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MDCCCLXXI.

A MONOGRAPH

OF THE

GYMNOBLASTIC OR TUBULARIAN

HYDROIDS.

IN TWO PARTS.

I.—THE HYDROIDA IN GENERAL.

II.—THE GENERA AND SPECIES OF THE GYMNOBLASTEA.

BY

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LONDON:

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ROBERT HARDWICKE, 192, PICCADILLY.

MDCCCLXXI.

Freuet euch des wahren Scheins,
Euch des ernsten Spieles;
Kein Lebendiges ist ein Eins,
Immer ist's ein Vieles.

Goethe, "*Epirrhema*," *in* '*Gott und Welt*.'

PRINTED BY J. E. ADLARD,
BARTHOLOMEW CLOSE.

I Dedicate this Book

TO

GEORGE BUSK, ESQ., F.R.S., F.L.S., &c.,

WHOSE ABLE AND CONSCIENTIOUS LABOURS IN THE FIELD OF RESEARCH TO WHICH ITS PAGES ARE

DEVOTED HAVE LARGELY CONTRIBUTED TO OUR KNOWLEDGE OF HYDROID ZOOLOGY,

WHOSE VARIED ACQUISITIONS, GATHERED FROM MANY A REGION OF BIOLOGICAL SCIENCE,

HAVE EVER BEEN, WITH GENEROUS DISINTERESTEDNESS,

PLACED AT THE DISPOSAL OF ALL WHO MAY BE WILLING TO USE THEM FOR

THE ADVANCEMENT OF KNOWLEDGE,

ONE OF MY EARLIEST FRIENDS AND MOST VALUED ASSOCIATES IN SCIENTIFIC WORK.

Weybridge;

1871.

PREFACE.

THE present work contains the result of many years' study of the remarkable group of animals to whose elucidation it is devoted, a group in the investigation of which ready access to the sea has afforded me special facilities.

My object has been to work out as exhaustively as possible the general natural history of the HYDROIDA, and besides this to give a complete descriptive Zoology of the Gymnoblastic or Tubularian forms of this Order.

The work is thus divided into two parts—the first devoted to the Morphology, Physiology, Distribution, and other general considerations bearing on the entire Order of the HYDROIDA; the second, to descriptions of all the known genera and species which compose one of its most important and interesting Sub-orders—that of the *Gymnoblastea*.

A very large proportion of the observations here recorded are entirely original, while it has, moreover, been my aim, in giving an account of the observations of others, to take nothing for granted which it was possible for me to subject to personal verification. It will be seen that the amount of labour thus involved is far from slight. Indeed, it is only by constant and widely extended explorations of the coast, both within the tidal zone and in the deeper sea regions, followed up by laborious microscopic investigations, that results of any value are to be expected.

The plates have all been drawn from nature by myself, and are from the living animal. The soft parts, which constitute the chief interest in these wonderful organisms, are thus represented as they show themselves while the animal is still beneath the waters of its native seas. This is all the more important in animals which, like the gymnoblastic hydroids, retain in their dried state not a single character of value, and which even in specimens preserved in spirits lose almost all their beauty and many of their important zoological characters. The figures of the species, too, are all coloured from life, so that not only will a more adequate idea of the beauty of these creatures in their living state be thus conveyed, but greater facilities will be afforded to the practical zoologist in the comparison and determination of species. The plates, moreover, contain numerous anatomical and embryological details; and, besides the magnified drawings of each species, I have in every case given a figure of the animal in its natural size.

It was originally my intention to restrict the descriptive portion of the work to the British representatives of the group. Further consideration, however, has led me to believe that its value would be much increased by including descriptions of all the known *Gymnoblastea*, whether British or foreign. The plates, however, are necessarily confined to British species. Indeed, independently of other reasons, this course was inevitable so long as I had resolved to make all my drawings from living specimens. Full reference, however, is always given to the places where published figures of the foreign species are to be found.

The same reason has obliged me to leave a few British species unfigured, as I have hitherto failed in my attempts to obtain living specimens of them. References, however, are here, as in the case of foreign species, always made to the works in which figures of them are given.

Besides the plates, numerous woodcuts are introduced into the text. Though a few of these have already appeared in my published memoirs, they are all from original drawings of my own, and will, it is hoped, serve to render clear various points of structure which it would be difficult to make intelligible without the aid of figures.[1]

For obvious reasons it is only those species whose trophosomes have been discovered which form the subject of the descriptive portion of the present work. There are still known to zoologists a large number of hydroid medusæ which have not yet been traced to their trophosomes. Since Forbes's Monograph, published among the earlier volumes of the Ray Society, much additional matter has been accumulated regarding these beautiful organisms, and many of them have been figured with structural details in the first part of the present work. I have still many unpublished notes on them, and, though it was impossible to treat them here systematically, I cannot dismiss the hope of being yet able to supplement the present volume by another which would be devoted to the natural history of these free hydroid medusæ, whether they have been traced to their trophosomes or not.

As the descriptive portion of this Monograph is based upon the entire organism, both trophosome and gonosome affording characters equally essential in the diagnosis, I have never been contented with specimens in which the gonosome as well as the trophosome was not present. It is only in one or two cases that I have failed in

[1] The use of the blocks employed in the illustration of my "Report on the Hydroida," published in the 'Transactions of the British Association for the Advancement of Science,' has been liberally granted by the Council of that body.

procuring examples provided with their gonosomes, and that I have been obliged to confine my figures to the trophosome alone.

The additions which the last few years have made to our knowledge of hydroid morphology have necessitated the introduction of new terms. Such terms as I have found it necessary to construct have been made as far as possible etymologically significant of the ideas intended to be expressed by them, while I have endeavoured to define them with a rigidity which may allow of no ambiguity in their application. The advantages to be derived from a significant and rigidly defined terminology are great, for it not only facilitates the recording and communication of scientific truths, but it even becomes, like the symbols in algebra, a direct aid in original research.

With the view of making the terminology as perfect as possible, I have not hesitated to alter some of the terms formerly introduced by myself. Terminology differs from nomenclature in priority of use not necessarily giving a fixity of tenure; and while capricious change of terms must be deprecated, no one ought to be precluded from substituting a better term for one already in use.

The labour of the drawings, which I could entrust to no hand but my own, and the necessity of procuring in every case living specimens as the subjects of them, have caused the work to be longer in preparation than I had originally anticipated, and I cannot avoid here expressing my obligations to the Council of the Ray Society for the patience with which they have borne the delay. One advantage, however, has followed from it, for I have been thereby enabled to carry up to the present standpoint of our knowledge this exposition of a rapidly developing department of research, in which every year has been bringing out new facts and more or less modifying old views.[1]

The coasts of the British Isles have afforded me the chief fields for exploration, and my dredgings and tidal coast work have extended from the south-western extremity of Cornwall to the furthest outliers of the Shetland Isles. Some investigations, however, have been also carried on in the Mediterranean, and I have thus obtained many facts in hydroid zoology from the northern shores of the Adriatic, from the coast of Naples, and from the eastern and western Riviera.

Continental museums, wherever accessible, have been consulted. These, on the whole, are very poor in all that concerns the zoology of the HYDROIDA, and few of them possess anything beyond some dried specimens of such common species as may be casually picked up on the sea-beach.

Some, however, have repaid the trouble of consultation, and I must here express my thanks to M. Milne-Edwards and to M. Lacase Duthiers for the liberal manner in

[1] Quite recent additions to our knowledge of hydroid life render necessary some modification of the statements contained in pp. 22, 23 regarding our want of evidence of the direct development of the medusa from the egg, without the intervention of a hydriform trophosome. The reader will accordingly correct and supplement these statements by the results of later observations detailed in p. 100.

which they placed the collections of the Jardin des Plantes at my disposal, and for the opportunity thus afforded me of critically examining the authentic specimens of Lamarck, as well as other interesting hydroid collections in the museum. To Professor Stossich, of Triest, I am also indebted for an opportunity of examining the collection of hydroids in the museum of that town, one of the best collections of these animals contained in any Continental museum which I have been able to consult.

To Professor Paolo Panceri, of the University of Naples, my thanks are especially due, not only for the liberal way in which he placed in my hands specimens for investigation, but for the valuable assistance I received from him in the examination of the Neapolitan coast.

To my friend Professor Schiff, of Florence, I owe my hearty acknowledgments for aid in consulting the museum of that city, and for many other ways in which he has facilitated my researches.

To the Marquis Giacomo Doria, who, in the disinterested love of science, has devoted his time and property to the advancement of natural history, pursued, at the sacrifice of health, amid the malaria of East Indian jungles, and has thus added another laurel to those which have already made the name of Doria illustrious in the annals of the great Genoese Republic, as well as to Dr. Gestro, his assistant, and to Professor Trinchesi, of the University of Genoa, I am indebted for much kindness, and for valuable guidance to the zoological localities of the Gulf.

To Dr. Giglioli, of Florence, I owe the opportunity of inspecting an extensive collection of drawings in which he records many important observations made on hydroid planoblasts and other pelagic forms met with during the circumnavigatory voyage of the "Magenta," which he accompanied as assistant-naturalist.

Dr. Du Plessis, of Nice, who has made the hydroids of the neighbouring coast a subject of special study, and has been singularly sucessful in keeping them in a healthy state in his vivarium, kindly acted as my guide to various hydroid localities with which he had become familiar in the beautiful bay of Villafranca; while I am also under much obligation to Professor Mecznikoff, of St. Petersburgh, who happened to be at the same time residing at Villafranca, where he was engaged in researches on the lower animals of the bay, and where he communicated to me some of the important results to which he had arrived.

To Professor Van Beneden, of Louvaine, and to the late venerable Professor Sars, I am indebted for presentations of their many important memoirs, and for the communication of specimens, while my thanks are also due to Professor Agassiz and to Mr. Alexander Agassiz, as well as to Professor Kölliker and to Professor Haeckel, for copies of many valuable memoirs bearing more or less directly on hydroid zoology.

And still further, I must express my obligations to Professor Costa, of the University of Naples; to Sig. Filippo Trois, of Venice; to Professor Savi, of Pisa; to Professor Oscar Schmidt, of Gratz; to Dr. Antoine Fritsch, of Prague; to Dr.

Brauer, of Vienna; and to Dr. Marshal, of Leiden, as well as to many other continental naturalists, for friendly assistance, either by freely placing at my disposal specimens which I could not elsewhere have obtained or by otherwise aiding me in the object I had in view.

To specify here the names of our own countrymen from whom I have received assistance would be to extend this list of obligations to a much greater length than space will allow. Reference to them in other parts of the work will show that I have not been unmindful of the aid they have afforded me. I cannot, however, avoid expressing in this place my obligations to Professor Wyville Thomson, Dr. Carpenter, and Mr. J. Gwyn Jeffreys, for having placed in my hands the whole of the hydroids procured in the deep-sea dredgings of the "Porcupine" expedition; and to Mr. Busk, for allowing me the free use of his collection of hydroids obtained from various parts of the world, and affording facts of much value in the geographical distribution of the order.

The earlier sheets of the present Monograph had been already printed before the publication of Mr. Hincks's work on the British Hydroids.[1] This will account for the absence of all allusion to it in the section devoted to the history of those labours which have contributed to bring our knowledge of the HYDROIDA to its present standpoint. And yet the literature of hydroid zoology demands a special reference to this valuable work. Eminently critical, with the descriptions accurate and lucid, and with the figures abundant and expressive, it is the most complete systematic work on the HYDROIDA hitherto published. The large amount of original observations gives it a special value, and its fulness of description and illustration renders it indispensable to every student of the HYDROIDA. The delay which has occurred in the publication of the second part of the present Monograph will enable me to cite unreservedly Mr. Hincks's work, without which the synonomy and literature of many of the species here described would be very deficient.

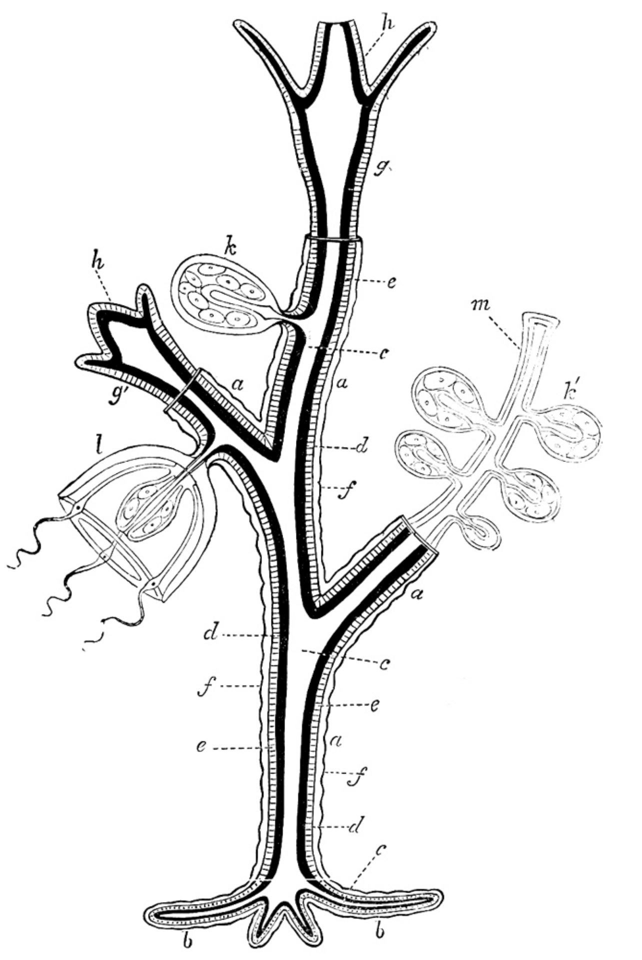
[1] 'A History of the British Hydroid Zoophytes.' By Thomas Hincks. London, Van Voorst, 1868.

GLOSSOLOGY.

Imaginary generalised Diagrams of Hydroids to illustrate the terminology.

In order better to distinguish the various parts and to render the respective limits of the trophosome and gonosome at once apparent, the endoderm and ectoderm of the gonosome are in both figures represented by simple outline, while in the trophosome the endoderm is throughout distinguished by a heavy line, the ectoderm by transverse hatching, and the perisarc by a simple wavy line.

I.



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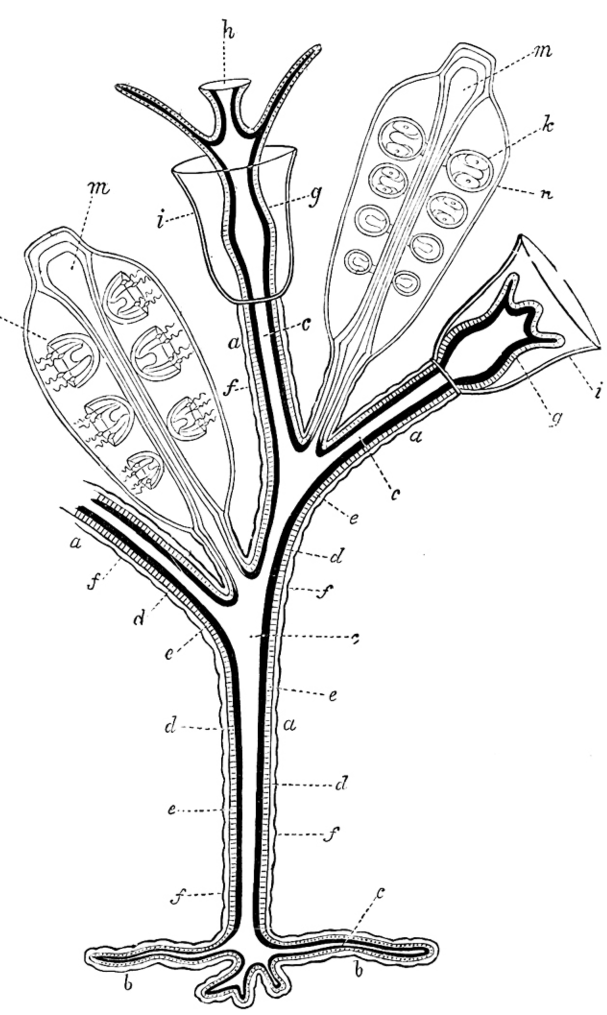

I. *Imaginary generalised Diagram of a Gymnoblastic Hydroid.*—*a, a, a, a.*—Hydrocaulus. *b, b.*—Hydrorhiza. } Hydrophyton. *c, c, c.*—Somatic cavity. *d, d, d.*—Endoderm of hydrophyton. *e, e, e.*—Ectoderm of hydrophyton. } Cœnosarc. *f, f, f.*—Perisarc. *g.*—Hydranth extended. *g'.*—Hydranth contracted. *h, h.*—Hypostome bearing the mouth at its extremity. *k.*—Sacciform gonophore (sporosac) springing from the hydrocaulus. *k'.*—Sporosac springing from a blastostyle. In *k, k'*, the spadix is seen to occupy the axis of the sporosac, and round the spadix are developed the generative elements. *l.*—Medusiform gonophore (planoblast). A manubrium occupies its axis, and in the walls of this the generative elements are directly developed. *m.*—Blastostyle.

II. *Imaginary generalised Diagram of a Calyptoblastic Hydroid.*— The letters *a* to *h* indicate the same parts as in I. *i, i.*—Hydrotheca. *k.*—Sporosac springing from a blastostyle, with the generative elements developed round a spadix which occupies the axis of the sporosac. *l.*—Planoblast springing from a blastostyle. *m, m.*—Blastostyle. *n.*—Gonangium.

TERMS APPLICABLE TO THE HYDROID COLONY IN GENERAL.

Hydrosoma (ὕδρα, hydra, mythological monster; σῶμα, body). The entire hydroid colony.

Ectoderm (ἐκτός, outside; δέρμα, skin). The more external of the two organized layers of which the body of every hydroid is composed. (Diagrams I and II, *e, e, e.*)

Endoderm (ἔνδον, within; δέρμα, skin). The more internal of the two organized layers of which the body of every hydroid is composed. (Diagrams I and II, *d, d, d.*)

Perisarc (περὶ, around; σὰρξ, flesh). The unorganized chitinous excretion by which the soft parts are to a greater or less extent invested. (Diagrams I and II, *f, f, f.*)

Zooids (ζῶον, animal; 'εἶδος, form). The more or less independent products of non-sexual reproduction; the members more or less individualized of which the hydroid colony is composed. (Diagrams I and II, *g, g', k, k', l, m.*)

Trophosome (τροφὴ, nourishment; σῶμα, body). The entire assemblage of zooids with their common connecting basis, destined for the nutrition of the colony.

Gonosome (γόνος, offspring; σῶμα, body). The entire assemblage of zooids destined for the sexual reproduction of the colony.

Thread-cells. Peculiar bodies consisting of a containing capsule and contained filament destined for urtication, and universally present as a histological element of the ectoderm. (Fig. 52, page 118.)

Palpocils (*palpo*, I feel; *cilium*, an eyelash). Microscopic, hair-like, non-vibratile processes of the ectoderm, probably organs of touch. (Fig. 48, page 112.)

Heteromorphism (ἕτερος, diverse; μορφή, form). Diversity of form among the component zooids of the colony.

Homomorphism (ὅμοιος, similar; μορφή, form). Similarity of form among the component zooids of the colony.

Polymerism (πολύς, many; μέρος, part). Simple multiplicity of the component zooids of the colony.

TERMS APPLICABLE TO THE TROPHOSOME.

Hydranth (ὕδρα, hydra; ἄνθος, flower). The proper nutritive zooid, or that part of it which carries the mouth and proper digestive cavity. (Diagrams I and II, *g, g'.*)

Hypostome (ὑπὸ, under; στόμα, mouth). The distal prolongation of the hydranth, which carries the mouth on its summit. (Diagrams I and II, *h.*)

Hydrotheca (ὕδρα, hydra; θήκη, receptacle). The cup-like chitinous receptacle which protects the hydranth in the calyptoblastic genera. (Diagram II, *i, i.*)

Hydrophyton (ὕδρα, hydra; φυτόν, plant). The common basis of the trophosome by which its zooids are connected into a single colony. (Diagrams I and II, *a, a, a, a, b, b.*)

Hydrorhiza (ὕδρα, hydra; ῥίζα, root). The proximal end of the hydrophyton by which the colony fixes itself to other bodies. (Diagrams I and II, *b, b, b, b.*)

Hydrocaulus (ὕδρα, hydra; καυλός, stem). All that portion of the hydrophyton which intervenes between the hydrorhiza and the hydranth. (Diagrams I and II, *a, a, a, a.*)

Cœnosarc (κοινὸς, common; σάρξ, flesh). The common organized fleshy portion of the hydrophyton; the living bond by which the zooids are organically united to one another. (Diagrams I and II, *d, d, d, e, e, e.*)

Nematophores (νῆμα, thread; φορέω, I carry). Peculiar bodies developed in certain genera from definite points of the trophosome (and of the corbulæ in the genus *Aglaophenia*), and consisting of a chitinous receptacle with sarcode contents in which thread-cells are usually immersed. They are characteristic of the family of the *Plumularidæ*. (Figs. 50 and 51, pages 116 and 117.)

TERMS APPLICABLE TO THE GONOSOME.

Gonophore (γόνος, offspring; φορέω, I bear). The ultimate generative zooid which gives origin directly to the generative elements, ova or spermatozoa. (Diagrams I, *k, k′, l,* and II, *k.*)

Sporosac (σπορὰ, sexual product, offspring; σακός, a sack). A sack-shaped gonophore destitute of obvious umbrella. (Diagrams I, *k, k′,* and II, *k.*)

Planoblast (πλάνος, wandering; βλάστη, a bud). A generative bud with a structure fitting it for a free locomotive life when detached from the hydrosome. (Diagrams I and II, *l.*)

Gonocheme (γόνος, offspring; ὄχημα, chariot). A medusiform planoblast whieh gives origin directly to the generative elements. (Diagram I, *l.*)

Blastocheme (βλάστη, bud; ὄχημα, chariot). A medusiform planoblast which gives origin to the generative elements, not directly, but through the medium of special sexual buds which are developed from it. (Diagram II, *l,* and Figs. 9 and 10, page 35.)

Blastostyle (βλάστη, bud; στύλος, column). A columniform zooid destined to give origin to generative buds. (Diagrams I and II, *m, m, m.*)

Perigonium (περί, around; γόνος, offspring). The walls of a sporosac by which the generative elements are confined, and in which, when fully developed, three laminæ may be demonstrated. (Fig. 7, page 32.)

Ectotheca (ἐκτός, outside; θήκη, sheath). The most external of the three laminæ of the perigonium. (Fig. 7, *c,* page 32.)

Mesotheca (μέσος, middle; θήκη, sheath). The middle one of the three laminæ of the perigonium. (Fig. 15B, *b,* page 44.)

Endotheca (ἔνδον, within; θήκη, sheath). The most internal of the three laminæ of the perigonium. (Fig. 7, *b,* page 32.)

Spadix (σπάδιξ, the fruit-shoot of a palm tree, a term used by botanists for a form of inflorescence). The hollow body which projects from the floor of the sporosac into its cavity, and round which the generative elements are developed. (Diagrams I and II, *k, k′,* and Fig. 7, *a,* page 32.)

Umbrella. The gelatinous bell of a medusiform planoblast. (Diagrams I and II, *l,* and Fig. 8, *c,* page 33.)

Manubrium (*manubrium*, handle). The axial portion which, in a medusiform planoblast, hangs from the summit of the umbrella, carrying the mouth at its extremity. (Diagram I, *l*, and Fig. 8, page 33.)

Atrium (*atrium*, a hall). An enlargement of the somatic cavity which occurs in many medusæ. It is situated at the base of the manubrium, and from it the radiating canals proceed. (Fig. 17, page 46.)

Codonostome (κώδων, bell; στόμα, mouth). The orifice of the umbrella through which its cavity communicates with the external water. (Fig. 8, page 33.)

Velum (*velum*, a veil). The membranous perforated diaphragm which stretches transversely across the codonostome. (Fig. 8, *h*, page 33.)

Ocellus (diminutive of *oculus*, eye). A heap of pigment-cells accompanied or not by a refracting body, and forming a coloured spot on definite points of the umbrella-margin in certain planoblasts. (Fig. 56, *g*, page 139.)

Lithocyst (λίθος, stone; κύστις, bladder). A sack-like body containing concretions, developed on definite points of the umbrella-margin in certain planoblasts. (Figs. 57, *c*, and 58, *h*, pages 140 and 141.)

Phanerocodonic (φανερὸς, manifest; κώδων, bell). The condition of a gonophore when it possesses a developed umbrella. (Diagram I, *l*.)

Adelocodonic (ἄδηλος, not manifest; κώδων, bell). The condition of a gonophore when no developed umbrella is present. (Diagram I, *k*, *k'*, and II, *k*.)

Gonangium (γόνος, offspring; αγγειον, vessel). An external chitinous receptacle within which, in the calyptoblastic genera, the sporosacs or planoblasts are developed. (Diagram II, *n*.)

Gubernaculum (*gubernaculum*, rudder, director). A common sack-like membrane which surrounds the generative buds within the gonangium, and aids in directing them or their contents towards the orifice of the gonangium. (Figs 18, *d*, and 19, *d*, page 48.)

Acrocyst (ἄκρος, on the top; κύστις, bladder). An external sac which in certain hydroids is formed upon the summit of the gonangium, where it constitutes a receptacle in which the ova pass through some of the earlier stages of their development. (Figs. 21 and 22, page 50.)

Meconidium (diminutive from μήκων, a poppy). Peculiar sporosacs, somewhat resembling a poppy capsule in form, and borne upon the summit of the gonangium in the genus *Gonothyræa*. (Fig. 28, page 57.)

Corbulæ (*corbula*, a basket). Basket-shaped receptacles which enclose groups of gonangia in certain plumularian hydroids. (Fig. 30, page 60.)

Planula (a diminutive noun, suggested by a supposed resemblance to a *Planaria*). The locomotive infusorium-like embryo into which the egg of most hydroids becomes directly developed. (Fig. 39, κ, page 86.)

Actinula (a diminutive noun found from ἀκτίς, a ray). The locomotive polypoid embryo into which, in certain genera, the egg becomes directly developed. (Plate XXI, fig. 6, Plate XXIII, fig. 16, &c.)

TERMS APPLICABLE TO CERTAIN CONDITIONS OF THE HYDROSOMA.—NAMES OF LEADING SYSTEMATIC GROUPS.

Gymnoblastic (γυμνὸς, naked; βλάστη, bud). The condition of a hydroid when no external protective receptacle (hydrotheca or gonangium) invests either nutritive or generative buds. GYMNOBLASTEA, the name of one of the sub-orders of HYDROIDA. (Diagram I, and the various plates illustrating the present Monograph.)

Calyptoblastic (καλυπτὸς, covered; βλάστη, bud). The condition of a hydroid when an external protective receptacle (hydrotheca or gonangium) invests either the nutritive or generative buds. CALYPTOBLASTEA, the name of one of the sub-orders of HYDROIDA. (Diagram II, and fig. 2, page 23.)

Eleutheroblastic (ἐλεύθερος, free; βλάστη, bud). The condition of a hydroid when the nutritive buds, instead of remaining permanently attached, become free and enjoy an independent existence. ELEUTHEROBLASTEA, the name of one of the sub-orders of HYDROIDA.

MONOPSEA (μόνος, single; ὄψις, appearance). The name of one of the sub-orders of the HYDROIDA, in which development from the egg takes place without the intervention of a hydriform trophosome.

RHABDOPHORA (ῥάβδος, rod; φορέω, I bear). The name of one of the sub-orders of the HYDROIDA. It corresponds to the extinct group of the Graptolites, in which a solid rod is developed in the walls of the chitinous perisarc.

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PART I.

THE HYDROIDA IN GENERAL.

SUPPLEMENTARY.

PART I.

THE

HYDROIDA IN GENERAL.

THE

HYDROIDA IN GENERAL.

PHYSIOGNOMY OF THE HYDROIDA.—DESIGN OF THE PRESENT MONOGRAPH.

Rooted in the transparent reservoirs which the retiring tide has left behind it in the rocky shore, or spreading over the fronds of the sea-weeds, or fringing the reef at low water with a mimic vegetation, or brought up by the dredge of the naturalist and the lines of the fisherman from the deeper regions of the sea, there may be obtained, on perhaps every coast and in every latitude, certain singular organisms which repeat with such unerring fidelity the forms of the vegetable kingdom that we can scarcely bring ourselves to believe that the hundred plant-like shapes which root themselves in that marvellous sea-garden, and stretch forth their branches, and unfold their buds, and spread abroad their starry flowers, have not the structure and the life as well as the form and the habit of the plant. And yet they are no plants, these strange plant-like dwellers in the sea, but genuine animals in all that constitutes the essence of animality.

When Marsigli, more than a century and a half ago, fished up from the Mediterranean Sea a piece of living coral, and for the first time in the history of science its branches were seen clustered with starry polypes, he believed that he had before him a blossoming plant; for in the branching stem which he had plucked from the rock where it had been rooted, and in its living bark and eight-petalled flowers he saw nothing but the evidence of vegetality, which surely proved that the great botanists of the day—Ray and Tournfort, and Cæsalpinus, and Bauhin, and Lobel, were right when they called corals plants, and assigned them to the Flora rather than to the Fauna of the sea. And so, also, the organisms with which the present monograph is to be occupied are no less plant-like than their relatives the corals, for they are rooted, and branch, and bud and blossom like them.

But more than this, the sea is filled with living and moving forms, floating bells of crystal, whose beauty no description can convey, whose multitude no thought can estimate. Unlike those animated flowers which root themselves to the sea-bed, these no less wonderful Medusæ, with functions higher and more varied, lead a life of freedom. They love the upper regions of the sea, and wherever over its wide surface the conditions suited to their welfare are to be found there will the towing-net encounter them. A thousand leagues away from land, where the ship lies motionless in the calm, there they are abroad in their unnumbered hosts; and where the gale is strong, and the wave breaks upon the rocky headland, there too they congregate and sport unharmed in the surf. And yet for days together the towing-net may sweep the sea without a trace of them, for they are sensitive to every changing mood of the atmosphere above them; they feel the gathering cloud and the summer shower; and when the sea freshens beneath the falling rain-drops, or the air rests upon its surface with influences unfavorable to their well-being, they sink into salter waters and find shelter in more genial depths.

But their life was not always one of freedom as it now is, for they once grew as buds upon those strange hydroids, which, with the life of the animal, root themselves to the sea-bed like a plant; they sprung forth from their sides, and drew their nourishment from the parent branch, and expanded and developed themselves until they became fitted for an independent existence, and then, full of a new and higher life, they broke away from their supporting stalk, active and energetic beings, unrivalled in the gracefulness of their motions and in the symmetry and beauty of their forms.

The true significance of all this budding and blossoming, of this imitation by the animal of the form and growth of the plant, lies at the foundation of a scientific knowledge of the HYDROIDA, and constitutes one of the most interesting and marvellous chapters in the morphology and physiology of animals.

It is my intention to devote the present work to an examination of the HYDROIDA in their general morphological and physiological relations as a great natural group; while to one large and important subdivision of this group, the *Tubularinæ*, a more special consideration will be given, and all the genera and species of which it is composed will be described in detail. Thus, a purely descriptive zoology of the *Tubularinæ* will be combined with a careful study of their structure and physiology, and of the structure and physiology of the entire order of the HYDROIDA, that more comprehensive group under which the *Tubularinæ* are immediately included.

When thus investigated, it will be found that the study of the HYDROIDA possesses an interest far beyond what we may at first be inclined to attribute to beings so simple in their structure and so apparently insignificant in the place allotted to them in the economy of nature, for we shall then learn that some of the most important facts in morphology and some of the highest laws in physiology find in them their expression and elucidation.

SYSTEMATIC POSITION.

The HYDROIDA of the present monograph include the *Hydrinæ*, *Tubularinæ*, *Campanularinæ*, and *Sertularinæ*, being so far exactly coextensive with the HYDROIDA of Johnston.[1] The group HYDROIDA, however, as here understood, necessarily embraces most of the so-called naked-eyed or gymnophthalmic Medusæ, for a large proportion of these are known to be the free generative

[1] George Johnston, 'A History of the British Zoophytes.' Second Edition, 1847.

zooids of the *Tubularinæ* and *Campanularinæ*, while those which have not yet been so traced—provided we have no reason to regard them as the free zooids of the *Siphonophora*—and even those which may be proved to be developed directly from the egg, cannot, in a philosophical system, be separated from the others.

I accept without hesitation the group CŒLENTERATA, with the characters assigned to it by Leuckart; and I further adopt the division of this group into two primary sections, with the names of *Actinozoa* and *Hydrozoa*, as proposed by Huxley. The following table will indicate the place of the HYDROIDA among the other members of the *Hydrozoa*:[1]

CŒLENTERATA . . .	ACTINOZOA.	
	HYDROZOA . .	Ctenophora.[2]
		Discophora.
		Lucernariæ.
		Hydroida.
		Siphonophora.

HISTORY OF THE PROGRESS OF OUR KNOWLEDGE OF THE HYDROIDA.

The history of the successive stages through which any important branch of human knowledge passes in its development from the first dawnings of its truths upon the mind to that more perfect phase which in the lapse of time it has attained, constitutes one of the most instructive subjects upon which the philosophic student can be engaged; and a history of this development, as it shows itself in the progress of our knowledge of the Hydroida may, therefore, with advantage precede that exposition of the present state of our knowledge of them which is the chief aim of the present work.

In order to avoid extending our historical sketch to an inconvenient length, the record of many important anatomical and physiological discoveries must be postponed to that part of the volume where these discoveries can be described with sufficient detail; and I shall here confine myself chiefly to the more important steps which have been made towards the determination of the systematic position of the HYDROIDA, and their recognition as a distinct group with the limits assigned to them in this monograph.

[1] I must for the present hesitate to include among the hydrozoal orders the tabulate and rugose corals. The hydrozoal affinities of these groups have been recently claimed for them by Agassiz as the result of an examination of living specimens of *Millepora alcicornis*, a tabulate coral, in which, if there be no error of observation, Agassiz has detected a true hydrozoal structure, while he believes himself supported by analogy in attributing this structure, not only to all the other genera of tabulate corals, whether living or extinct, but even to the entirely extinct group of *Rugosa*. (See his 'Cont. Nat. Hist. United States,' vol. iv.) The observations, however, on which this view has been based are plainly not yet as complete as could be desired for a determination so important, and even startling. Of the generative system more especially we are entirely ignorant. Under these circumstances I believe it will be safer to wait for such verification as may be expected from further researches.

[2] In adopting the more usual view, in accordance with which the *Ctenophora* are placed among the *Hydrozoa* rather than among the *Actinozoa*, as originally indicated by Leuckart, and more decidedly insisted on by Huxley, I believe myself borne out by a careful study of the structure of *Beroe*.

We have no evidence whatever to show that the Greek and Roman naturalists were acquainted with any member of the HYDROIDA. Aristotle and the naturalists of Greece and Rome who followed him had some knowledge of corals, sea-anemones, and steganophthalmic Medusæ; but this was very imperfect, while no mention is made by them of a single hydroid, and it is not until the eighteenth century that we find in the writings of naturalists anything beyond the most obscure indications of an acquaintance with the animals now included in the order HYDROIDA.

It was in the beginning of the eighteenth century that the fresh-water *Hydra* was discovered by Leeuwenhoeck, and its faculty of budding like a plant accurately described. Leeuwenhoeck communicated a notice of this discovery to the Royal Society of London in 1803.[1]

The first grand impulse, however, to the study of the Hydroida was given some years later by Trembley. Abraham Trembley was born in Geneva in 1700, and in 1743 was awarded the Copley medal by the Royal Society of London, of which he had been elected a Fellow. It was while residing at the Hague with his two pupils, the sons of the Count de Bentinck, that he obtained, in the pond at Sorgvliet, the country house of the count, the hydras which enabled him to make that remarkable series of observations on the reproductive powers of these animals which resulted in the discovery of phenomena hitherto unsuspected in the animal kingdom, and of the highest significance in physiology; for they established the fact that the animal organism may not only multiply itself by budding in the manner of a plant, as Leeuwenhoeck had already demonstrated, but that it may possess the power of enduring repeated subdivision, and may suffer with impunity the most extensive mutilations, the fragments of the divided *Hydra* not only recovering from the operation, but becoming endowed, after a time, with all the parts of which they had been deprived by the act of division.

The discoveries of Trembley were communicated to Réaumur, and recorded by him, in 1742, in the preface to the sixth volume of his 'History of Insects;'[2] and in 1744 an extended account of them was published by Trembley himself, in his celebrated treatise on 'Fresh-water Polypes.'[3] In this remarkable work the species of *Hydra* known to Trembley are described with copious details of their general structure and habits, and of the curious experiments to which he subjected them. The work consists of four memoirs, and is abundantly illustrated with figures of great beauty exhibiting the *Hydra* in various conditions and under various modes of treatment, all from the pencil and most of them from the graver of the celebrated Lyonet; while the quaint but expressive vignettes from another hand, which are placed at the heads of the four memoirs, and which represent various parts of the grounds of Sorgvliet, with the author and his two pupils engaged in the capture and observation of the Hydræ, give an additional charm to a work which must be regarded as the most important step yet made towards a scientific knowledge of the HYDROIDA.

The progress of discovery in the natural history of the HYDROIDA, however, is so intimately connected with various observations which had been about this period made on certain corals and other Actinozoa, that it is impossible to follow the one without some knowledge of the other.

The researches of Trembley were preceded by Peysonelle's demonstration of the true nature of the polypes of coral. The coral polypes were discovered towards the beginning of the last

[1] Ant. de Leeuwenhoeck in 'Phil. Trans.' for 1803.

[2] René-Antoine Ferchaud de Réaumur, 'Histoire des Insectes.' Paris, 1742.

[3] 'Mémoires pour servir à l'Histoire d'un genre de Polypes d'eau douce à bas en forme de Cornes.' Leyden, 1744.

century by the Count de Marsigli.[1] Marsigli, however, regarded them as the flowers of the coral, and saw in them a proof of the vegetable nature of the supposed sea-plant which bore them; and his discovery was at once received as a full confirmation of the views entertained by the leading botanists of the time, who all regarded the corals as genuine members of the vegetable kingdom.

Jean Antoine Peysonelle, however, during a residence at Marseilles and on the Mediterranean shores of Africa, and subsequently at Guadaloupe, applied himself to the study of living corals and madrepores, and soon became convinced that the coral flowers of Marsigli were truly animals closely allied to the *Actiniæ*, or " *Urticæ marinæ*," as they were called by the naturalists of that day.

Peysonelle's views were communicated by Réaumur to the Academy of Sciences in 1727, where they were received with discredit, and even contempt, Réaumur himself, who believed in the vegetable nature of coral, not even mentioning the name of the author whose communication he undertook to present, so that Peysonelle's discovery remained almost unknown until 1742, when he forwarded to the Royal Society of London a long memoir, which was published in abstract in the 'Philosophical Transactions' of that year.

The discoveries of Peysonelle, however, had arrested the attention of the celebrated botanist, Bernard de Jussieu, and, with the view of verifying them, he determined to visit the sea-coast of Normandy. Though the shores of Normandy afforded to Jussieu no true corals, he found there the nearly allied *Alcyonium*, which enabled him to confirm the views of Peysonelle. He at the same time convinced himself that the plant-like Flustras were truly animals; and, what has a more direct importance in its bearing upon the present history, he observed the polypites of *Tubularia indivisa*, and was thus enabled to refer this hydroid to the animal kingdom. The results of de Jussieu's visit to Normandy were published in the 'Mémoires de l'Académie' for 1742,[2] where he gives a figure of *Tubularia indivisa*, which in truthfulness and expression has never since been surpassed.

Réaumur, unable to resist the accumulated evidence of the animality of corals and hydroids, now fully accepted the views of Peysonelle, which he had some years before scarcely deemed worthy of a serious thought.

At this time Linnæus was carrying out those wonderful reforms in classification and nomenclature which were destined to exert an influence on the progress of natural history greater than anything which had been effected since the days of Aristotle, and which mark out the eighteenth century as the most significant in the history of the natural sciences.

The discoveries of Peysonelle, of Jussieu, and of Trembley, however, had not yet brought conviction to the great systematist, and in 1745 we find him, in a dissertation on the fossil corals of Sweden,[3] after contrasting the various opinions regarding the nature of coral in accordance with which it was assigned either to the mineral, the vegetable, or the animal kingdom, candidly confessing that he was unable to decide between these rival views.

[1] See Luigi Ferd. Marsigli, 'Histoire physique de la Mer.' Amsterdam, 1725. Translated, under the care of Boerhaave, from the original Italian edition of 1711.

[2] Bernard de Jussieu, " Examen de quelques productions Marines qui ont été mises au nombre des plantes, et qui sont l'ouvrage d'une sorte d'Insectes de Mer;" 'Mém. de l'Acad. Roy. des Sciences,' Paris, 1742, p. 392.

[3] Carolus Linnæus, 'De Coralliis Balticis.' Upsaliæ, 1745.

