, 2 vols., 1851–4.

As a type of the *Macroura*, we describe in detail the genital organs of *Astacus*. The sexes are distinct; and in external form the testis and ovary have each the outline of a gland composed of three lobes (Fig. 77). They also occupy a similar position in the body—viz., behind the stomach and below the heart. There are two vasa deferentia which are united, one on each side of the junction of the three lobes of the testis. These ducts are long and coiled, and terminate in apertures, situated on the coxopodites of the fourth pair of ambulatory limbs.* Each lobe of the testis is composed of small cæca in which the spermatozoa (see Fig. 76, *e*) are developed. The spermatozoa are united into masses, which become invested by a fine membrane secreted by the cells of the vasa deferentia (Fig. 77, *d*); thus forming the spermatophores. The ovary is composed of three large cæca, and the ova are developed in this organ. The oviducts are short tubes, which open on the coxopodites of the second pair of ambulatory limbs. The internal walls of the ovary are lined with epithelial, nucleated

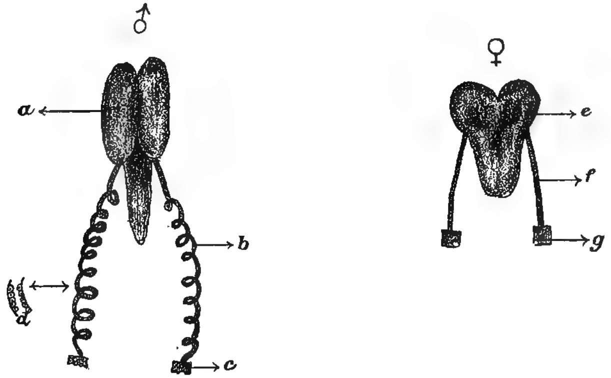

FIG. 77.—REPRODUCTIVE ORGANS OF ASTACUS.

a = testis or spermarium. *b* = vas deferens. *c* = coxopodite of fourth ambulatory limb. *d* = cells of vas deferens which secrete the spermatophores. *e* = ovary. *f* = oviduct. *g* = coxopodite of second ambulatory limb.

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* In the land crabs the male genital aperture is situated on the last segment of the body.

cells, which give rise to ovisacs. (See Fig. 76, *g*). An ovisac consists of a mass of cells; a central cell, however, grows until it forms an ovum (containing a germinal vesicle and spot, vitellus, and vitelline membrane). The ovisac ultimately bursts, liberating the ovum, which falls into the cavity of the ovary. It then passes down the oviduct to the exterior, where it becomes attached by a viscous matter (covering the vitelline membrane) to one of the swimmerets. The viscous matter hardens, and consequently encloses the egg in a tough case, which is suspended from the swimmeret by a peduncle, which is in reality a prolongation of the substance of the case. The ova are fecundated while in the female. The fecundated ovum undergoes partial segmentation of the vitellus; and after the formation of a short, round, primitive streak, the limbs develop, and the embryo passes through the *Nauplius* stage. After this the embryo develops further, and is hatched in the general form of the adult, the *Zoœa* or *Copepod* stage being rapidly assumed and discarded during the embryonic existence. After moulting, the abdominal feet are developed, and the young *Astacus* becomes altogether similar to the adult form.

In the *Macroura* and *Paguridœ*, the male genital apertures are "surrounded by a soft sphincter, without any trace of a penis, but out of which the ductus ejaculatorius is perhaps protruded during copulation. But with the *Brachyura* and short-tailed *Anomoura*, on the contrary, there are two longer or shorter tubular penes, always covered by the tail, which is pressed against the abdomen. In many *Decapoda*, the two feet of the first caudal segment are transformed into pedicellated processes (secondary penes), the extremity of which is sometimes grooved. In some short-tailed *Anomoura*, the feet of the second post-abdominal pair take part also in the act of copulation, and, for this purpose, are prolonged into stalk-line organs." *

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* The forms assumed by the spermatozoa of *Pagurus*, *Pisa*, and *Grapsus* are illustrated in Fig. 76, p. 412.