The only hydroid which, up to this time, had been examined in a living state with results of any value to science was the *Tubularia indivisa*, which, as already mentioned, had been studied by De Jussieu on the coast of Normandy ; a most important accession, however, to our knowledge of the HYDROIDA was now about to be made by the observations of Ellis.

John Ellis was a London merchant devoted to the study of natural history, which he pursued in the intervals of his mercantile labours, with an enthusiasm and a success which renders his name familiar to every student of the HYDROIDA. He was elected a Fellow of the Royal Society, and was awarded the Copley Medal in recognition of the esteem in which his researches were held by that body.

An examination of dried specimens of various hydroids had already led Ellis to suspect that these plant-like productions really belonged to the animal kingdom, and determined him to study them in a living state. With this view he repaired with his microscope to the Island of Sheppey, and some other parts of the south-eastern shores of England, accompanied by Mr. Brooking, a distinguished painter of sea-pieces, and by the celebrated botanical painter Ehret. He had there abundant opportunity of studying a great number of living hydroids, and soon convinced himself that "these apparent plants were ramified animals in their proper skins or cases." In this remarkable assertion we have the first philosophic expression of the true nature of the fixed plant-like hydroids, and thus was finally settled the animality of these organisms. The results of his observations were published in 1755, in a work[1] whose beautiful and accurate figures and admirable descriptions render it at this day indispensable to the student.

Nothing was now wanting to produce general conviction of the animality, not only of the true corals, but of all those flexible, plant-like productions whose external form had so long caused their real nature to be overlooked. Even Linnæus himself was at last convinced by the discoveries of Ellis, and now declared himself a believer in their genuine animality.

Besides the generally very expressive vernacular names employed by Ellis, his species are, in accordance with the usual practice of the day, indicated by short Latin descriptions rather than by systematic designations. Linnæus's grand invention of the binomial nomenclature was, however, making its way among systematists. The 'Systema Naturæ' had already passed through several editions, and in 1766 we find the various species of HYDROIDA then known enumerated by Pallas under their binary designations in his admirable 'Elenchus Zoophytorum.'[2] In this work the species are characterised by a precision which leaves little to be desired; a complete synonomy is prefixed to each, and in their arrangement the celebrated Prussian naturalist affords evidence of an insight into those affinities on which the more natural classifications of subsequent systematists have been based.

In the tenth fasciculus of his 'Spicilegia Zoologica,'[3] published in 1774, Pallas describes and

[1] John Ellis, 'An Essay towards a Natural History of the Corallines and other Marine productions of the like kind commonly found on the coasts of Great Britain and Ireland. To which is added the description of a large Marine Polype taken near the North Pole by the Whale-fishers in the summer of 1753.' London, 1755.

[2] Petr. Sim. Pallas, 'Elenchus Zoophytorum sistens generum Adumbrationes generaliores et specierum cognitarum succinctas descriptiones cum selectis Auctorum synonymis.' Hagæ-Comit., 1766.

[3] Petr. Sim. Pallas, 'Spicilegia Zoologica quibus novæ imprimis obscuræ Animalium species iconibus, descript. atque commentariis illustrantur,' tom. i, fasc. i—x, Berolini, 1767—1774; tom. ii, fasc. xi—xiv, Berolini, 1776—1780.

figures two new hydroids. One of them is a *Coryne,* a genus which he adopts from a MS. of Gaertner; the other has no generic name assigned to it by Pallas; it can, however, be easily recognised as a *Clava,* a genus founded a few years afterwards by Gmelin for the *Hydra squamata* of Müller. Pallas's figures, however, though sufficient for identification, cannot be compared, either in beauty of execution or in truthfulness, to those of Trembley, Jussieu, or Ellis.

A much better figure of a *Clava* was given shortly afterwards by the Danish naturalist and traveller, Forskål, in his 'Icones Rerum Naturalium,'[1] where the species is named *Hydra multicornis;* and in the same work, besides two other tolerable figures of hydroid trophosomes, we find some very expressive and, indeed, up to that time, the only really recognisable ones of true hydroid Medusæ.

Among the means which tend most powerfully to advance the progress of the natural history sciences is an accurate and expressive iconography. The beautiful figures of Trembley and of Ellis hold in this respect the first rank. As we have already seen, Jussieu had given an admirable figure of *Tubularia indivisa,* and Forskål some very good ones of other hydroids, while some tolerable figures of a *Tubularia* and of some Sertularian and Campanularian hydroids had been published by Baster;[2] but hitherto no attempt had been made at the publication of coloured drawings. Between 1777 and 1780, however, were issued the first two fasciculi of the 'Zoologia Danica' of O. F. Müller,[3] which after Müller's death was continued with additions by Abildgard. It contains coloured figures of Scandinavian animals, mostly invertebrate, from the surrounding seas, and amongst them several hydroids. In the accuracy, beauty, and abundance of the figures, too much praise cannot be given to the 'Zoologia Danica,' which marks out an era in zoological iconography.

The posthumous work of Ellis and Solander,[4] published in 1786, contains many hundreds of figures, chiefly of corals, but having also among them several hydroids. Many of the figures contained in this work are masterpieces of iconography.

Esper also gives us a most laborious iconography, partly copied, partly original, consisting of coloured figures of corals, sponges, &c., as well as of numerous hydroids.[5] Where the hydroid figures are not copied from Ellis they are vastly inferior to those of the English naturalist.

The naturalists who during the eighteenth century contributed most to advance our knowledge of the HYDROIDA close with the name of Cavolini. Cavolini, like Ellis, studied the Hydroida in a living state. His investigations were made in the Bay of Naples, where he discovered many hydroids previously unknown, and determined many points of interest in their structure and physiology. He was the first to observe a Medusiform gonophore in connection

[1] 'Icones Rerum Naturalium quas in Itinere Orientali depingi curavit Petrus Forskål.' Copenhagen, 1776. The descriptions are contained in a separate volume, published in 1775.

[2] Jobi Basteri, 'Opuscula Subseciva.' Harlemi, 1762.

[3] Otho Fredericus Müller, 'Zoologiæ Danicæ seu Animalium Daniæ et Norvegiæ variorum et minus notorum Icones.' Hafniæ, 1777—1780.

[4] 'The Natural History of many curious and uncommon Zoophytes collected from various parts of the Globe, by the late John Ellis, F.R.S. Systematically arranged and described by the late Daniel Solander, M.D., F.R.S.' London, 1786.

[5] 'Die Pflansenthiere in Abbildungen nach der Natur mit Farben erleuchten nebst Beschreibungen,' von Eugenius Johann Cristoph Esper. Nuremberg, 1791—1797.

with the trophosome, and has described the radiating canals and the included ova of this body in his *Sertularia pennaria* (*Pennaria distycha*, Goldfuss), without, however, exactly comprehending its true significance or its relations to a free hydroid Medusa. He also insisted on the vegetality of the proper corallines or nullipores, which, on the establishment of the animality of corals, were carried with these into the animal kingdom. The results of his researches were published in 1785, in a work[1] full of valuable information, and illustrated with excellent figures of living hydroids, corals, and Polyzoa.

In the 'Elenchus Zoophytorum' of Pallas, published in 1766, all the known hydroid trophosomes were distributed among three genera—*Hydra*, *Tubularia*, and *Sertularia*. In the 'Spicilegia' Pallas adds the genus *Coryne* from Gaertner MS. Gmelin, in his edition of the 'Systema Naturæ,' 1788, while he overlooks the genus *Coryne*, adds the new genus *Clava*. Besides these different genera of hydroids, all characterised from their trophosomes, several true hydroid Medusæ had been at this date known and described; but they were all included along with steganophthalmic forms, and with *Siphonophora* and *Ctenophora*, under the common generic name of "Medusa," given to them by Linnæus.

The state of the natural history of the Hydroida at the date of the publication of the thirteenth edition of the 'Systema Naturæ' (Gmelin's) may thus be stated in a few words:—The animality of the Hydroida was fully acknowledged. Such species as were known by their trophosomes were distributed under five genera—*Hydra*, *Tubularia*, *Sertularia*, *Coryne*, and *Clava*, while such free gonophores as were known were thrown together with all the other free forms of *Hydrozoa* under the common name of *Medusa*.

The natural history of the Hydroida, which during the latter half of the eighteenth century had been thus steadily advancing in the hands of Trembley, Jussieu, Ellis, Pallas, Forskål, O. F. Müller, and Cavolini, was, with the commencement of the nineteenth century, destined to receive a fresh impulse.

The famous voyage of Peron and Lesueur[2] inaugurates the natural history labours of the nineteenth century. It was commenced in 1800, and in 1804 the voyagers returned laden with new and important facts for science. No expedition could have afforded better opportunities of studying the pelagic forms of invertebrate animals; and soon after their return Peron and Lesueur undertook a systematic description of the Medusæ which they had observed in the great seas which their ships had traversed, as well as of other species which they had studied in expeditions afterwards made to the coasts of Normandy and to the Mediterranean. In the two memoirs[3] in which they publish the results of their researches they propose an entirely new classification of the Medusæ. The old Linnean genus *Medusa* is broken up into numerous separate genera, and

[1] Filipo Cavolini, 'Memorie per servir alla storia de Polypi Marini.' Naples, 1785. Translated in 1813 into German by Sprengel.

[2] 'Voyage de Découvertes aux Terres Australes, fait par ordre du Gouvernement sur les corvettes "le Géographe," "le Naturaliste," et la goëlette "la Casuarina," pendant les années 1800 à 1804, rédigé par Peron et continué par M. Louis de Freycinet,' 2e édit. revue, corrigée, et augmentée, par M. de Freycinet. Paris, 1824, 1825.

[3] Peron et Lesueur, "Notions préliminaires sur les Méduses," 'Ann. du Muséum,' 1809, p. 218; and 'Tableau des Caractères génériques et spécifiques de toutes les Espèces de Méduses connues jusqu'à ce jour,' id., p. 325. The plates referred to all through the second memoir have, unfortunately, never been published.

many true hydroid Medusæ are described; but the authors had as yet failed to recognise the fundamental differences between the hydroid Medusæ and the proper *Discophora*.

In 1812 Cuvier published a sketch[1] of his celebrated arrangement of the animal kingdom, which he divides into four primary groups. To the last of these he assigns the name of "Animalia Zoophyta seu Radiata." The group *Radiata* of Cuvier thus includes all the HYDROIDA, but though more precise and definite than the "Vermes" of Linnæus, it is still a heterogeneous assemblage, and as it fails to recognise the distinction between grade of development and morphological plan, it necessarily contains forms which belong to very different types.

The beautiful researches of Savigny on the compound Ascidians were published in 1816,[2] and by proving that a large number of organisms which, under the common name of *Alcyonium*, had been hitherto associated with true cœlenterate forms, are in reality Ascidians, these researches must be regarded as an important step towards the final limitation of the primary groups of the animal kingdom.

For some time past a vast amount of material for the zoology of the invertebrate animals was being accumulated, and a period had now arrived when a systematic arrangement of the whole was loudly called for. It was in this state of things that a work destined to exert great influence on the study of the lower animals made its appearance. The second volume of the 'Histoire Naturelle des Animaux sans Vertèbres' of Lamarck[3] was published in 1816. In this celebrated work three new genera of hydroids are instituted from their trophosomes, namely, *Campanularia*, *Antennularia*, and *Plumularia*. Among Medusæ, however, Lamarck recognises only a portion of the genera established by Peron and Lesueur, and in thus attempting to simplify the classifications of his predecessors he falls behind the famous voyagers in the actual requirements of science.

While Lamarck was engaged in the preparation of his 'Animaux sans Vertèbres,' Lamouroux was occupied with the study of a set of flexible, plant-like organisms forming a heterogeneous group, which included not only most of the hydroid trophosomes then known, but also a large number of *Actinozoa* and *Polyzoa*, and even many indubitable plants; and in the same year with the publication of the second volume of Lamarck's work there appeared a natural history of these organisms by Lamouroux. Lamouroux[4] has here defined some good additional genera of hydroids characterised by their trophosomes; though some of them are identical with genera instituted by Lamarck under other names. The names given by Lamarck, however, have found more general acceptance with subsequent authors; and whatever doubt may be entertained regarding actual priority of publication, the zoologist of the present day will scarcely hesitate to give them the precedence, especially when it is remembered that Lamouroux had complete access to all Lamarck's specimens which had been deposited in the Museum of the Jardin des Plantes, and which had been already labelled with the names given to them by the illustrious author of the 'Histoire des Animaux sans Vertèbres.'

[1] G. Cuvier, "Sur un nouveau rapprochement à établir entre les classes qui composent le Règne Animal." 'Annales du Muséum,' 1812.

[2] Marie Jul. Cæsar Lelorgue de Savigny, 'Mémoires sur les Animaux sans Vertèbres,' part ii, Paris, 1816.

[3] J. Bapt. P. Ant. de Monnet Lamarck, 'Histoire Naturelle des Animaux sans Vertèbres,' 7 vols., Paris, 1815—1822.

[4] J. V. F. Lamouroux, 'Histoire des Polypiers Coralligènes flexible vulgairement nommés Zoophytes,' Caen, 1816.

Almost precisely at the same time appeared the first edition of the 'Règne Animal' of Cuvier.[1] The general division of the animal kingdom, of which, as we have already seen, a sketch had previously appeared, is here adopted and carried into detail. In his association of the free Hydrozoa into a distinct class under the name of Acalepha, Cuvier now takes an important step, though its value is deteriorated by the admission of Actinia into the same group. Independently of the advance which the natural history of the HYDROIDA has thus directly received, the great influence which Cuvier has exerted on the studies of the zoologist, by taking anatomical structure rather than external resemblance as the basis of classification, renders it impossible in the history of any department of zoology not to see in the publication of the 'Règne Animal' a well-marked era of development.

The voyage of Peron and Lesueur, which had such valuable results for zoology, was only the first of a long series of scientific expeditions which, fitted out under the auspices of various governments, brought back with them rich stores of materials, and mark out the first half of the present century as eminently the era of the naturalist voyager.

Between the years 1815 and 1826 two exploratory expeditions round the world were fitted out by the Russian Government.[2] They were entrusted to the command of Kotzebue, and were accompanied by Chamisso and Eschscholtz as naturalists. The expeditions afforded fine opportunities for the observation of pelagic forms of *Mollusca* and *Cœlenterata*, and are rendered memorable by Chamisso's famous discovery of the "alternation of generations" in *Salpa*—a discovery which was destined to exert great influence on the study of the HYDROIDA and the interpretation of their marvellous life-history.

The study of the cœlenterate animals observed during these voyages was specially undertaken by Eschscholtz, and after the return of the voyagers from their second expedition we find this philosophic naturalist publishing a general work on the Medusæ and allied forms[3]—a work by far the most important which had as yet appeared upon the animals of which it treats, and one which, even at the present day, the student is unable to dispense with.

It is here that, for the first time, we find the hydroid Medusæ, under the name of "Discophora cryptocarpa," separated as a distinct and well-defined group from the proper *Discophora*, to which Eschscholtz assigns the name of "Discophora phanerocarpa;" and though the characters on which this dismemberment was based were but imperfectly understood by Eschscholtz, and have since undergone considerable modifications, the conception of the hydroid Medusæ as a separate section is a step of primary importance, and could have been entertained only by one who was able to recognise the fundamental differences and appreciate the true affinities of the group among which these organisms had been hitherto indefinitely distributed.

Cuvier had already[4] recognised an essential difference of structure between the actinozoal and hydrozoal forms included in his group of "Polypes," when he pointed out the presence of a digestive sac, with differentiated walls in the former, and its absence in the latter; but the

[1] Geo. Leop. Chr. Fred. Dajob. Cuvier, 'Le Règne Animal distribué d'après son organisation, pour servir de base à l'Histoire Naturelle des Animaux et d'introduction à l'Anatomie comparée,' Paris, 1817.

[2] Otto v. Kotzebue, 'Voyage of Discovery into the South Sea and Behring's Straits, undertaken in 1815-18, in the ship "Rurick,"' London, 1821; and 'New Voyage round the World in 1823-26,' London, 1830.

[3] Joh. Friedr. Eschscholtz, 'System der Acalephen,' Berlin, 1829.

[4] 'Le Règne Animal,' 1817, tome iv, p. 79.

structure of most of the animals constituting the *Radiata* of Cuvier was still so very imperfectly known that this important character failed to receive its due weight in classification.

In 1828 it was brought out with greater distinctness and force by M. Milne-Edwards in an account of his zoological researches in the Chausey Isles[1]; but still the fixed plantlike hydroids continued to be associated with the true corals and *Polyzoa,* under the common name of "Polypi," for, notwithstanding the deep-lying difference which had been indicated by Cuvier, and more definitely insisted on by Milne-Edwards, between the hydrozoal and actinozoal types, yet its full value as a classificatory character still continued unappreciated. As Eschscholtz, however, had seen in the reproductive system of the medusæ a ground for their separation into two primary groups, so in the same year Professor Rapp, of Tubingen, proposed to divide the polypoid *cœlenterata* into two sections, also based upon the peculiarities of their reproductive system.[2] Observing that in the hydroid trophosome the ovigerous buds were produced externally, while in *Actinia* and the corals the reproductive organs projected into the interior of the body-cavity, he assumed this difference as a basis for the definition of two distinct groups, to which he gave the names of *Endoarii* and *Exoarii.* Though the real nature of the peculiarity on which this dismemberment of the fixed cœlenterata rests was, like that in accordance with which Eschscholtz had already based his subdivision of the Medusæ, scarcely comprehended by its author, the proposal of Rapp must, nevertheless, be regarded as an important step towards the determination of the systematic position of the HYDROIDA.

Among the results of Milne-Edwards's investigations carried on in the Chausey Isles, the most important was his demonstration of a type of structure in the *Flustræ,* entirely different from that of the cœlenterate animals with which they had been associated by his predecessors. A similar conclusion had been just arrived at by Grant,[3] but the British zoologist had not worked out the structure with that completeness which characterised the investigations of Edwards, who now showed[4] that the *Flustræ* were constructed on a plan in all essential points identical with that of the compound Ascidians, with whose organisation Savigny had already made us acquainted in his masterly memoirs.

Though M. Milne-Edwards had thus proved the existence of a true molluscoid type of structure in *Flustra,* no comprehensive name had yet been given to the group so characterised. While Grant and Edwards, however, were thus engaged in their anatomical examination of *Flustra,* J. V. Thompson, then residing on the coast of Cork Harbour, was occupied with a series of similar investigations, and, quite independently of any knowledge of the labours of Grant and Edwards, had determined not only the molluscoid structure of *Flustra,* but had in a very complete way demonstrated an entirely similar structure in other plant-like organisms hitherto associated with true cœlenterate forms. To the organisms thus characterised by this common type of structure Thompson, while fully recognising their relation to the Ascidians, gave, in 1830, the name of *Polyzoa.*[5]

[1] J. Victor Audouin and H. Milne-Edwards, "Résumé des Recherches sur les Animaux sans Vertèbres, faites aux Isles Chausey," 'Ann. des Sci. Nat.,' 1828.

[2] Wilhel. Rapp, 'Ueber die Polypen in Allgemeinen und die Actinien insbesondere,' Weimar, 1829.

[3] Robert E. Grant, "Observations on the Structure and Nature of Flustræ," 'Edinb. New Phil. Journ.,' vol. iii, 1827.

[4] Op. cit.

[5] John Vaughan Thompson, 'Zoological Researches and Illustrations,' Cork, 1830. The date is

In 1831[1] Ehrenberg employs the term *Bryozoa* in a sense exactly equivalent to that of Thompson's *Polyzoa*, and in 1833[2] we find him proposing a new classification of the heterogeneous and unscientific group of the "Polypi," by dividing them into the *Anthozoa*, which embraced the cœlenterate forms, and the *Bryozoa* to which all the molluscoid forms were referred.

In the same memoir Ehrenberg also forms a separate group for the fixed *Hydrozoa*, which, under the name of "Zoocoralia oligactinia," he separates from the *Actinozoa*. He further gives a synopsis of such genera and species as were then known, and makes some valuable reforms in the limitation and arrangement of the genera; but the most important point in which this memoir has advanced our knowledge of the HYDROIDA will be found in the ascription of an independent zooidal significance to the so-called "egg-capsules" of these animals, and the consequent determination of a distinct sexuality among the zooids which compose a hydroid colony. This capital discovery, whose true import, however, was but partially comprehended by Ehrenberg, has in the hands of subsequent investigators undergone further development, and must be viewed as the starting-point for all those more recent researches which have so largely contributed to bring about the philosophical views now entertained regarding the structure, physiology, and systematic position of the HYDROIDA.

In 1834 De Blainville published his 'Manuel d'Actinologie.'[3] The important reforms of Eschscholtz, Rapp, and Ehrenberg are not adopted by De Blainville; and the 'Manuel d'Actinologie,' except in so far as it constituted a useful work of reference and description for the student, cannot be regarded as in any way advancing the systematic arrangement, or aiding in a philosophic conception of the HYDROIDA.

The notes and drawings of Medusæ made by Mertens during his voyage round the world as naturalist to the Russian exploring ship "Seniavin," were, after Mertens' death, entrusted to Brandt, who has given us an account of them in two important memoirs. The first, published in 1833,[4] consists in a synopsis of the genera and species observed by Mertens, among which are several new genera of both hydroid Medusæ and Discophora proper; while in the second[5] he gives us a more detailed account of them, and now publishes the numerous and beautiful figures made by Mertens from the living animals. Brandt does not adopt Eschscholtz's division of the Medusæ, so that the hydroid Medusæ are here mixed up with the *Discophora* proper. He gives us detailed anatomical descriptions of the Medusæ, so far as their structure was at that time known; but the chief value of the labours of Mertens and Brandt will be found in their rendering us acquainted with new forms, and in their giving us the most beautiful and accurate figures of Medusæ which had been up to that time published.

not printed on the title-page, but it will be found on the paper wrapper in which the publication was originally issued.

[1] Chr. Gdfr. Ehrenberg, 'Symbolæ Physicæ,' iv, Berolini, 1831.

[2] Corallenthiere.

[3] Henri Marie Ducrotay de Blainville, 'Manuel d'Actinologie ou de Zoophytes,' Paris, 1834.

[4] J. F. Brandt, "Prodromus descriptionis Animalium ab H. Mertensio in Orbis Terrarum circumnavigatione observatorum." 'Recueil des Actes de la Séance publique de l'Académie Impériale des Sciences de St. Pétersbourg,' 1833-34.

[5] Ibid. "Ausführliche Beschreibung der von C. H. Mertens auf seiner Weltumsegelung beobachteten Schirmquallen," 'Mém. de l'Acad. Impér. des Sciences de St. Pétersbourg,' vi sér., Sci. Nat., tom. ii, Pétersbourg, 1838.

In 1838 Dr. Johnston published his 'History of British Zoophytes.'[1] The "zoophytes" of Johnston include not only the plant-like hydroids, but the *Actinozoa* and *Polyzoa*. He does not, however, confound the natural boundaries of these groups, and proposes for the hydroid forms the name of *Hydroida*, which thus coincides with the HYDROIDA of the present Monograph in all respects, except in the fact of its not including the hydroid Medusæ, whose relation to the plant-like trophosomes had not yet been definitely recognised.

Without the originality of Ellis's classical 'Essay,' Johnston's 'History of British Zoophytes' is still a work of great utility for the student. The descriptions of the species are very good, and are accompanied by a copious and valuable synonomy; and the figures, though mostly drawn from the dried hydrosome, and certainly not equal in artistic feeling to those of Ellis, are often excellent, and always of great use in aiding in the determination of the species. The value of the 'British Zoophytes,' however, lies in its character as a descriptive work, and with its publication we may date a new impulse to the study of the HYDROIDA, similar to that which nearly a century before, Ellis's 'Natural History of Corallines' had exercised in the same direction. In 1847 a second edition of the 'British Zoophytes' made its appearance. A great number of additional species are described in it, and many new plates are added to those which were contained in the first.

The observations of Cavolini[2] in the last century, and afterwards those of Wagner[3] and Loven,[4] had already made us acquainted with certain facts which show that the hydroid trophosome may give rise to buds presenting a close resemblance to Medusæ; while the beautiful researches of Sars had shown that among the *Discophora* phenomena occur which in many points resemble this budding of Medusæ among the HYDROIDA, and have an intimate relation with it.[5] The true significance of these observations, however, was but imperfectly appreciated when Steenstrup, in 1842, combining them with analogous ones in other groups of animals, correlated with great skill all the known facts, and generalised the phenomena under the name of "alternation of generations," an expression already employed by Chamisso when describing the gemmation and generation of *Salpa*.[6]

Though in the terms in which Steenstrup enunciates his law of alternation of generations a false conception of the phenomena may appear to be involved, it is evident that his own view of them is a correct one, and the modification which Steenstrup's expression of the law has since undergone can never deprive it of its value in opening up more philosophic views of the morphology of the invertebrate animals, and marking out a new era in their study.

[1] George Johnston, 'A History of the British Zoophytes,' Edinburgh, 1838.

[2] Op. cit., 1785.

[3] Rudolf Wagner, 'Neue im Adriatischen Meere gefundene Art von nacktem Armpolypen,' Isis, 1833, iii, p. 256.

[4] S. L. Loven, "Beitrag zur Kenntniss der Gatungen *Campanularia* und *Syncoryne*," 'Müller's Archiv,' 1837.

[5] Martin Sars, 'Beskrivelser og Jagttagelser over nogle mœrkelige eller nye i Havet ved den Bergenske Kyst levende Dyr,' &c., Bergen, 1835; and 'Ueber die Entwickelung der *Medusa aurita* und der *Cyanea capillata*,' in 'Wiegm. Arch.,' 1841.

[6] Joh. Japetus Steenstrup, 'Ueber den Generationswechsel oder die Fortpflanzung und Entwickelung durch abwechselnde Generationen, eine eigenthümliche Form der Brutpflege in den niedern Thierclassen. Uebers. von Lorenzen,' Kopenh., 1842. Also translated for the Ray Society, by Busk, London, 1845.

Nearly at the same time some beautiful additional observations were made by Dujardin,[1] who traced various known forms of free hydroid Medusæ to their fixed trophosomes, and had seen them produce eggs; from this epoch we may regard as definitely established the genetic relation between the free hydroid medusa and the fixed trophosome.

In 1843 two memoirs on the Campanularian and Tubularian Hydroids were presented by Van Beneden to the Royal Academy of Brussels.[2] The structure and gemmation of several species are described at length, and the memoirs are accompanied by very beautiful figures. He has seen and described with much detail the free medusoid gonophores, as well as the fixed sporosacs, but he mistakes the former for embryos destined by direct metamorphosis to become changed into the form of the polypoid trophosome. He founds the new genus, *Hydractinia*, for the *Alcyonium echinatum*, of Fleming, and calls attention to the polymorphism of the zooids in this interesting and remarkable hydroid.

The voyage of the French corvette, "La Coquille," under the command of Duperrey, during the years 1822—1825,[3] afforded to Lesson, who, along with Garnot, accompanied the expedition as naturalist, fine opportunities for the study of the Medusæ; and in 1843 we find him publishing, as a volume of the "Suites à Buffon," his 'Histoire Naturelle des Acalephes.'[4] Lesson's work contains a great mass of information, and shows that its author must have had a very extensive acquaintance with the Medusæ, and yet we cannot say that, beyond the description of some new forms, our knowledge of the HYDROIDA has received from him any advance. Indeed, he does not avail himself as he might of the discoveries of his predecessors, while in his classification the Hydroid medusæ are, as usual, mixed up with the *Discophora* proper.

Up to this point of our history it is plain that the systematic writers who came after Eschscholtz have fallen behind him in their appreciation of the Hydroid medusæ as a natural group; for though Eschscholtz misunderstood the peculiarities of organization on which he founded his "Discophora cryptocarpæ," this group is not the less a natural one, and the *cryptocarpæ* of Eschscholtz must be recognised in every system which would aim at expressing the true position and affinities of the various members of that large and heterogeneous assemblage of organisms which have been included under the common name of Medusæ.

It was not, indeed, until 1846 that the Eschscholtzian division of the Medusæ into two grand groups was distinctly accepted by any other naturalist. In this year, however, a paper was read before the British Association by Edward Forbes,[5] in which the author divides the Medusæ into two groups, corresponding with the *phanerocarpæ* and *cryptocarpæ* of Eschscholtz.

The erroneousness of Eschscholtz's interpretation of the characters on which he founded his subdivision had by this time become apparent, and Forbes accordingly, while admitting the value of the groups, bases them on other characters than those employed by Eschscholtz; for he finds in the condition of the marginal bodies and of the gastro-vascular canals points of structure

[1] Fél. Dujardin, "Observations sur un nouveau genre de Medusaires (*Cladonema*) provenant de la Métamorphose des Syncorynes," 'Ann. Sci. Nat.,' 2e sér., 1843.

[2] P. J. Van Beneden, 'Recherches sur l'Embryogenie des Tubulaires, et l'Histoire Naturelle des différents genres de cette famille qui habitent la côte d'Ostende,' Bruxelles, 1843.

[3] 'Voyage autour du Monde sur la Corvette la Coquille, pendant les Anneés 1822, 1823, 1824 et 1825, par M. L. J. Duperrey, capitaine de frégate, commandant l'expédition.'

[4] René Primevère Lesson, 'Histoire Naturelle des Zoophytes. Acalephes.' Paris, 1843.

[5] Edward Forbes, "On the Pulmograde Medusæ of the British Seas," 'Brit. Assoc. Rep.' for 1846.

by which the two divisions may be anatomically characterised. In 1848 Forbes's views were further developed in a beautiful monograph on the Naked-eyed Medusæ of the British seas,[1] in which every known British species of hydroid Medusa is described and illustrated by an original figure. In this work he distinguishes the two groups by the names of "Steganophthalmia," corresponding with the *Discophora phanerocarpa* of Eschscholtz, and "Gymnophthalmia," corresponding with his *Discophora cryptocarpa*. With Forbes's monograph we may date the definite acceptance of the hydroid Medusæ as a well-marked and legitimate group.

The *Radiata* of Cuvier, which, by the elimination of various groups originally included in it, had been gradually attaining to a form more in accordance with the requirements of a natural classification, was in 1847 subjected to an important revision by Leuckart,[2] who insisted on the necessity of attending to a remarkable type of structure, which was common to certain members of the *Radiata* as then accepted by zoologists, namely, the free communication of the general body-cavity with the external world through the mouth. He saw in this feature a character of great value by which, after the exclusion of the *Polyzoa*, the whole of the Cuvierian "polypi" and "acalepha" would require to be united into a distinct group apart from the *Echinodermata*. To the group thus constituted Leuckart gave the name of *Cœlenterata;* while soon after Huxley was led to adopt similar views, and, quite independently of Leuckart, proposed the construction of an exactly equivalent group, under the name of *Nematophora*, suggested by the universal presence of thread-cells in the tissues of the animals composing it.[3]

The relation between the fixed hydroid trophosomes and the free hydroid medusæ, which, as we have seen, had already become apparent, received about this time additional light from the researches of Dalyell,[4] an acute, laborious, and conscientious observer, though without that technical precision in his descriptions which indicates a special zoological training, and without much acquaintance with what had been already done by others. Dalyell has recorded many additional instances of the development of Medusæ from the hydroid trophosome; and the accumulation of such facts now began to exert an influence on the classification.

We accordingly find Carl Vogt in 1851 combining the fixed hydroids with the whole of the *Discophora* of Eschscholtz, in order to form a single group, to which he gives the name of *Hydromedusæ*.[5]

In 1853 we find Kölliker employing the name of *Hydromedusida*,[6] but restricting it to a group composed of the gymnophthalmic Medusæ of Forbes, the Siphonophorous genus *Velella*, and all the non-natatory hydroids, except *Hydra*, which he unites with the rest of the *Siphonophora* to form his group *Hydroidea*, while he confines the name *Discophora* to the *Steganophthalmia* of Forbes, or *Discophora phanerocarpa* of Eschscholtz.

These proper Hydrozoal groups are, along with the *Ctenophora*, united to the *Actinozoa*, in order to form his division *Radiata molluscoida*, which would thus constitute a great natural

[1] Edward Forbes, 'A Monograph of the British Naked-eyed Medusæ,' London, 1848. Published by the Ray Society.

[2] Hnr. Frey und Rud. Leuckart, 'Beiträge zur Kenntniss wirbelloser Thiere,' Braunschweig, 1847.

[3] Th. H. Huxley, "An Account of Researches into the Anatomy of the Hydrostatic Acalephæ," 'Brit. Assoc. Rep.' for 1851.

[4] Sir John Graham Dalyell, 'Rare and Remarkable Animals of Scotland,' London, 1847.

[5] Carl Vogt, 'Zoologische Briefe,' Frankfurt-a-M., 1851.

[6] Albert Kölliker, 'Die Schwimmpolypen oder Siphonophoren von Messina,' Leipsig, 1853.

group corresponding to the *Cœlenterata* of Leuckart, were it not that Kölliker unfortunately combines with the cœlenterate forms the *Polyzoa*, so as to form by the union of the two his *Radiata molluscoidea*.

The same year Leuckart[1] proposed to divide the whole of the *Cœlenterata* into three classes —the *Ctenophora* of Eschscholtz, composed of the Beroes and their allies; the "Medusæ" (Scheibenquallen), and the "Polypes," which last name he confines to the Actinozoal *Cœlenterata*. Under the "Medusæ" of this classification are comprised three orders—the *Discophora* proper, the *Hydroida* with their Medusæ, and the *Siphonophora*.

The union thus nearly simultaneously proposed by Kölliker and by Leuckart of the non-natatory forms of hydroids with the gymnophthalmic Medusæ so as to form a group distinct from that of the steganophthalmic Medusæ, is the first expression we have of a natural relation which all subsequent research has only tended to confirm.

In 1856 Leuckart published his Supplement to Van der Höven's 'Manual of Zoology.[2] In this valuable little work we find him distributing the gymophthalmic Medusæ between two groups. Those which he believes to undergo a direct metamorphosis without the intervention of a hydroid trophosome are combined into one order, to which he gives the name of *Ceratostera*, from the rigid habit of their marginal tentacles; while those which are known to be produced as buds from a trophosome are associated with their trophosomes, and with other fixed hydroids in which the gonophore never assumes the form of a free medusa, so as to constitute his order *Hydroidea*.

In the same year Huxley[3] proposed to divide the group *Cœlenterata* into two classes, which he names *Hydrozoa* and *Actinozoa*. Instead of assigning to the *Ctenophora* the value of a distinct class, he regards them as *Actinozoa*, thus bringing them into immediate relation with *Actinia*.

In 1857 Gegenbaur published a very valuable paper on the Medusæ,[4] in which he describes and figures many new forms of *Gymnophthalmia*, the subordinate groups of which he revises and limits more in accordance with the natural affinities of the animals than had been hitherto attempted. He adopts the Eschscholtzian subdivision; but instead of basing it on the characters assumed by Eschscholtz, or on those proposed by Forbes, he finds the grounds of the subdivision in the presence or absence of the membranous diaphragm which extends horizontally inwards from the margin of the umbella, and which Forbes had already designated by the name of "Velum." In accordance with this view Gegenbaur divides the Medusæ into the *Acraspeda*, or those in which no velum is developed, and which correspond to the *Steganophthalmia* of Forbes, and the *Craspedota*, or those which are provided with a velum, and which correspond to the *Gymnophthalmia* of Forbes.

In 1858 McCrady published an important paper on the "Gymnophthalmic Medusæ,"[5] in which many new forms are described and figured. Instead, however, of limiting his group *Gymnophthalmia* within the bounds of that to which Forbes had already assigned this name, he extends

[1] Rud. Leuckart, 'Zoologische Untersuchungen.' Erstes Heft. Giessen, 1853.

[2] Rud. Leuckart, 'Nachträge und Berichtigungen zu dem ersten Bande von J. Van der Höven's Handbuch der Zoologie,' Leipsig, 1856.

[3] Thomas Henry Huxley, "Lectures on General Natural History," in 'Medical Times' for 1856.

[4] Carl Gegenbaur, "Versuch eines Systemes der Medusen," 'Zeitsch. für Wissensch Zoologie,' 1857.

[5] J. McCrady, the *Gymnophthalmata* of Charleston Harbour, 'Proc. of the Elliott Society of Natural History,' Charleston, 1858.

it by uniting with the medusoid form which constitutes the *Gymnophthalmia* of Forbes, not only the polypoid forms of hydroids, but also the *Siphonophora*. The *Gymnophthalmia* of M'Crady thus correspond to the *Hydromedusida* and *Hydroidea* of Kölliker united.

In a small treatise on the alternation of generations among the hydroids,[1] Gegenbaur had already contributed some valuable observations to our knowledge of the generative phenomena and life-history of the HYDROIDA; while, as we have seen, he had also made the so-called naked-eyed Medusæ a subject of careful systematic study. In his 'Outlines of Comparative Anatomy,' published in 1859,[2] he retains his divisions of *Acraspeda* and *Craspedota*, uniting them into a single order, *Medusida*, while he combines the various non-natatory hydroid colonies into another order under the name of *Hydroida*.

In 1859 Huxley gave us a monographic treatise on the *Siphonophora* observed during the circumnavigatory voyage of H.M.S. "Rattlesnake."[3] The "Rattlesnake" was fitted out in 1846, under the command of Captain Owen Stanley, for the purpose of surveying the channel lying within the great barrier reef which extends along the east coast of Australia, and for the exploration of the neighbouring seas; and the expedition was accompanied by Mr. Huxley as assistant-surgeon. Owing to the refusal of the Admiralty, on the return of the expedition, to furnish the means of publication, the results of Huxley's observations remained unpublished, until, after many fruitless attempts to obtain the aid of Government, and many years of vexatious delay, the Ray Society undertook the task of publication. In this valuable work the *Siphonophora* are described under the designation of *Oceanic Hydrozoa*. The special part of the treatise is preceded by a general introduction, which abounds in original and philosophic views of the morphology of the HYDROIDA and of their relation to the other groups of *Hydrozoa;* and the author proposes a new and comprehensive terminology, much of which has been adopted in the present Monograph. In his systematic arrangement of the *Hydrozoa;* he does not venture to unite into a single group with the polypoid phases of the HYDROIDA those hydroid Medusæ which have not been proved to proceed from a polypoid trophosome, but prefers to arrange them as a distinct order of *Hydrozoa* under the name of *Medusidæ,* attaching, however, only a provisional significance to the group thus constituted.

Between 1860 and 1862 there appeared the third and fourth volumes of Agassiz's 'Contributions to the Natural History of the United States.'[4] These volumes are devoted to the *Hydrozoa,* which are treated of under the designation of Acalephæ. We learn from the preface to the first volume that the author has been assisted by Prof. H. J. Clark, to whom the microscopical researches which form so valuable a portion of the work are mainly due. Many new genera and species of hydroids are described, and their trophosomes as well as gonosomes represented in elaborate and beautiful figures drawn from the living animal, while the number and beauty of the drawings expressing anatomical and embryological details give to

[1] Carl Gegenbaur, 'Zur Lehre vom Generationswechsel und der Fortpflauzung bei Medusen und Polypen,' Wurzburg, 1854.

[2] Carl Gegenbaur, 'Grundzüge der Vergleichenden Anatomie,' Leipzig, 1859.

[3] Thomas Henry Huxley, 'The Oceanic Hydrozoa; a Description of the Calycophoridæ and Physophoridæ observed during the Voyage of H. M. S. "Rattlesnake," in the years 1846-50.' London, printed for the Ray Society, 1859.

[4] Louis Agassiz, 'Contributions to the Natural History of the United States of America,' Boston, 1857—62.

this work a special value, and place it among the most important contributions we possess to the natural history of the HYDROIDA.

Agassiz here divides his "Acalephæ" into three orders, *Ctenophora*, *Discophora*, and *Hydroida*, which last embraces the *Gymnophthalmia* of Forbes, the admitted polypoid forms of *Hydrozoa*, and the *Siphonophora* and *Lucernariæ;* and he also, contrary to the universally entertained opinion of previous naturalists, maintains that the corals constituting the still living group of the *Tabulata*, and those forming the entirely extinct groups of the *Tubulosa* and *Rugosa*, have a true hydroid structure, and that they must accordingly be removed from the *Actinozoa*, with which they had been hitherto associated, and take their place among the genuine HYDROIDA.

It will be seen that Agassiz here follows Kölliker, Leuckart, and M'Crady in uniting the polypoid forms of *Hydrozoa* with the gymnophthalmic Medusæ as elements in a group equivalent in value with that of the *Discophora*, a name which he employs in the limited sense adopted by Kölliker to indicate the *Discophora phanerocarpa* of Eschscholtz.

In 1861 Greene published his excellent little Manual of the Cœlenterata,[1] a work which gives us in a condensed form a very complete view of the structure, development, and relations of the various members of this group. He adopts the name of *Hydrozoa* in the sense in which it was limited by Huxley, while he combines the gymnophthalmic Medusæ into a distinct order from which the polypoid forms are excluded, and thereby as, I believe, fails to express the true relations of these organisms.