THE POLYZOA.

Reproduction in these animals takes place by gemmation, parthenogenesis, and gamogenesis. Where gemmation occurs, the buds produced usually remain adherent to the stock; but in *Pedicellina* and *Loxosoma*, they become separated. Gemmation occurs throughout the whole colony of polypides. In the fresh water *Polyzoa*, a kind of parthenogenesis is the mode of reproduction. In these animals, gemmules, statoblasts, or unfecundated ova, are developed in the funiculus. A statoblast is usually biconvex in form, covered by two chitinous shells, and gives rise to an animal which, when hatched, resembles the adult. It soon becomes fixed and produces (by gemmation) a new colony of organisms. Sexual reproduction or gamogenesis always takes place in the *Polyzoa*. As a rule they are usually hermaphrodites. The male and female organs are groups of cells, the former being developed either in the upper portion of the funiculus or at its base; and the latter on the internal surface of the anterior part of the endocyst. The ova fall into the perivisceral cavity, where they are fecundated by the spermatozoa, which are also present in the same cavity. The fecundated ovum (in marine *Polyzoa*) passes into the ovicell—a dilatation of the body wall. The ovum becomes segmented in the ovicell, forming a morula, and subsequently a blastula. Finally, the embryo is hatched as a ciliated free swimming larva (Trochosphere). After swimming about for some time, the larva becomes stationary and develops a tentacular crown and "cell." New zooids are then produced by gemmation, and so a new colony is gradually formed.

THE BRACHIOPODA.

Most of these animals are diœcious; and the genital organs are situated in the body cavity or its prolongations. They consist of paired, glandular bands; and the spermatozoa and ova pass into the body or perivisceral cavity, and from thence they pass to the pallial chamber by the excretory ducts. After fecundation the ovum becomes completely segmented, and a free swimming gastrula is formed by invagination. After this a free swimming, segmented, ciliated larva, like that of the *Annelida*, is produced. This larva is composed of three segments—the cephalic, thoracic, and caudal; it ultimately becomes fixed, and the shell develops from the thoracic segment.

THE MOLLUSCA.

In the *Lamellibranchiata*, the sexes are usually distinct, but these animals are sometimes hermaphrodites.* The genital organs in both sexes are somewhat similar to each other. They are paired, lobed, or racemose glands; and occupy the upper portion of the foot. Taking *Anodonta* as a typical example of the *Lamellibranchiata*, these glands vary in size with the season. In the spring and winter, they are larger than at any other season. The genital ducts (of both sexes) open into the cloaca. The testes are white or yellow (due to the spermatic fluid), and the ovaries are red (due to the colour of the ova). The fecundation of the ovum takes place in the branchial chamber of the female; it then passes into the branchial spaces of the external gills. The segmentation is unequal, and the embryo passes through a morula (blastomeres), a gastrula, and a free-swimming, ciliated, or veligerous condition.

The *Gasteropoda* are either diœcious or hermaphrodite.† As a typical example of the *Pulmogasteropoda*, we describe the reproductive organs of *Helix*. This animal is hermaphrodite; and its genital apparatus consists of a single gland—the ovotestis (Fig. 78) composed of branched tubules. In this

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* *Cyclas*, *Cardium* (some species), *Pecten* (some species), *Ostrœa*, *Pandora*, &c.

† The *Scaphopoda* and *Heteropoda* are diœcious, while the *Polyplacophora* are hermaphrodites.

gland the spermatozoa and ova are developed, but never at the same time. In terrestrial snails the maturity of the spermatozoa precedes that of the ova; the object of this arrangement being to prevent self-impregnation. The narrow, common, hermaphrodite duct leads from the ovotestis, but soon dilates. In this dilated portion it receives the secretion of a large albumin gland. Beyond this point it divides into two ducts—one for the spermatic fluid, and the other for the ova. The oviduct passes into the vagina, while the narrower branch of the common duct is continued into a separate vas deferens, the extremity of which leads into a long penis.