Though Greene's Manual lays no claim to originality, it discusses in a philosophic spirit various questions bearing on the subject with which it is occupied, and constitutes one of the most valuable aids to the general study of the *Cœlenterata* which can be placed in the hands of the student.

In the first volume of the 'Manual of Zoology,' by Peters, Carus, and Gerstaecker,[2] published in 1863, J. Victor Carus gives us among other articles an excellent one on the *Cœlenterata*. The *Hydromedusæ* which form his third order of *Cœlenterata* are here divided into the *Siphonophora* and *Hydroidea*, the latter embracing both the free gymnophthalmic Medusæ and the polypoid colonies. The article contains an account of the leading anatomical and embryological features of the HYDROIDA; and the subordinate groups under which the author believes that they ought to be distributed are characterised. It also contains a very useful synopsis with diagnoses of all the genera of hydroids.

Observations on both the hydriform and medusiform elements of the HYDROIDA had been thus for several years accumulating, and the time had already come when it seemed possible to assign to the free hydroid Medusa its proper place in a comprehensive system of the HYDROIDA. The importance of uniting the two elements in the definitions of genera had been already recognised by M'Crady, Agassiz, and Victor Carus; but notwithstanding the prominence which these authors, and especially Agassiz, had given to the medusiform buds, it did not seem that a thoroughly natural distribution of the HYDROIDA under legitimately limited genera had yet been effected, and this belief led me in 1864 to attempt a revision of the older genera of all tubularian and campanularian hydroids whose hydriform element was known.[3]

[1] Joseph Reay Greene, 'A Manual of the Sub-kingdom Cœlenterata,' London, 1861.

[2] Wilh. C. H. Peters, Jul. Victor Carus, und C. E. Adolph Gerstaecker, 'Handbuch der Zoologie,' Leipzig, 1863.

[3] Allman, 'On the Construction and Limitation of Genera among the Hydroida.' 'Ann. and Mag. of Nat. Hist.' for May, 1864.

In the diagnoses of the genera I regarded the reproductive zooid, whether fixed or free, of as much importance as the nutritive, and the resulting classification, in so far as it applies to the subject of the present Monograph, is, with such modifications as further investigations rendered necessary, that which I have here adopted.

At this period the *Æginidæ* constituted a group of Medusæ whose structure was but imperfectly understood, and whose systematic position and affinities had given rise to much discussion. In 1865, however, Ernst Haeckel published some very valuable observations[1] which no longer leave any doubt that these Medusæ possess a true hydroid structure, by which they become associated with the ordinary hydroid or gymnophthalmic Medusæ; while he still further made the remarkable discovery that *Cunina*, a typical Æginidan, is produced as a bud from *Geryonia*, a medusa of an entirely different form, and one whose true hydroid affinities had never been doubted.

In the same year, Alexander Agassiz published his illustrated Catalogue of the North American Hydrozoa contained in the Museum of Comparative Zoology at Harvard College.[2] In this work, besides other hydrozoal groups, a large number of hydroid Medusæ, occasionally accompanied by their trophosomes, and including many new forms, are described and illustrated by very expressive woodcuts. The views of Prof. Louis Agassiz on almost all that concerns nomenclature, generic groups, and systematic position and affinities are throughout adopted by his son; but whether these views be in all points accepted or not, we cannot but regard the work of Alexander Agassiz as tending in no small degree to advance to our knowledge of the zoology of the HYDROIDA.

In 1866, while the present sheets were passing through the press, M. Van Beneden published in the 'Memoirs of the Royal Academy of Belgium' a treatise on the Natural History of the *Cœlenterata* of the Belgian Coast, a group for which he uses the general name of "polypes."[3]

The greater part of the work is devoted to the HYDROIDA; it is illustrated by many beautiful plates, and is one of the most elaborate treatises which has been hitherto published on these animals. M. Van Beneden describes and figures not only a considerable number of the fixed forms, but also many free medusiform gonophores; and the work must be regarded as a valuable contribution to the iconography and descriptive natural history of the Hydroida, though the author's opinions on many points, more especially such as concern the synonomy and determination of species, cannot receive our assent, and will be discussed in another part of the present Monograph.

While the natural history of the HYDROIDA was thus gradually advancing towards perfection in all that appertains to descriptive Zoology and systematic arrangement, the anatomists were developing it from a structural and embryological point of view. The introduction of the achro-

[1] Ernst Haeckel, 'Ueber eine neue Form des Generationswechsels bei den Medusen, und über die Verwandeschaft der Geryoniden und Aegmiden Monatsbericht der Könige Akad. der Wiss. zu Berlin,' 2 Feb., 1865. Translated in the 'Ann. of Nat. Hist.' for Jan. 1865.

Id., 'Beiträge zur Naturgeschichte der Hydromedusen,' Leipzig, 1865.

[2] 'Illustrated Catalogue of the Museum of Comparative Zoology at Harvard College.' No. II. "North American Acalephæ." By Alex. Agassiz. Cambridge, U.S., 1865.

[3] P. J. Van Beneden, "Recherches sur la Faune littorale de Belgique.—Polypes." 'Mém. de l'Acad. Roy. de Belg.,' tome xxxvi. Published also in a separate form.

matic microscope had already placed in their hands a new and powerful instrument of investigation, and discoveries in the anatomy and physiology of the lower animals had begun to accumulate with a rapidity hitherto unprecedented. We have already referred to the important light which the microscope in the hands of Ehrenberg, Sars, Dalyell, Steenstrup, Dujardin, Leuckart, and Gegenbaur had thrown upon the mutual relations and life-history of these animals, and we have seen the influence it has thus had on their classification, while within the last twelve years the microscopical investigation of the HYDROIDA has been pursued with an assiduity greater than at any former period, and has yielded the results which might have been expected from the numerous able observers who have been engaged in it. To give, however, in the present historical sketch even an imperfect analysis of the various discoveries by which recent anatomical research has enriched our knowledge of the HYDROIDA, would be impossible without extending our introductory pages far beyond the limits within which it is expedient to confine them, and the reader must accordingly be referred for an account of such discoveries to the parts of this work where they will be specially considered.

The steps which in the history just sketched have exerted the greatest influence in determining the boundaries and systematic position of the HYDROIDA, in the sense in which this group is limited in the present Monograph, would seem to be the following:—

1. The discoveries of Trembley in the anatomy and physiology of *Hydra*.

2. The researches of Ellis among the marine forms, which resulted in the complete establishment of the animality of the fixed plant-like HYDROIDA—results to which the observations of Peysonelle and De Jussieu had led the way.

3. The establishment of the *Radiata* by Cuvier as one of the four primary divisions of the animal kingdom.

4. The recognition by Eschscholtz of two types of form among the Medusæ, and his consequent subdivision of these organisms into the *Phanerocarpa* and *Cryptocarpa*.

5. The recognition by Cuvier, Milne-Edwards, and Rapp, of the difference of structure which separates the actinozoal from the hydrozoal forms of the so-called "Polypi."

6. The determination by Ehrenberg of the sexuality of the HYDROIDA.

7. The discovery of a genetic relation between certain free gymnophthalmic Medusæ and the fixed Hydroids, by Loven, Sars, Dalyell, Dujardin, and others, and the correlation of this with analogous phenomena by Steenstrup.

8. The gradual rectification of the *Radiata* of Cuvier by the successive elimination of the Nullipores, Worms, *Infusoria*, *Rhizopoda*, and *Polyzoa*.

9. The further analysis by Leuckart of the amended *Radiata*, resulting in his establishment of the group *Cœlenterata*.

10. The union by Kölliker and Leuckart of certain free gymnophthalmic Medusæ with the fixed HYDROIDA, so as to constitute a single group equivalent in value with that of the *Discophora* or steganophthalmic Medusæ.

MORPHOLOGY OF THE HYDROIDA—TERMINOLOGY.

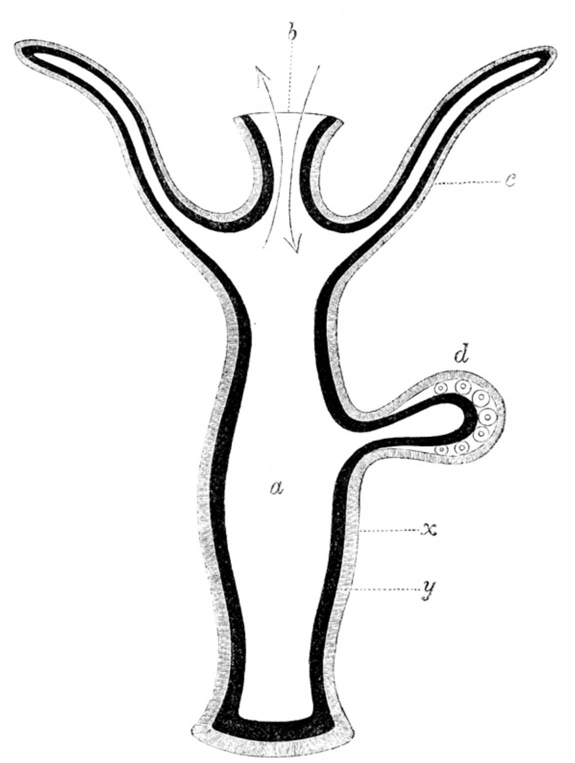
I. The Hydrosoma in general.

1. *Generalised conception of a Hydroid.*

We shall best bring this part of our subject before the mind, if we first endeavour to conceive of hydroid organisation freed from all non-essential complication.

Let us, then, imagine an open sac (woodcut, fig. 1), whose walls consist of a double membrane (*x*, *y*), and whose orifice (*b*) is surrounded by a circle of tubular tentacles (*c*) formed by cæcal offsets from its cavity. Let us further suppose that there projects from some part of the walls of this sac another sac (*d*), also composed of a double membrane. To the morphological conception thus acquired, let us add the physiological one which we obtain by regarding the walls as endowed with irritability; and as a further physiological element in our ideal picture, let us imagine that while the former sac subserves the function of a digestive cavity, the latter, which has been emitted as an external bud from its side, is destined to give origin to generative elements which are formed between the two membranes which constitute its walls; and we shall then have as general an idea, morphological and physiological, as it is possible to form of a hydroid.

Fig. 1.



Diagramatic section of a Hydroid.

a, Body cavity; *b*, orifice serving for ingestion and egestion; *c*, tentacle; *x*, outer membrane of body walls (ectoderm); *y*, inner membrane of body-walls (endoderm); *d*, generative sac, containing eggs. The endoderm is throughout indicated by a darker shading than that of the ectoderm.

The hydroid organism, however, which we have thus reduced to its simplest expression, admits of much and varied complication, while the actual forms which we meet with in nature present a beautifully graduated series, in which the law of specialisation is expressed with a distinctness and significance in the highest degree instructive, and whose study possesses a peculiar interest in leading us to those wider generalisations in which other groups of the *Hydrozoa* may be included, and by which we are enabled to assert a morphological unity of the whole.

2. *General Structure—Ectoderm and Endoderm.*

Every hydroid is composed of two membranes, an outer or *ectoderm* (woodcut, fig. 1, *x*), and an inner or *endoderm* (*y*), the ectoderm having its free surface in direct relation with the medium in which the animal lives, while the free surface of the endoderm is turned inwards, and forms the boundary of the gastric cavity and of all its prolongations through the organism. A similar composition may be demonstrated not only in all the rest of the *Hydrozoa,* but in the whole group of the *Cœlenterata.* For the important generalisation which thus asserts the composition of every cœlenterate animal out of two membranes—a generalisation which forms the basis of the whole morphology of the *Cœlenterata*—we are indebted to Prof. Huxley, who first enunciated it as a great anatomical truth.[1]

Another character which the HYDROIDA possess in common with the entire group of Cœlenterata is the presence of the peculiar bodies known as *thread-cells.* These bodies, which will be afterwards more particularly examined, are developed in the ectoderm, where they are frequently aggregated in definite groups very characteristic of the species.

3. *Composite character of the Hydroida—Trophosome, and Gonosome.*

The HYDROIDA, wherever our knowledge of them is sufficiently complete to justify us in arriving at any well-founded conclusion regarding the entire life of the individual are all, with only a single apparent exception, composite animals at some one period of their existence, each consisting then of an assemblage or colony of zooids,[2] in organic union with one another (woodcut, fig. 2). The colony thus formed constitutes the "hydrosoma" of Huxley.

It will be shown in the sequel that, except in the solitary—and, perhaps, after all, only

[1] Huxley, "On the Anatomy and Affinities of the Medusæ," 'Phil. Trans.,' 1849.

[2] For the introduction of the very convenient term "zooid" into the language of zoology, we are indebted to Prof. Huxley, who, in defining the "individual" as "the total result of the development of a single ovum," proposed to designate by the term zooid all more or less independent forms which may be included as elements in this total result. (See Huxley, "Observations on *Salpa,*" &c., in 'Phil. Trans.,' 1851; "Lecture on Animal Individuality," 'Ann. Nat. Hist.,' June, 1852; and his review of J. Müller's "Researches on the Development of the Echinodermata," in 'Ann. Nat. Hist.,' July, 1851. See also Carpenter, 'Principles of Gen. and Comp. Physiology,' 1851, p. 906, and 'Brit. and For. Med.-Chir. Rev.' for Jan. 1848 and Oct. 1849, where the same idea is clearly supported, Dr. Carpenter using the expression "a generation" for all that intervenes between one act of true or sexual generation and another.

The distinction between a "zooid" and an "organ" is not always easy, and may indeed sometimes appear to be arbitrary. I believe, however, that we may define a zooid as *a more or less individualised animal organism, which may or may not be capable of independent existence, and which constitutes one of a series whose members are related to each other by some form of non-sexual reproduction, and morphologically repeat one another either actually or homologically.* In this sense not only are the free medusiform buds of the *Hydroida* true zooids, but we must also regard as such the fixed hydranths and those fixed gonophores which never attain a developed medusiform structure, as well as the simple generative sacs which are developed on the radiating canals of *Obelia, Thaumantias,* &c. (see p. 35).

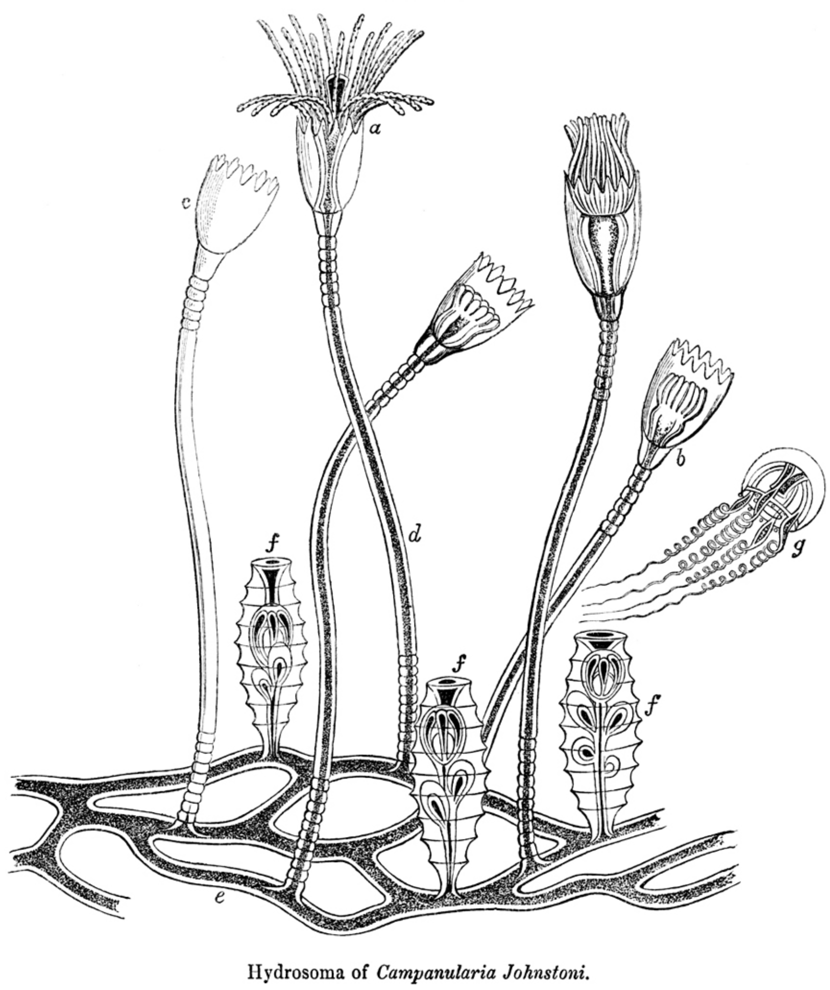
On the other hand, from the above definition are necessarily excluded all mere *organs,* however capable they may be for a longer or shorter period of self-maintenance, such, for example, as the *Hectocotylus* of the Hectocotylus-forming *Cephalopoda.*

Many zooids may combine to form the true *zoological Individual* —the logical element of the *species.*

apparently exceptional—case here referred to, and which will be afterwards more particularly described, those which have been adduced as affording exceptions to this phenomenon are in every instance based upon incomplete observations; that they may or may not be confirmed when opportunities of more extended observation shall have been afforded; and that accordingly, in the present state of our knowledge, we are not justified in accepting them.

The associated zooids are always of two kinds. In one (*a*, *b*), the zooid is destitute of all power of true or sexual generation, and has as its proper function the general nutrition of the colony. The other group of zooids (*f*, *g*) has nothing to do with the general nutrition of the colony; it has as its proper function true generation, and the zooids which compose it give origin to the generative elements—ova or spermatozoa—either directly or after having first developed a special sexual bud. For the whole assemblage of the former, or nutritive zooids, with their common connecting basis, I propose the name of *trophosome*, while I shall designate the entire association of generative zooids by the name of *gonosome*. Every hydroid, therefore, with whose life-history we are acquainted consists essentially—with the solitary exception already alluded to—of a trophosome destined for the preservation of the individual, and of a gonosome for the perpetuation of the species.

FIG. 2.



Hydrosoma of *Campanularia Johnstoni*.

a, *b*, *c*, *d*, *e*, Various portions of the trophosome; *f*, *f*, *f*, *g*, of the gonosome. *a*, Hydranth expanded; *b*, hydranth contracted; *c*, empty hydrotheca; *d*, free portion of hydrophyton (hydrocaulus); *e*, adherent portion of hydrophyton (hydrorhiza); *f*, *f*, *f*, gonangia, containing generative buds, which in this genus are blastochemes; *g*, a blastocheme just after its escape from the gonangium.

4. *Orientation.*

The attached extremity of the fixed hydrosoma, or its equivalent in the free one, is described by Huxley as the *proximal* end; that which is placed diametrically *opposite* to this is the *distal* end. In the present Monograph I shall employ the terms proximal and distal in the sense thus proposed. Beyond these two aspects none other can be definitely distinguished in the HYDROIDA. The determination of a right and a left side is impossible, for though an apparent bilateralism occasionally occurs, as, for example, in the planoblasts of *Corymorpha* (Pl. XIX), and in those of *Gemmellaria* (Pl. VII) and *Dicoryne* (Pl. VIII); these conditions must be regarded rather in the light of an arrest or retardation of the development which in the vast majority of cases results in the symmetrical disposition of the parts radially round a common axis.

II. MORPHOLOGY OF THE TROPHOSOME.

1. *Hydranths.*

Two distinct portions enter into the composition of the trophosome, namely, the hydranths and the hydrophyton.

The proper nutritive zooids (woodcut, fig. 2, *a*, *b*) which constitute the essential part of the trophosome of the Hydroida have been usually known in common with the zooids of the *Actinozoa*, or proper coral-animals, by the name of "polypes." It will be more convenient, however, to restrict this term to the *Actinozoa*, to which Réaumur originally applied it, borrowing the word from Aristotle, who used it, not for cœlenterate animals at all, but for the cuttle-fishes; while for the alimentary zooids of the HYDROIDA I shall in the present work employ the term *hydranth*.[1]

The hydranth consists essentially of a digestive sac opening at one end by a mouth. Behind the mouth are situated tubular offsets from the sac; these are known as *tentacula*. The mouth itself is borne on the summit of a more or less distinctly developed proboscis-like extension of the sac, and to this the name of *hypostome* may be given.

The hydranth is developed on some part of the hydrophyton, which usually forms for it a hollow, stem-like support (*d*), on whose summit or sides it is carried, and with whose cavity its own is directly continuous.

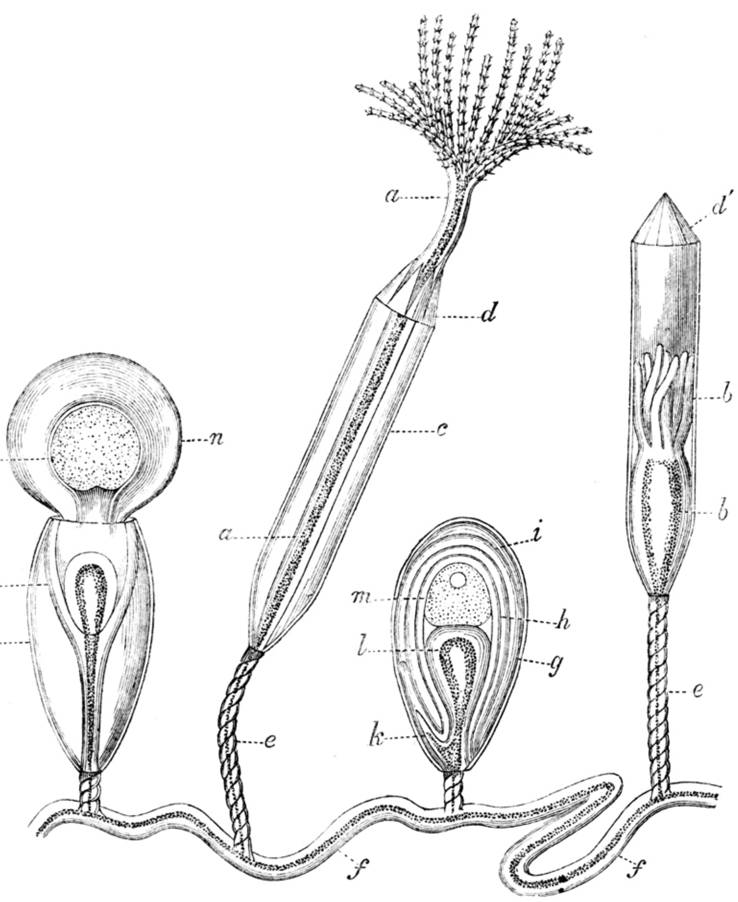
The form of the hydranth varies. It may be flask-shaped, or fusiform, or nearly cylindrical; but is in every case more or less mutable, constantly changing its shape as the result of various states of contraction. The hypostome may pass imperceptibly into the body of the hydranth (*Hydra*, *Perigonimus*), or it may be strongly differentiated from it, and it then usually presents a trumpet-like form, though frequently acquiring at the same time increased contractility and

[1] Huxley uses in the same sense the term *polypite*, and in former publications of my own I followed him in the employment of this word. As, however, a virtually identical term (polypide) is in use for the exsertile and retractile portion of a polyzoon, an objection similar to that which renders inexpedient the use of the word polype may be urged against the employment of polypite in the terminology of the Hydroida.

mutability of outline (*Eudendrium*, *Campanularia*, woodcuts figs. 2 and 13). The tentacles vary in form, number, and arrangement in the different species, and thus afford excellent characters for the purposes of classification. Their axial tube may be continued throughout (*Hydra*), or it may be more or less obliterated (*Coryne*, *Campanularia*). They are usually simple filiform processes, as in *Hydra*, *Clava*, *Hydractinia*, *Campanularia*, &c.; but in some cases their extremity presents a knob-like enlargement, as in *Coryne*, when they are said to be "capitate." Their number may be as low as two (*Lar*), or it may amount to more than 100 (*Corymorpha nutans*). They may be arranged in a single circlet (*Campanularia*),[1] or in two (*Vorticlava*), or in several (*Stauridium*), or they may be scattered over the body of the hydranth (*Coryne*), or may be partly verticillate, partly scattered (*Pennaria*). Finally, they may be all of one kind (filiform, as in *Clava*, capitate, as in *Coryne*), or the same hydranth may carry both filiform and capitate tentacles (*Stauridium*).

In a great number of hydroids the hydranth is destitute of any external protection (*Tubularia*, *Coryne*, &c.). In others, however, there exists a cup-shaped receptacle, within which

FIG. 3.



Portion of the Hydrosoma of *Calycella syringa*, showing the operculate hydrothecæ, &c.

a, *a*, The hydranth extended; *b*, *b*, hydranth retracted; *c*, hydrotheca; *d*, operculum open for the exit of the hydranth; *d'*, operculum closed after the retraction of the hydranth; *e*, *e*, hydrocaulus; *f*, hydrorhiza; *g*, gonangium with its contents previous to the escape of ovum; *g'*, gonangium after the passage of the ovum into an acrocyst; *h*, walls of sporosac; *i*, gubernacular sac; *k*, remains of blastostyle; *m*, ovum still contained within the sporosac; *n*, acrocyst; *o*, ovum after its escape into the acrocyst; *p*, empty sporosac, still enclosing the spadix.

[1] A single circlet may be absolutely simple or it may result from the close approximation of two or more verticillate series of tentacles.

4

it may be partially or totally withdrawn, and from which it may again spontaneously extend itself (*Campanularia, Sertularia,* &c.). To this receptacle, which is characteristic of a large section of the Hydroida, the name of *hydrotheca* has been given by Huxley.

The hydrotheca is formed of a chitinous membrane continuous below with the perisarc or common chitinous investment of the hydrophyton, to be presently described. Its margin may be quite even, or it may be divided into minute teeth (woodcut, fig. 2); the cup may be permanently open (woodcut, fig. 2), or it may be provided with a kind of operculum formed of triangular segments, united, as by a hinge, to the margin, and capable of completely closing over the cup when the hydranth is retracted (woodcut, fig. 3). Sometimes the operculum consists of a flexible membranous continuation of the cup-margin, and then, during the retracted state of the hydranth, falls together in loose folds.

In a few hydroids (*Bimeria*, Pl. XII, fig. 1) the chitinous perisarc is continued from the hydrophyton for a greater or less distance over the hydranth, which it closely invests without forming anything like a free hydrotheca. In others (various species of *Bougainvillia*, Pl. IX and X) the perisarc continued over the hydranth invests it so loosely that in extreme contraction the hydranth seems to be withdrawn into a cup; but this apparent cup has nothing of the permanent form or rigid texture of a true hydrotheca, and is always thrown into more or less distinctly marked transverse folds or rugæ by the contraction of the hydranth.

2. *Hydrophyton.*

The term *hydrophyton* is used to designate the common basis by which the various zooids of the hydrosoma, or general colony, are kept in union with one another.

Cœnosarc and Perisarc.—The hydrophyton consists mainly of a fleshy tubular basis, composed, like all the zooids which it supports, of an ectoderm and an endoderm. I shall designate this fleshy and only essential portion of the hydrophyton by the name of *cœnosarc.*

In every member of the Hydroida, however, with whose trophosome we are acquainted, excepting only the fresh-water *Hydra*, and possibly also *Nemopsis* and *Acaulis*, whose trophosomes, like that of *Hydra*, are stated—though without sufficient evidence—to be free, the ectoderm excretes from its outer surface an unorganised pellicle, chemically identical with chitine, and forming an external tubular investment for the soft organised ectoderm.[1] This unorganised excretion, which must be placed in a totally different category from that of the ectoderm and endoderm, I shall designate as the *perisarc.* In some cases it is confined to the hydrophyton; in others it extends, not only over the entire hydrophyton, but is continued for a greater or less extent, and in a more or less modified form, over the various zooids of the colony. In the *Sertularinæ* and *Campanularinæ* it forms the cup-like receptacles or *hydrothecæ* already described, into which the hydranths are retractile; as well as peculiar receptacles—the *gonangia* (woodcuts, fig. 2, *f*, and fig. 3, *g*)—destined for the protection of the sexual buds. It varies greatly in thickness, from a tough investment, in which numerous layers of deposition can be detected, to a delicate, scarcely recognisable pellicle, and is invariably absent from those zooids (fig. 2, *g*) which have detached themselves from the colony in order to lead an independent life in the open sea. In the adult *Hydractinia* and *Podocoryne* it presents the very exceptional condition of not only investing the

[1] If future observations should confirm the view entertained by Agassiz, as to the hydroid nature of the tabulate and rugose corals, we shall then have examples of calcareous as well as chitinous skeletons among the HYDROIDA.

ectoderm, but being itself overlaid by a soft naked expansion of the cœnosarc, for which it thus forms an internal framework, recalling the sclerobasic corallum of certain *Actinozoa.*

Hydrorhiza and Hydrocaulus.—In almost every case the general colony, or hydrosoma, is attached to some foreign body, such as rocks, shells of mollusca and crustacea, sea-weeds, floating timber, &c., to which it is fixed by some part of its surface (woodcuts, fig. 2, *e*, and fig. 3, *f*). In many cases this is effected by a definite organ of attachment, as in the fresh-water *Hydra,* where, by means of a disc-like expansion of the end diametrically opposite to the mouth, the animal can attach itself to the stems and leaves of aquatic plants, from which it can again spontaneously free itself; or, as in a great number of marine HYDROIDA, in whose young state a disc occupying a similar position (Pl. XIII, figs. 12—16) also becomes an organ of fixation, differing, however, from the corresponding organ in *Hydra* by its not admitting of spontaneous detachment, and by its being usually replaced, as the animal grows older, by adherent tubular offsets, or *stolons,* given off from the same part. For the definite organ of fixation the term *hydrorhiza,* as suggested by Huxley, may be employed; while for the whole of that portion of the hydrophyton which intervenes between the hydrorhiza and the hydranth (woodcuts, fig. 2, *d*, and fig. 3, *e*) it will also be very useful, especially in descriptive zoology, to have a distinct name, and that of *hydrocaulus* may therefore be conveniently used to designate it.

In many cases, however, all trace of a definite hydrorhiza disappears as the animal grows old, and continues to complicate itself by the formation of new buds and branches; and we then find fixation effected by some part of the general surface of the hydrosoma, as in certain creeping Campanularians, &c., in which a greater or less extent of the hydrocaulus itself becomes the medium of attachment. Sometimes it is the hydrocaulus which is suppressed, and the hydranth will then be sessile on the hydrorhiza, as in *Hydractinia* (Pl. XV).

It is occasionally very uncertain whether the part which fixes the hydrosoma ought to be regarded as a true hydrorhiza or as an adherent hydrocaulus. Most usually, however, some peculiarity of structure or of form will justify a decision. Thus, in the *Campanularia* represented in woodcut, fig. 2, the tendency of the adherent portion to form a network of inosculating branches, so very different from anything exhibited by the free stems, will fully entitle us to regard this adherent network as a true hydrorhiza, and to place it in a category distinct from that of the free hydrocaulus.

Again, it is by no means always easy to say where the hydranth ends and where the hydrocaulus begins. In by far the majority of cases the distinction is easy enough, as in the whole of the calyptoblastic hydroids, and in *Tubularia, Corymorpha,* and many others among the gymnoblastic genera, in all of which the line of demarcation is indicated by a marked change of form, and frequently of structure. In some other cases among the *Gymnoblastea,* however, the hydranth passes so imperceptibly into the hydrophyton that it is difficult to say how much we ought to give to the one, and how much to the other.

The limit of the perisarc, or common chitinous investment, will often help us in this. Thus in *Clava* (Pl. I), where the hydranth possesses a very much elongated form, one might easily be led to regard as hydrocaulus what is really part of the hydranth. Here, however, if we consider the whole of the naked portion of the trophosome as belonging to the hydranths, we shall have a distinct though rudimental hydrocaulus in the very short, narrow tubes, invested by a perisarc, which arise from the upper surface of the hydrorhiza, but which have usually been overlooked in the description of this genus. It must, however, be admitted that there are cases among the gymnoblastic hydroids in which the boundary can scarcely be regarded as otherwise than arbitrary.

Besides the fresh-water *Hydra,* two cases have been described in which the entire hydrosoma occurs in a free state. This very exceptional condition is stated to exist in two North American genera, *Nemopsis* and *Acaulis,* whose trophosomes have been found floating free in the open sea. *Acaulis,* however, is described as becoming attached at a later period of its life.[1]

In most cases the hydrophyton becomes developed into a ramified, tree-like growth (*Eudendrium ramosum, Bougainvillia ramosa, Laomedea dichotoma,* &c.). In other cases it consists of a creeping adherent, usually ramified stolon, with simple free tubes sent off from it at intervals (certain species of *Clava, Campanularia,* &c.); while sometimes, as in *Hydractinia* and *Podocoryne,* it forms a continuous stratum, spreading over the surface of some foreign body which the hydroid has selected for its abode.

Nematophores.—In hydroids belonging to the family of *Plumularidæ* certain very remarkable appendages are developed at definite and constant points from the hydrophyton. They have been named *nematophores* by Busk;[2] and though the part they perform in the economy of the hydroid cannot be regarded as strictly determined, they may be here described more appropriately than anywhere else. They consist each of a cup-like receptacle containing a sarcode mass, which can extend itself from the cup in the form of simple or branching processes, and again completely withdraw itself, so as in every respect to resemble the pseudopodial prolongations of a rhizopod. There is usually a cluster of thread-cells immersed in the sarcode.[3]

The receptacle is formed of a chitinous membrane like that of the hydrothecæ, and may either consist of a single chamber (*Aglaophenia pluma*) or its cavity may be divided by a transverse diaphragm into a distal and a proximal chamber, which freely communicate with one another through an orifice in the diaphragm (*Antennularia*).

The nematophores may be attached to the hydrosoma by a broad base, or be adnate to it for a greater or less extent (*Aglaophenia*), or they may taper away to a fine point of attachment at their proximal ends (*Antennularia*).

In *Aglaophenia pluma* there is a nematophore always situated immediately in front of each hydrotheca. It is here adnate to the walls of the hydrotheca, with whose cavity that of its own receptacle communicates by means of a common lateral aperture, through which the sarcode prolongations of the nematophore can freely pass into the interior of the hydrotheca.

In the singular Campanularian genus *Ophiodes* Mr. Hincks has described certain appendages which take the place of the nematophores in the nematophore-bearing genera.[4] They consist of very extensile tentacula-like bodies, which are carried both upon the hydrocaulus and the hydrorhiza. They terminate at their distal extremity in a spherical capitulum loaded with thread-

[1] See M'Crady's account of *Nemopsis,* in Proc. Elliot, 'Soc. of Nat. Hist.' vol. i; and Stimpson on *Acaulis,* in his 'Fauna of Grand Manon,' published in the Smithsonian Contributions. These floating trophosomes, however, are probably only the detached hydranths of fixed forms, while the statement that *Acaulis* becomes subsequently attached is almost certainly founded on an error.

[2] Busk, 'Hunterian Lectures' (MS.), delivered at the Royal College of Surgeons, London, 1857.

[3] Figures of nematophores are given below in the section which treats of the physiology of the Hydroida.

[4] T. Hincks on *Ophiodes,* in 'Ann. Nat. Hist.' for Nov., 1866.

cells and are surrounded at their base by a chitinous sheath. During the life of the hydroid they may be seen to be in a state of great activity, stretching themselves out and twisting about in every direction.

III. Morphology of the Gonosome.

1. *General view of the Gonosome.*

The zooids which compose the gonosome may remain permanently attached to the rest of the hydrosome, or they may become free and lead henceforth an independent existence in the open sea. It will be found very convenient to have a common term to express all these free zooids of the gonosome, and I accordingly propose for them the name of *planoblast*.[1] With one rare exception, they are all in the form of the so-called gymnophthalmic medusæ.

Under the planoblasts, however, must be included certain comparatively rare instances in which the medusiform zooid, though having its natatory organ well developed, remains, from some unknown cause, attached to the trophosome, and attains to sexual maturity without ever actually becoming free. It is capable, however, when accidentally detached, of swimming by the systole and diastole of a true natatory umbrella, and cannot, therefore, be placed in a different category from that of the essentially free planoblast.

The gonophore is the *ultimate generative zooid*,—that on which devolves the duty of giving immediate origin to the generative elements which are always produced from it between its own ectoderm and endoderm without the intervention of any other zooid. It is the only essential part of the gonosome, being never absent. It may remain attached during its whole lifetime, or it may sooner or later separate itself from the rest of the hydrosome, and thus become a free generative bud or planoblast. It presents either the form of a "gymnophthalmic medusa" or else that of a zooid in which the form of the medusa is more or less disguised, or its parts more or less suppressed, but which can nevertheless be always referred by an easy comparison to the essential type of the medusa.

The planoblasts may either be the direct producers of the generative elements, and are then true gonophores, or may never produce the generative elements directly, but only through the intervention of another bud which is developed from them. For this latter form of planoblast, which is thus, strictly speaking, non-sexual, and which, notwithstanding its resemblance to a gonophore, should be carefully distinguished from it, I have given the name of *blastocheme;* while the proper sexual medusiform planoblast may be designated by the term *gonocheme*.

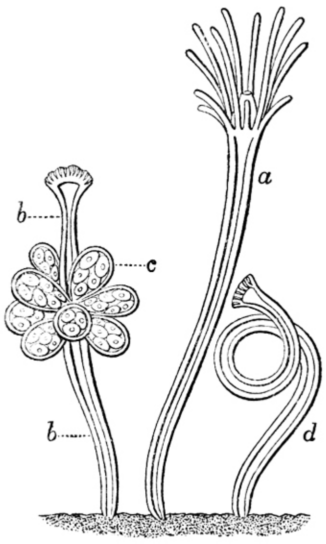
Among the fixed zooids of the gonosome there is very frequently one which, like the blastocheme, takes only a subordinate part in the generative function, being, like it, destined for the production of other generative buds which are developed from some part of its surface, and which may be either gonophores or blastochemes. It is never medusiform, but may be regarded as a peculiarly modified hydranth, having its alimentary function suppressed. It is referred to in the present work under the name of *blastostyle*.

The gonophore is always borne as a bud, either directly upon some part of the trophosome, or upon a blastostyle, or upon a blastocheme. While it is constructed essentially on the plan of a gymnophthalmic medusa, it varies greatly in the degree of completeness in which this plan is expressed in it. It may be referred to one or other of two principal types, based respectively on

[1] "Wandering buds"—πλανομαι and βλαστὸς.

the greater or less approach to the completely formed medusa. The peculiar condition by which one of these types is characterised may be termed *phanerocodonic*, while that which distinguishes the other may be designated as *adelocodonic*—conditions, however, which, it must be borne in mind, pass into one another by numerous gradations.

Fig. 4.



Group of zooids from a colony of *Hydractinia echinata*, taken from near the margin of the colony.

a, alimentary hydranth; *bb*, blastostyle; *c*, gonophores which have been produced as buds from the blastostyle, and are filled with ova; *d*, spiral hydranth, developed close to the margin of the colony. The alimentary and spiral hydranths are connected to one another and to the blastostyle by a common basal expansion or cœnosarc.

The phanerocodonic condition is found in those gonophores (Pl. X, &c., and woodcut, fig. 8) which present an obvious medusa-form, and which are distinguished by having a well-developed umbrella, provided with the wide aperture, or *codonostome*, which characterises the complete medusa; the umbrella, except in one remarkable form—that presented by *Clavatella*, Hincks (woodcut, fig. 5), and *Eleutheria*, Quatrefages—being eminently contractile, and fitted for natation. The adelocodonic condition is found in the bodies to which I have elsewhere given the name of *sporosac;* these bodies (Pl. I, &c., and woodcuts, fig. 4, *c*, and fig. 7) have either no umbrella, or, if this be present, it is in an incompletely developed state, never provided with a wide, open codonostome, and quite incapable of acting as a locomotive organ.

The phanerocodonic gonophores, in by far the greater number of instances, detach themselves from the hydrosoma after they have attained a certain degree of maturity, and lead henceforth an independent existence, during which they increase in size, often develop new parts, and sooner or later give origin to ova or spermatozoa.

In some cases, however, they develope and discharge their reproductive elements while still attached, and then wither away, without ever becoming free, notwithstanding their well-developed contractile umbrella apparently fitting them for an independent natatory existence. If an observation of Agassiz be not really made on two different species instead of one, as he himself believes, it would seem that this condition is dependent, in one case at least, on the season of the year; for he informs us that he found the gonophores of *Coryne mirabilis*, Agass., in the earlier months of the year, detach themselves from the trophosome and swim away as gymnophthalmic medusæ before the development in them of ova or spermatozoa; while, somewhat later, he has seen the gonophores attain to sexual maturity, without ever becoming free.[1] It is possible, however, that the two conditions here described by Agassiz belong to two quite different species.

The free phanerocodonic gonophore is in one rare form (woodcut, fig. 5) ambulatory: in all others it is natatory; locomotion being effected by alternate systole and diastole of the umbrella. In the ambulatory form the umbrella is incapable of evident systolic and diastolic movements, and locomotion is performed by marginal tentacles peculiarly modified for creeping over solid bodies. This very exceptional form has been met with only in *Clavatella*, whose trophosome has been

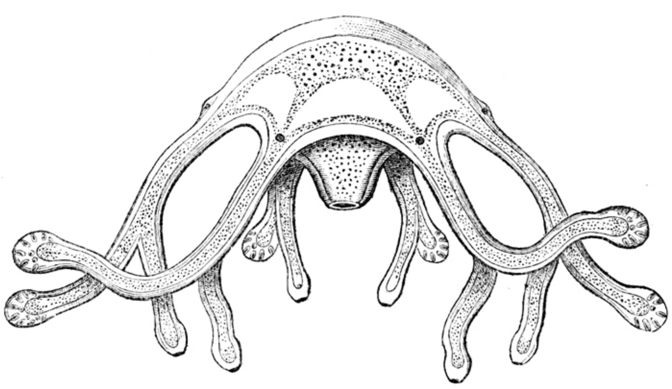
[1] Agassiz, 'Contributions to the Nat. Hist. of the United States,' vol. iv, p. 189.

[2] The gonophores of the siphonophorous group *Calycophoridæ* properly come under the designation of phanerocodonic, though they may never become free, and though we find them departing from the typical form of the gymnopthalmic medusæ by the non-development of the marginal appendages of the umbrella.

discovered by Hincks, and in the nearly allied *Eleutheria* of De Quatrefages, whose trophosome has not yet been detected.

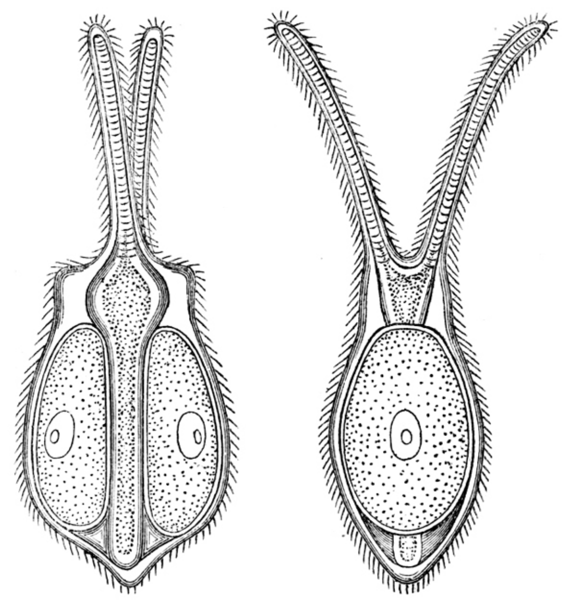
While all the leading features of a gymnophthalmic medusa are thus at once obvious in the phanerocodonic gonophore, the adelocodonic gonophores, on the other hand, present the medusoid structure only in a disguised or undeveloped condition. They have the form of sacs, and, except in a single known instance, the whole gonophore remains permanently attached to the hydrosoma, giving rise within it to the generative elements, which, after attaining a certain degree of maturity, are ultimately discharged from its cavity. The single exception is afforded by the

Fig. 5.



Ambulatory Medusa of *Clavatella prolifera*.

Fig. 6.



Free locomotive sporosac of *Dicoryne*. The figure represents two aspects of the female sporosac when swimming in the open sea, and viewed in planes at right angles to one another.

genus *Dicoryne*, Allm. (woodcut, fig. 6), in which, before discharging its generative products, the gonophore liberates itself from its external investment or ectotheca, and thus, becoming a free planoblast, swims about actively by the aid of vibratile cilia.

The following tabular view will exhibit at a glance the various parts which may occur in a hydroid gonosome:

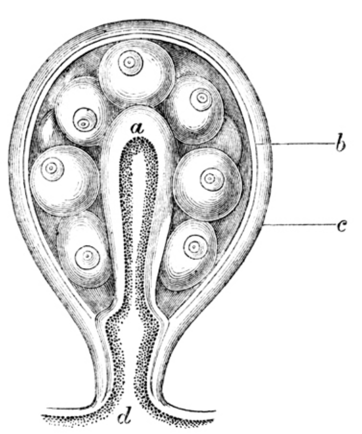
Gonosome.	Zooids directly sexual (*Gonophores*)	Adelocodonic or sacciform (*Sporosacs*)	fixed.	
			natatory.	*Planoblasts.*
		Phanerocodonic or medusiform (*Gonochemes*).	natatory.	
			ambulatory.	
	Zooids not directly sexual, but giving origin to sexual buds.	Medusiform (*Blastochemes*)	natatory.	
		Styliform (*Blastostyles*)	fixed.	

Whether the gonosome remains during its whole lifetime connected with the trophosome, or detaches itself as one or more independent zooids, it is manifest that it constitutes an essential element in the character of the species, and the study of no one species of hydroid can be regarded as complete unless it embrace both trophosome and gonosome. Since, however, in many cases we are acquainted with only the free gonophore, or the free blastocheme, not having yet discovered the trophosome to which it belongs, while in other cases the trophosome alone is known to us, we have been in the habit of treating such instances without regard to the missing zooids, and as if they afforded examples of independent species; but it must never be forgotten that the data on which we thus assign to them the rank of determinate species, or genera, are insufficient for the purposes of a philosophic system: such genera and species must be regarded as purely provisional; for the zoologist is no more justified in accepting such incomplete characters as sufficient for the accurate determination of his hydroid, than would the botanist be in regarding the flower alone on the one hand, or the root, stem, and leaves alone, on the other, as affording characters sufficient for the definition of any flowering plant whose exact determination he would attempt.

The gonosome is that part of the hydroid which presents the most marked variation among the different members of the group, and it is here that we find most distinctly manifested those beautiful gradations of form which, by throwing light not only on one another, but on forms belonging to other groups of the *Hydrozoa,* possess for the morphological student a profound significance. It will therefore be necessary to enter into a more detailed examination of the gonosome in its various modifications among the HYDROIDA.

2. *The Adelocodonic Gonophore* (*Sporosac*).

FIG. 7.



Adelocodonic gonophore of *Hydractinia echinata.*
a, Spadix surrounded by the ova, the whole enveloped by the perigonium, which here consists of *b,* endotheca, and *c,* ectotheca, the mesotheca being absent; *d,* communication of the cavity of the spadix with that of the blastostyle.

The adelocodonic gonophore (woodcut, fig. 7) is a sac-like body, which presents the following parts:

1. An internal hollow process, the *spadix* (*a*), which occupies the axis, and whose cavity is in communication with the general somatic cavity of the hydrosome.

2. The generative elements, *ova* or *spermatozoa,* which are developed round the spadix.

3. A sac (*perigonium*) which surrounds the generative elements, and retains them in their place. This sac may be simple or its walls may present two or even three layers, in which last case it will consist of (1) an internal layer (*endotheca*), which lies immediately on the generative elements; (2) a middle layer (*mesotheca*); and (3) an external layer (*ectotheca*). The mesotheca, moreover, may have a system of canals developed in it.

Of the adelocodonic gonophore we have examples in such forms as the so-called generative sacs of *Clava, Hydractinia, Eudendrium,* &c.

3. *The Phanerocodonic Gonophore* (*Gonocheme. Sexual Medusa*).

The phanerocodonic gonophore (woodcuts, figs. 8 and 17) is bell-shaped, and in its most developed form presents the following parts:

1. A central tubular body, the *manubrium* (*a*), which carries a mouth (*i*) at one extremity.

2. The generative elements (*b*), which are developed between the inner and outer membranes (endoderm and ectoderm), which compose the walls of the manubrium.

3. A contractile bell, *umbrella* (fig. 8, *c*), from the summit of whose concavity the manubrium is suspended, and in whose walls is always developed a system of canals (*gastrovascular*), consisting of —1. A set of equidistant longitudinal canals (*d d*), mostly four in number, which radiate from the base of the manubrium, into which or into a special cavity (*atrium*, fig. 17) which often exists at its base—they open at their origin; and 2, of a circular canal (*e*) which surrounds the *codonostome*, or orifice of the bell, and receives the distal extremities of the radiating canals.

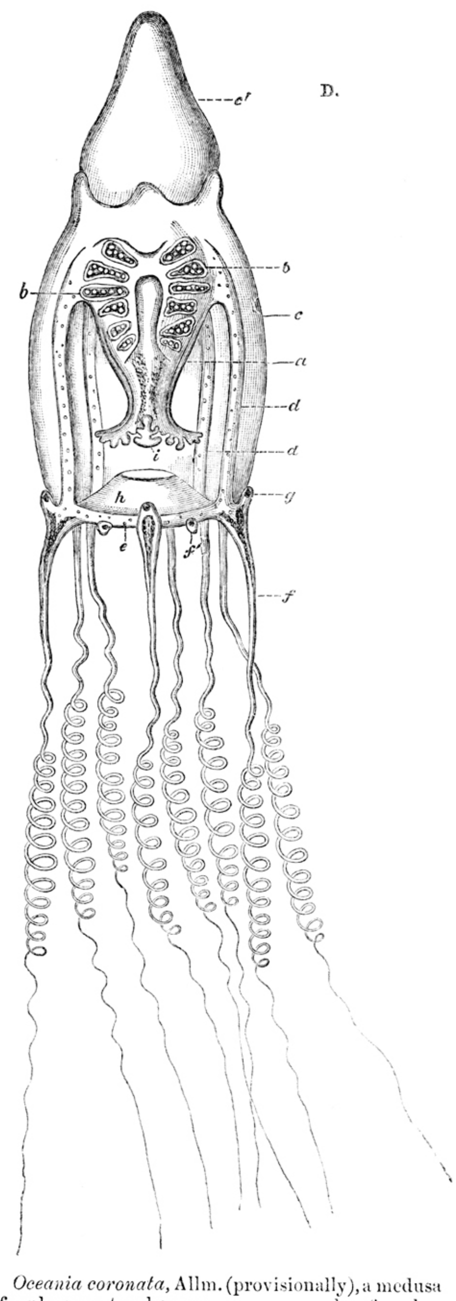
4. Contractile *tentacula* (*f*), which spring from the margin of the umbrella, and often carry at their bases definite accumulations of pigment-granules (fig. 8, *g*, and fig. 17, *c*) named *ocelli*.

5. A membranous extension, *velum* (*h*), of the margin of the umbrella over the codonostome where it forms a thin, muscular diaphragm, perforated in the centre by a circular opening of greater or less diameter.

The body composed of the various parts now enumerated constitutes one form of the so-called "gymnophthalmic medusa,"[1] and in its young state is usually invested by an external protective membrane, the *ectotheca*, the homologue of the external layer of the perigonium in the sporosac.

Of the form of medusa presented by the phanerocodonic gonophore we have examples in the types described by authors under the names of *Sarsia*, *Steenstrupia*, *Oceania*, &c.[2]

FIG. 8.



Oceania coronata, Allm. (provisionally), a medusa of unknown trophosome, as an example of a phanerocodonic gonophore.

a, Manubrium; *b*, generative elements (ova) developed between endoderm and ectoderm of manubrium; *c*, umbrella; *c′*, peculiar development of the solid tissue of the umbrella, which occurs in the present species; *dd*, radiating gastrovascular canals; *e*, circular gastrovascular canal; *f*, marginal tentacles; *f′*, rudimental marginal tentacles; *g*, ocellus; *i*, mouth surrounded by its four fimbriated lips.

4. *The Blastostyle.*

The blastostyle, as has been already said, must be regarded as a hydranth whose alimentary functions have become suppressed, and which, though not, properly speaking, sexual itself, is entirely destined for the production of sexual buds or gonophores, either directly or through the medium of a non-sexual bud, the blastocheme. A good idea of this form of zooid may be obtained from the so-called "fertile polypes" of *Hydractinia echinata* (Pl. XV, and woodcut, fig. 4, *b b*). These are bodies of a cylindrical shape, which are scattered among the alimentary hydranths, and which in all respects they resemble except in the

[1] Another form is presented by the blastocheme described below.

[2] The structure above described is that of the phanerocodonic gonophore in its most completely

fact that the tentacles are entirely suppressed, their place being taken by small clusters of thread-cells, and that the mouth, if not wholly obliterated, is reduced to a very minute perforation, which probably never subserves the function of ingestion. Near the distal extremity of these bodies the gonophores (*c*) are borne as a dense cluster of buds.

In the whole of the *Campanularian* and *Sertularian* hydroids the blastostyle, with its buds, is enclosed in an external chitinous capsule, the *gonangium* (woodcut, fig. 2, *f*), which is never present in the *Tubularinæ*. The gonangium is of very definite form for each species, and affords good characters for diagnosis.

Though it is necessary to distinguish the blastostyles from the hydranths, it cannot be overlooked that they may pass into them by certain transitions. Agassiz[1] describes a mouth in the blastostyles of the *Hydractinia polyclina* of the North American coast, but as the tentacles are entirely suppressed, it is doubtful whether the orifice which here exists can be regarded as destined for the ingestion of nutriment. In certain *Eudendria* the hydranths which carry the gonophores grouped round their base present a perfectly developed form while the gonophores are young; but as these continue to grow, the hydranths which carry them frequently become atrophied, losing their tentacles and mouth; and by the time the gonophores have attained to maturity the hydranths have assumed the condition of blastostyles. Again, among the *Sertularinæ* we find in *Halecium halecinum* (woodcut, fig. 29) the female blastostyle developing from its summit a pair of perfect hydranths with tentacles and mouth, and with their digestive cavity in communication with that of the blastostyle; but I know of no more instructive demonstration of the relation between blastostyle and hydranth than what is afforded by the female gonangium and its contents in *Sertularia rosacea*, *S. tamarisca*, and *S. falax*. In these hydroids (woodcuts, fig. 23—26) the blastostyle develops from its summit a set of peculiarly formed tentacles, which, after becoming invested with a perisarc, continuous with the chitinous walls of the gonangium arch, over the summit of the gonangium, so as to form the walls of a special chamber, which constitutes a marsupial receptacle, in which the ova, after their discharge from the gonangium proper, may undergo further development. These, however, are all exceptional cases, and do not render less valid the association of the blastostyle with the gonosome rather than with the trophosome, while they are important as showing the homological identity between the hydranth and the blastostyle.

Notwithstanding the transitions which may be thus traced between the hydranth and the blastostyle, we must carefully avoid the confounding of a true blastostyle, whose characteristic form and suppression of nutritive function show themselves *before* the appearance of the generative buds, and those pseudo-blastostyles which are caused by the exhaustive action of the generative buds on an ordinary hydranth.

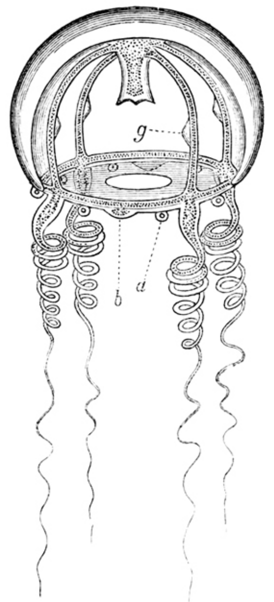
developed form. Such complete differentiation, however, is not always attained even in the HYDROIDA, while among the SIPHONOPHORA a hydrozoal group possessing the closest relations with the HYDROIDA, the margin of the gonocalyx or umbrella of the medusiform gonophore in the *Calycophoridæ* carries neither tentacles, ocelli, nor lithocysts, and the manubrium develops, at least usually, no mouth upon its extremity.

[1] Agassiz, 'Contrib. to the Nat. Hist. of the United States,' vol. iv, p. 230.

5. The Blastocheme (non-sexual Medusa).

It has been already stated that the blastocheme presents, like the phanerodoconic gonophore, the form of a completely developed gymnophthalmic medusa. It differs, however, from the gonophore, not only in never producing generative elements directly, and in being thus, properly speaking, non-sexual, but also in certain points of structure; for it is almost universally characterised by the absence of ocelli, and by the presence of peculiar capsules called *lithocysts*, which are attached to the margin of the umbrella, and enclose one or more transparent refractile corpuscles.[1]

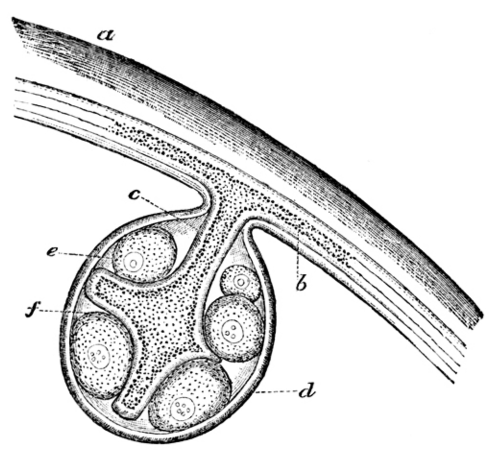
FIG. 9.



Medusa of *Campanularia Johnstoni*, shortly after liberation from the gonangium, illustrating the peculiarities of the blastocheme.

a, Lithocyst; *b*, incipient tentacle; *g*, incipient sporosac, formed as a bud upon the radiating canal.

FIG. 10.



Sexual zooid (sporosac budding from a radiating canal in the blastocheme of *Obelia geniculata*.

a, Portion of the umbrella, and *b*, radiating canal of the blastocheme; *c*, spadix of sporosac; *d*, perigonium consisting here of a single membrane; *e*, ovum with germinal vesicle and spot; *f*, ovum with numerous germinal spots in the germinal vesicle.

[1] An exceptional condition in this respect is presented by a few medusæ referable to the type of the blastocheme. *Thaumantias*, as limited by Gegenbaur, has ocelli instead of lithocysts, and the same is the case, according to Agassiz, in *Staurophora*, Brandt, and in *Laodicea*, Lesson; while in *Melicertum*, Oken, there are neither lithocysts nor ocelli.

In *Tiaropsis diademata*, Agas., a well-defined pigment spot has been described by Agassiz as existing in the base of the lythocyst, a statement which I can confirm by my own observations on a species of *Tiaropsis* captured in the Firth of Forth. As will be afterwards seen, however, I do not regard the pigment spot of *Tiaropsis* as representing a true ocellus. According to Strethill Wright, a medusa, which has been described by him under the name of *Goodsirea* ('Edin. N. Phil. Journ.,' July, 1859), is a true gonocheme, and yet it has lithocysts instead of ocelli. As to *Oceania octona*, Fleming, and *O. turrita*, Forbes—medusæ belonging to the type of the gonocheme—the statement of Forbes, that they have a lithocyst imbedded in the base of the tentacle, is founded on an error of interpretation

While it is itself non-sexual, the blastocheme always gives origin to special sexual buds, or gonophores, which are borne upon some part of the radiating canals.

As characteristic examples of the blastocheme, we may adduce the planoblasts of *Campanularia Johnstoni* (woodcuts, fig. 2, *g*, and fig. 9)—which are medusiform zooids referable to the deep-belled section of Gegenbaur's genus *Eucope*—and those of *Laomedea dichotoma* and *L. geniculata* (woodcut, fig. 10) of authors—medusæ referable to Peron's type of *Obelia*. In none of these are sexual elements ever directly developed, but instead of the direct formation of ova and spermatozoa, there is produced a new zooid, which no longer presents the complete medusal type, but is formed upon the plan of the adelocodonic gonophore. This zooid (woodcuts, fig. 9, *g*, and fig. 10) springs as a bud from the radiating canals of the medusa, and is constructed upon precisely the same plan as that which we meet with in the gonophore of *Clava* or *Hydractinia*, except that the perigonium would seem to be simple. It has an axile spadix (woodcut, fig. 10, *c*), whose cavity is in direct communication with that of the radiating canal (*b*) from which it springs. Immediately investing the spadix are the generative elements (*e*, *f*) ova or spermatozoa; while these are themselves surrounded and confined by a true perigonium (*d*), which becomes at last ruptured for the liberation of its contents.

The zooidal nature of these buds is nowhere more distinct than in the genus *Aglaura*, Pér., a form not yet traced to a polypoid trophosome. Here the generative elements are produced in eight sac-like processes which surround the base of the manubrium, which is itself borne on the extremity of a stalk dependent from the summit of the umbrella. These sacs are undoubtedly true buds, and are entirely homologous with the gonophores of *Clava;* and it is plain that they are developed from the proximal extremities of the radiating canals, just where these canals pass off from the manubrium in order to run along the sides of its stalk before reaching the umbrella.[1]

In some blastochemes the sexual bud extends over a greater length of the radiating canal, and presents, in consequence, a less defined and individualised appearance than in the instances just mentioned, so as to lead one at first to hesitate as to the propriety of regarding it as a true zooid. Such, for example, is its character in the medusæ referable to the types of *Thaumantias*, *Tima*, and *Melicerta*, in all of which, while the generative buds are situated as in *Obelia*, on the radiating canals, they occupy with their extended base so much of the canal as to be readily mistaken for mere organs—ovaries or spermaries. Notwithstanding this, however, they are constructed upon essentially the same plan as the others, and offer no exception to the view here taken.

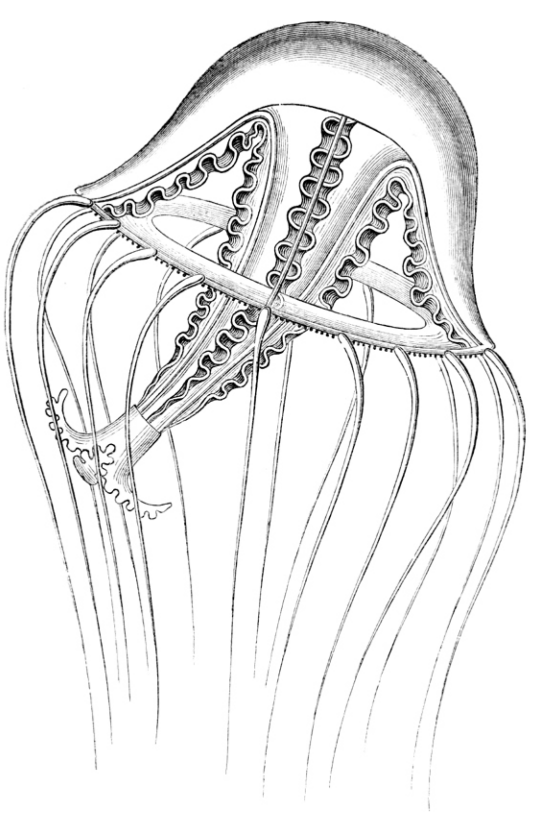
In *Tima*, indeed (woodcut, fig. 11), we have an extreme case of this extension of the base of the generative buds, which here present themselves in the form of four long, flattened, sinuous frill-like bands, each attached by one edge along the whole length of a radiating canal. When a section is made from the free to the attached edge of this band (woodcut, fig. 12), the generative elements

while the view of the structure of *Slabberia*, Forbes, which would make this medusa to be a blastocheme, having ocelli instead of lithocysts, is also, as will be shown below, based on an error. Though it is thus very rare to find a blastocheme without lithocysts, the absence of ocelli in the gonocheme is quite common.

[1] See Leuckart's description of *Aglaura Péronii* ('Wiegmann's Archiv,' 1856, Erster Band, S. 10). Leuckart recognises in the generative sacs of *Aglaura* the significance of true zooids, though he refrains from extending this view to the generative sacs of other medusæ.

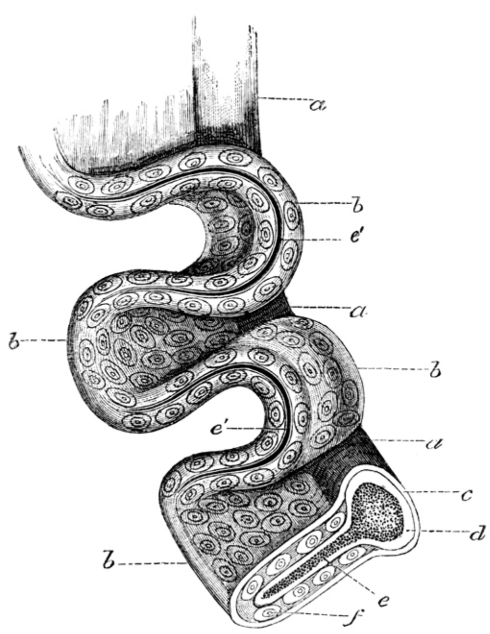
are seen to be disposed upon each side of a hollow longitudinal septum (*e*). This septum consists of a diverticulum of the endoderm of the radiating canal; it admits into its interior the fluid which circulates in the radiating canal, and is plainly homologous with a laterally extended and flattened spadix; while the generative elements are externally confined by an ectodermal covering, which is in the same way the homologue of the perigonium in an ordinary sporosac, but here flattened out like the spadix, in accordance with the ribbon-shaped form of the gonophore.

FIG. 11.



Medusa (*Tima Bairdii*), a blastocheme of unknown trophosome, showing the convoluted and ribbon-shaped sporosacs along the course of the radiating canals.

FIG. 12.



Portion of the ribbon-shaped sporosac, much enlarged in a female specimen of *Tima Bairdii*.
a, a, a, radiating canal; *b, b, b*, sporosac; *c*, ectoderm; *d*, endoderm; *e*, cavity of the spadix; *e′, e′*, distal edge of the spadix, seen through the ectodermal layer; *f*, ova.

The blastocheme is thus essentially a free non-sexual medusa, which, like the blastostyle, gives origin to sexual buds, but which, unlike the blastostyle, is endowed with the locomotive powers of a medusa, so that it carries those buds from place to place by the contractions of an umbrella.

In the account here given of the blastocheme, I have confined this term to such medusæ as develop distinct sexual buds upon the gastro-vascular canals. In some of those medusæ, however, in which the sexual elements are produced in the walls of the manubrium, we find the portions of the walls which give origin to the ova or spermatozoa more or less differentiated from the general walls of the manubrium, and presenting a lobulated appearance, which might easily lead to the belief that the manubrium emitted from its sides true sexual buds. I am not, however, prepared to place any of these cases in the same category with the blastocheme.

The condition alluded to is especially well marked in the medusa of *Cladonema* and of *Bougainvillia*, and in certain forms of *Oceania*, in the sense in which this group has been restricted by Forbes and Gegenbaur, and generally accepted by the German zoologists; and an opportunity of studying an undescribed medusa of this type (woodcut, fig. 8), which I obtained abundantly in the autumn of 1865, on the west coast of Scotland, has plainly shown that the generative lobes of the manubrium cannot be regarded as true zooids. The generative elements are here simply produced between the endoderm and ectoderm of the manubrium, and the lobes are nothing more than a puckered or sacculated condition of the walls in those parts where the ova or spermatozoa originate. I do not, however, deny the possibility of the manubrium as well as of the gastrovascular canals giving origin to true buds, to which the development of the sexual elements may be confined; when this has been shown to be the case, the medusa presenting it must take its place among the blastochemes.

Whether the medusæ referable to the type of *Geryonia* and its allied forms ought to be regarded as blastochemes is as yet uncertain, though my own opinion is in favour of so viewing them. The parts which in these medusæ give origin to the generative elements have been described as leaf-like expansions of the radiating canals. Haeckel's observations have led him to deny to them the significance of true zooids,[1] while he sees in them nothing more than mere lateral expansions of the canal, a portion of whose epithelium becomes here differentiated into ova or spermatozoa. This question as regards the *Geryonidæ* is, as we shall afterwards see, one of considerable importance. Having had no opportunity of examining for myself specimens of these medusæ, I can bring no direct personal observations to bear upon it; but the account given by Haeckel, who has so admirably worked out the structure and history of the *Geryonidæ*, does not appear, as I shall afterwards show, to necessitate the conclusion to which he arrives, or to be inconsistent with the zooidal nature of the reproductive pouches. Further observations, however, instituted for the express determination of this point will be needed before we can regard the question as thoroughly cleared up.

6. *Homological parallelism between Sporosac and Medusa.*

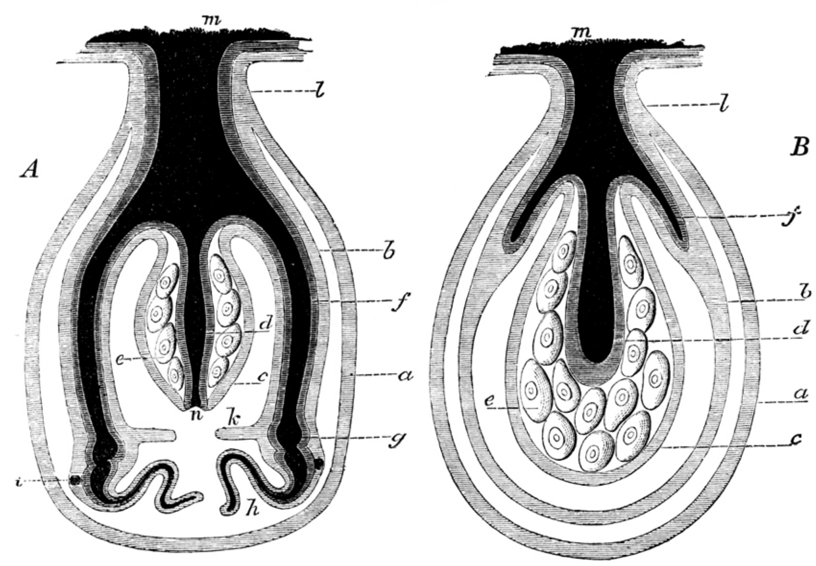
While it will be found very convenient to insist upon the differences pointed out above between the adelocodonic gonophore on the one hand, and the phanerocodonic gonophore and blastocheme on the other, it must not be supposed that these two forms are constructed upon plans widely different from one another. We find, on the contrary, that the most exact parallelism admits of being demonstrated between them; for though they may at first sight appear very different, it can nevertheless be shown that the closed generative sac of a *Clava* or a *Hydractinia* is an easily understood modification of a medusa.[2]

[1] Haeckel, 'Die Famille der Rüsselquellen,' Vorwort, viii.

[2] It is now many years since I endeavoured to demonstrate that the so-called "ovarian vesicles" of the *Tubularinæ*, and the fixed sacs contained within the gonangium of the *Sertularinæ* and *Campanularinæ*, are in all cases strictly homologous with the free medusa, that they possess a true medusal structure in a more or less degraded or disguised condition. ("On the Anatomy and Physiology of *Cordylophora*," 'Phil. Trans.,' June, 1853.)

In comparing the two classes of bodies with the view of determining their homological relations, their composition out of the two membranes ectoderm and endoderm must be carefully kept in mind.

FIG. 13.



Diagrammatic sections of phanerocodonic and adelocodonic gonophores.
A, Phanerocodonic, and B, adelocodonic gonophore.
a, Ectotheca; *b*, mesotheca or umbrella; *c*, endotheca, or ectodermal layer of manubrium; *d*, spadix, or axile tube of manubrium; *e*, ova; *f*, radiating gastrovascular canals; *g*, circular gastrovascular canal seen in transverse section; *h*, marginal tentacle; *i*, ocellus in bulbous base of tentacle; *k*, velum; *l*, peduncle of gonophore; *m*, general cavity of cœnosarc; *n*, mouth of medusa.
In both sections the endoderm is distinguished from the ectoderm by giving it a darker shade.

Commencing with the central parts of a hydroid medusa, and comparing these with the central parts of a sporosac, we shall find that in the medusa (woodcut, fig. 13, *A*) we have a manubrium in the form of a more or less elongated tubular body occupying its axis. The walls of the manubrium are composed of two layers, an internal or endodermal layer (*d*) and an external or ectodermal (*c*); and in all phanerocodonic gonophores or hydroid medusæ of the sexual type, these two layers become ultimately more or less separated from one another by the development of the generative elements (*e*) between them.

In the sporosac or adelocodonic gonophore also (*B*) we have a double-walled tubular body, between whose two walls the generative elements are developed exactly as in the medusa; but while in the medusa this body is in almost every case perforated by a terminal mouth, in the sporosac it is completely closed, so that it assumes, by the increasing volume of the generative elements, the appearance of a sac, filled with ova or spermatozoa, and having a cæcal diverticulum (spadix) plunged into the middle of the mass. This cæcal diverticulum (*d*) is plainly the equivalent of the endodermal portion of the manubrium in the medusa, while the wall (perigonium) of the sac represents more or less completely the structures which in the medusa lie external to the generative elements.

When the perigonium presents its highest degree of development it consists as we have already seen of three layers. Of these the inner (*c*) (endotheca) is the equivalent of the ectodermal layer of the manubrium in the medusa; the middle layer (*b*) (mesotheca) corresponds to the umbrella, and like it may have a system of canals (f) more or less completely developed in it, and may even present a rudimental codonostome, while the most external layer (a) (ectotheca) corresponds to a similar external layer frequently present in the young medusa bud.

It would seem that in no case is a velum or its homologue developed in the adelocodonic gonophore, even though the representative of the umbrella should possess as in *Tubularia* a rudimental codonostome, while the marginal tentacles of the medusa are, except in the "meconidium" (see below, p. 57), also without their representative in this form of gonophore; for the tentacula-like tubercles which crown the summit of the sporosac of some of the *Tubularidæ* (*Tubularia larynx*, for instance, Pl. XXI) are of an entirely different significance, being merely processes of the ectotheca.

7. *Homological parallelism between Hydranth and Medusa.*

While we have been thus enabled to trace a close parallelism between the medusa and the sporosac, another comparison of great interest in this inquiry suggests itself, that, namely, between the medusa and the hydranth. Now there can be little difficulty in finding in the distal portion of the hydranth the homologue of the manubrium of the medusa;[1] but the equivalents of the umbrella and gastrovascular canals of the medusa are not at first sight so obvious. I believe, nevertheless, that these are not totally unrepresented in the hydranth. It will be kept in mind that the tentacula of the hydranth are merely tubular radiating prolongations of the digestive cavity, though with the cavity of the tube usually more or less obliterated by the peculiar condition of the endoderm, and that for some distance from their origin they are necessarily included in the thickness of the body-walls of the hydranth, where they consist merely of radiating canals extending through these walls and lined by a layer of endoderm. Now this included portion I regard as the true representative of the radiating canals of the medusa; and if we were to imagine the ectoderm of the hydranth in a *Eudendrium* or *Campanularia* to acquire unusual thickness in a zone corresponding in position to the roots of the tentacles, we should have a disc-like extension of the

[1] Huxley ('Oceanic Hydrozoa') strongly insists on this relation, and is so impressed with the closeness of the homology between manubrium and hydranth, that he uses the same term, "polypite," for both.

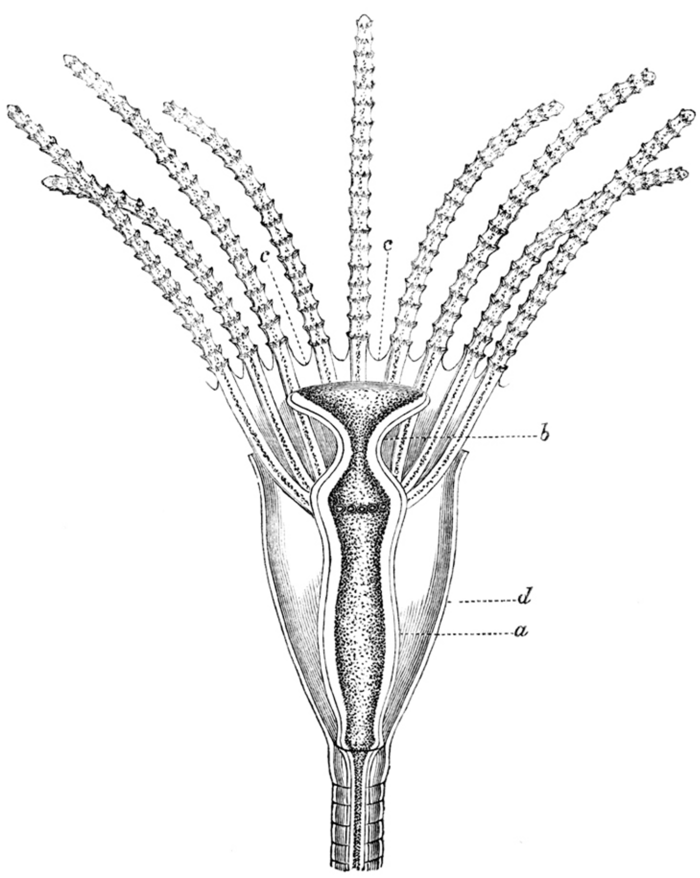
Agassiz (op. cit., vol. iv, p. 226) has witnessed the very simple adelocodonic gonophore in male specimens of his *Rhizogeton fusiformis*, instead of withering away after the discharge of its contents, elongate itself, develop tentacles, and become transformed into a hydranth. I have myself, on one occasion, seen an analogous phenomenon in the female gonophore of *Cordylophora lacustris*, in which, after the discharge of the ova, the spadix had become elongated through the ruptured chitinous investment of the original gonophore, had developed an ectoderm, thrown out tentacles from its summit, and become metamorphosed into an ordinary hydranth. In the case of *Cordylophora* the transformation is confined to the spadix, while, according to Agassiz, the entire gonophore of *Rhizogeton* takes part in the metamorphosis.

I believe that in both cases the phenomenon is an abnormal one; it certainly is so in *Cordylophora*, for, in the ordinary conditions to which this hydroid is exposed, no metamorphosis of the kind takes place.

ectoderm traversed in a radiating direction by tubular extensions of the endoderm which lines the body-cavity of the hydranth, and this disc would only need to become still further expanded in order to show itself as an unmistakable umbrella, with radiating gastrovascular canals, while the hypostome or proboscidiform extension of the body, which in these genera advances far in front of the base of the tentacles, would resemble in all essential points the manubrium of the medusa.

Now, the commencement of such an expansion is evident in the hydranth of many *Campanularidæ,* while in certain species, as *Laomedea flexuosa* and *Campanulina acuminata,* the ectoderm of the body is actually extended as a thin disc for a considerable distance in the plane of the tentacles, which acquire in consequence the appearance of being connected at their bases by an intervening web (woodcut, fig. 14).

Fig. 14.



Longitudinal section through the hydranth and hydrotheca of *Laomedea flexuosa,* showing the web-like membrane by which the bases of the tentacles are connected to one another.

a, Body of hydranth; *b,* hypostome, carrying the mouth on its summit; *c, c,* intertentacular web; *d,* hydrotheca.

While the portion of the tentacles included in the thickness of the body-wall of the hydranth will thus be the equivalent of the radiating canals of the medusa, their free portion is plainly homologous with the free tentacles, which in the medusa hang from the margin of the umbrella at the points corresponding to the entrance of the radiating into the circular canal, and which must be regarded as strictly the continuation of the radiating canals beyond their apparent termination in the circular canal. The tentacles, which in many medusæ spring from the intervening spaces upon the margin of the umbrella, and are therefore not directly continuous with the radiating canals, make their appearance probably in all cases later than the others, and are frequently less developed. These inter-radial tentacles must be placed in the same category with the lithocysts as simple marginal appendages, to be carefully distinguished from the primary tentacles, and, like the lithocysts, have no representative in the hydranth.

It cannot be urged, as an argument against this view, that the circular canal of the medusa is not represented in the hydranth; for the absence of a developed umbrella in the hydranth necessarily brings with it the absence of this canal; and it is for the same reason that velum, lithocysts, and secondary tentacles, are also absent. Neither can it be said that those cases in which the tentacles of the hydranth are not arranged in a single verticil, but are repeated regularly or irregularly in different planes upon the body, are inconsistent with the homological relations here insisted on; for such cases can be regarded only as special modifications of the more typical plan which has directly suggested our comparison.

Huxley, believing the difference in structure and development between the locomotive disc of the gymnophthalmic and that of the steganophthalmic medusæ to be so great as to place them in different categories, would confine the term "umbrella" to the disc of the *steganophthalmata*, and would designate that of the *gymnophthalmata* by the terms "nectocalyx" and "gonocalyx." I was at first disposed to adopt the same view; but an investigation of the mode in which this part makes its appearance in the gymnophthalmic forms has convinced me that the development is essentially the same in both cases, and that, notwithstanding some marked structural differences, there is sufficient unity between the two to render it more convenient to speak of them under the same term as strictly homologous organs. In both cases they are formed by an outgrowth of the walls of the polypoid manubrium, and the fact that the steganophthalmic medusa is produced by successive transverse divisions of a "scyphostoma," while the gymnophthalmic medusa is formed as a lateral bud from a hydrosome, is no valid argument against this approximation; for every segment of the "scyphostoma" is strictly comparable to the bud of the hydroid, and developes its umbrella by an outgrowth from its sides in quite the same way.

A very instructive example, which strikingly bears out the comparison I have here attempted to make between the hydranth and the medusa, is afforded by the remarkable locomotive zooid which forms the gonophore of *Dicoryne*. This little zooid (woodcut, fig. 6) is essentially a free medusa, reduced to the condition of an ova-bearing or spermatozoa-bearing manubrium, from whose base two free tentacula in form and relations like those of a hydranth are developed. Now, there is here no umbrella, locomotion being affected by the action of cilia; but it is evident that we have only to imagine the ectoderm of the manubrium projected as a disc, in the way already supposed, in the horizontal plane passing through the base of the two tentacles so as to include the basal portion of these tentacles in its thickness, in order to have an umbrella with two radiating canals added to the manubrium.