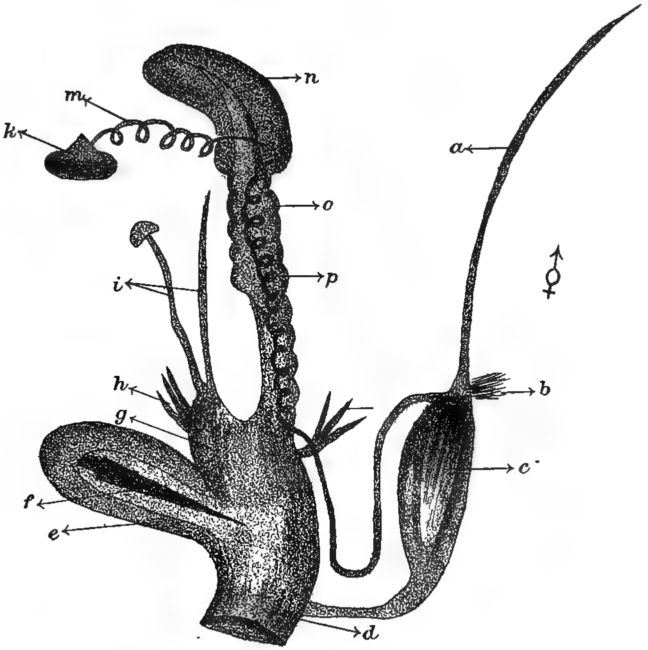

FIG. 78.—REPRODUCTIVE ORGANS OF HELIX.

a = flag or sperm gland. *b* = retractor muscle of penis. *c* = penis.
d = genital vestibule. *e* = dart sac. *f* = dart. *g* = vagina.
h = mucous glands. *i* = spermatheca. *k* = ovotestis. *mo* = hermaphrodite duct. *n* = albumin gland. *p* = prostate.

Projecting from the vas deferens is the flag or flagellum. The vagina and the male aperture (at the end of the penis) open into a common cloaca, which bears filamentous glandular appendages or mucous glands. These secrete albumin. The muscular dart-sac (which contains a "calcareous" or "chitinous" dart or rod *) also opens into the common cloaca. In connection with the female genital aperture, there is a receptaculum seminis or spermatheca. Although *Helix* is hermaphrodite, cross-fertilisation takes place. When two individuals copulate, the dart or spiculum amoris is protruded; and no doubt acts as a stimulating organ. The dart is usually broken up during copulation, but is afterwards replaced. During coition, the semen of one individual, after being discharged, is stored in the spermatheca of the other individual. The ova are impregnated in the duct, and are invested in albumin, which is enclosed within a calcified chorion. The development is direct, and the young is hatched in the form of the adult.

"The *Branchiogasteropoda* fall into two distinct series, of which the one is hermaphrodite (the genital gland being an ovotestis), and invariably opisthobranchiate; while the other is unisexual, and usually prosobranchiate."

In some genera the penis is not developed (*e.g.*, *Murchisonia*, *Pleurotomaria*), while in others the organ is developed (*e.g.*, *Natica*, *Turritella*, *Voluta*, *Cypræa*).

The *Pteropoda* are hermaphrodites, provided with an ovotestis, which develops spermatozoa and ova. As in *Helix* these two generative elements are not mature at the same time. The ovotestis has a single duct, the termination of which may be provided with a receptaculum seminis, and connected with a penis. Cross-fertilisation takes place, and the ovum gives rise to young, provided with a rudimentary shell, velum, and probably an operculum. In some forms (*Hyalæa*) the shell is retained, while in others (*Clio*) it disappears.

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* In some species the dart contains silica.

The *Cephalopoda* are diœcious, and the genital organs are unlike those of other *Mollusca*. "They consist, in both sexes, of lamellar or branched organs, the cellular contents of which are metamorphosed into ova and spermatozoa, and which are attached to one point or line of the wall of a chamber, which communicates with the pallial cavity by two symmetrically disposed oviducts, in the females of some species; but in most female and almost all male Cephalopods it has only one duct, the termination of which is situated on the left side, but may be near the middle line (male *Nautilus*), or even on the right side (female *Nautilus*)."

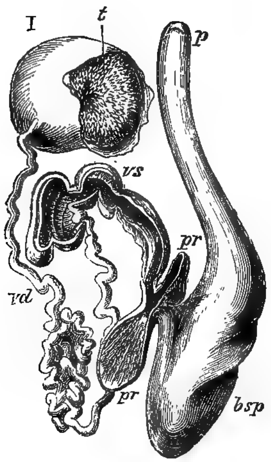

FIG. 79.

MALE REPRODUCTIVE ORGANS OF SEPIA.

(*After* DR. A. VON MOJSISOVICS.)

t = testis. *p* = penis. *vd* = vas deferens. *pr* = prostate.
bsp = receptacle of spermatophores.
vs = vesicula seminalis.

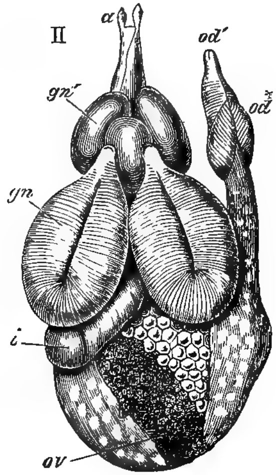

FIG. 80.

FEMALE REPRODUCTIVE ORGANS OF SEPIA.

(*After* MILNE-EDWARDS.)

a = anus. *ov* = ovary. *gn* = nidamental glands. *gn′* = accessory glands. *od* = oviducal gland.
od′ = oviducal aperture. *i* = intestine.

In the male *Sepia* (Fig. 79) the genital organs consist of a well-developed testis, a vas deferens, which passes into a vesicula seminalis, at the termination of which is the prostate. The prostate forms the spermatophores, which are discharged into a receptacle (Fig. 79). The receptacle or sperm-sac then leads into a muscular penis, at whose extremity is situated the genital aperture. "The projection of the sperm-sac occurs at the moment when, during coition, the spermatophores pass from the penis of the male into the sac of the mouth of the female. A true intromission of the penis into the female genital opening appears impossible in these animals, so that coition consists only in a simple juxtaposition of the genital organs." (Von Siebold.)

In the female *Sepia* (Fig. 80) the genital organ consists of an ovary, with an oviduct which opens near the anus. The oviduct presents an enlargement called the oviducal gland. In addition to these, there are nidamental and accessory glands. These glands secrete a substance which invests the ova as they pass from the oviduct, and which serves to glue them to foreign bodies. The fecundated ovum undergoes partial segmentation; but for the further development of the embryo, the reader is referred to Professor Lankester's paper in the *Quarterly Journal of Microscopical Science*, 1875; Grenacher's paper in the *Zeitschrift für Wissenschaftliche Zoologie*, 1876; and Mojsisovics's *Cephalopoden der Mediterranen.*

THE TUNICATA.

These animals are hermaphrodites; but cross-fertilisation takes place as the spermatozoa and ova reach maturity at different times. The testes and ovaries are racemose glands, which usually lie among the viscera in the hinder portion of the body. In many simple Ascidians, however, these organs are situated in the lateral walls of the atrium, into which their ducts* open more or less in the vicinity of the anus. The impregnated ovum becomes completely segmented, and passes through the morula and gastrula stages. Afterwards

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* The ovaries and testes of *Appendicularia* are devoid of ducts.

a free-swimming tailed larva is developed. Just before reaching maturity, the larva attaches itself by means of papillæ, and undergoes a series of changes, of which the following are the most important: The tail aborts, the muscles and notochordal sheath degenerate, and the notochordal axis contracts. The nervous system and organs of sense degenerate, and the cavity in the nerve-cord and cerebral ganglion disappear. The pharynx increases largely, and the branchial slits become visible. After this the adult state is reached.*

At this point we give a diagram (Fig. 81) which indicates roughly the evolution of the *Invertebrata.*

CONCLUDING REMARKS.