But development, as we shall afterwards see, entirely coincides with anatomy in pointing to the same conclusion; and it is only necessary to trace the formation of the umbrella and radiating canals in the budding medusa, in order to become convinced that their origin is essentially that here insisted on); while the interesting observations of Johannes Müller on the development of *Æginopsis*, and of M'Crady on that of *Cunina*—observations which will be specially referred to below—show that in these genera the umbrella grows out as a horizontal disc from the walls of a free polypoid manubrium, which bears a close resemblance to the generative zooid of *Dicoryne*. It would appear, however, from the observations of Fritz Müller,[1] and of Haeckel,[2] that in certain geryonidan medusæ the umbrella is formed by the excavation of a solid spherical embryo; but it must be noted that neither of these observers had seen their embryo medusæ at a period anterior to the commencement of the developing umbrella.

The parallelism which I have thus endeavoured to demonstrate may be expressed in the following scheme:

PHANEROCODONIC GONOPHORE AND BLASTOCHEME. (MEDUSA.)	ADELOCODONIC GONOPHORE. (SPOROSAC.)	HYDRANTH.
Ectotheca	Ectotheca	0
Umbrella	Mesotheca	Web-like membrane uniting the bases of the tentacles in *Laomedea flexuosa*, &c.
Gastrovascular canals	Canals of Mesotheca	Base of tentacles extending through the thickness of the body walls, and through the web-like membrane.
Ectoderm of manubrium	Endotheca	Ectoderm of hypostome.
Endoderm of manubrium	Walls of spadix	Endoderm of hypostome.
Manubrium	Spadix + endotheca	Hypostome.
Primary or radial marginal tentacula	Primary tentacula in the meconidium.	Free portion of tentacula.
Secondary or interradial marginal tentacula.	Secondary tentacula in the meconidium.	0
Ocelli and lithocysts	0	0
Velum	0	0
Generative elements in gonocheme	Generative elements	0

8. *Further modifications of the Gonosome.*

Besides the great leading differences already described, many others of a more subordinate kind are met with. The adelocodonic gonophore in particular exhibits many special modifications, and presents us with a regular series of gradations in complexity, which throw much light on its morphology.

The simplest form is probably that which we meet with in the female gonophores of the freshwater *Hydra*. Here there would seem to be no differentiation of an ectotheca, while the

[1] 'Wiegm. Archiv,' 1859, p. 310.
[2] 'Die Familie der Russelquallen (Geryonidæ),' 1866.

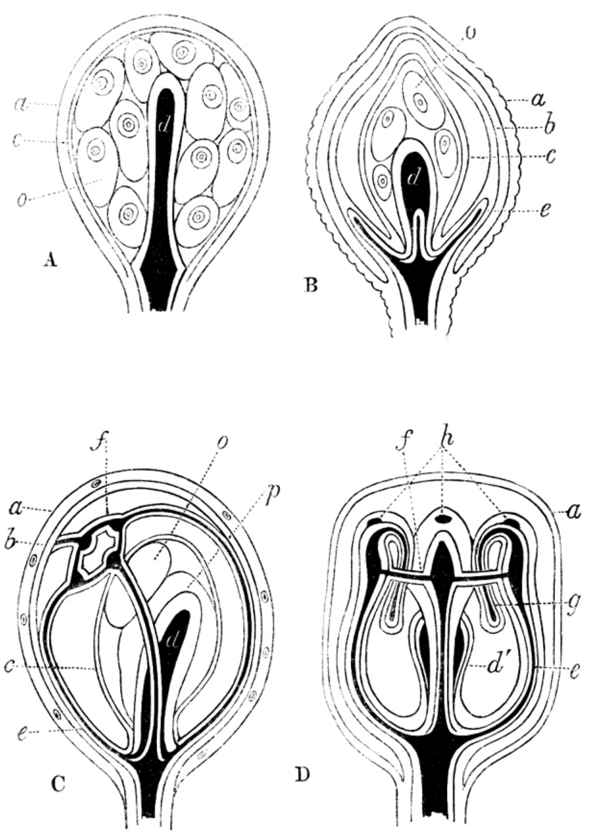
spadix itself remains in a rudimental condition, being scarcely elevated above the base of the gonophore, whose whole cavity becomes at an early period occupied by the ovarian mass.

An advance over this condition is seen in the sexual bud which is borne by that form of medusa described above, under the name of "blastocheme." Here we have the ultimate sexual bud quite destitute of ectotheca, and reduced to the condition of spadix and endotheca separated from one another by the intervening generative elements (fig. 10, p. 35).

In *Clava*, *Hydractinia*, &c., we have a still further advance in complexity. The gonophore has here the form of a simple closed sac, whose axis is occupied by a cylindrical or club-shaped spadix, round which the generative elements are clustered (woodcut, fig. 15, *A*). Careful examination, however, will show that the walls of the sac consist of two membranes, an outer or ectotheca and an inner or endotheca. The mesotheca is entirely absent.

In *Garveia nutans*, I have found a mesotheca to be distinctly demonstrable; but it is closed at the summit, and destitute of circular canal, while four short radiating canals may be seen in its walls extending from the base of the spadix for about a third of the height of the sac (woodcut, fig. 15, *B*).

FIG. 15.



Types of Gonophores.

A, *Hydractinia echinata*. B, *Garveia nutans*. C, *Tubularia indivisa*. D, *Syncoryne eximia*.
a, ectotheca; *b*, mesotheca; *c*, endotheca; *d*, spadix; *d′*, manubrium; *e*, radiating gastrovascular canals; *f*, circular gastrovascular canal; *g*, marginal tentacles; *h*, ocelli; *o*, ova; *p*, ovarian plasma in *Tubularia*.

In *Tubularia indivisa* the mesotheca presents the highest degree of development which it attains in any adelocodonic gonophore, if we except the peculiar body described below under the name of "meconidium." It is perforated at its summit, and the perforation is surrounded by a distinct circular canal, which receives four radiating canals, which open into it by small bulbous expanions (woodcut, fig. 15, *C*). We thus find almost entirely the conditions of a medusa —a medusa, however, which never divests itself of its ectotheca, and accordingly never becomes free, while the spadix remains as a simple cæcal diverticulum, and the codonostome is reduced to a mere perforation of the mesotheca, this last exhibiting but the faintest traces of contractility, and being quite incapable of acting as a locomotive umbrella.

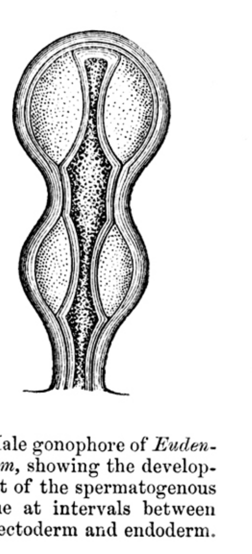
From the sporosac of *Tubularia indivisa* it is thus but a single step to the true phanerocodonic gonophore, such as we find in *Corymorpha nutans*, or *Syncoryne eximia*, where the mesotheca assumes the condition of a contractile locomotive umbrella, with a well-developed codonostome and velum, and, the manubrium now becoming perforated by a mouth, the gonophore is no longer dependent on the trophosome for its nutrition, but can become free and lead an independent life in the open sea (woodcut, fig. 15, *D*).

The typical and ordinary condition of the spadix is that of a hollow cylindrical or clavate body, occupying the axis of the adelocodonic gonophore. Occasionally, however, it departs from this condition and becomes more or less branched, as in *Cordylophora lacustris* (Pl. III), *Plumularia pinnata*, *Laomedea caliculata*, &c.

The gastrovascular canals in the adelocodonic gonophore may, as we have already seen, be either entirely suppressed or present the condition of simple, short, blind tubes, radiating from the base of the gonophore, or be continued from this point as fully developed radiating canals to the distal extremity of the gonophore, where they become united by a circular canal. In certain free medusæ (*Willia*, *Cladonema*—Pl. XVII) the radiating canals subdivide before reaching the circular canal.

The usual condition of the adelocodonic gonophore is that of a simple, more or less spherical or oval sac. In *Eudendrium*, however, the male gonophores present the form of a simple sac only at first; for by the time that their contents have approached maturity, new spermatogenous tissue becomes apparent between the endoderm and ectoderm of their supporting peduncles, and these two membranes thus become separated from one another so as to form a second sac immediately below the first, while a third may in the same way be formed below the second, the gonophore thus acquiring the peculiar moniliform or polythalamic conformation characteristic of this genus (woodcut, fig. 16). It will be at once apparent that the separate chambers presented by this peculiar form must not be regarded as so many distinct gonophores; the whole moniliform series ought rather to be viewed as a simple adelocodonic gonophore, in which the perigonium is not uniformly separated from the spadix by the intervention of the spermatogenous tissue, but remains at intervals permanently adherent to it. Among the planoblasts an entirely analogous phenomenon occurs in a *Sarsia*-like medusa of unknown trophosome, which I captured in the towing-net on the south-west coast of Ireland (woodcut, fig. 17). In this the manubrium, which is extraordinarily extensile, and can be projected to a great length beyond the umbrella, was enlarged at distinct intervals by the development of the generative elements between its ectoderm and endoderm. The specimen captured was a male, and the manubrium, when extended, presented, by the mode in which the spermatogenous tissue was developed in its walls, five elongated cylindrical enlargements, separated from one another by long thin intervening portions, in which the ectoderm and endoderm of the manubrium continued in direct contact with one another, no generative elements being there developed. The spermatogenous mass which occupied the free end of the manubrium was divided into two by a shallow strangulation. The peculiar mode in which the generative elements are developed in the manubrium of *Dipurena*, a nearly allied genus described by M'Crady,[1] would seem to afford an example of an analogous phenomenon.

Fig. 16.



Male gonophore of *Eudendrium*, showing the development of the spermatogenous tissue at intervals between the ectoderm and endoderm.

Fig. 17.

Medusa (*Sarsia strangulata*, Allm., provisionally) of unknown trophosome.

a, very extensile manubrium opening at its proximal end into a special cavity, the atrium; *b*, *b*, *b*, male elements developed at intervals between the ectoderm and endoderm of the manubrium; *c*, ocellus.

The gonophore may be borne upon a distinct peduncle, which may be simple (*Syncoryne eximia*, &c.) or branched (*Tubularia indivisa*, *Corymorpha nutans*, &c.), each branch then bearing a gonophore on its summit; or the peduncle may be obsolete, and the gonophore become sessile (*Laomedea flexuosa*, &c.)

The gonophores, whether phanerocodonic or adelocodonic, may be destitute of any further

[1] M'Crady, op. cit., p. 135.

covering, and will then, while still forming part of the hydrosoma, have their surface in immediate contact with the surrounding water (*Syncoryne*, *Clava*, *Hydractinia*, &c.)

In other cases the blastostyle, with the gonophores which bud from it, may be surrounded by a close case or capsule, formed by a layer of ectoderm with an external chitinous investment (*Campanularia* and *Sertularia*) (woodcut, fig. 2, *f*). I have elsewhere designated this capsule by the name of "*gonangium*."[1] The blastostyle extends through the axis of the gonangium as a cylindrical column, bearing the gonophores as buds upon its sides, and generally expanded at its summit into a conical plug or disc, by which the gonangium is here closed.

In some cases the contents of the gonangium escape, when mature, by the simple rupture of the summit (*Plumularia*, &c.). In others, however, the summit is separated as a distinct lid, which is then either cast off at once (*Sertularia pumila*, &c.), or it remains movably attached by one spot of its edge, as by a hinge, to the margin of the aperture thus formed in the summit of the gonangium (*Sertularia operculata*, *Antennularia antennina*).

In every instance where a gonangium exists the hydranths also are protected by a hydrotheca, while the absence of a gonangium is always associated with the absence of a hydrotheca. The difference thus involved in the presence or absence of these parts corresponds to two primary sections of the Hydroida, and I have distinguished all hydroids which possess a gonangium and hydrotheca by the name of calyptoblastic, while the gymnoblastic hydroids are those which—with the exception of the freshwater Hydras which constitute a separate section—are destitute of these protective coverings.

In by far the greater number of cases the blastostyle in the calyptoblastic genera carries numerous buds, which are either sporosacs or blastochemes, and which always increase in maturity as they recede from the base and approach the summit of the gonangium (woodcuts, fig. 2, *f*, and figs. 18 and 19). In some cases, however, the blastostyle bears but a single bud; and then it often happens that this enlarges to such an extent as to fill nearly the entire cavity of the gonangium, the blastostyle being pushed aside out of the axis, and becoming often partially absorbed, so as to render it difficult to demonstrate its existence[2] (woodcut, fig. 3, *k*).

It usually happens that a fleshy membrane abounding in thread-cells may be seen passing over the whole of the generative buds while still attached to the blastostyle within the gonangium (woodcuts, figs. 18, *d* and 19, *d*). It closely confines them as in a common sac, and is probably an internal layer which has separated from the original formative ectoderm on whose outer surface the gonangium had been excreted. It performs an important office in the economy of the hydroid by confirming the generative buds and guiding them or their contents towards the orifice of the gonangium. I shall refer to it under the name of *gubernaculum*.

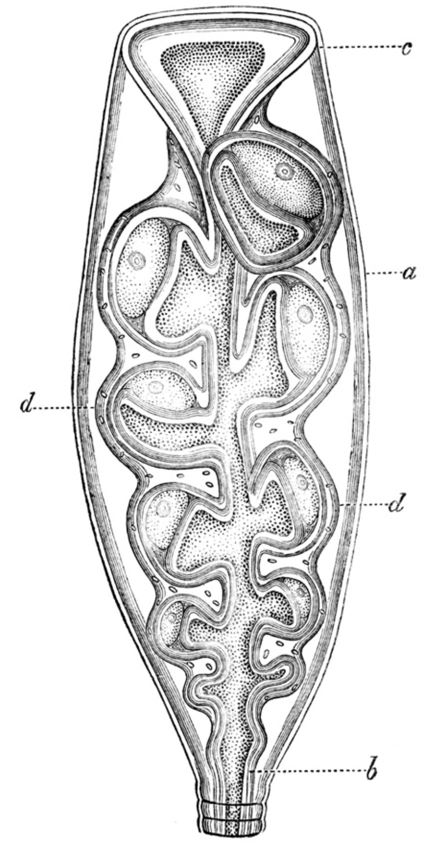
Sometimes the blastostyle, though in the very young state quite simple, soon breaks up, from a common point near the base, into several distinct tubes, which again unite in the

[1] "On the Structure and Terminology of the Reproductive System in the Corynidæ and Sertulariadæ," 'Ann. Nat. Hist.,' July, 1860.

[2] The difference presented by the gonangia, according as they contain numerous gonophores or only a single one, is regarded by Gegenbaur ('Generationswechsel,' p. 38) as of sufficient importance to induce him to distinguish the gonangia into "polymeric" and "monomeric." I am not disposed however, to give much weight to this difference, the number of gonophores which a gonangium may contain varying with particular conditions of development.

common cavity of the plug-like summit. This has been shown by Agassiz to be the case in his *Laomodea* (*Clytia*) *poterium*, and I have myself seen it in a nearly allied species from the east

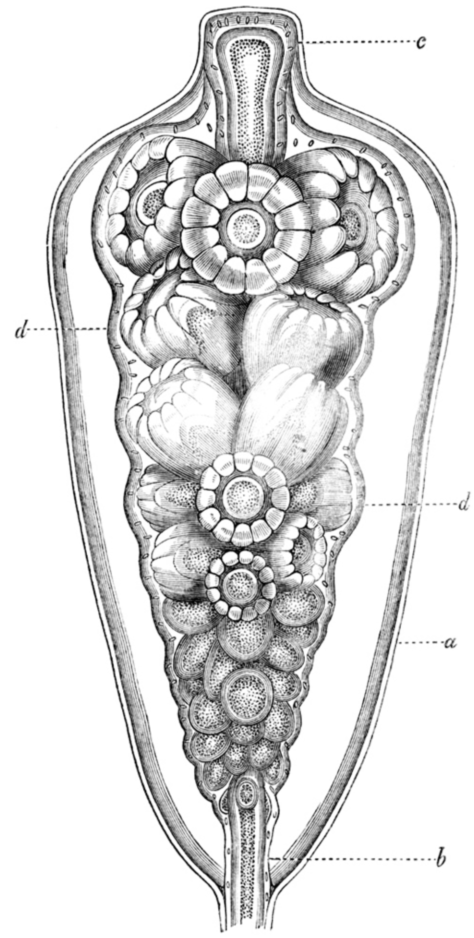
Fig. 18.



Gonangium, with its contents from *Laomedea flexuosa*.

a, Gonangium; *b*, blastostyle, carrying gonosacs, which increase in maturing from below upwards; each containing a single ovum in which the germinal vesicle and germinal spot are conspicuous; *c*, opercular summit of blastostyle; *d*, common investing membrane of the contents of the gonangium.

Fig. 19.



Gonangium, with its contents, from *Obelia geniculata*.

a, Gonangium; *b*, blastostyle loaded with medusæ (blastochemes), which increase in maturing from below upwards; *c*, opercular summit of blastostyle; *d*, *d*, common membrane, investing and confining the medusæ.

coast of Scotland (woodcut, fig. 20). It is entirely analogous to the breaking up of the cœnosarc which will be described below as occurring in the stem of *Antennularia*.

In most cases the gonophore discharges its generative elements directly into the surrounding water. In the females of some calyptoblastic species, however, the ova, instead of escaping directly from the gonophore into the water or the cavity of the gonangium, are retained for some time in a peculiar receptacle, where they undergo further development, and which is supported upon the summit of the gonangium, and lies entirely external to its cavity (woodcuts, figs. 3, *n*, 21 and 22). It will be found convenient to employ a special term for this receptacle, which confers upon the gonosomes in which it occurs a very characteristic feature. I have already designated it by the name of "*acrocyst*.[1]" It may be seen in *Sertularia pumila*, *S. cupressina*, *S. polyzonias*, *Calycella syringa*, *Calycella lacerata*, &c., and would seem to be in every instance confined to the female.

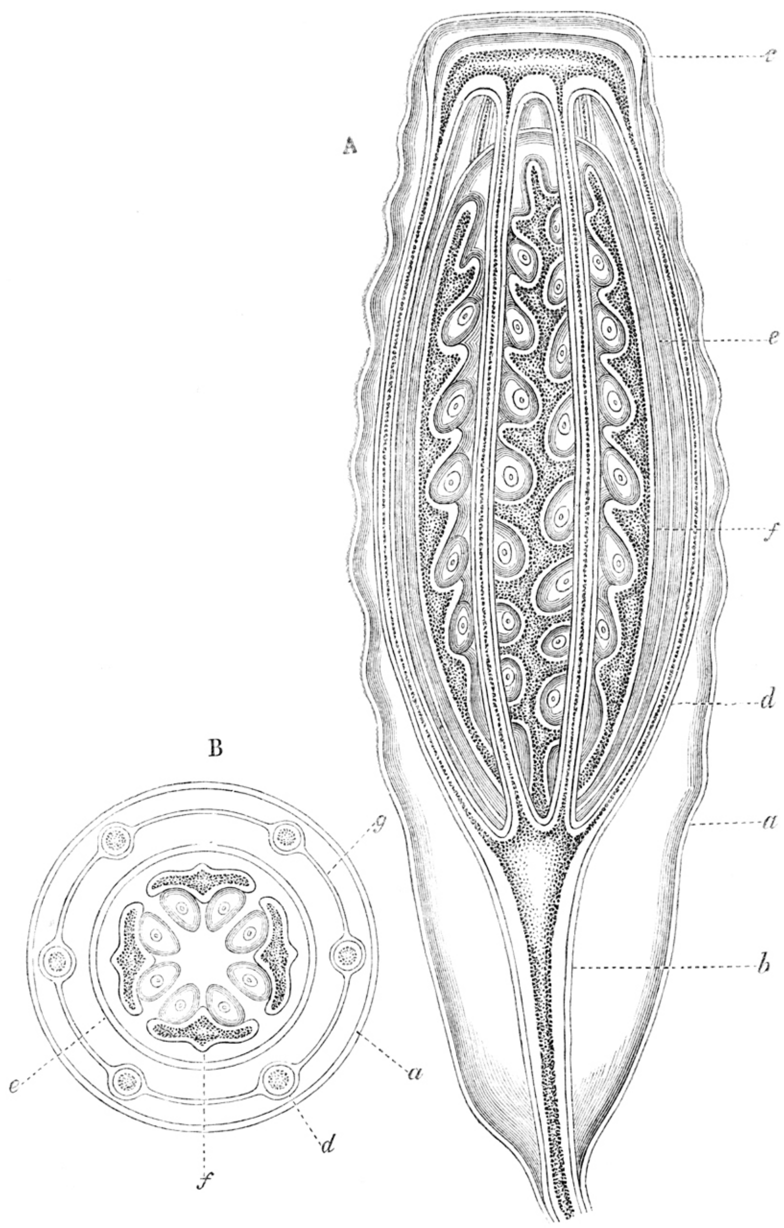
[1] 'Proc. Roy. Soc. Edin.,' 1858.

There is some difficulty in determining the exact morphology of the acrocyst. In its usual form it seems to consist of a simple extension of the endotheca of the gonophore, protruded as a hernia-like sac through the summit of the gonangium, when the whole becomes surrounded by a thick gelatinous-looking envelope, which is excreted from the outer surface of the sac, and which shows no appearance of true structure, though distinct zones of deposition may occasionally be observed in it.

In *Calycella lacerata* the spadix itself, as was first shown by Dr. S. Wright, is, with the surrounding endotheca and ova, carried upwards upon the blastostyle, by whose elongation these various parts are protruded from the summit of the gonangium, and the endotheca thus becomes a true acrocyst and excretes from its outer side the usual thick gelatinous investment (woodcut, fig. 22). The peculiarity of the acrocyst in this case is found in the presence within it of the spadix, which, however, is depressed by the enlarging ova, and forced back into the bottom of the sac.

In the interior of the acrocyst the ova pass through certain stages of their development, and ultimately escape as free ciliated embryos by the rupture of its walls.

FIG. 20.



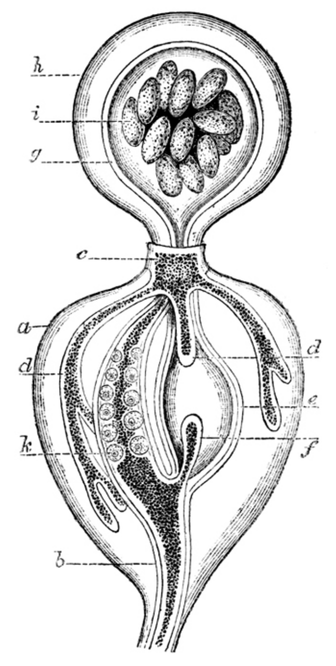
Gonangium, with its contents, from *Laomedea repens*, Allm., showing the compound blastostyle.

A, General view; B, plan of transverse section. *a*, gonangium; *b*, lower portion of blastostyle continuing simple; *c*, opercular summit of blastostyle; *d*, separate tubular branches into which the blastostyle has become divided; *e*, the endotheca; *f*, ramifications of spadix; *g*, an ectodermal membrane, connecting the divisions of the blastostyle with one another.

From the observations of Strethill Wright it would appear that in *Wrightia* (*Atractylis*) *arenosa*, a gymnoblastic species, the ova escape, by the rupture of the sporosac, into a gelatinous mass which is a secretion from the outer surface of the summit of the sporosac, to which it remains adherent, and that in this gelatinous nidus they become converted into planulæ, and then escape into the surrounding water. It is plain, however, that the simple gelatinous secretion which thus affords a protective nidus for the developing ova cannot be confounded with a true acrocyst, which is found only in the calyptoblastic hydroids.

In the cases above described the acrocyst is destitute of any further covering, and has its walls with their gelatinous investment freely exposed to the surrounding water. In *Sertularia rosacea*, *S. fallax* and *S. tamarisca*, however, an additional covering is provided for the acrocyst, and there is thus formed a curious and complicated receptacle, in which the ova, as in a sort of

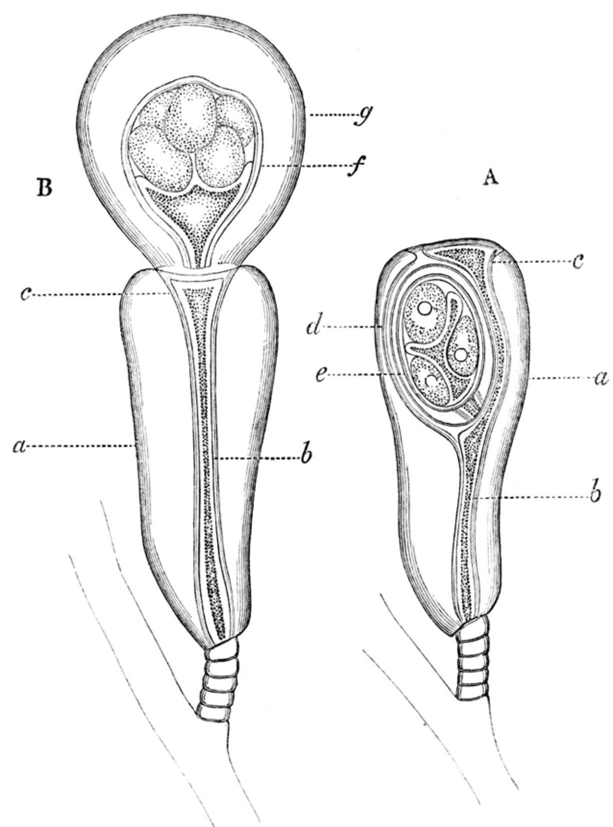
Fig. 21.



Female gonangium, with acrocyst of *Sertularia pumila*.

a, gonangium; *b*, blastostyle; *c*, opercular summit of blastostyle; *d d*, cæcal offsets from the summit of the blastotyle; *e*, gonophore after having discharged its contents into the acrocyst; *f*, spadix; *g*, proper sac of acrocyst; *h*, external gelatinous investment of acrocyst; *i*, ova contained in acrocyst; *k*, young ova in blastostyle.

Fig. 22.



Female gonangium with acrocyst of *Calycella lacerata*.

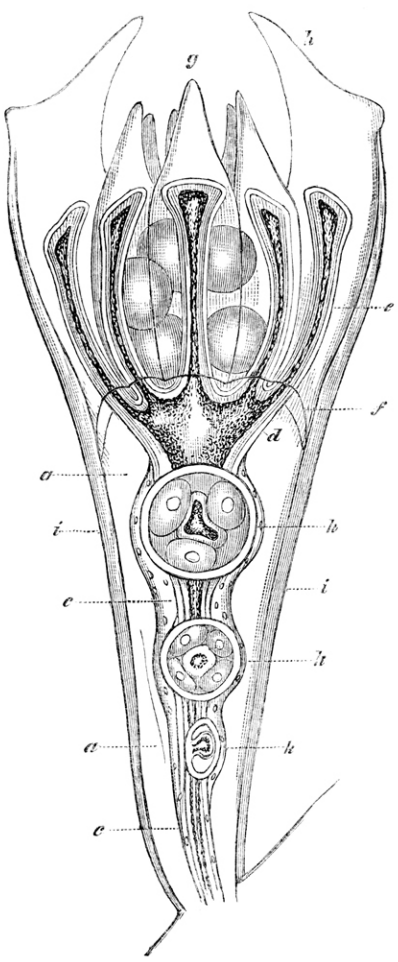
A, Young gonangium, with its contents before the formation of the acrocyst. B, older gonangium, bearing an acrocyst.

a, gonangium; *b*, blastostyle; *c*, opercular summit of blastostyle; *d*, membrane passing over the gonosac while still confined within the gonangium; *e*, gonosac still within the gonangium, and containing ova which surround a lobed spadix; *f*, proper membrane of acrocyst; its gelatinous investment. Within the acrocyst are seen ova already somewhat advanced in development, and the spadix depressed towards the bottom of the sac by their enlargement.

marsupium, pass through certain early stages of their development, previously to being discharged into the surrounding water.

The nature and morphology of this receptacle in *Sertularia rosacea* (woodcut, fig. 23) will be best understood by tracing its development. The young female gonangium (woodcut, fig. 25) is a conical body, with eight slightly projecting longitudinal ridges, and with the broad end of the cone constituting the distal end or summit of the gonangium. A blastostyle occupies its axis, having upon its sides, one over the other, the young budding gonophores, and expanding at its summit into a broad thick disc, which closes, as with a plug, the free end of the gonangium. Upon the outer side of this disc a thin chitinous investment is excreted, becoming continuous at

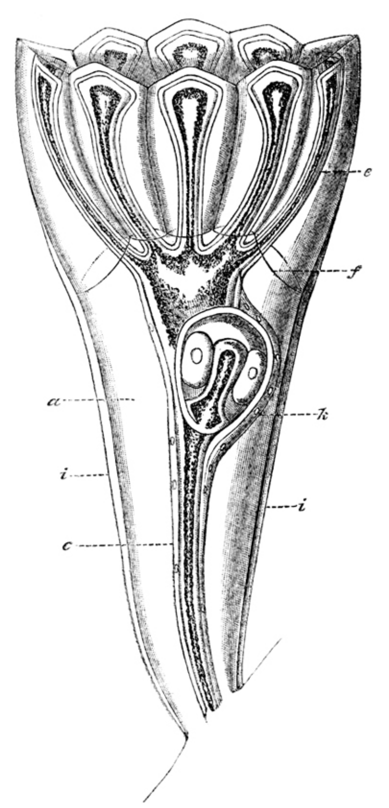
FIG. 23.



Mature female gonangium with marsupial chamber in *Sertularia rosacea*.

a, a, Cavity of the proper gonangium; *c, c,* blastostyle; *d,* opercular summit of blastostyle; *e,* one of the eye's radiating arms which are given off from the summit of the blastostyle, marked by a chitinous sheath *f,* which is prolonged from the walls of the gonangium; the arms are seen surrounding the marsupial chamber, which contains ova advancing towards the condition of planulæ; *g,* the six shorter spines which crown the marsupium; *h,* the two longer lateral spines; *i, i,* the two lateral ridges of the gonangium, which are continued into the longer spines; *k, k, k,* gonophores in various stages of development, all surrounded by the gubernacular membrane.

FIG. 24.



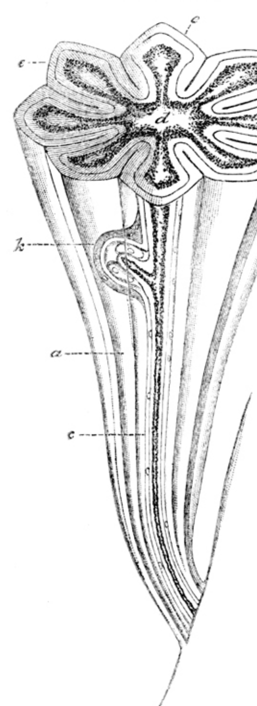
Young female gonangium of *Sertularia rosacea,* showing the formation of the marsupial chamber.

a, Cavity of the proper gonangium; *c,* blastostyle; *e,* radiating arms prolonged from the opercular summit of the blastostyle; *f,* chitinous sheath of arms; *i, i,* lateral ridge of gonangium; *k,* gonophore surrounded by its gubernacular membrane.

the edge of the disc with the chitinous walls of the gonangium, while in the centre of the disc the chitinous investment is deficient, leaving here the summit of the blastostyle naked.

The edge of the disc soon becomes produced into eight thick symmetrically radiating lobes (*e, e*) which gradually elongate themselves, carrying with them a continuation of the chitinous excretion, which forms a wide tube around each; and now bending upwards, in the form of eight arms with enlarged extremities, they remind one of the disposition of the petals in a flower, and present altogether an appearance of great elegance (woodcut, fig. 24, *e*). These eight radiating arms are composed of ectoderm and endoderm, and have their axis occupied by a tubular cavity, which communicates with that of the blastostyle. As the arms continue to elongate, we find them next with their free extremities bending towards one another, until finally (woodcut, fig. 23), they completely enclose a space, which becomes entirely shut in by the lateral coalescence of the wide chitinous tubes with which the radiating processes are each invested.

Fig. 25.



Very young female gonangium of *Sertularia rosacea.*

a, Cavity of the gonangium; *c*, blastostyle; *d*, opercular summit of blastostyle; *e*, radiating lobes from summit of blastostyle, about to be prolonged into arms; *k*, young gonophore.

In the mean time the eight longitudinal ribs of the gonangium continue themselves upon the radiating arms, and ultimately extend beyond their extremities as free pointed processes (*g*, *h*). Two of them, however, situated opposite to one another, greatly surpass the others in size, and mainly contribute to the peculiar and characteristic form of the gonangium. Into the marsupial chamber thus formed the ova make their way, enclosed apparently in a proper acrocyst.

A very similar condition is presented by *Sertularia fallax*. Here, however, the summit of the blastostyle is prolonged into four instead of eight lobes; but the subsequent history of these is in all essential points the same as in *Sertularia rosacea*.

If we compare the structures now described with an ordinary hyrandth, we shall have no difficulty in recognising an exact parallelism; for the tubular processes which are developed from the summit of the blastostyle may be regarded as homologous with the tentacles of a hydranth. They have, however, undergone a special modification, by which they become subservient to an entirely different function from that of the tentacles of the hydranth; for, no mouth being developed on the blastostyle, they are no longer prehensile organs administering to the alimentation of the colony, but, like the blastostyle itself, have assigned to them functions appertaining to reproduction rather than nutrition, and are destined to circumscribe a cavity for the retention and development of the ova.

The ova would seem to continue in the marsupial cavity until they have acquired the condition of ciliated embryos.

The modification of marsupial receptacle which occurs in *Sertularia tamarisca* is also very interesting. The female gonangia (woodcut, fig. 26 B) are here of an oval form for about the proximal half of their length, and then become trihedral, with the sides diverging upwards, while the whole is terminated by a three-sided pyramid. The sides of the pyramid are cut into two or three short teeth along their edges, and each of their basal angles is prolonged into a short spine.

The trihedral portion, with its pyramidal summit, is formed of three leaflets (g, g', g'') which merely touch one another by their edges, without adhering, so that they may be easily pushed aside from one another by the dissecting needle, or by the embryo during its escape.

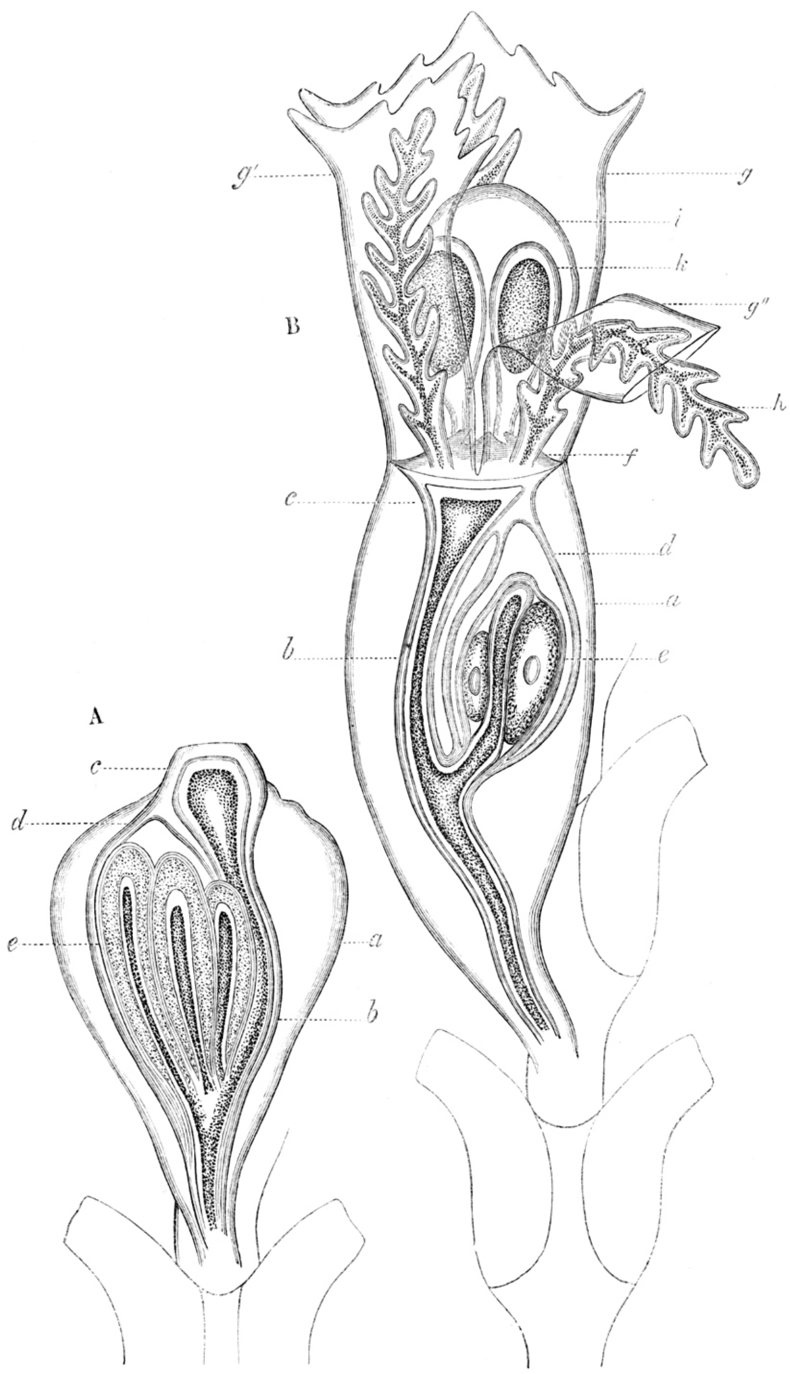
On laying open the gonangium the oval or proximal portion of it is seen to be occupied by a blastostyle (*b*), which gives origin to one or more gonophores. It terminates upwards by closing round the distal extremity of the blastostyle, where it forms a ring (*f*) with tooth-like processes, by which the extremity of the blastostyle is encircled. This oval portion constitutes the gonangium proper, and is the only part developed in the male (fig. 26 A).

From the summit of the blastostyle three tentacula-like processes (*h*) are given off. They constitute ramified cæcal offsets of the cavity of the blastostyle, and are composed of an ectodermal and an endodermal layer. Immediately after their origin from the blastostyle they enter the terminal leaflets, and now lie between the two laminæ of which these leaflets are composed.

The leaflets, with their contained cæcal offsets from the blastostyle, surround a membranous sac (*i*) which is borne on the summit of the oval portion, or proper gonangium, and contains one or two ova, which are usually in an advanced stage of development. Each ovum is immediately invested by a delicate structureless sac (*k*), which is continued by a neck-like prolongation to the summit of the blastostyle.[1]

The homological relations

FIG. 26.



Male and female gonangia of *Sertularia tamarisca.*

A, Male gonangium; B, female, with its marsupial chamber.

a, Proper gonangium; *b*, blastostyle with *c*, its opercular summit; *d*, gubernaculum; *e*, gonophores, having the spadix surrounded by the spermatozoa in the male and by the ova in the female; *f*, chitinous roof of the gonangium proper in the female, perforated by a central denticulated aperture; *g*, *g'*, *g''*, the three leaflets, forming the walls of the marsupial chamber, and each containing within it a ramified cæcal process, *h*, from the summit of the blastostyle; *g''* is cut across and depressed; *i*, acrocystal sac; *k̄*, ovum, included in a special sac.

[1] The account here given of the marsupial receptacle of *Sertularia tamarisca* differs in some

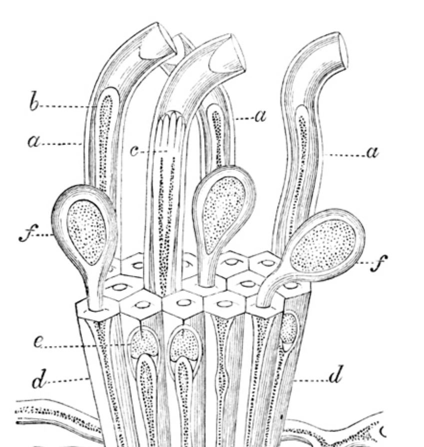
between the marsupial receptacles of *Sertularia rosacea* and *Sertularia fallax* on the one hand, and *Sertularia tamarisca* on the other, are at once apparent, and are very interesting. The ramified tubes of *S. tamarisca* are manifestly the representatives of the simple tubes in *S. rosacea* and *S. fallax;* while the three broad chitinous leaflets within which the ramified tubes are contained are homologous with the hollow chitinous processes of the gonangium, which in *S. rosacea* and *S. fallax* enclose the simple tubes, and subsequently coalesce to form with their prominent ridges and spines an external capsule-like covering for the sac, into which, as in *S. tamarisca,* the ova are expelled from the gonangium proper.

The structures just described in *Sertularia rosacea, S. fallax,* and *S. tamarisca* will, I think, enable us to explain a peculiar feature observed in *S. pumila,* and probably some other species. In *S. pumila* the blastostyle of both male and female gonangia gives off from its enlarged opercular summit several more or less ramified cæcal tubular processes (woodcut, fig. 21, *d, d*), which, instead of developing themselves externally, are found entirely within the gonangium, where they hang freely from the summit of the blastostyle. Their walls are composed both of endoderm and ectoderm, and their cavity communicates with that of the blastostyle, so that the peculiar coloured corpuscles which circulate within the cavity of the blastostyle are freely admitted into the cæcal tubes, where they may occasionally be seen in active motion. The tubes can be most satisfactorily examined in the younger gonangia. In the older ones they will frequently be found to have contracted adhesions to the gonangium, to have become atrophied, and, finally, even to have disappeared.