This chapter has its moral—that *like always begets like.* It does not matter by what mode of reproduction it has been produced, the offspring is always of the same kind as the parent. It appears that transformation or pleomorphism does not exist in the animal kingdom. The life-cycles of the lowest as well as the highest animals repeat themselves according to a well-known law. "To one who has fully comprehended the meaning and the operation of the Darwinian law, it will be at once apparent that there must be error somewhere in the matter of pleomorphism." How can *Bacillus subtilis* be transformed into *Bacillus anthracis;*† or an amœba into a gregarina by the experimentalist? "If the law of actual variation," says Dr. Dallinger, "with all that is involved in the survival of the fittest, *could be so readily brought into complete operation, and yield so pronounced a result,* where would be the

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* In some of the *Tunicata*, the development of the embryo takes place within the parent, and there is a *placenta.* See also Giard's papers in *Revue Scientifique*, 1874; *Comptes Rendus*, 1874–5; *Archives de Zoologie Expérimentale*, 1872.

† See Dr. Griffiths' book: *Researches on Micro-Organisms*, p. 41 (Baillière & Co.).

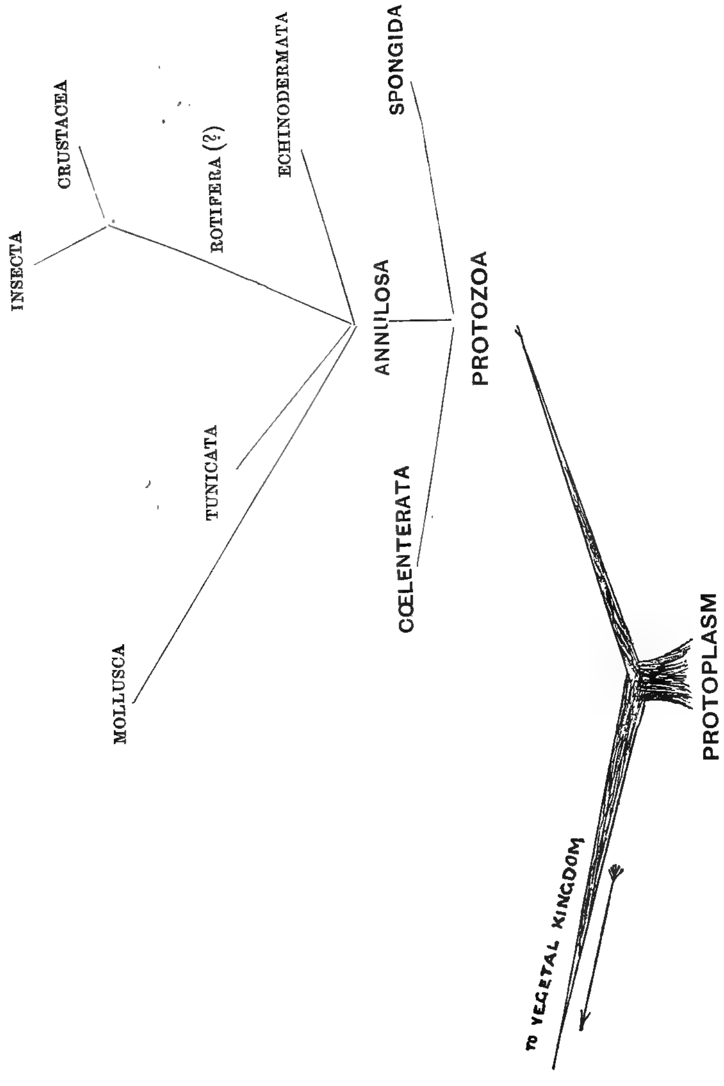

Fig. 81.—A Rough Diagram indicating the Evolution of the Invertebrata.

stability of the organic world? Nothing would be at one stay.