I believe that these tubes are the exact equivalents of those which in *Sertularia tamarisca* and *S. rosacea* are given off from the same part of the blastostyle, but where, instead of growing into the cavity of the gonangium, they are developed in an outward direction, and assist in the formation of the peculiar receptacle which surrounds the acrocyst in those species.[1]

Among the most remarkable modifications of the trophosome is that of *Coppinia arcta* (woodcut, fig. 27). In this singular hydroid the hydrothecæ and gonangia spring directly from a creeping retiform hydrorhiza, while the gonangia, which are very numerous, become closely adherent to one another by their sides, so as to form with the proximal portion of the hydrothecæ and with the hydrorhiza a continuous encrusting basis spreading over the surface to which the

FIG. 27.



A portion of the hydrosoma of *Cophinia arcta.*

a, a, a, Hydrothecæ; *b,* a hydranth retracted and destitute of tentacles; *c,* a hydranth retracted and with its tentacles present; *d, d,* basal encrusting portion formed by the juxtaposition and adhesion of tubular gonangia; *e,* sporosac, enclosing a solitary ovum; *f, f,* acrocysts, enclosing the ovum in a more advanced stage of development; *g,* retiform stolon, forming the hydrorhiza.

respects from my original description of the same part ('Brit. Assoc. Report on HYDROIDA'), subsequent more favorable examinations having caused certain modifications of my former views.

[1] It is evidently the tubes here described to which Agassiz ('Nat. Hist. U. S.,' vol. iv, p. 329, pl. xxxii, figs. 10, 10[a]) refers as occurring in a North American hydroid which he regards as identical with the *Sertularia pumila* of the European coasts. He views them, however, as simply representing the fleshy bands which may frequently be seen in the trophosome of the Hydroida, extending from the outer

hydroid had attached itself. Each gonangium in the female contains a single sporosac with a single ovum; and this ovum, after a time, becomes extra-capsular in order to undergo within an acrocyst some of the earlier stages of its development.[1]

But there is, perhaps, no modification of the gonosome more interesting than that which we meet with in *Gonothyræa Lovéni*, Allm., and at least one other allied species. In this calyptoblastic hydroid there are borne upon the summit of the gonangium, and altogether external to its cavity, certain very peculiar gonophores, which convey the impression of small, fixed, imperfectly developed medusæ (woodcut, fig. 28). It was to these extracapsular gonophores

surface of the cœnosarc to the inner surface of the chitinous periderm, and which these tubes certainly resemble when they become more or less atrophied and adherent to the walls of the gonangium. They are also described and figured by Lindström in a paper "On the Development of *Sertularia pumila*" ('Oefversigt af Köngl. Vetenskap-Akademiens Förhandlingar,' 1855).

[1] As the nature of *Coppinia arcta* has been hitherto very imperfectly understood a more detailed description of it may here be given.

The hydrosoma forms small sponge-like masses on the stems of the larger hydroids, and is especially abundant on *Sertularia abietina* and *Plumularia falcata* from deep water.

Even on a superficial inspection it may be seen to consist of two distinct portions. Of these, one constitutes a continuous encrusting base, and the other consists of curved cylindrical tubes which project from the free surface of the base. In each of these tubes is contained an exsertile and retractile hydranth. The tubes are thus true hydrothecæ. The hydranths are conspicuous by their fine lemon-yellow colour, and are furnished with a verticil of filiform tentacles disposed round the base of a short conical hypostome. They are, however, often imperfect and apparently destitute of mouth and tentacles.

The encrusting base which forms the most remarkable part of the hydroid has never yet been correctly described.

The hydrothecal tubes can be traced through it to its attached surface, while vertical and transverse sections show that the rest of the crust is mainly composed of vertical chitinous tubes rendered polygonal by mutual pressure. They adhere to one another by their sides, and each, as had been long ago shown by Dalyell, opens on the free surface of the crust by a small circular aperture.

These tubes are true gonangia; within each is a solitary sporosac which seems to have originally budded from a blastostyle, which soon, however, becomes suppressed by the growing sporosac. A sufficiently obvious spadix may be recognised in the sporosac which contains a single large lemon-yellow ovum, in whose earlier stages there may be seen a distinct germinal vesicle, while the place of the germinal spot is taken by numerous clear spherical bodies which disappear in a few seconds after the ovum is pressed out of the sporosac and exposed to the action of the surrounding water.

Segmentation commences while the ovum is still within the gonangium, and the ovum becomes thereby converted into a mass so plastic that it allows of its being forced through the small aperture in the summit of the gonangium. In its exit it carries out with it a hernial extension of the attenuated walls of the sporosac, which thus form for it an acrocyst in which it is still for some time confined. It ultimately, by the rupture of the acrocyst, escapes as a planula into the surrounding water. The planula and its development into a hydranth enclosed in a chitinous tube have already been observed by Dalyell.

Both hydrothecæ and gonangia spring from an adherent retiform hydrorhiza without the intervention of a hydrocaulus.

A knowledge of the structure of *Coppinia* will enable us to give a more correct generic that Lovén long ago[1] called attention when he supported and developed the doctrine, just then announced by Ehrenberg, of the sexuality of the HYDROIDA—a doctrine which, though in its mode of statement not absolutely correct, was yet full of significance.

The bodies (*g, g'*) in question are nearly spherical sacs, and occur in both the male and female colonies. In their walls may be demonstrated an ectotheca, mesotheca, and endotheca. The generative elements are formed within the endotheca, and surround a well-developed spadix. The endotheca, however, is generally of short duration, becoming absorbed or ruptured under the increasing volume of its contents. In the female four very distinct radiating canals may frequently be seen; these spring from the base of the spadix, and thence run in the walls of the mesotheca towards the opposite end of the sac. In many cases, however, I was unable to detect any trace of these canals, and could never find them in the male. We should, however, be scarcely justified in asserting that in such cases they are altogether absent; for it is quite possible that emptiness or some other peculiar condition at the time of observation may have caused them to escape detection—a supposition which receives confirmation from the fact that, even in cases where they are obvious, they become obliterated under slight pressure.

At the summit of the sac the mesotheca is perforated by a circular aperture, round which its walls appear to be thickened, and seem to contain here a circular canal in which the radiating canals terminate; at least, the presence of a line of coloured granules at this place affords an indication of the existence of such a canal. The ectotheca, which is loaded with thread-cells, is also perforated by an aperture corresponding to that of the mesotheca; and the gonophore is crowned by a circle of short tentacles, which seem to originate from the thickened margin of the perforation in the summit of the mesotheca.

These tentacles possess, like the marginal tentacles of a true medusa, considerable contractility. They may frequently be seen of very different lengths in different gonophores of the same colony; and this, which is really the result of different degrees of contraction, may be easily taken for different degrees of development, the tentacles being especially sluggish in the acts of extension and contraction. Their length, when fully extended in the female gonophore, will equal about half the diameter of the gonophore. While under external irritation, they will slowly contract to a third of their original length, and will then show themselves as a little stellate crown on the summit of the gonophore, reminding us of the sessile stigma in the pistil

diagnosis than was possible so long as we were ignorant of the true nature of this curious hydroid, and the following may be taken as expressing the essential characters of the genus:

COPPINIA, Hassall.

Trophosome.—Hydrocaulus absent; hydrothecæ tubiform, springing from an adherent retiform hydrorhiza.

Hydranths with a single verticil of filiform tentacles.

Gonosome.—Gonosphores adelocodonic; gonangia tubiform, sessile on the hydrorhiza, and forming, by the close approximation of their sides, a continuous incrusting mass surrounding the bases of the hydrothecæ which project from it at intervals.

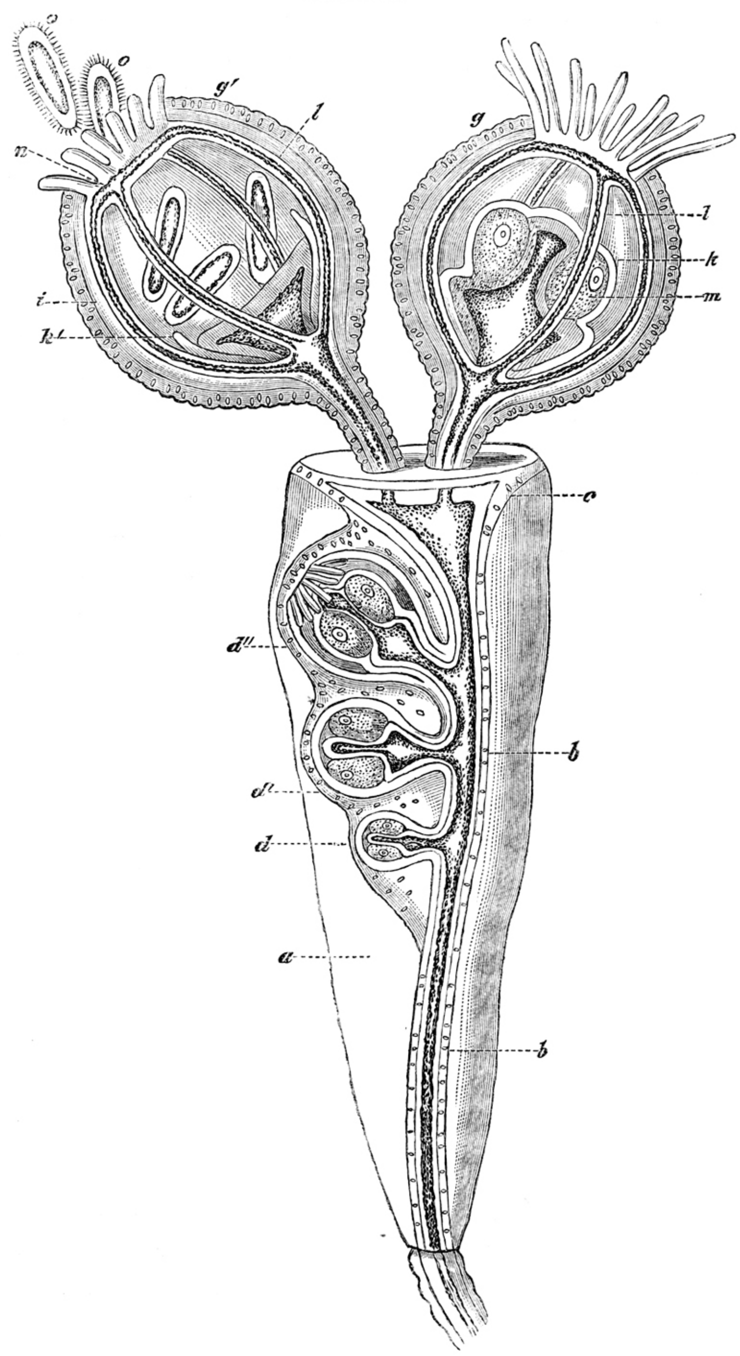
[1] Lovén, "Beiträge zur Kenntniss der Gattungen *Campanularia* und *Syncoryne*," 'Wiegm. Arch., 1837. Lovén names the hydroid in which he witnessed the extracapsular gonophores *Campanularia geniculata*, which is certainly a wrong determination of the species. See "Notes on the Hydroida," 'Ann. Nat. Hist.' for August, 1859.

of a poppy. They vary in number; I have counted in the female from eight to sixteen or twenty. They are composed of ectoderm and endoderm, the ectoderm containing thread-cells, and the endoderm presenting the usual septate appearance. They are less numerous and less developed in the male than in the female.

The contents of the sacs are, as in an ordinary gonophore, either ova or spermatozoa, and the sexes are invariably found separated on distinct colonies. The ova, while contained within them, pass through the various stages of development up to that of ciliated embryos, in which state, as has been already shown by Lovén, they are discharged into the surrounding water through the orifice in the summit.

If we follow the development of these extracapsular gonophores, we shall find, as, indeed, Lovén had already pointed out, that they are originally produced within the gonangium where they originate, exactly like intracapsular gonophores, as buds from the blastostyle. By the growth of the blastostyle the gonophores are carried upwards with it, in the order of their maturity—the oldest ones, while within the gonangium, being always nearest the summit of the blastostyle; but instead of discharging their contents and then withering away on their arrival at the orifice of the gonangium, as in ordinary adelocodonic forms, they are here carried out through the orifice, become truly extracapsular, and in this state undergo, with their contents, further development, while the growing blastostyle always keeps its extremity truncated on a level with the summit of the gonangium, whose orifice it continues to close by a plug-like expansion, which at the same

Fig. 28.



Gonangium with Meconidia of *Gonothyræa Lovéni* (female).

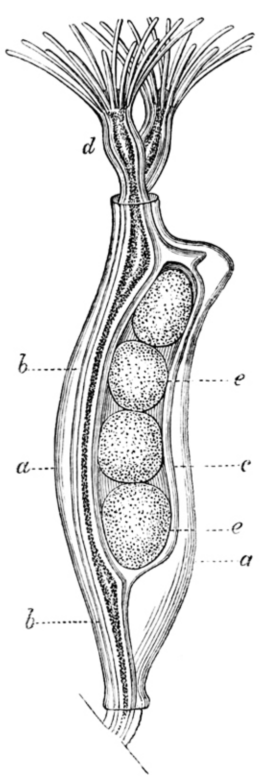
a, Cavity of gonangium; *b*, *b*, blastostyle, with *c*, its opercular summit; *d*, *d'*, *d''*, gonophores in various stages of maturity still within the gonangium, all surrounded by the gubernacular membrane; in *d''* the tentacles are seen already formed and lying back on the walls of the gonophore; *g*, *g'*, meconidia, *g'* being more advanced than *g*; *i*, mesotheca, external to which may be seen the ectotheca loaded with thread-cells; *k*, endotheca; *k'*, remains of endotheca in the more advanced meconidium; *l*, radiating canals, united by the circular canal, *n*; *m*, ovum with germinal vesicle and spot; *o*, *o*, embryos, escaping in the form of ciliated planulæ.

time affords a support for the gonophores after they have become extracapsular. Two or three of these extracapsular gonophores, in different stages of development, may be usually seen, borne each by a short peduncle upon the opercular summit of the blastostyle, with whose cavity that of their spadix freely communicates through the tubular axis of the peduncle.

While the gonophore is still contained within the gonangium, the mesotheca has become developed in it, and in the more advanced ones (d'') the rudimental tentacles may be seen thrown back in their walls in the form of a little star.

That the bodies now described belong to the class of adelocodonic rather than to that of phanerocodonic gonophores must, I think, be admitted. In all essential points, except in the presence of entacles developed from the mesotheca, they agree with the gonophores of *Tubularia indivisa*, which must certainly be classed among the adelocodonic forms, notwithstanding their possession of a well-developed mesotheca and gastrovascular canals. In both the aperture of the mesotheca is reduced to a mere perforation, and in neither is the mesotheca ever developed as a locomotive organ.

Fig. 29.



Gonangium with gonangial hydranths in *Halecium halecinum.*

a, a, Gonangium; *b, b*, blastostyle; *c*, gubernacular membrane, still confining the ova, *e, e*, which are here in an advanced stage of development, the proper gonophore having become absorbed after discharging its contents; *d*, gonangial hydranths.

It must also be borne in mind that, when planoblasts are produced in the *Campanularinæ*, they are in almost every instance blastochemes; in other words, they belong to the type in which the generative elements are produced, not directly, as in *Gonothyræa*, between the ectoderm and endoderm of the manubrium, but are formed in special zooids developed from some parts of the gastrovascular system; *Leptoscyphus tenuis*, Allm.,[1] affording the only known exception to this rule.

The extracapsular gonophores of *Gonothyræa Lovéni* are thus of no little interest in the morphology of the Hydroida, and it will be found convenient to speak of them under a special name. Their resemblance to a pomegranate, or perhaps still more obviously to a poppy-capsule, with its sessile stellate stigma, will instantly strike us; and it is this comparison which has suggested to me the name of *meconidium*,[2] by which I have elsewhere found it useful to designate them.

A very remarkable feature, which one is at first sight tempted to place in the same category with the formation of meconidia, but which is in reality of an entirely different significance, is presented by *Halecium halecinum*. In this hydroid there is borne upon the summit of the female gonangium, in a situation precisely similar to that of the meconidia of *Gonothyræa Lovéni*, a pair of hydriform bodies (woodcut, fig. 29 *d*). These bodies present no appreciable difference by which they may be distinguished from the ordinary hydranths of the trophosome. They are of an elongated oval form, with the mouth situated on the summit of a short conical hypostome, which is surrounded by a circle of filiform tentacles. They are always two in

[1] "Notes on the Hydroid Zoophytes," 'Ann. Nat. Hist.,' Nov., 1859.

[2] A diminutive noun, formed from μήκων, a poppy. "Notes on the Hydroid Zoophytes," 'Ann. Nat. Hist.,' August, 1859.

number, and diverge from a common point of attachment, while their wide gastric cavities, after contracting below, communicate here with one another and with the tubular cavity of the blastostyle.

I have never been able to discover any direct relation between these gonangial hydranths and the generative functions of the hydroid. The ova, so far as I can determine, seem to be produced in the usual way in a sporosac which springs from the blastostyle, and are then discharged into a chamber formed by the gubernacular sac (*c*), the sporosac itself entirely disappearing after the loss of its contents. In the sort of internal marsupium thus formed the ova pass through certain stages of their development before their ultimate liberation as planulæ through the summit of the gonangium, which takes place, probably, after the disappearance of the gonangial hydranths.

I may here mention a very singular body, whose exact significance I have never been able satisfactorily to determine, and which may be seen in the female gonangium of *Antennularia antennina*, where it is of frequent occurrence. It is always found floating free in the cavity of the gonangium, along with the ova which had escaped from the ruptured gonophores, and resembles an imperfectly developed medusa, with a large and apparently imperforate manubrium, but with its umbrella closed, and without any trace of gastrovascular canals, the walls of the umbrella being separated from the manubrium by a considerable space, which is filled with a clear fluid. It may be compared to a free sporosac; but it is much smaller than the ordinary sporosacs of the *Antennularia;* and I have never observed in it any trace of generative elements. It is possibly an undeveloped sporosac, produced, like the perfect sporosacs, as a bud from the blastostyle, and becoming separated at an early stage; but I can offer no decided opinion either as to its origin or its ultimate destination. It may be a parasite, though it is not easy to reconcile its peculiar structure with this view.

In almost every case the gonangium, when present in the Hydroida, is destitute of any further covering. In certain hydroids, however, belonging to the family of the *Plumularidæ*, the gonangia are developed in groups, and each group is contained in a common receptacle, which confers upon the hydroid in which it exists a very striking and characteristic feature. This receptacle must be carefully distinguished from a proper gonangium, with which, indeed, it has been confounded in various descriptive works on the HYDROIDA. It will therefore be very convenient to give it a special name, and I have already proposed for it the term *corbula*, suggested by its basket-like form.[1]

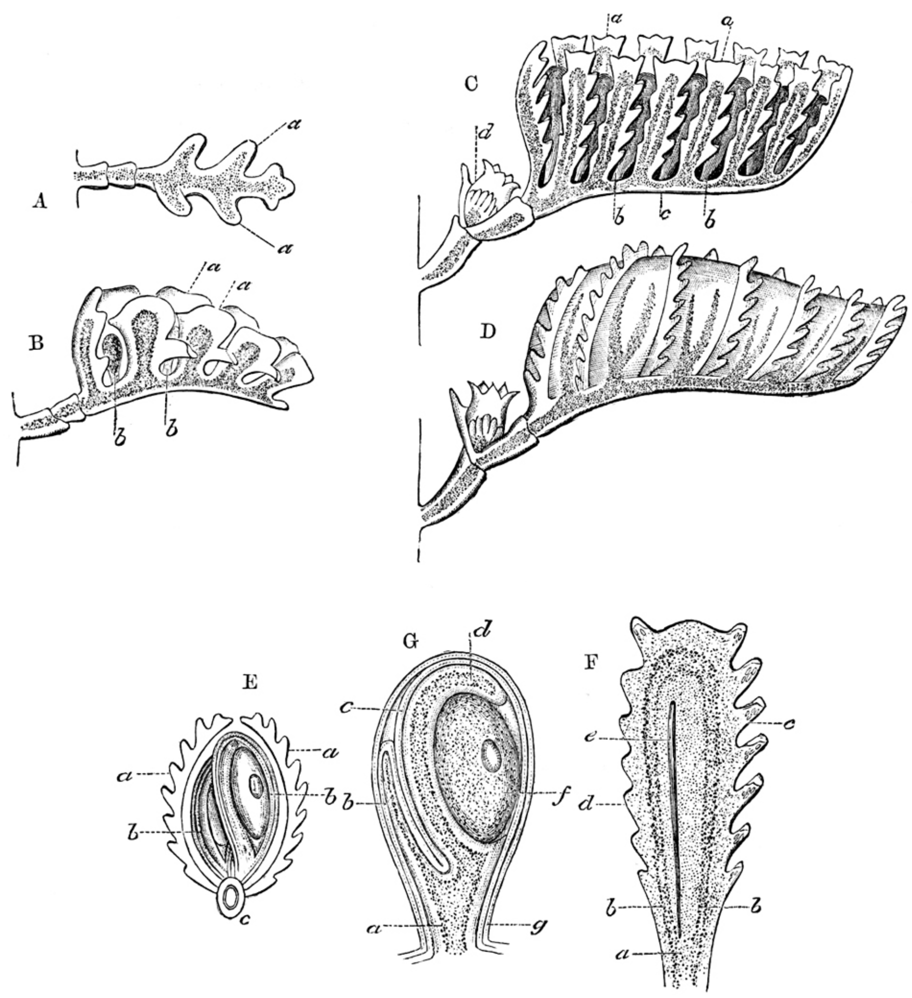
In *Aglaophenia pluma* the corbulæ (woodcut, fig. 30, D) may be plainly seen to be metamorphosed ramuli. The peculiar metamorphosis of a ramulus, which results in the formation of a corbula, consists here in the suppression of the hydrothecæ, accompanied by the development on each side of the ramulus of numerous oval, hollow, alternately placed leaflets; each leaflet consisting of a diverticulum from the cœnosarc of the ramulus, invested by a continuation of the general perisarc.

In the earliest stages of these leaflets (A, *a*) their edges are entire, but they soon become deeply serrated by the formation of hollow tooth-like processes, more especially upon the edge which is turned towards the distal extremity of the ramulus. Upon the proximal edge of the leaflet these processes usually remain in an imperfectly developed state, though they are occasionally equally

[1] 'Proc. Roy. Soc. Edin.,' 1858.

well developed on both edges. The processes which are thus developed on the edges of the leaflet are in all respects similar to the lateral nematophores of the trophosome (see p. 28). They are filled, like these, with soft granular protoplasm, in which is immersed a cluster of fusiform thread-cells, and which is in direct communication with the cœnosarc filling the cavity of the leaflet. They are also, like these, perforated at their extremity by an oblique aperture; but I have never seen the nematophores of the corbulæ emit, like those of the trophosome, pseudopodial prolongations of their contents.

Fig. 30.



Development of the Corbula in *Aglaophenia pluma*.

A, Very young corbula; B, corbula more advanced; C, corbula in a still more advanced stage; D, the mature corbula; E, transverse section of mature corbula, showing two gonangia, each containing a single gonophore. *a*, *a*, leaflets of corbula; *b*, *b*, gonangia; *c*, ramulus supporting the leaflets; *d*, a hydrotheca.

F, Separate leaflet from mature corbula. *a*, continuation of the somatic cavity into the leaflet, where it divides into two branches, *b b*; *c*, nematophores forming tooth-like processes on the distal edge of the leaflet; *d*, imperfectly developed tooth-like processes on the proximal edge; *e*, septum, dividing the cavity of the leaflet.

G, Gonangium from mature corbula. *a*, continuation of somatic cavity into gonangium; *b*, blastostyle, partially suppressed by the enlarging gonophore; *c*, gonophore; *d*, spadix; *f*, ovum; *g*, wall of gonangium.

As the young leaflet continues to grow, its cavity becomes partially divided by a chitinous septum (F *e*) which stretches across from the outer to the inner side, parallel to the axis of the leaflet, but always nearer to the proximal edge. At the free end of the leaflet the septum is incomplete; so that here the contents of the cavity at one side of the septum communicate with those upon the other side, both sides communicating at the base of the leaflet with the common cavity of the cœnosarc.

The leaflets, as they increase in size (B, C), direct themselves vertically from the upper surface of the ramulus, and those of one side arch over so as to approach those of the opposite. They are at first free, but they afterwards become intimately united at their edges, the nematophores continuing to project as tooth-like processes, and forming an elegant serrated ridge between every two leaflets. Ultimately the leaflets of one side coalesce with those of the other by their summits, and thus form a completely closed chamber (D).[1]

In the receptacle thus formed the gonangia are produced. They spring from the upper side of the metamorphosed ramulus, near the point where the leaflet leaves it, and represent the hydrothecæ which exist on an ordinary ramulus, and whose place they here take. They begin to be produced at an early stage of the corbula, and may be easily examined in the young corbula before it has become closed (B *b*, C *b*). The metamorphosed ramulus generally remains unchanged for a short distance from its origin, and may be here seen bearing one or two ordinary hydrothecæ.

About twelve gonangia are usually contained in each corbula. They are of a very simple type (G), of a regular oviform figure, and with their chitinous walls thin and delicate. Each gonangium seems to contain but a single sporosac, which soon comes to occupy almost its whole cavity. A long, nearly cylindrical spadix extends from the base to the summit of the sporosac, passing in the male through the axis of the mass of spermatogenous tissue, but in the female pushed to one side by the development of the large single ovum, which here occupies almost the whole remaining portion of the cavity of the sporosac.

There may appear some difficulty in deciding as to whether the corbula ought to be regarded as properly belonging to the trophosome or to the gonosome. The truth is, that it holds a place exactly intermediate between the two, and may in this respect be compared to the bracts in plants; for these are in the same way intermediate between the ordinary leaves and the proper floral verticils. As the bracts, however, are usually treated of in connection with the *inflorescence*, whose limitation they frequently determine, we shall, perhaps, here also find it convenient to speak of the corbula in connection with the gonosome rather than with the trophosome.[2]

[1] In some other species (*Aglaophenia myriophyllum*) the leaflets never coalesce, and the corbula remains permanently open.

[2] In a very ingenious paper, "On the Morphology of the Reproductive System in the Sertularian Zoophytes," by Professor E. Forbes ('Ann. of Nat. Hist.,' 1844, vol. xiv, p. 385), the author recognises in the corbulæ of *Aglaophenia pluma*, and some other allied species, their true significance as metamorphosed branches. He mistakes, however, the nature of the metamorphosis, while, in accordance with the prevailing view, he sees in the receptacles in question bodies in all respects corresponding to the proper gonangia of the other hydroids.

Forbes, moreover, extends his generalisation, applying it to the gonangia of the other Sertularians, which he believes must be all regarded as peculiarly metamorphosed branches, with metamorphosed and confluent hydrothecæ, exactly in the same way that the floral verticils in plants may be referred to verticillate, metamorphosed, and variously combined leaves. "The vesicle," he says, "is formed from a branch or pinna through an arrest of individual development, by shortening of the spiral axis, and, by a transformation of the stomachs (individuals) into an ovigerous placenta, the dermato-skeletons (or

As a general rule, there is no perceptible difference between the male and female colonies of the same species of hydroid, either in the trophosome or the gonosome, beyond what is, of course, presented by the generative elements themselves. In some cases, however, the difference is sufficiently well marked. Thus in *Sertularia tamarisca* the male and female gonangia (woodcut, fig. 26) differ strikingly from one another; for the male gonangia are compressed, somewhat obcordate receptacles, with a short terminal tubular aperture; while the female are oval for about the proximal half of their height, and then become trihedral with the sides diverging upwards, the whole being terminated by a three-sided pyramid whose edges are cut into two or three short teeth, and the basal angles prolonged into a short spine.[1]

So also in *Sertularia rosacea* a well-marked difference may be seen. The male gonangia are here of a conical form, curved near the apex, which is their point of attachment, and provided with six longitudinal ridges in the form of thin projecting lamellæ, each of which terminates at the distal extremity in a free-pointed process which arches over the summit of the gonangium. In the female gonangium (woodcut, fig. 23) the longitudinal ridges are eight in number, while two opposite ones being greatly more developed than the others give to the gonangium the very elegant and striking form which caused Ellis to compare it to a " lily or pomegranate-flower just opening." A very similar difference exists between the male and female gonangia of *Sertularia fallax*, and generally in the group which under the name of *Diphasia*, Agassiz has separated from *Sertularia*. In all these cases the difference depends on the formation in the female of the remarkable marsupial chamber whose structure has been already described (see p. 52).

It will also be borne in mind that, in those species which develop an acrocyst on the summit of the gonangium, this body is formed only in the female; while it is on the female gonangium alone of *Halecium halecinum* that the little geminate hydranth already described (p. 58) is produced; and to these cases we may also add the difference presented by the male and female meconidia in *Gonothyrea Lovéni* (see p. 56).

Among the gymnoblastic hydroids, also, certain differences may be occasionally observed between the male and female. Thus, the tentaculoid tubercles which, in certain *Tubulariæ*, crown the gonophore are in some species more fully developed in the female than in the male; but the most striking difference is found in the genus *Eudendrium*, whose male gonophores are situated in a verticil on the body of the hydranth, and present the remarkable polythalamic condition already described, while the female gonophores originate irregularly for some distance backwards on the branch, and are always monothalamic (see Pls. XIII and XIV). This difference between the male and female gonophores in *Eudendrium* struck Cavolini long before the presence of a male element in the HYDROIDA was suspected, and led him to suppose that *Eudendrium* reproduced

cells) uniting to form a protecting capsule or germen; which metamorphosis is exactly comparable with that which occurs in the reproductive organs of flowering plants, in which the floral bud (normally a branch clothed with spirally arranged leaves) is constituted through the contraction of the axis and the whorling of the (individual) appendages borne on that axis, and by their transformation into the several parts of the flower (reproductive organs)."

The theory, however, involved in the above statement, attractive though it be, is contradicted by the actual development of the parts in question. When Forbes wrote, so little was known of the structure and development of the HYDROIDA, that this accomplished and lamented naturalist may well be excused if some parts of his very suggestive paper have refused to stand the test of subsequent research.

[1] It is apparently the male gonangia which Ellis has figured in his description of this species.

itself by two different kinds of eggs. In accordance with this view, he called the female gonophores in his *Sertularia* (*Eudendrium*) *racemosa* "uova a racemo," and the male gonophores "uova a corimbo."[1]

The differences above described between the male and female are all confined to the gonosome; the trophosome, however, does not appear to be always exempt from a participation in sexual difference, for in *Hydractinia polyclina*, Agass., the hydranths of the male colony are described by Agassiz as differing from those of the female colony by their more elongated proboscis.[2]

We may now consider how the principal modifications which we have described as presented by the gonosome are distributed among the leading groups of the HYDROIDA.

There is no fully established instance of the same species of hydroid producing both phanerocodonic and adelocodonic gonophores, either simultaneously or consecutively; and Sars[3] is certainly in error when he includes under his *Podocoryne carnea*, two forms of hydroids, one with developed medusæ, and the other with sporosacs. Neither is there any known instance of a species with blastochemes producing gonophores in any other way than through the medium of the blastocheme, and there can be little doubt that Van Beneden[4] has made some confusion between two distinct species when he figures a portion of a hydroid colony, which he names *Campanularia geniculata*, with two kinds of gonangia, one containing medusæ and the other sporosacs.

Among the gymnoblastic hydroids the gonophores may be borne either by the trophosome directly or by blastostyles, but they are never included within a gonangium. We have here some species with phanerocodonic and others with adelocodonic gonophores, and the two forms would seem to be pretty equally distributed through the group. Unless *Nemopsis* should prove an exception, there is no known example of the occurrence of a blastocheme among the *Gymnoblastea*. It is, however, by no means impossible that the sexual lobes of *Nemopsis* whose bases extend over portions of both the manubrium and radiating canals, ought to be regarded as true zooids. If this be so, then the *Nemopsis* medusa must be regarded as a blastocheme, though M'Crady has shown that its trophosome is that of a true tubularian.

Among the *Campanularinæ* we meet with medusiform planoblasts, as well as with fixed sporosacs, both forms being produced in nearly equal proportion. The planoblasts, however, belong, with only a single known exception,—that, namely, which is afforded by *Leptoscyphus tenuis*— to the type of the blastocheme. Both planoblasts and sporosacs are in the *Campanalarinæ* always developed upon blastostyles within a gonangium.

The *Geryonidæ*, a group composed of medusæ which have not yet been traced to a hydraform trophosome, must probably, as we shall see below, be regarded as true blastochemes.

Finally, among the *Sertularinæ* we know as yet of no instance of a planoblast, the generative elements being among these hydroids always produced in fixed sporosacs, which, as in the *Campanularinæ*, are invariably borne on the blastostyle of a gonangium.

[1] Cavolini, 'Mem. Polypi Marini,' 1785.
[2] Agassiz, 'Nat. Hist. United States,' vol. iv, p. 228.
[3] Sars, 'Fauna lit. Norv.,' p. 7, pl. ii, fig. 5.
[4] Van Beneden, 'Mém. sur les Campanulaires,' pl. iii, figs. 1—6.

9. *The Generative Elements.*

I have thus far endeavoured to give a complete account of the morphology of those parts which are destined for the origination and protection of the generative elements. These elements themselves may next be examined.

The existence of generative elements—ova and spermatozoa—has now been fully determined in every important group of the HYDROIDA.

Ova.—The hydroid ovum (woodcut, fig. 40 A), in all those cases where its structure has been satisfactorily seen, consists of a granular vitellus enveloping (except in the genus *Tubularia* and probably the other *actinula*-producing hydroids) a distinct, more or less excentric, germinal vesicle, in which one or more germinal spots may be almost always demonstrated, and occasionally with one or more puncta or nucleoli in the interior of the germinal spot. The whole is invested by an exceedingly delicate vitellary membrane, which, though it sometimes escapes detection, is probably always present, at least during some period in the existence of the ovum. In the genus *Tubularia* the most careful investigation has as yet failed in detecting any trace of germinal vesicle or spot.

From some observations which I have been enabled to make on certain very early stages of the ovum, it would seem that the germinal vesicle shows itself before any distinctly differentiated vitellus has begun to envelope it, and that the vitellus afterwards accumulates round the germinal vesicle as round a separate centre of differentiation. (See below, where this process is more fully described in the physiological section.)

In *Coryne pusilla* and many other species, the ova, when escaping from the gonophore under the pressure of the compressorium, present a peculiar appearance. They are then seen to be each invested by a special membrane of great delicacy, which is continued backwards by a narrow neck-like prolongation; so that in this state the whole ovum presents a pyriform shape. This membrane is probably nothing more than the vitellary membrane of the ovum, which, from the mode in which the pressure is applied, assumes the form described.

In no hydroid ovum have I found any evidence of a micropyle.

Spermatozoa.—The spermatozoa possess the form which so generally characterises those bodies throughout the animal kingdom, being here in all cases active caudate corpuscles (woodcut, fig. 31 D *d*). The caudal filament is sometimes of such extreme tenuity as to render it very difficult of detection, while the head varies in form, being usually conical—and then with the filament attached to the wide end of the cone—but sometimes spherical, or cylindrical, or "guitar-shaped,"[1] according to the species. In *Eudendrium ramosum* a very minute granule may always be seen attached to one side of the head of the spermatozoon, where it looks like a parietal nucleus. (Pl. XIII, fig. 17.)

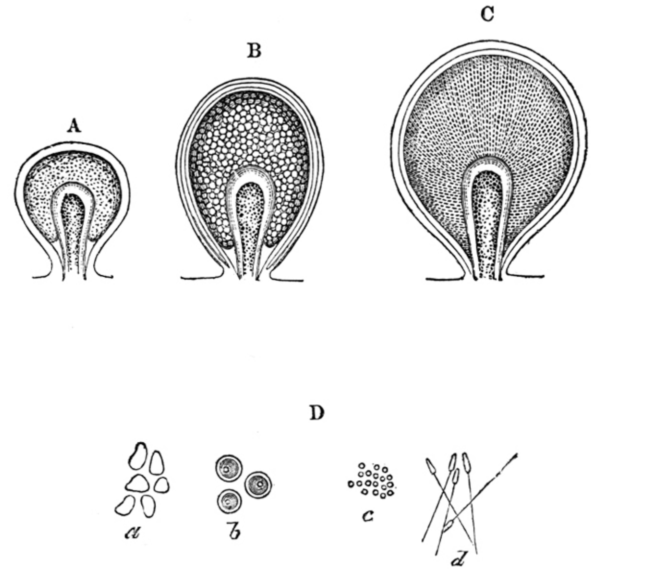
The spermatozoa seem to be always developed in true sperm-cells, which are themselves

[1] The spermatozoa of *Eudendrium dispar,* Agass., and some other species, are so described by Agassiz. 'Nat. Hist. United States,' vol. iv.

frequently contained as a brood in the interior of mother-cells, as may be very well seen in *Sertularia polyzonias*, where the cells which give immediate origin to the spermatozoa form groups of from two to four enclosed within a common mother-cell. The spermatozoon itself seems due to the metamorphosis of the nucleus of the sperm-cell.

In *Laomedea flexuosa* I have carefully followed the progress of the spermatogenous tissue from a very early period to the formation of the mature spermatozoon. In the very young gonophore of this hydroid (woodcut, fig. 31 A) the spadix may be seen surrounded by a nearly transparent mass, which is destined to become developed into spermatozoa, but which presents as yet no obvious structure beyond a minutely granular condition, which under the action of acetic acid becomes more distinct.

Fig. 31.



Development of the Spermatozoa in *Laomedea flexuosa*.

A, Very young male gonophore, showing the spermatogenous plasma interposed between the ectoderm and the endoderm.
B, Gonophore further advanced.
C, Mature gonophore.
D, Structure of spermatic tissue at various stages; *a*, spermatic tissue from B; *b*, the same after treatment with acetic acid; *c*, spermatic tissue, from a gonophore somewhat further advanced than B; *d*, mature spermatozoa from C.

In a stage a little further advanced (B) the gonophore has increased in size, and the spermatogenous mass has become more voluminous and has acquired a manifest structure, being now plainly formed of a peculiar tissue which, when liberated from the confinement of the gonophore and spread over the field of the microscope, is seen to consist of a multitude of bodies of a rather irregularly pyriform or conical shape, and about $\frac{1}{3000}$th of an inch in diameter (D *a*). These bodies, when set free, present for the most part an evident vibratory movement, which seems distinct from mere molecular motion, though as yet no filament or other source of the motion can be detected. When treated with acetic acid, they assume a regularly spherical form, and have then all the appearance of thick-walled cells with an undoubted nucleus in their interior (D *b*).

In a more advanced stage the contents of the gonophore have still further increased in opacity, and are now seen to be entirely composed of very minute spherical corpuscles (D *c*) about $\frac{1}{9000}$th of an inch in diameter, and presenting a close resemblance to the nuclei of the cells composing the spermatogenous tissue in the stage last described. They exhibit distinct but not active motion under the microscope, though no filament can as yet be demonstrated in them.

In the next stage (C) the gonophore has attained maturity, and the spermatogenous mass has become still more opaque than in the preceding stage, and presents a peculiar striated appearance, the striæ radiating from the sides of the spadix to the walls of the gonophore. Soon after the gonophore has attained this condition it bursts, and allows its contents to escape into the surrounding water as mature active spermatozoa (D *d*). These spermatozoa have an ovoconical head, with a caudal filament of extreme tenuity; the head is about $\frac{1}{3000}$th of an inch in its longer diameter, and about $\frac{1}{9000}$th in its shorter. The tail is attached to the wide end.

In attempting an interpretation of the above appearances, we must, I think, regard the nucleated cells which constitute the contents of the gonophore in the second of the stages (woodcut, fig. 31 B) just described as spermatic cells which in the next stage have set free their nuclei; these nuclei, after liberation from the cells, acquiring a more elongated form, developing a filament, and becoming converted into true spermatozoa.

Allusion has been just made to the peculiar striated appearance presented by the mature spermatic mass while yet contained within the gonophore. This appearance, which is very common in the mature male gonophores of the HYDROIDA, suggests to us the idea that the corpuscles composing the mass are confined in an exceedingly fine tubular tissue. I have, however, in vain sought for any indubitable evidence of tubes, and I believe that the appearance in question is the result of a mere arrangement of the corpuscles—a condition induced in the plastic mass by the pressure exerted on it by the resisting walls of the gonophore as the mass within increases in volume; for the component corpuscles have now become changed from the spherical form of the previous stage to a more oval form, and their axes are compelled by the surrounding pressure to take a definite direction. It is a phenomenon which in this view would be purely physical, and which we cannot avoid comparing to that of slaty cleavage, though occurring in an organized and living mass.

IV. DEVELOPMENT.

There can be no doubt that the phenomena of development, involving as these do the changes of form undergone by the organism in successive periods of time, constitute a department of MORPHOLOGY, and should, when possible, be treated in connection with other morphological phenomena instead of being included under the head of PHYSIOLOGY, as is the usual, and perhaps in some cases the more convenient, practice.

In the account already given of various parts of hydroid organisation, it has been found necessary to dwell with more or less detail on their development. A more systematic treatment of hydroid development may now be attempted. This may be best considered under two heads, the one treating of the development of the bud, the other of that of the embryo.

These two kinds of development, notwithstanding certain differences which necessitate their separate consideration, possess close analogies with one another. The progress of the bud in its development, like that of the embryo, is always from the general to the special; and just as it is impossible at first to point out any difference between embryos which are destined to branch off into widely separated types, so in their early stages it is impossible to distinguish from one another buds which are destined to become developed into very different forms. Thus, no difference whatever can be detected on their first appearance between three buds, one of which is destined to become a hydranth, another a sporosac, and another a medusa; and the analogy will appear still closer when we bear in mind that buds formed by entirely different bud-bearing types may in their early stages be undistinguishable from one another.

While the hydroid embryo, however, continues to develop as an independent organism, the bud remains for a longer or shorter time dependent on the parent stock; but it will yet be seen that the stage of differentiation on which the bud stands at the earliest period at which any differentiation is perceptible corresponds to that of the embryo at the moment when the ectoderm and endoderm of the planula become differentiated as distinct structures, and the further development of the planula and of the hydranth-bud present a close parallelism with one another.

1. *Development of the Bud.—Zooidal Development.*

Reproduction by budding or gemmation is the phenomenon which, of all others, most vividly impresses us in our study of the Hydroida, and is that which confers upon this remarkable group of organisms its peculiar and characteristic physiognomy. It struck with all its force the earlier observers, and united with the flower-like form of the hydranth in suggesting the term "zoophyte," by which the wonderful budding and blossoming plant-like animals which adorn our rocks at low water, and are dredged up at various depths from the bottom of the sea, have long been known to the naturalist.

Gemmation in the Hydroida has for its object, 1, the extension of the trophosome; 2, the origination and extension of the gonosome.

The primordial trophosome (Pl. I, fig. 11; Pl. III, fig. 8; Pl. XIII, fig. 16) is quite simple; but it soon begins to complicate itself by budding, and this complication is frequently carried to a great extent, the primary buds giving rise to secondary buds, and these again to tertiary, while buds of a fourth, fifth, or even higher order, may continue to be produced in succession; and as every bud may develop itself into a branch, the result will be the production of those complicated dendritic groups (Pls. III, IV, IX, XIII, &c.) which attain to such perfection in numerous species among the *Tubularian*, *Campanularian*, and *Sertularian* hydroids.

The complex trophosomes which thus result from successive buddings may present symmetrical and asymmetrical forms. Symmetrical forms are, as a general rule, presented throughout the *Sertularians;* the hydranths, with their hydrothecæ, being in these hydroids developed upon points which are symmetrically disposed in relation to a common axis or a common plane; while the ramification of the trophosome is here also usually symmetrical—distichous in most species, verticillate in others. The *Campanularians*, on the other hand, and especially the *Tubularians*, present in most cases an asymmetrical disposition of their branches. The genus *Pennaria* among the *Tubularians* affords a remarkable exception in this respect, its gemmation being so singularly symmetrical as to give to the entire trophosome a close resemblance to that of a *Plumularia*—so close, indeed, as to have led the earlier systematists to place it in that genus.

Under the general head of Gemmation, we may here consider the development of the hydranth, the development of the blastostyle, the development of the sporosac, and the development of the medusa.

a. Development of the Hydranth.

It is exceedingly rare to find the trophosome retaining through life the simple condition which it presents during its primordial state. Cases, however, of permanently simple trophosomes occur. We meet with them, for example, in *Corymorpha* (Pl. XIX) and certain allied forms. The curious free trophosome of *Nemopsis* as described by M'Crady, and of *Acaulis*, as described by Stimpson, are probably only the detached hydranths of some fixed Tubularians which may possess the habit of throwing off their hydranths, as we know to be the case in certain European species of *Tubularia*.

Hydranth-bud in the Gymnoblastea and Eleutheroblastea.—When a hydranth-bud is about to become developed from any part of the cœnosarc in the gymnoblastic hydroids, the two layers of the cœnosarc are seen at this spot to be pushed outwards as if by an incipient hernia, and the little hollow tubercle thus produced forces before it the investing perisarc, which is first extended over the advancing bud, and—except in the very young parts, where it is still in the condition of a mere film—is at last absorbed or ruptured.

The little bud, however, has been in the mean time clothing itself with a new perisarc, which, now that it has escaped from the confinement of the old one, is seen to cover it with a very delicate, transparent, structureless pellicle. The bud continues to increase in size, becoming longer and thicker, with its endoderm and ectoderm very distinct, and with its cavity opening freely into that of the branch from which it springs, and admitting into its interior the fluid with the floating granules which fill the general cavity of the cœnosarc, and which are kept in a state of active rotation within the bud. It continues to enlarge, but has its distal extremity still closed, while the entire bud is still invested by its delicate perisarc (Pl. II, fig. 5, &c.).

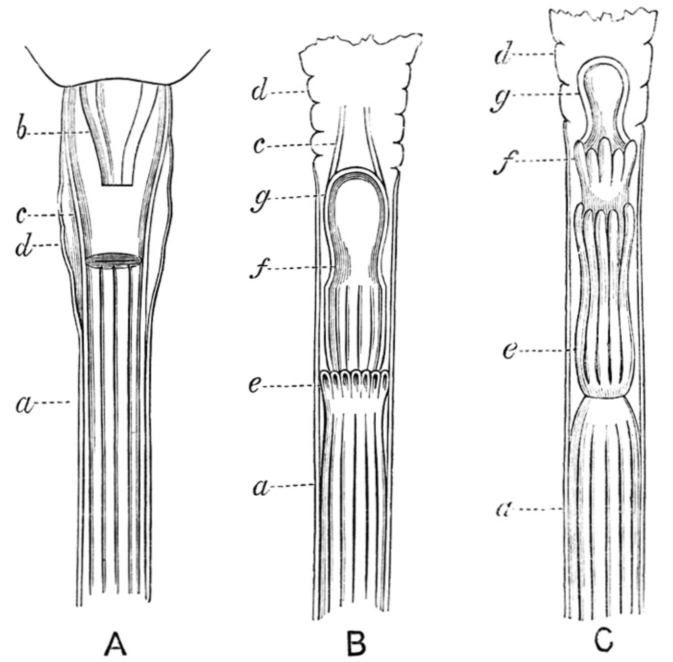
We next find that the little bud has acquired a somewhat clavate form by the enlargement of its distal extremity. While the perisarc which clothes the growing bud continues, by means of new layers deposited upon its inner surface, to increase in thickness over the proximal part of the bud, these new layers cease, in almost every case, at a very early period to be excreted from the free extremity of the bud, and the perisarc here accordingly remains in the condition of a transparent structureless pellicle of extreme tenuity, which at last, in most cases, entirely disappears. We now find tentacles begin to grow out from the enlarged extremity of the bud, and a terminal mouth to become developed; the form is thus gradually assumed which is to characterise the adult hydranth.

In some cases, however (*Coryne vaginata*, Hincks (Pl. IV, fig. 8), and *Eudendrium vaginatum*, Allm. (Pl. XIV, fig. 7)), the perisarc which clothes the free extremity of the growing branch attains considerable thickness, and does not disappear until a later period; but it ceases in such cases to be in close contact with the ectoderm, and forms an outer chitinous capsule, within which the hydranth continues to become developed; and this development proceeds to the formation of tentacles and the assumption, more or less, of the adult form of the hydranth-bud, before the rupture of the enclosing capsule places the young hydranth in direct relation with the surrounding water.

The development of the hydranth-bud in *Hydra*—our only representative of the *Eleutheroblastea*—seems to be in all essential points the same as in the *Gymnoblastea*, the most important differences being those which depend on the absence of a perisarc in *Hydra*. The ultimate destination of the bud, however, is very different in the two cases; for while in the *Gymnoblastea* it remains fixed as a permanent part of the hydrosoma, it is in *Hydra* destined to become detached and enjoy henceforth an independent existence.[1]

Spontaneous Decapitation and Re-formation of successive Hydranths.—Our account of the development of the hydranth-bud in the *Gymnoblastea* would be incomplete without some reference to a very remarkable phenomenon presented by certain species of *Tubularia*, namely, the periodical shedding and renewal of the hydranths. This phenomenon was several years ago observed by Dalyell,[2] and described with all his usual accuracy by this excellent observer. I cannot find, however, that any author has followed the process with that exactness which is necessary to enable us to form a correct idea of its nature. My own observations have been principally made on *Tubularia indivisa*, where I have bestowed upon the process in question a very careful examination.

Fig. 32.



Shedding and Renewal of the Hydranth in *Tubularia indivisa*.

A, Part of a stem in which a breach of continuity has just taken place below the hydranth; *a*, the perisarc, closely investing the proximal segment of the stem; *b*, the endodermal tube of the distal segment, which has become separated and retracted from the proximal segment and from its own ectoderm; *c*, the detached ectoderm of the distal segment; *d*, the perisarc, where it forms a loose membranous sheath, just below the old hydranth.

B, Early stage of the new hydranth, with the commencement of the proximal zone of tentacles; *a*, the perisarc, where it invests the stem just below the new hydranth; *c*, remains of the ectoderm, which had belonged to the detached part of the stem; *d*, remains of the perisarc, where it had formed a loose, thin membranous sheath, below the old hydranth; *e*, commencement of new proximal tentacular zone; *f*, distal constriction, from which the distal circlet of tentacles is to become developed; *g*, the truncated extremity of the proximal segment, now closed over, and containing a cavity formed by the coalesced canals of the endoderm.

C, More advanced stage of the new hydranth, showing the formation of the second or distal circlet of tentacles; *a*, perisarc, closely investing the stem just below the new hydranth; *d*, remains of the distal part of the perisarc, where it had formed a loose membranous sheath; *e*, proximal zone of tentacles, now much elongated; *f*, distal zone of tentacles: *g*, terminal part of the proximal segment, forming the hypostome of the new hydranth.

When the hydranth of this species, with its clusters of gonophores, has acquired full maturity, the time is come when it is to be cast off (woodcut, fig. 32 A), and its place taken by a successor. A breach of continuity now occurs in the endoderm of the stem at a short distance behind the hydranth; while the ectoderm (*c*) having already become detached from the endoderm (*b*)

[1] The curious free reproductive bodies which occur in *Corymorpha nutans*, and which probably originate as gemmæ, though their exact significance has not yet been determined, will be described below.

[2] 'Rare and Remarkable Animals,' 1847, vol. i, p. 4.

in the space between this breach and the base of the hydranth, the upper end of the stem slips out of its ectoderm, carrying the hydranth with it, and leaving behind it the empty ectoderm as a thin, collapsed, membranous sheath, surrounded by the perisarc, which here exists as a delicate loose pellicle (*c*).

The hydranth thus detached falls to the ground, where it retains for some time its vitality, the gonophores which still hang from it discharging such of their contents as had not escaped before the decapitation.

In the mean time the wound which had been formed in the cœnosarc by the detachment of the hydranth heals over, and the truncated end of the cœnosarc becomes closed.

Two slight constrictions, one a little behind the other, are next seen (B) to take place in the cœnosarc at a short distance from the decapitated extremity, while the peculiar tubular lacunæ which exist in the cœnosarc of the *Tubularia,* and which had hitherto extended as separate canals through the whole cœnosarc of the stem, now coalesce in front of the anterior constriction (*f*), where they form a single cavity by the breaking down of the partitions of endoderm which had upon this time separated them from one another.

A girdle of minute tubercles (*e*) may next be seen budding forth from the cœnosarc, at the site of the posterior constriction. These soon become extended into tentacles (C *e*), which embrace the distal part of the cœnosarc.

In the next stage a similar zone of tubercles (*f*), becoming, like the others, elongated into tentacles, shows itself close below the anterior constriction; and there are thus established the two sets of tentacles, the proximal and distal ones of the new hydranth.

By the elongation of the cœnosarc from below, the new hydranth is gradually lifted up out of the tube of the perisarc, when the tentacles, having room to expand, immediately fall into their normal position, while the rudimental clusters of gonophores may be seen as minute lobulated elevations between the anterior and posterior series of tentacles, and the free extremity of the hydranth has by this time become perforated by a mouth.

The hydranth now increases in size, raised higher and higher on the elongating cœnosarc, which clothes itself with a perisarc as it lengthens, and the hydranth with its clusters of gonophores, having finally attained complete maturity, is then in its turn cast off, to be succeeded in an entirely similar way by a new one.

The formation of successive hydranths is always accompanied by a periodical elongation of the stem, and this is indicated by annular markings of the periderm separated by rather wide intervals, each interval corresponding to a single decapitation and renewal.

From the above description it will be seen that the formation of successive polypites is not so much a process of ordinary budding, as a true metamorphosis of the decapitated extremity of the cœnosarc.

Polarity of the Hydroid.—In connection with the phenomena now described, those which accompany the artificial section of the stem deserve special notice. When the stem is cut across, the cœnosarc of the upper segment soon heals over at the place of section, the tubular lacunæ become again closed, and the cœnosarc now begins to grow downwards through the cut extremity of the periderm, presenting the same lacunar structure as in the older portions, and excreting upon its surface a very delicate perisarc. The well-known cyclotic currents may generally be seen with great distinctness in the fluid which fills the tubular lacunæ of the young elongated cœnosarc.

The lower segment, on the other hand, instead of pushing forth from the cut extremity a simple continuation of the cœnosarc, develops from this extremity a hydranth.[1] There is thus *manifested in the formative force of the Tubularia-stem a well-marked polarity*, which is rendered very apparent if a segment be cut out from the centre of the stem. In this case, no matter in what position the segment may lie, that end of it which was directed downwards or proximally while it formed a part of the unmutilated hydroid will never develop a hydranth, but will extend itself as a simple cylindrical prolongation of the cœnosarc; while the upper or distal end, instead of becoming simply elongated, will shape itself into a true hydranth; and all this though, of course, not the least difference in structure or form, can be detected between the two extremities at the time of section.

It is further manifest from these facts that, when the hydroid is placed under conditions which allow of perfect freedom of growth, there is no such thing as a stationary extremity, both ends being really growing ends, while there exists in every segment a neutral plane midway between the two ends.

Hydranth-bud in the Calyptoblastea.—In the development of the bud, the Campanularian and Sertularian hydroids differ in some important features from those which characterise the process just described. The development may be easily watched in many species, as, for example, in *Laomedea flexuosa*. We may here (woodcut, fig. 33) see it proceed, in the first place, to the formation of a hollow cylindrical branch (*a*), whose cavity is in free communication with that of the cœnosarc, and whose distal extremity ends in a cul-de-sac invested, like the rest of the young branch, by the chitinous perisarc. Up to this point the phenomena are precisely similar to what we have just seen in the *Tubularians;* but now the distal extremity of the branch begins to enlarge, and at the same time continues to coat itself with a chitinous perisarc in the form of a capsule, which acquires increased thickness by successive deposits of new matter to its inner surface, thus contrasting with the much thinner pellicle which forms the temporary capsule in certain *Tubularians.*

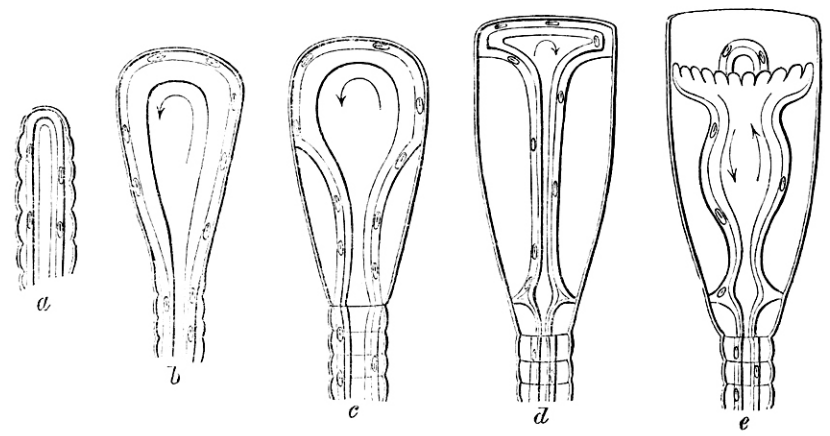
The extremity of the branch (*b*) now presents the shape of an inverted cone, plainly recognisable as the body of the budding hydranth, invested with a strong chitinous covering, which is closely applied over its whole surface, and is continuous below with the perisarc covering the rest of the branch. The interior of the young hydranth is hollowed out into a wide cavity lined by a layer of loose cells—the most internal cells of the endoderm—which are filled with a granular pigment.

The conical enlargement at the extremity of the branch continues to increase in size (*c*), and we soon see the soft parts within become contracted towards the proximal end of the cone, where they withdraw themselves from contact with the walls of the chitinous capsule, which had up to this time closely embraced them. At the wide or distal end of the cone they still remain adherent to the capsule for some distance downwards, while at the proximal end itself there is also a distinct but narrow zone of contact and adhesion maintained between the internal soft parts

[1] The first observations on this subject are those of Dalyell, who has made numerous experiments on the section of the stem in *Tubularia indivisa,* with results similar to those here recorded. (See Dalyell, 'Rare and Remarkable Animals,' vol. i, p. 23.)

and the external chitinous capsule. In the cavity which occupies the interior of the soft contents of the capsule very distinct rotating currents may be now seen, excited, doubtless, by the action of vibratile cilia, though a direct view of these cilia cannot be obtained through the thickness of the walls.

FIG. 33.



Development of Hydranth and Hydrotheca in *Laomedea flexuosa*.

a. Very early condition, in which the bud forms a simple cylindrical cæcal offset from the cœnosome.
b. The distal extremity of the bud has become enlarged, so as to present the form of an inverted cone.
c. The cone has increased in size, and the soft parts towards its proximal end have become retracted from the external chitinous walls.
d. The internal structures have still further withdrawn themselves from the chitinous walls, with which they are now in contact only by a narrow proximal and a wider distal zone, between which they present the form of a tubular cylindrical column.
e. The distal zone of contact has become retracted from the summit of the cup-like envelope of chitine, tentacles have begun to sprout from its circumference, and a hypostome has risen from its centre. The leading features of the completely formed hydranth are thus established, and its chitinous envelope has become the hydrotheca.
The arrows in the figures indicate currents in the somatic fluid.

Between the proximal and distal zones of contact the internal structures become more and more withdrawn from the walls of the capsule, while the whole body continues to elongate (*d*); and this may now be seen in the form of a cylindrical column occupying the axis of a conical cup of chitine, and expanded below into a narrow ring, which at this point connects it with the walls of the cup, while above it expands into a broad disc, which fills up the distal extremity of the cup like a lid or plug. The axis of the column is permeated by a tubular cavity in continuation below with the cavity of the branch, and expanding above into a wide chamber, which occupies the interior of the plug-like enlargement of its distal end. It is now plain that, while the soft contents of the cup are the developing hydranth, the cup itself is to become the hydrotheca.

The excreting of the chitine and the shaping of the hydrotheca would seem to devolve on the terminal plug-like disc alone, from the time that the lower parts of the nascent hydranth had withdrawn themselves from contact with the walls of the external capsule; and as the hydranth continues to elongate itself, the surrounding cup is extended at the same rate, by addition to its wider end from the sides of the disc, while the lower parts of the cup undergo little or no change.

The upper surface of the disc has been all along covered with a thin layer of chitine, whose periphery is continuous with the chitinous walls of the cup, but which does not interfere with the growth of the young hydranth; for as the latter continues to extend itself, the layer of chitine on the upper surface of the disc is carried onwards before it, without becoming thereby detached from the side of the cup—a fact which we can scarcely explain otherwise than by supposing considerable extensibility in the recently deposited chitine of the cup. At last the hydrotheca has attained its complete size and shape, and now the young hydranth becomes more or less retracted within it, the terminal plug-like disc withdrawing itself from the layer of chitine which it had excreted on its upper surface, and which is now left behind as a roof closing over the mouth of the cup.

The whole circumference of the retracted disc now begins to develop a circle of minute tubercles (*e*), which gradually elongate themselves into short thick tentacles, while the central part becomes elevated into a blunt conical proboscis (hypostome), and the cylindrical tubular column which occupies the axis of the hydrotheca has become dilated into a more oval-shaped body, with a wide internal cavity—the stomach of the developing hydranth.

The young hydranth, still included within a completely closed cup, presents greater and greater contractility, now withdrawing itself towards the bottom, and now extending itself through the entire height of the surrounding cup. The tentacles in the mean time have become longer, the extremity of the terminal cone has become perforated by a mouth, and at last the hydranth pushes off the chitinous roof of its hydrotheca, and emerges into free contact with the surrounding water.

b. Development of the Blastostyle.

In the gymnoblastic genera the development of the blastostyle is essentially similar to that of the first stages of the hydranth. Instead, however, of proceeding to the development of prehensile tentacles, an arrest takes place, sporosacs bud from its sides, and the nutrition of the colony, to which the hydranth is destined, becomes replaced by the duty of supporting the sexual buds. In the calyptoblastic genera the development of the blastostyle is accompanied by some additional features which render necessary a more detailed description.

Laomedea flexuosa will afford here too a very convenient subject for tracing the process of development. The blastostyles of this hydroid arise close to the axillæ of the branches, and present the form of a long cylindrical column, expanded at its summit into a disc, occupying the axis of a spacious gonangium, and carrying along its whole length adelocodonic gonophores, which increase in maturity as they approach the summit of the column. The whole is elevated on a short annulated peduncle.

The blastostyle here originates in a bud precisely in the same way as a hydranth; and up to the stage to which we have already followed the development of the hydranth and hydrotheca, when these parts present the condition of a conical enlargement of the extremity of the branch, there cannot be found any difference between the hydranth-bud and the blastostyle-bud. It would seem, however, that at this stage the soft parts, instead of absolutely withdrawing themselves from contact with the external chitinous capsule, present in their ectodermal layer a number of lacunæ, which, increasing in size, become confluent with each other, and the ectoderm thus becomes split into two layers by a true *chorization*. The external layer remains in contact with the chitinous capsule, while the internal layer, remaining adherent to the endoderm, becomes more and more withdrawn towards the axis of the bud, where it now constitutes the external or ectodermal layer of an axile column or blastostyle. The capsule thus becomes lined with a thin layer of ectoderm, which is continuous with the ectoderm of the blastostyle only at its distal and proximal extremities, these two membranes being in the whole of the intermediate region separated from one another by a wide interval. This interval, which constitutes the cavity of the developing gonangium, is thus nothing more than a large lacuna; and it is in this lacuna that the sporosac or blastocheme now begins to bud forth from the axile column. The excreting and modelling of the chitinous gonangium would seem to devolve for some time still on the ectodermal lining instead of being, as in the hydranth-bud, transferred at a very early period exclusively to the disc-like summit of the axis. After a time, however, the lining membrane entirely disappears, and henceforth the excreting and modelling of the gonangium seems to devolve on the terminal disc of the blastostyle. While the gonangium is yet young, numerous irregular fleshy bands may be seen stretching across the cavity from the blastostyle to the external wall. These bands are the remains of the original union between the two layers into which the ectoderm has split. They are generally torn, and disappear as the gonangium, increasing in size, has its walls more and more widely separated from the blastostyle; but they are also occasionally more or less visible in the full-grown gonangium.

A comparison between the developing hydranth and its hydrotheca, on the one hand, and the developing blastostyle and its gonangium on the other, affords a most instructive parallelism, showing the close connection between the hydranth and the blastostyle. If in the hydranth-bud the development were arrested at the point to which it arrives just before the terminal disc has withdrawn itself from the roof of the young hydrotheca (woodcut, fig. 33 *d*), in order to develop its tentacles, we should have in almost every particular a gonangium with its blastostyle (see woodcut, fig. 18). The development of a mouth and tentacles, however, points towards a different destination; and now, instead of producing zooids destined for generation, the hydranth applies itself solely to the nutrition of the colony.

The gonangium does not always present the simple form which we find in *Laomedea flexuosa*, and we have already seen the remarkable modification which it undergoes in the female colonies of *Sertularia rosacea*, *S. fallax*, and *S. tamarisca*, by the formation of a marsupial chamber for the protection of an extra-capsular sac, in which the ova are retained during the earlier periods of their development.

c. Development of the Sporosac.

The development of the sporosac or adelocodonic gonophore, in its simplest form, may be easily studied in *Hydractinia echinata*. In this hydroid the gonophores are borne on a blastostyle (Pl. XV, and woodcut, fig. 4 *bb*, *c*), which here, just as in the blastostyle of the *Sertularians* and *Campanularians*, is morphologically nothing more nor less than an arrested hydranth, but in *Hydractinia* never developing a gonangium.

In their earlier stages the sporosacs may be seen as minute hollow tubercles, projecting from the sides of the blastostyle. They are composed of two layers, endoderm and ectoderm, directly continuous with the corresponding layers of the blastostyle, with whose cavity that of the young bud is in free communication. At first we can detect no change beyond a simple increase in size; but we soon find the ectoderm separated from the endoderm by the interposition of a minutely granular mass between them. This mass constitutes the basis of the generative elements, and is afterwards to become ova or spermatozoa. In the mean time the ectoderm has itself become differentiated into two layers; and we have thus laid down the foundation of all the parts which we meet with in the full-grown gonophore. The wall of endoderm which surrounds the central cavity of the developing gonophore, and is itself immediately surrounded by the generative elements, is the spadix; the more internal of the two layers into which the ectoderm has divided is the endotheca, the more external the ectotheca.

The sporosac now becomes more and more distended by the increasing volume of the generative mass, while the spadix at the same time continues to grow, and now constitutes a club-shaped hollow organ, extending through the axis of the mass, while floating particles from the cavity of the blastostyle are freely admitted into its interior, where they may be seen performing active rotatory movements.

The sex of the gonophore becomes evident at an early period, by the appearance of ova with their germinal vesicle and spot in the generative plasma of the female, while in the male the interval between the spadix and endotheca continues still to be occupied by a uniform grumous plasma, in which, at a somewhat later period, spherical cells and ultimately free-moving spermatozoa may be detected.

The gonophore of *Hydractinia echinata* does not pass to any higher grade of development than that here described; but in some other forms of adelocodonic gonophore a further differentiation takes place by the development of an additional membranous sac or mesotheca, with gastrovascular canals, between the endotheca and ectotheca (*Tubularia indivisa*—Pl. XX, fig. 3, and Pl. XXIII, figs. 8 and 11). I have never succeeded in following the development of the mesotheca, and cannot say under what condition it begins, or how it proceeds, the membrane appearing always fully formed from the moment it is recognisable.

It will be seen that in the above account I differ in some important points from the interpretation given by Agassiz to the appearances which present themselves in the development of the adelocodonic gonophore. In his account of this process in his *Clava leptostyla*, Agassiz[1] regards the perigonium or walls of the gonophore as simple, and as homologous with the umbrella of a medusa. In *Clava multicornis*, however, the existence of two membranes may with care be demonstrated in these walls, though I admit that I have frequently failed in detecting more than a single one. In no case, however, can the walls of the gonophore in *Clava* be regarded as the homologue of an umbrella. When two membranes can be demonstrated in them, these will be an endotheca and ectotheca; if only a single membrane be present, as Agassiz believes to be the case in his *Clava leptostyla*, this will be an endotheca, while the part which would really represent an umbrella, namely, a mesotheca, is not developed.[2]

[1] *Op. cit.* vol. iv, p. 221.

[2] In my earlier researches into the anatomy of the reproductive system in the *Hydroida* ("On the Anatomy and Physiology of *Cordylophora*," Phil. Trans. 1853), I entertained the view here advo-

Again, in the gonophores of *Hydractinia polyclina*, Agass., *Tubularia* (*Parypha*) *crocea*, Agass., and *Tubularia* (*Thamnocnidia*) *spectabilis*, Agass., Agassiz correctly figures the two membranes which enter into their walls; but he assuredly assigns an incorrect origin to the more internal of these membranes when he describes it as rising, subsequently to the formation of the generative mass, from the proximal end of the gonophore in the manner of a cup closely pressed against the outer wall, and, at least in *Hydractinia* and *Tubularia spectabilis*, ultimately closing over the contained structures so as to form a continuous internal wall.

Now, the internal wall in the gonophore of *Hydractinia* is undoubtedly formed, not *after*, but simultaneously with the appearance of the generative mass, and is nothing more than the internal of the two layers into which the ectoderm of the primary bud has become divided simultaneously with its separation from the endoderm by the interposition of the generative elements; it is thus the endotheca of the sporosac, while the more external layer is the ectotheca.

Having had no opportunity of examining the development of the gonophores in either of the two *Tubulariæ* cited above, I am unable to bring any direct observation into opposition with the views of Agassiz as to the gonophores of these hydroids; but the analogy of *Hydractinia* and of other hydroids, whose adult gonophores correspond in all essential points with those of the American forms, leads me to believe that the process is in all the same as in *Hydractinia*.

It is only in those cases where a mesotheca becomes developed, as in *Tubularia indivisa*, that the adelocodonic gonophore presents any true representative of the umbrella of a medusa, the mesotheca being properly the homologue of this part. Agassiz, in his account of *Tubularia Couthouyi*, Agass., ignores the existence of any membrane between the well-developed mesotheca of this species and the generative mass which surrounds the spadix. In *Tubularia indivisa*, however, this membrane cannot be overlooked, especially in the male, though in the female it would seem to disappear at an early period, and may thus escape detection.

d. Development of the Medusa.

The medusa, whether gonocheme or blastocheme, shows itself at first in every case as a minute hernia (woodcut, fig. 34 A), consisting of endoderm and ectoderm, and having its cavity in free communication with that of the blastostyle, or of the trophosome from which it springs; thus in no respect differing at this period from the corresponding stage in the development of the adelocodonic gonophore, or, indeed, in that of a hydranth branch.

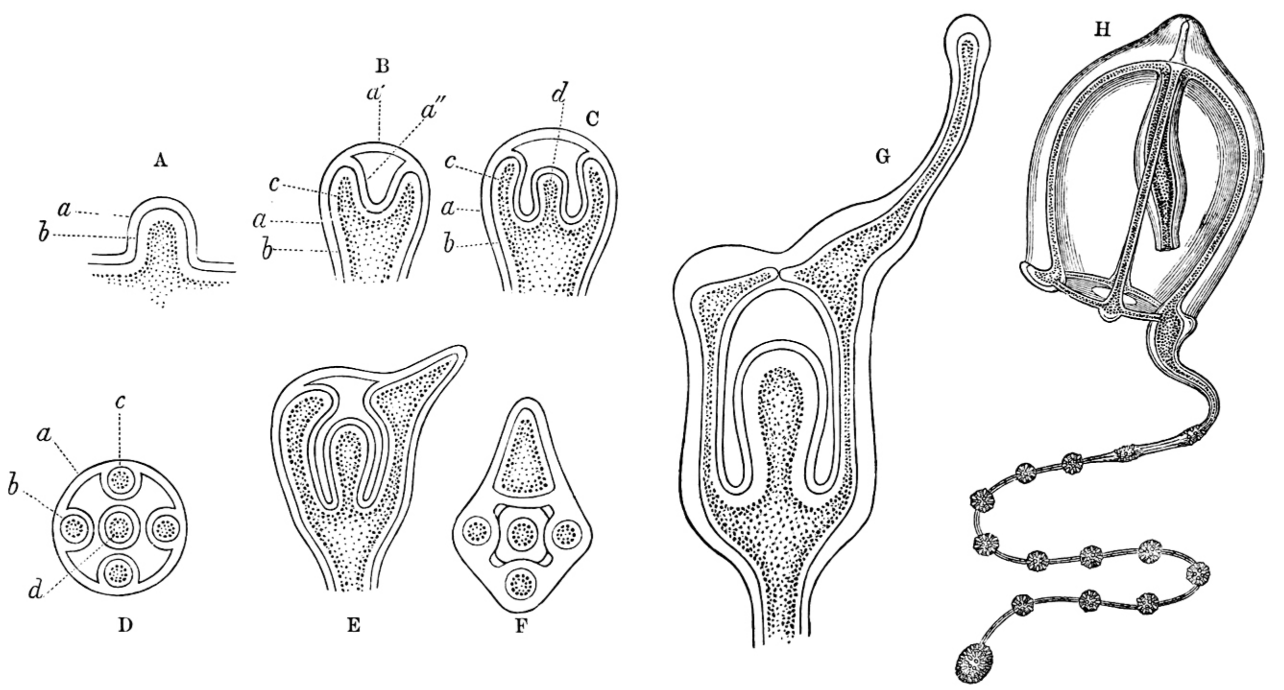
It is very difficult to follow satisfactorily the several steps by which this primordial tubercle becomes ultimately converted into a medusa. I have bestowed great attention on it in different species of HYDROIDA, and have more recently subjected the development of the medusa bud

cated by Agassiz, as to the homology of the parts in question. Subsequent more extended observations, however, have induced me to modify in some respects the views then expressed, and to adopt those which are advocated in the present Monograph. (See my paper "On the Reproductive Organs of *Sertularia tamarisca*," in the Report of the British Association for the Advancement of Science, 1858.)

in *Corymorpha nutans* to a laborious examination, which has led me to adopt the process now about to be described, as the true interpretation of the phenomena presented in this hydroid.

We first find that four equidistant processes (woodcut, fig. 34 B *c*), consisting of endoderm and ectoderm, with an included cavity, which is a continuation of that of the hernia-like tubercle just mentioned, have begun to grow upwards from a circle round the summit of this primordial bud. These, however, do not show themselves as free processes; for simultaneously with their appearance the ectoderm of the summit of the bud becomes split into two layers (*a′*, *a″*), which become more and more widely separated from one another as the processes continue to elongate, the outer layer arching over the space which is surrounded by the four processes. During this elongation the ectodern which occupies the four intervals between the roots of the processes is carried upwards as a continuous membrane, stretching across from one process to another in the manner of a web.

FIG. 34.



Development of the Planoblast in *Corymorpha nutans*.

A, Very early stage of the medusa-bud when it presents the form of a simple hernia-like tubercle, whose cavity is in communication with the somatic cavity of the hydroid; *a*, ectoderm; *b*, endoderm.
B, More advanced stage. *a*, ectoderm; *b*, endoderm; *a′*, the more external of the two layers, into which the ectoderm of the bud has split; *a″*, the more internal of these two layers; *c*, commencement of radiating canals.
C, Stage still more advanced, *a*, ectoderm; *b*, endoderm; *c*, radiating canals; *d*, manubrium.
D, Transverse section of C. *a*, ectoderm; *b*, endoderm; *c*, radiating canals; *d*, manubrium.
E, A stage still more advanced than C. The distal ends of the radiating canals have become dilated into bulb-like expansions, one of which has begun to extend itself as a marginal tentacle.
F, Transverse section of E.
G, A stage somewhat more advanced than E. The bulbous terminations of the radiating canals have coalesced, and one of them has become projected into a thick tentacle.
H, Medusa, just after liberation from the trophosome.

The result of this is, that we have now the distal portion of the bud in the form of a deep cup, closed over by a layer of ectoderm, and having its walls traversed by four equidistant cæcal tubes, whose cavity is continuous with the original cavity of the bud, and which are lined by a continuation of the endoderm of the bud. There is no difficulty in recognising in these tubes the radiating canals of the future medusa, and in the web of ectoderm which unites them the umbrella.

From the central point of the area included between the bases of the four canals another hernial process (C *d* and D *d*) has already begun to make its appearance, composed of ectoderm and endoderm, and containing a prolongation of the original bud cavity. It advances as a thick process in the axis of the cup, and is at once recognisable as the future manubrium.

The four peripheral processes continue to elongate, and are soon seen to be dilated into bulb-like expansions at their extremities (E, F). The bulbs increase in size, and come in contact by their sides; while one of them, enlarging much more rapidly than the three others, gives a marked preponderance to its side of the bud, and makes the distal end of the bud appear as if obliquely truncated. It then begins to extend itself beyond this distal end into a thick, hollow tentacle.

In the mean time the four bulbs which had come in contact have coalesced, and their cavities now communicate with one another (G); but, by the gradual enlargement of the distal end of the bud, the bulbous ends of the radiating canals are again drawn away from one another. The communication, however, between their cavities is not thereby interrupted, but continues to be maintained by a tubular elongation of their original points of union; and in this tube we now recognise the circular canal of the medusa.

The cavity of the umbrella is still closed by the more external of the two laminæ into which the ectoderm had originally split at the distal end of the bud. In the final stage this lamina is either perforated in the centre, in order to form the velum, or, what I now believe to be more probable, it entirely disappears, and the velum is formed by a centripetal extension of the ectoderm on a plane with the bulbous extremities of the radiating canals, at the time when these bulbs are withdrawn from contact with one another, in order to form the circular canal.

The manubrium, previously imperforate, has now acquired a mouth at its extremity. The solitary tentacle, too, has now become elongated, and presents its characteristic moniliform structure, the umbrella rapidly contracts and expands with vigorous systole and diastole, and the medusa at last hangs on its stalk, a true *Steenstrupia*, ready to break away from the restraint of its fostering hydranth, and enter upon an independent existence (H, and Pl. XIX, fig. 5).

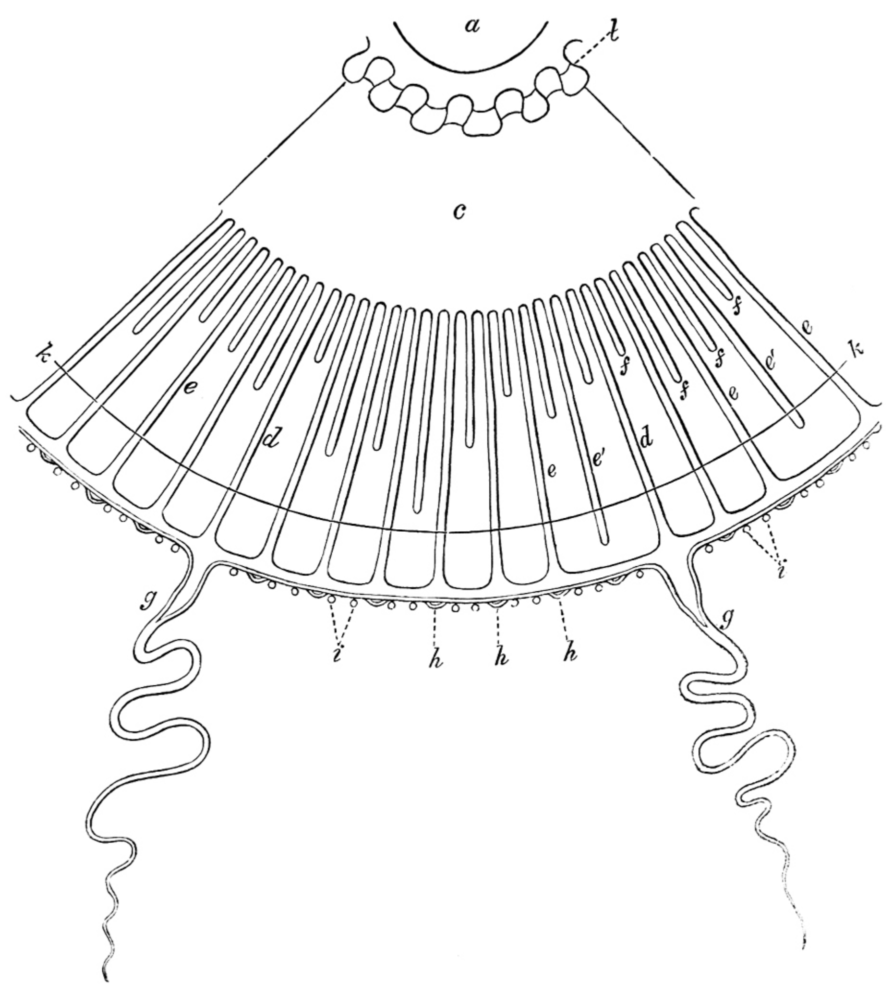
From the above account of the development of the medusa bud, it will be seen that here also I am not entirely in accordance with the views expressed by Agassiz on this subject. The distinguished American naturalist gives a very detailed account of the process as he has interpreted it in the development of the medusa-bud springing from his *Syncoryne mirabilis*, and in which he describes this development as starting with the separation of the endoderm from the ectoderm in the primordial tubercle, and the inversion of the endoderm into itself, so as to form the cup of the future umbrella. "In doubling on itself the retreating fold does not press closely on all points upon the stationary one, but leaves four equidistant spaces into which the chymiferous fluid penetrates."[1] These four spaces are the foundation of the four radiating canals, which would thus originate in an entirely different way, and have a significance entirely different

[1] 'Natural History of the United States,' vol. iv, p. 192, &c.

from what my observation of the process in *Corymorpha* and other genera has led me to regard as the true one.