"There could be no permanence in anything living. The philosophy of modern biology is that the most complex forms of living creatures have derived their splendid complexity and adaptations from the *slow and majestically progressive variation and survival from the simpler and the simplest forms.* If, then, the simplest forms of the present and the past were not governed by accurate and unchanging laws of life, how did the rigid certainties that manifestly and admittedly govern the more complex and the most complex come into play? If our modern philosophy of biology be, as we know it is, true, then it must be very strong evidence indeed, that would lead us to conclude that the laws seen to be universal break down, and cease accurately to operate, where the objects become microscopic,* and our knowledge of them is by no means full, exhaustive, and clear. Moreover, looked at in the abstract, it is a little difficult to conceive why there should be more uncertainty about the life-processes of a group of lowly living things, than there should be about the behaviour, in reaction, of a given group of molecules. The triumph of modern knowledge is a knowledge—which nothing can shake—that Nature's processes are immutable. The stability of her processes, the precision of her action, and the universality of her laws, are the basis of all science, to which *biology* forms no exception. Once establish, by clear and unmistakable demonstration, the life-history of an organism, and truly some change must have come over Nature as a whole, if that life-history be not the same to-morrow as to-day; and the same to one observer, under the same conditions, as to another.

"No amount of paradox would induce us to believe that the combining proportions of hydrogen and oxygen had altered in a specified experimenter's hands in synthetically

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* Büchner, Sattler, Grawitz, and others state that certain microbes are capable of being transformed into other microbes.

producing water. We believe that the melting-point of platinum and the freezing-point of mercury are the same as they were a hundred years ago, and as they will be a hundred years hence. Now carefully remember that, so far as we can see at all, it must be so with life. Life inheres in protoplasm; but just as one cannot get *abstract* matter—that is, matter with no properties or modes of motion—so one cannot," says Dr. Dallinger, "get *abstract* protoplasm. Every piece of living protoplasm we see has a history: it is the inheritor of countless millions of years. Its properties have been determined by its history. It is the protoplasm of some definite form of life which has inherited its specific history. It can be no more false to that inheritance than an atom of oxygen can be false to its properties. All this, of course, within the lines of the great secular processes of the Darwinian law, which could not operate at all if caprice formed any part of the activities of Nature."

In addition it may be remarked that pleomorphism is entirely opposite to the Darwinian law, but abiogenesis (as already stated at the commencement of the present chapter) is not in opposition to evolution. It is one of the theories which have been brought forward to explain the origin of life in the world. Protoplasm consists of carbon, hydrogen, oxygen, nitrogen, with a little sulphur and phosphorus, and still fainter traces of other elements, combined in extreme complexity. "Given the matter which composes it, and the play of forces and energies of which that matter is the vehicle, wherein lies the difference which gives as one result non-living substance, and as another result living substance? The answer obviously is that, the ingredients being the same, the difference must lie in the mixing;" and it is this "mixing" which the scientist has to find out to explain the *origin of life*, or, before abiogenesis can be considered to be more than one of the theories which have been put forth during historic times to account for it.

APPENDIX.

I. THE COMPOSITION OF HÆMOCYANIN.

THE author* has ascertained the approximate composition of hæmocyanin (see p. 142 *et seq.*). The hæmocyanin derived from the blood of *Homarus, Sepia*, and *Cancer* respectively was submitted, after purification, to chemical analysis. The percentage composition of this important substance is very constant. In this respect it differs from hæmoglobin. We are, therefore, justified in calculating an empirical formula for hæmocyanin as follows:—

$$C_{867}H_{1363}N_{223}CuS_4O_{258}.$$

The blood of the lower, and some of the higher, Invertebrates is a watery fluid, called the hydrolymph. But in the majority of the higher Invertebrates, the blood is less watery and much richer in albuminoids; it is sometimes termed a hæmolymph.

II. INVERTEBRATE CARTILAGE.

Invertebrate cartilage is very similar, chemically and histologically, to that of the *Vertebrata*. Dr. W. D. Halliburton† has recently examined the head cartilage of *Sepia*, and the entosternite of *Limulus*. "The basis in both structures is chrondrin; there is, however, in addition, a certain proportion of chitin, in the case

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* *Comptes Rendus de l'Académie des Sciences*, tome 114, p. 496.

† *Proceedings of Royal Society*, vol. 38; and *Quart. Jour. Micro. Science*, vol. 25.

of *Limulus* 1.01, and in that of *Sepia* 1.22 per cent. These results are especially interesting, as showing that chitin is not a substance which is exclusively epiblastic in origin, but here, at least, we have it occurring in mesoblastic structures."

III. Chitin and other Substances.

Chitin.—This substance, which is frequently impregnated with salts (calcareous salts in the *Crustacea*, silica in the lingual ribbon of certain *Mollusca*), "has a very wide distribution among the *Invertebrata*. It is in the *Arthropoda* that it is found to the greatest extent; it forms the membrane of the ovum, the cuticle of the adult, with its appendages, the supporting substance in the tracheæ of insects, &c. It is also found in the *Mollusca* (jaws and odontophore); and in worms (*e.g.*, the setæ of the *Annelida*). It forms the membrane of the ova in other groups, and the cyst-wall in encysted forms of the *Protozoa*, &c."

Chitin is readily prepared by treating the shells of crabs and lobsters with HCl, so as to dissolve out the calcareous salts. It is also obtained by digesting the wings of beetles and other insects in a solution of NaHO. In both cases the chitin remains undissolved. The residue is then dissolved in strong HCl, and re-precipitated from this solution by the addition of water. This operation is repeated two or three times, when the chitin is obtained in a state of purity.

Chitin is a colourless substance, devoid of crystalline structure, and is only soluble in strong mineral acids. When *heated* with strong acids, it is decomposed into acetic acid and glucosamine:—

$$2C_{15}H_{26}N_2O_{10} + 2H_2O = 3C_2H_4O_2 + 4C_6H_{13}NO_5.$$

Conchiolin ($C_{30}H_{48}N_9O_{11}$) is the skeletin or basis of the shells of the *Gasteropoda*.

Cornein ($C_{30}H_{44}N_9O_{13}$) is the skeletin of *Gorgonia* and other corals.

Spongin is the skeletin of the *Porifera*. Its composition is unknown.

Fibrorin is the substance of which the webs of spiders are composed.

These four substances all yield leucin and glycocine on decomposition.

Hyalin is allied to chitin, and is found in the *Echinodermata* and other Invertebrates. It has the following composition:—$C = 45.3$ to 44.1; $H = 6.5$ to 6.7; $N = 5.2$ to 4.5; $O = 43$ to 44.7 per cent.

Tunicin is the carbohydrate found in the *Tunicata*, *Ophrydium*, &c. It is represented by the formula $(C_6H_{10}O_5)_n$.*

IV. THE INK-BAG OF SEPIA.

The secretion of the ink-bag (see p. 73) is used to colour the water and cover the flight of the animal. It contains from 70 to 87 per cent. of solids, of which the black or brown pigment is the chief constituent; it also contains mucin, magnesium carbonate, sodium sulphate, calcium carbonate, and sodium chloride. According to Nencki and Sieber,† the pigment contains an acid, which has been termed sepiaic acid.

It has been suggested that the ink-bag corresponds to a liver; but its secretion contains neither biliary acids nor glycogen, and it has no digestive properties.

V. WAVE-LENGTHS.

The sign λ (p. 151 *et seq.*) denotes wave-lengths. For instance, λ506 means a wave-length equal to 506 millionths of a millimetre. Sometimes the letters W.L. are used instead of λ.

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* For further information, see Gautier's *Chimie Biologique* (1892), pp. 163, 165, 188; and Halliburton's *Chemical Physiology and Pathology*.

† *Chem. Centralblatt*, 1888, p. 587.

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SUBJECT INDEX.

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ERRATA.

Page 20, line 7, *for* assimilation, *read* assimilated.
,, 86, ,, 28, *for* Some *Ascares marginatæ*, *read* Some worms (*Ascaris marginata*).
,, 289 ,, 12, *for* predominate, *read* predominates.

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