M'Crady[1] believes that those medusæ which occur among the gymnoblastic hydroids, where, as we have already seen, they belong to the type of the gonocheme, are developed in a different way from those which we find among the *Campanularians*, and where they present the type of the blastocheme. He describes the umbrella in the former as produced by an excavation of

FIG. 35.



Segment of a young *Æquorea* captured off the west coast of Scotland, showing the development of the radiating canals.

a. Mouth; *b*, frill-like lip; *c*, floor of the greatly expanded base of the manubrium, from whose circumference the radiating canals are emitted; *d*, *d*, primary radiating canals; *e*, *e*, canals developed later, and already united with the circular canal; *e′*, *e′*, canals which have not yet reached the circular canal; *f*, *f*, *f*, *f*, canals still less developed, on their way to the circular canal; *g*, *g*, developed marginal tentacles; *h*, *h*, *h*, rudiments of marginal tentacles; *i*, *i*, lithocysts; *k*, *k*, margin of velum.

the substance of the young bud, forming thus a completely closed cavity in which the manubrium is included, and which only at a subsequent period becomes perforated at its summit to form the

[1] Op. cit. p. 110.

orifice of the umbrella. In the *Campanularians*, on the other hand, he believes that the umbrella grows up from below as a ring round the manubrium, which is thus never included in a closed cavity, but is from the first directly exposed to the surrounding medium. In accordance with these views, M'Crady divides the gymnophthalmatous or hydroid medusæ into the "endostomata" and the "exostomata." My own observations, however, will not allow me to adopt this division of M'Crady. In the medusa of *Campanularia* at all events the development is essentially the same as that just described in the medusa of *Corymorpha*.

The medusa has not necessarily attained its complete development at the time when it has become fitted for an independent existence, and has detached itself from the trophosome in order to spend its future life in the open sea. It is very common to find both tentacles and lithocysts less numerous at the time of liberation than at a more advanced period; while in some cases (*Æquoria*) the radiating canals continue to increase in number with the age of the free medusa[1] (woodcut, fig. 35).

In every case in which I have had an opportunity of observing the formation of new radiating canals, these have been developed in a centrifugal direction. They commence as offsets from the base of the manubrium (woodcut, fig. 35, *f*), or from the previously existing canals, and then becoming elongated in the gelatinous substance of the umbrella, they direct themselves towards the umbrella margin until they meet the circular canal with which they inosculate. This penetration of previously formed tissue by the nascent canals, their invariable maintenance in it of a definite direction, and their inosculation with a canal already completed, are phenomena not without their general significance in the formative forces of living beings.

In some cases still more striking transformations have been witnessed in the free medusa. Thus Gegenbaur observed that the *Trachynema ciliatum*, Gegenb., a medusa not yet traced to a polypoid trophosome, is in its young state a free-swimming flask-shaped body, with three or four minute tentacles in a circle round the base of its contracted neck-like portion, and with a clothing of vibratile cilia over its whole surface. It subsequently developes an umbrella and gastrovascular canals, and becomes provided with numerous imperfectly contractile tentacles.[2]

It is, however, in the family of the *Geryonidæ* to which the *Æginidæ*, as follows from Haeckel's observations, must now, notwithstanding their very different form, be united, that we meet with medusæ which, during their free state in the open sea, undergo the most striking change, passing through a series of metamorphoses which consist, not only in the development of new parts, but in the loss of organs which, being destined to enjoy only a transitory existence, disappear, as is described below, to make way for permanent ones of an entirely different form. It is true that none of these medusæ have as yet been traced to a hydraform trophosome; but they are not on that account of less importance in the general history of hydroid development.

[1] Alexander Agassiz has shown that in their order of succession the marginal tentacles of the Hydroid Medusæ obey a law very similar to that which Milne-Edwards and Jules Haimes have shown to regulate the formation of the successive septa in the Actinozoa. A. Agassiz in 'Proc. Bost. Soc. Nat. Hist.,' vol. IX, Aug. 1862.

[2] 'Generationswechsel,' p. 51.

An exceedingly interesting case of metamorphosis in an Æginidian medusa has been described by M'Crady.[1] He observed, lying free in the umbrella-cavity of an Oceanidan medusa, to which he gives the name of *Turritopsis nutricula* multitudes of little organisms, presenting various forms, from that of a minute club-shaped hydroid to that of a well-developed medusa belonging to the type of the *Æginidæ,* and all undoubtedly connected with one another as stages of a simple developmental process.

Though he at first believed these to be the proper offspring of the *Turritopsis* in which they occurred, he afterwards rejected this notion, and recognised in them the young of a species of *Cunina* (*Cunina octonaria,* M'C.), which had selected the umbrella-cavity of the Oceanidan in order to spend there as parasites the early stages of their existence.

The untentaculated, club-shaped larva (the earliest stage observed) was followed by a bitentacular hydroid form with long imperforate proboscis and distinct internal digestive cavity, and he noticed the interesting fact that this bitentacular stage freely repeats itself by budding. Next, two other tentacles make their appearance symmetrically between those first formed, while the extremity of the proboscis seems now to be perforated by a mouth. The umbrella next begins to make its appearance by an annular extension of the circumference of the body close to the oral side of the roots of the tentacles; and four new tentacles begin to sprout between those already formed, while lithocysts become developed on the margin of the incipient umbrella. After this the larva assumes the form of an adult *Cunina* in all essential points, except in the possession of a long proboscis, like that of a *Geryonia,* in which stage it leaves the umbrella-cavity of the *Turritopsis* to spend a free life in the surrounding water. It is only after it has quitted the medusa on which it had been hitherto living as a parasite that it loses its proboscis, and that the digestive cavity thereby assumes the form characteristic of the family of the *Æginidæ.* M'Crady views this case as presenting an instance of direct development from the ovum, believing that the *Cunina* originally gained access to the umbrella of the *Turritopsis* in the condition of a free-swimming planula.

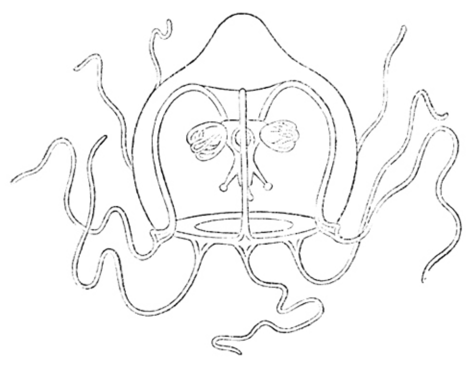
Fritz Müller[2] has given an excellent account of the metamorphosis of a Geryonidan medusa, *Liriope cathariensis,* Fr. Müller; and his observations have been confirmed and extended by Haeckel,[3] who has described similar metamorphoses in two other Geryonidans, *Glossocodon* (*Liriope*) *eurybia* and *Carmarina* (*Geryonia*) *hastata.* In all these cases the medusa in its earliest observed condition was found swimming free in the open sea. The youngest medusa noticed presented the form of a minute hyaline gelatinous sphere; on one point of whose surface was a small pit-like depression closed over by a perforated diaphragm; and the most striking feature in the subsequent metamorphosis consisted in the development of two sets of peculiar larval tentacles, of which one or both sets were destined after a period to disappear, their place being supplied by an entirely different set, which remained as permanent organs during the life of the medusa. The larval tentacles are solid and rigid, and have no connexion with the gastrovascular system; while the permanent tentacles are hollow offshoots from the circular canal, and are eminently flexible and extensile.

While we are entirely ignorant of the origin of the free-swimming bodies which have been

[1] Proc. Elliott, 'Soc. Nat. Hist. Charleston, 1856,' p. 55.
[2] 'Wiegmann's Archiv,' 1859, p. 310.
[3] Haeckel, 'Die Familie der Rüsselquallen.'

thus traced through a series of metamorphoses into adult Geryonidans, it has been proved that certain other free medusæ of the Æginidan type have originated as buds from adult forms. This, however, leads us to consider the formation of buds by the medusa.

FIG. 36.



Medusa, probably young *Lizzia*, captured in the open sea, with medusa-buds springing from the base of the manubrium.

Formation of Buds by the Medusa. — The phenomenon of medusa-budding does not necessarily find its extreme term in the formation of the medusa itself. Many free-swimming medusæ, some of which are known to have originated in hydroid trophosomes, complicate themselves by gemmation, which manifests itself in the production of other medusa-buds upon various parts of their bodies. A fine example of this phenomenon is afforded by the medusa of the tubularian hydroid, *Hybocodon prolifer*, Agass. In this beautiful animal, Agassiz[1] describes the base of the solitary tentacle which is continued from the distal extremity of one of the radiating canals of the medusa as itself producing a cluster of medusa-buds, which in time assume the form of the primary medusa, and may themselves repeat the same process, through the production of successive broods of similar buds, before they become detached as free natatory medusæ. Steenstrup[2] has observed buds developed from the base of the tentacles in a medusa which he believes to have originated in a Coryne-like trophosome, which he names *Coryne fritillaria;* Greene has described the production of buds, not only from the bulbous base of the tentacles, but also along the course of the tentacles themselves in a nearly allied medusa, *Diplura*, Greene;[3] while the emission of buds by medusæ has also been described by Forbes,[4] Sars,[5] Busch,[6] and others.

I have several times witnessed this phenomenon in medusæ captured while swimming in the open sea. In some of these cases the buds were borne on the base of the manubrium (woodcut, fig. 36), in others, on an elongated tubular peduncular extension of the manubrium (woodcut, fig. 37), and in others upon the bulbous bases of the marginal tentacles (woodcut, fig. 38). The singular ambulatory medusa of Clavatella also multiplies itself by budding from the intertentacular spaces on the umbrella-margin (see Pl. XVIII, fig. 5). In these various cases the buds seem destined to assume the form of the medusa which gave origin to them, but observations on

[1] Op. cit. vol. iv, p. 245, pl. 24.

[2] J. J. Steenstrup, 'Alternation of Generations,' p. 26; Roy. Society's Translation, 1845.

[3] J. R. Greene, in 'Nat. Hist. Rev.,' 1857, vol. iv. The Medusæ is there named *Diplonema*, but from this name having been already given to a genus of plants, it was subsequently changed by Greene to *Diplura*. See my paper "On the Genera of the Hydroida," in 'Ann. Nat. Hist.' for May, 1864.

[4] 'British Medusæ.'

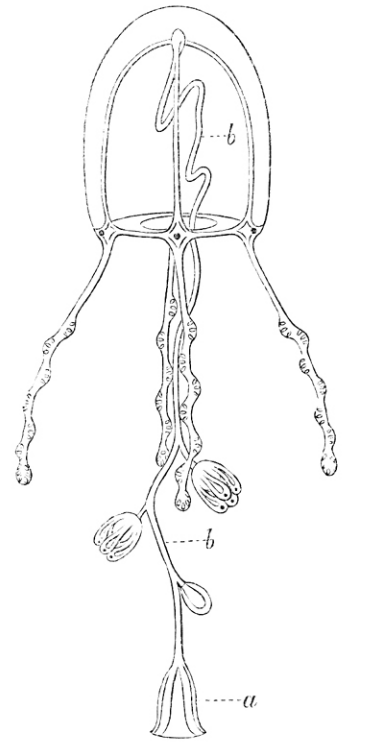
[5] 'Fauna lit. Norveg., erste Lieferung.'

[6] 'Beobachtungen ueber Wirbellos. Seethieren.'

their history after detachment from the parent-medusa are still wanting, in order to enable us to speak positively on this point.

In certain medusæ belonging to the family of the *Geryonidæ* it would seem, from the observations of Gegenbaur,[1] Kölliker,[2] Krohn,[3] Fr. Müller,[4] Keferstein and Ehlers,[5] and, above all, from the remarkable researches of Haeckel,[6] that the formation of buds within the cavity of the stomach is a constant and normal phenomenon. It would further appear that these buds, for the most part, detach themselves while still in a very immature state, and that after becoming free they undergo a metamorphosis before arriving at their adult condition; and, still further, it has been shown that in at least some of these cases there is a heteromorphism, the buds becoming developed into a form very different from that of the medusa which gave rise to them.

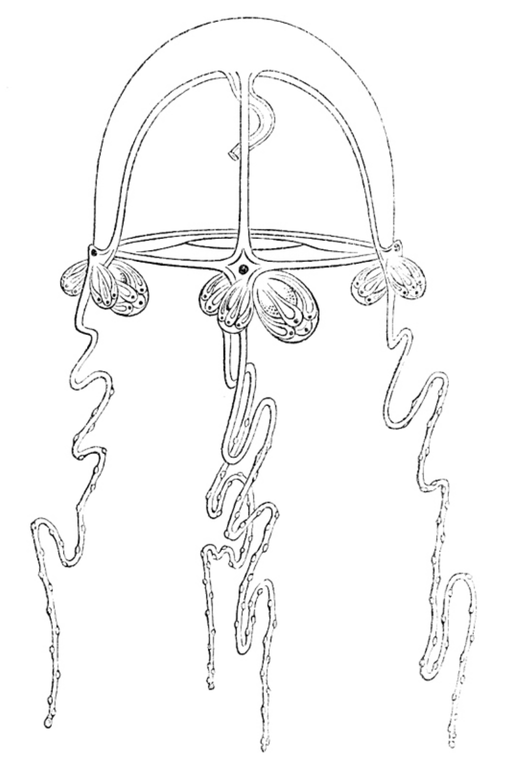
FIG. 37.



Sarsia, captured in the open sea, with medusa-buds borne by the manubrium.

a, Wide oral extremity of the manubrium; *b*, *b*, attenuated proximal portion of the manubrium, carrying the buds in various stages of development.

FIG. 38.



Medusa, probably the planoblast of a *Syncoryne*, captured in the open sea, and bearing clusters of medusa-buds on the bulbous bases of the marginal tentacles.

This last phenomenon has been witnessed in a case recorded by Fritz Müller,[7] who describes the formation of ciliated buds from the internal surface of the stomach in an eight-tentacled *Cunina*, which he names *C. Köllikeri*. He traced these buds through various stages until he

1 'Generationswechsel,' p. 56.

2 'Zeit. f. wissen. Zool.' 1843, p. 327.

3 'Archiv. fur Naturgesch.' 1861, p. 168.

4 Ibid., p. 51.

5 'Zoologische Beiträge,' 1861.

6 'Die Familie der Rüsselquallen (Geryonida),' 1865, p. 115, &c.

7 'Wiegmann's Archiv,' 1861.

saw them detach themselves and swim free in the cavity of the stomach. Here they underwent further development, which he continued to observe until he saw them transformed into true *Cuninæ*, differing, however, from the parent by the fact of their having twelve tentacles and twelve stomach-pouches, instead of eight, the number characterising the medusa which gave origin to them. Beyond this point Müller lost sight of them, and we are accordingly ignorant of their further changes and destination.

But in no recorded case of the production of one medusa from another by budding is the heteromorphism between the budding medusa and the buds produced by it so striking, and nowhere has it been so fully traced as in the observations of Haeckel, described in his remarkable memoir on the *Geryonidæ*, in which he has shown that a sexually mature Geryonidan medusa (*Carmarina hastata*, Haeckel), having its segments a multiple of six, produces upon the tongue-like process which in this genus projects from the fundus of the stomach into its cavity a multitude of buds which become developed, not into a six-rayed form resembling that of the Geryonidan which gave rise to them, but into true *Cuninæ*, Æginidan medusæ having eight instead of six elementary body-segments, and like all the Æginidan medusæ belonging to a type which had been previously regarded as possessing no relation whatever with the *Geryonidæ*.

It is not alone in the fact that the buds belong to a very different medusa-type from the budder that the phenomena described by Fritz Müller and by Haeckel present features peculiar and anomalous; for the situation of the buds within the stomach cavity of the bud-producing medusæ is without parallel in any other group of HYDROIDA. In every case where medusa-buds have been observed among other families of the HYDROIDA, the somatic cavity of the bud has been in communication with some part of the somatic cavity of the hydroid which produces it; while here such a communication is impossible before the development of the mouth in the bud shall enable the young Æginidan to receive nutriment through this orifice from the stomach cavity of the supporting medusa.

Two other cases, however, both among the Æginidan type of the *Geryonidæ*—namely, that of *Cunina prolifera*, described by Gegenbaur,[1] and that of *Ægineta gemmifera*, described by Keferstein and Ehlers[2]—have also been recorded, in which the young medusæ are formed as buds within the cavity of the stomach, in both of these instances the buds having been developed from the internal surface of the stomach walls. In all these cases the buds must have been formed in a very different way from that which takes place in the ordinary cases of budding medusæ—so different, indeed, that were it not for the competency of the observers who have described them as cases of true budding, we should be disposed to regard them as suggesting parasitism, rather than gemmation.

It is not, however, only in the *Geronyidæ* that we meet with cases of heteromorphic budding from the medusa; for the blastocheme, as we have already seen, is constructed on the plan of a fully developed hydroid medusa; while its sexual buds are simple sporosacs.

[1] 'Generationswechsel,' p. 56. [2] 'Zeit. fur wissen. Zool.,' 1853, p. 352.

2. *Development of the Ovum.—Embryonal Development.*

The general form and structure of the ovum has already been considered; the phenomena presented by the development of the embryo now remain for discussion.

Development of the Embryo from the commencement of the segmentation of the Vitellus to the attainment of the free locomotive stage.—I shall here describe this process as I have observed it in *Laomedea flexuosa*, which may be regarded as affording a type of embryonal development throughout the HYDROIDA. In this species the gonophores, which belong to the adelocodonic class, are included within a gonangium, where they are borne along the whole length of a blastostyle, regularly increasing in maturity as they recede from the base towards the summit of their supporting column (woodcut, fig. 18). Each gonophore in the female colony contains but a single ovum—a fact which facilitates the observation of the development.

The mature-ovum (woodcut, fig. 39 A), previous to the commencement of segmentation, is about 0·01 inch in diameter; it is of a granular structure, and contains a very distinct clear germinal vesicle about 0·002 of an inch in diameter, situated very excentrically, and easily separated from the surrounding vitellus, when it may be isolated as a perfectly spherical vesicle upon the stage of the microscope. There is occasionally a single germinal spot, but its place is usually taken by several (2 to 10) minute more or less spherical or oval bodies, which lie in the perfectly transparent and colourless fluid contents of the germinal vesicle. When the germinal vesicle is freed from the surrounding vitellus, and floated in sea-water on the stage of the microscope, these bodies almost instantly disappear without leaving a trace behind, being apparently dissolved by water absorbed from without through the walls of the vesicle. If, however, a little tincture of iodine be previously added to the water, they continue visible, and are now plainly seen to be themselves vesicles, containing within them a few minute granules which have been rendered obvious by the action of the iodine.

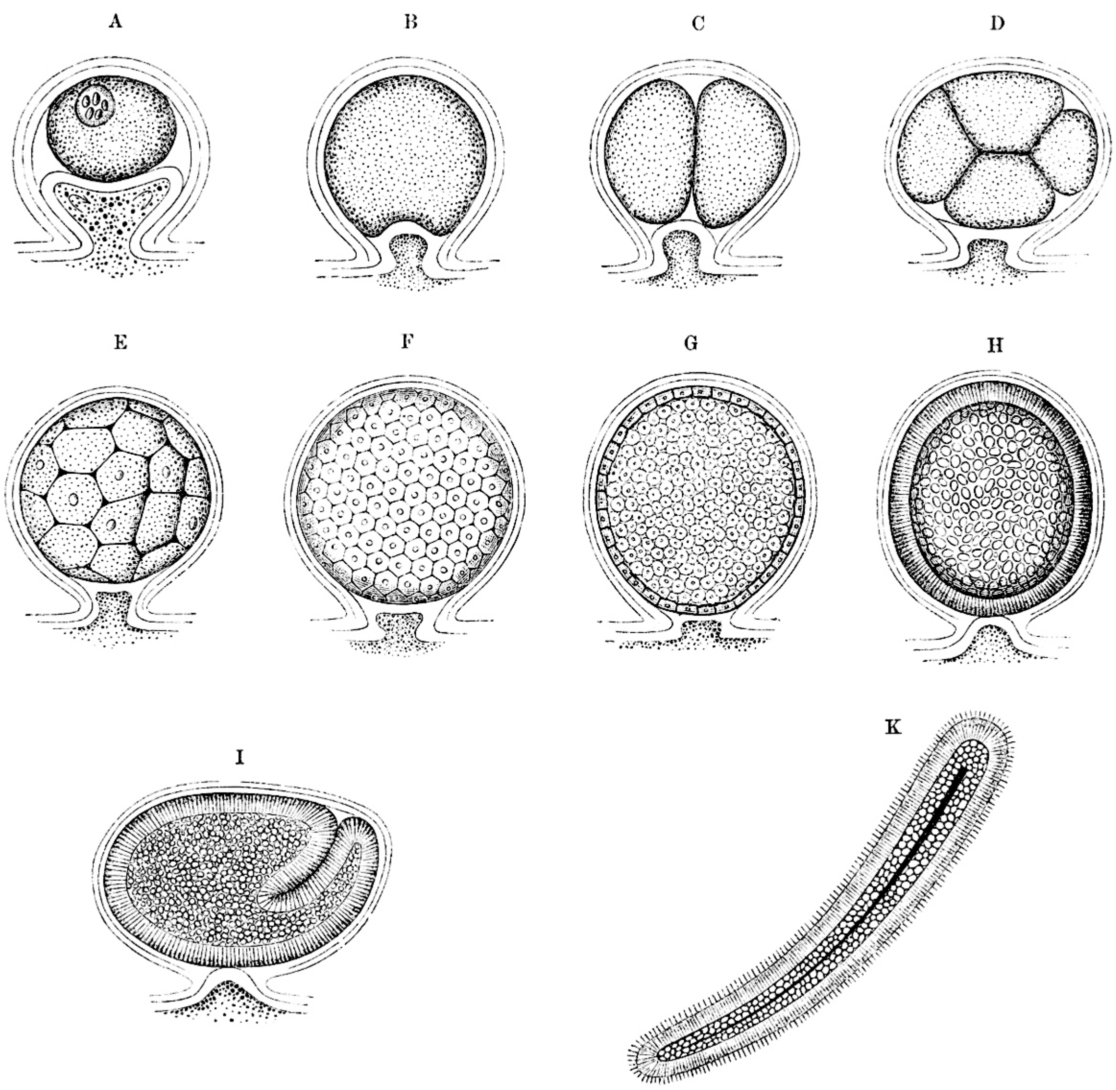
The vitellus is entirely composed of minute spherical corpuscles of apparently homogeneous structure, about 0·0002 of an inch in diameter, along with granules so small as not to admit of measurement. There is no obvious vitellary membrane in the mature ovum, but I have satisfied myself of its presence while the ovum is still in a very young state. In other species, *Hydractinia echinata* for example, this membrane is very obvious in the ovum just before segmentation. There is no trace of a micropyle in the ovum of this or of any other hydroid which I have examined.

As already said, there is never more than a single ovum in each gonophore of *Laomedea flexuosa;* and as this ovum continues to enlarge, it presses back the spadix until the latter is reduced to a small hollow projection in the bottom of the gonophore.

Up to this time the germinal vesicle continues quite distinct, but it now entirely disappears (B). The disappearance of the germinal vesicle is unaccompanied by any apparent change in the structure of the ovum, which retains the same peculiar composition of spherical corpuscles and granules. I have little doubt that the vesicle now ceases to exist, and that its disappearance is not due to its being merely concealed in the mass of the vitellus. It has probably burst, and in so doing must have liberated its peculiar contents, which will then, of course, be no longer visible in the vitellus. The disappearance of the germinal vesicle is probably the immediate result of impregnation; for I have seen active spermatozoa a little before this time in the cavity of the female gonophore.

Until, however, we have further evidence of what really becomes of the germinal vesicle,

Fig. 39.



Development of the ovum in *Laomedea flexuosa*.

A, Young ovum in the gonophore previously to the disappearance of the germinal vesicle; the germinal vesicle is here seen to contain several germinal spots. B, The germinal vesicle and spots have disappeared. C, The vitellus has become cleft into two segmentation-spheres. D, The ovum after the second cleavage. E, The segmentation-spheres have become numerous, and many of them now show a distinct nucleus. F, The segmentation-spheres have greatly increased in number, and a nucleus may now be detected in each of them. G, The segmentation-spheres have still further increased in number, while the most superficial have become arranged into a stratum distinguishable from the deeper portion of the ovum. H, The superficial stratum has become more distinct, and is now seen to be composed of long prismatic cells. I, The ovum has begun to elongate itself, and one end has become folded on the remainder. K, The embryo just after its escape in the form of a ciliated planula.

it is useless to speculate upon the influence which the supposed liberation of its contents may exert in exciting the new series of phenomena which are now about to take place in the ovum; at all events, shortly after the disappearance of the germinal vesicle, the process of segmentation sets in. This process is certainly not preceded by the visible occurrence of a new nucleus destined to take the place of the germinal vesicle. It is quite possible, however, that such a nucleus may exist, though, from its small size, and from being so deeply imbedded in the mass of the vitellus, it may have eluded our attempts to discover it.

The first step observable in the segmentation-process is the cleavage of the yolk into two segments (C), immediately followed by the cleavage of these into other two, so that the vitellus is now composed of four cleavage-spheres (D). In none of them, however, can a nucleus be as yet demonstrated.

The segmentation would now appear to proceed very rapidly, but not always with absolute regularity; for it would seem occasionally to advance more rapidly in some of the previously formed spheres than in others. By the time that the vitellus presents about thirty-six or more cleavage-spheres (E) we begin to recognise in some of these spheres a distinct nucleus; while, as the spheres become smaller and more numerous, the nuclei become more and more apparent, until at last there may be seen in every minute sphere, of which the segmented yolk is composed (F), a brilliant nucleus, visible not only in the superficial spheres, but also in the deeper ones which come into view when the ovum is broken down under the compressor. It is, therefore, highly probable that in the earlier stages also a nucleus exists in every cleavage-sphere, but that in consequence of the thickness and opacity of the enveloping vitellus it is withdrawn from observation. The cleavage-spheres at this stage present the same peculiar structure which we find in the yolk just before the commencement of segmentation, consisting, as they do, of minute spherical corpuscles, with still more minute granules. When the vitellus has thus become broken up into a great number of minute spheres, it is evident that the most superficial of these spheres have arranged themselves into a distinct stratum, consisting of a single layer of spheres, and completely enveloping the more internal parts (G).

We next find that the spheres composing this layer have increased in number, while at the same time they have become longer in the direction of the radius of the ovum, and now form a rather thick layer of undoubted cells, arranged with their long axes perpendicular to the surface of the ovum, having their sides in close contact and investing, as with a continuous wall, the whole interior of the mass (H).

It is impossible not to see in the entire process here described an exact parallelism with the early stages in the development of the holoblastic vertebrate ovum, while the superficial layer of cells, to the formation of which we have just arrived, must—though as yet showing no obvious tendency to a splitting into distinct laminæ—be at once recognised as the representative of the vertebrate blastoderm.

The nuclei, which were previously visible in the cleavage-spheres, have now ceased to be distinguishable, while these spheres at the same time show a distinct investing membrane. In fact, on now carefully breaking down the ovum under the microscope, its interior is found to consist entirely of loosely aggregated cells, some spherical, some more elongated, and all with a more or less copious endogenous brood of secondary cells within them.

The external enveloping layer having thus attained a considerable thickness, and a well-defined differentiation between it and the more internal parts having been established, the ovum begins to elongate itself, and at the same time the interior has undergone a further change; for we no longer find in it the large mother-cells with their endogenous brood, but a multitude of small, free, clear vesicles, of various sizes, mingled with minute granules, similar to those which had all along formed a part of the constituents of the segment spheres.

At this point we may conveniently, though somewhat arbitrarily, designate the developing body as the "embryo." We next find that one end of the oval embryo begins to be prolonged beyond the rest, upon which it becomes bent back as it continues to elongate itself (I). By this time the embryo has become endowed with evident contractility, as manifested by sluggish changes of contour.

Shortly after this the embryo escapes from its confinement by the rupture of the walls of the gonophore, when it speedily straightens itself, and then, in the form of an elongated, nearly cylindrical body, slightly tapering towards one end, is discharged through the summit of the gonangium into the surrounding water (K).

We now find that its whole surface is clothed with vibratile cilia, by whose aid it moves slowly along the bottom of the vessel, while the cells and granules which occupied its deepest parts seem to have undegone a kind of liquefaction, resulting in the formation of an elongated cavity in the axis of the embryo which is thus, at this period, a nearly cylindrical sac, without, as yet, any appearance of a mouth, but with an endoderm and ectoderm already differentiated, while multitudes of very minute elongated oval bodies, with a high refractive power, soon make their appearance in the ectoderm; these are most probably thread-cells, though no sign of a filament can as yet be discovered in them.

I am unable to form any decided conclusion as to whether the endoderm, which thus about this period becomes demonstrable, is to be regarded as the remains of the more central cells of the segmented ovum, or as an inner lamina formed by a differential splitting of the peripheral layer or blastoderm. The appearances are rather in favour of the former view; but if the latter be the true interpretation, the analogy up to a certain point with the development of the vertebrate ovum will be the closer. At all events there can be little doubt that the two membranes which now make their appearance and continue as the endoderm and ectoderm of the developing hydroid are functionally equivalent, the endoderm to the internal or vegetative layer, and the ectoderm to the external or animal layer of the vertebrate blastoderm. It will be seen in the sequel that the parts which are concerned in digestion and in generation have their seat in the endoderm, while those which are destined for the functions of sensation, locomotion, and protection, originate in the ectoderm—a state of things which has its exact parallel in the two laminæ of the vertebrate blastoderm.[1]

We have thus arrived at the ciliated and locomotive stage of the embryo. To this stage Sir John G. Dalyell has given the name of "planula"—a name, however, suggested by a mistaken view of its form, which he compares to a *Planaria*. In this comparison he has probably been led astray by the imperfection of his microscope; for the locomotive embryo has no tendency whatever to a flattened shape, as indicated by the name of "planula," but is always conical or cylindrical. Instead of "planula," therefore, one is strongly tempted to employ for

[1] The comparison of the structure of the Hydrozoa to the early stages in the development of the highest animals has been very distinctly made by Professor Huxley. "The outer and inner membranes appear to bear the same physiological relation to one another as do the serous and mucous layers of the germ; the outer becoming developed into the muscular system and giving rise to the organs of offence and defence; the inner, on the other hand, appearing to be more closely subservient to the purposes of nutrition and generation."—"On the Anatomy and Affinities of the Medusæ." 'Phil. Trans.,' 1849, p. 426.

this form of embryo some term which shall not tend to convey a false impression of its figure. The term "planula," however, has passed into such general use, and has, moreover, become so intimately associated with the memory of one to whose admirable and conscientious observations our knowledge of the HYDROIDA owes so much, that the defects of the term will hardly justify our suppression of it.

Further Development from the Planula to the attainment of the Adult Form.—The further progress of the animal, up to that stage in which it has acquired all the essential features of the adult, admits of being easily traced in many different species. I shall take as a good type of the changes which the ciliated embryo undergoes in this progress the development of *Eudendrium ramosum* (Pl. XIII), in which I have satisfactorily followed the various steps.

After the embryo (Pl. XIII, fig. 10) has enjoyed for a period (which probably extends over two or three days) its locomotive existence, it loses its cilia, and with them all power of active locomotion, though still apparently retaining the power of slowly creeping from place to place by the contractility of its body. It may now be occasionally seen with one end dilated, so as to assume a flask-shaped form (fig. 11).

We next find that the animal has attached itself to some fixed object by the enlarged extremity of its body, which becomes flattened over the surface to which it thus adheres (fig. 12). From the centre of this enlarged base the rest of the embryo rises perpendicularly as a little cylindrical or somewhat clavate hollow column. The base now expands laterally, while, at the same time, it becomes compressed vertically, so as to acquire the condition of a little circular disc of adhesion; and simultaneously with these changes the embryo becomes enlarged a little behind its distal or free extremity by the formation of a slightly prominent circular ridge, while an exceedingly delicate perisarc has been excreted as a scarcely perceptible film over its whole surface (fig. 13).

It will next be seen that a remarkable change has taken place in the disc of attachment by the division of this part into lobes separated from one another by radiating fissures, which commence as shallow notches at the circumference, and thence gradually increase in depth until they nearly reach the central vertical column (fig. 14). These lobes, like the rest of the young hydroid, consist of a layer of endoderm enveloped by one of ectoderm, while each contains a prolongation from the cavity of the column, and is invested by a delicate perisarc, which may be traced into the bottom of the dividing fissures. The lobes of the disc increase in number by successive dichotomous division, though absolute regularity is not usually maintained.

In the mean time the young *Eudendrium* has increased in size, and the circular ridge has become more pronounced, while the part at the distal side of this ridge has in the same proportion become more decidedly marked off from the rest of the body, and the perisarc has here become more distinct by the partial withdrawal from it of the included structures.

Soon after this the circumference of the ridge will be found to have extended itself as a circle of about ten short, thick tentacles, while at some distance behind these the body is seen to be narrowed into a short, nearly cylindrical stem, springing directly from the centre of the basal disc; and the more contracted portion which lies at the distal side of the circle of rudimental tentacles is now plainly recognisable as the proboscis or hypostome of the future hydranth. The tentacles now rapidly multiply by the intercalation of others between those already formed (fig. 15). The second set may at first be easily distinguished by their shortness; but the bases of all seem to be on the same level, and the whole appear to constitute a single uninterrupted series. The tentacles, though short and thick, will have thus soon attained the full number which we meet with in the adult. They consist in this stage of an endodermal and an ectodermal layer, the ectoderm apparently formed of a single layer of prismatic cells, while the endoderm seems to fill the entire axis with a mass of minute, spherical, loosely aggregated cells. Just behind the tentacles the body of the young hydranth is seen to be excavated by a large cavity, in which is a multitude of loose spherical cells, filled with a red granular pigment, and undoubtedly thrown off from the inner surface of the walls.

The whole of the young hydroid is still completely enveloped by the delicate chitinous perisarc, which forms a sheath extending over even the distal free extremity, and within which the various changes just described, including even the formation of the tentacles, have been going on. We now find, however, that this sheath (which has for some time lain loosely over the distal parts of the hydroid, and which it seemed to invest as in a sac) becomes ruptured in front of the tentacles, so that the water gains direct access to the surface of the young hydranth, and the tentacles have full freedom to extend themselves. It would seem, too, that the distal extremity of the proboscis had now, for the first time, become perforated by a mouth; for up to this stage, no undoubted evidence of an oral aperture could be detected.

The young *Eudendrium* has thus acquired the form of a true hydranth borne on the extremity of a short simple cylindrical stem, which still springs from the centre of the radiating disc (fig. 16). The stem elongates itself, and the body, tentacles, and hypostome rapidly acquire all the characters of the adult. It still, however, remains for it to develop from its base a creeping stolon which will take the place of the primordial disc, and which would seem to originate in the elongation of some of the lobes of this disc, to complicate itself by the budding of new hydranths and the development of branches, and, finally, by the formation of sexual zooids, to combine a gonosome with a trophosome, in order that the little hydroid whose progressive changes we have been thus following may attain the condition of the adult *Eudendrium* (figs. 1 and 2).

Development by Actinulæ.—The developmental phenomena above described are, in all their essential points, so far as we know, universal among the HYDROIDA, with the exception of the genera *Tubularia*, *Hydra*, and, probably, also *Myriothela* and *Actinogonium*.

In *Tubularia* a minutely granular plasma, which, except in its more obviously cellular structure, is entirely similar to that which in other Hydroida becomes differentiated into ordinary ova, may be seen enveloping the spadix of the young gonophore. Instead, however, of becoming transformed in the usual way into ova, portions become detached from the mass and lie loose in the cavity of the gonophore, where they undergo a development into free embryos in the manner to be presently described, while the residual plasma continues to detach from its mass fresh fragments, which are in their turn transformed into embryos (Pl. XX, fig. 3, and Pl. XXIII, figs. 11, 13, 14, 15, 16, 23, 24).

In the portions (Pl. XXIII, figs. 11 *g* and 23 *g*) thus successively detached from the central plasma (*f*) it is impossible to detect any decided trace of germinal vesicle or germinal spot, and yet we should certainly not be justified in regarding them as mere gemmæ, or in attributing to them any other significance than that of true ova,[1] though, possibly, of ova after they had already passed

[1] Agassiz calls the central plasma in *Tubularia* the "germ-basis," and refuses to regard as ova the masses which are thrown off from it and become developed into hydriform young. (*Op. cit.*, vol iv, pp. 255 and 269.)

the earlier stages of their development. The plasma in which they originate holds in the gonophores which contain it a position precisely similar to that held by the undoubted spermatogenous tissue in the male gonophores (figs. 8 *f*, 9 *f*, and 21 *f*) of the same species; and as nothing else is presented by the hydroid which can in any way be regarded as ova, we should, by denying to these the essential attributes of ova, be reduced to the anomalous alternative of admitting the existence of the male element without the correlative female one.

The fact, however, that the plasma at a very early period, as well as the masses which have been detached from it in order to become developed into embryos, consist almost entirely of cell-like elements, indicates a difference between the matter composing them and the more simple protoplasmic matter of the unfecundated vitellus in other hydroids.

The phenomena connected with the development of the embryo in *Tubularia indivisa* and *T. larynx*, in both of which I have carefully examined them,[1] will afford a good example of the difference between this form of development and that which is usual among the Hydroida; they would seem to be in all essential points similar in the other species of *Tubularia*.

In the very young female gonophore of *Tubularia larynx*, while yet only $\frac{1}{200}$th of an inch in diameter, the spadix may be seen lying in the axis of a cavity bounded externally by a double wall (Pl. XXIII, fig. 19). Surrounding the spadix, and occupying the whole of the space between it and the wall of the cavity, may be seen the generative plasma (*f*), consisting of a uniform mass of small spherical cells, about $\frac{1}{2000}$th of an inch in diameter. When liberated from the young gonophore, and floated in water, these cells seem perfectly transparent, their contents appearing to consist of a clear colourless fluid, with a somewhat higher refractive power than the surrounding water. Under the action of acetic acid their contents become granular, and a nucleus-like particle usually becomes visible in the midst of the granular contents (fig. 20).

At a slightly more advanced stage (fig. 21) the gonophore has reached to about $\frac{1}{120}$th of an inch in diameter, and the apical tubercles (*a'*) which characterise the mature gonophore have begun to make their appearance. The inner layer (*b*) of the walls of the gonophore may now be seen to have become separated from the outer (*a*), and thereby rendered more distinct. This inner layer is plainly composed of minute spherical cells, and is thinner than the outer wall, which is composed of prismatic cells, among which thread-cells are already developed. At this period the gonophore begins to become perforated at its summit by an aperture, which opens externally between the bases of the apical tubercles.

The tubercles continue to increase in size with the enlarging gonophore; the plasma becomes more voluminous, and among its component cells may be seen several of somewhat larger size than the rest; under the action of acetic acid these larger cells show a very distinct nucleus, with nucleolus, in the midst of granular contents (fig. 22). It is just possible that these cells may represent germinal vesicles with the germinal spot and its contained *punctum*, but with no vitellus as yet differentiated around them. The plasma, retaining the same structure, continues to increase in volume with the growth of the gonophore; while the inner layer of the wall—that which had immediately invested the plasma, and must be regarded as the endotheca—would seem to undergo absorption, and finally to disappear. We now find that a portion (fig. 23 *g*) of the plasma has become detached from the mass, and soon undergoes a special development into an embryo within the cavity of the gonophore. As has been said, no obvious trace of germinal

[1] "Notes on the Hydroid Zoophytes," 'Ann. Nat. Hist.,' July, 1859.

vesicle or spot can be found either in the entire mass or in any of the detached portions, unless the nucleated cells just referred to (fig. 22) can be so regarded; so also the phenomenon of yolk-cleavage, if present at all, is very obscure, but the detached mass may be easily broken up into cells filled with secondary cells.

The ovum (for I have no hesitation in so designating the mass detached from the primitive plasma, notwithstanding its anomalous character) lies in contact with the remainder of the plasma, and while in this position becomes developed into an actiniform embryo, as has been already noticed by Van Beneden,[1] Mummery,[2] myself,[3] and others. In the act of development, as shown in figs. 11—16, which represent the corresponding process in *Tubularia indivisa*, it becomes first (fig. 13) extended as a disc over the residual plasma. In this disc we can always recognise a differentiation between its peripheral and central portions. Next (fig. 14), from the circumference of the disc short and thick processes radiate all round, and these soon elongate themselves into tentacles (fig. 15); the disc at the same time gradually becomes more gibbous on the side turned away from the axis of the gonophore, its interior has already become hollowed out into a digestive cavity, and a mouth now makes its appearance in the centre of the opposite side, or that in contact with the plasma. The embryo now retreats from the plasma, the mouth is seen to be elevated on a conical prominence (fig. 16 *a*, fig. 24 *h'*), while the side opposite to the mouth becomes more and more prolonged with the general cavity of the embryo continued into it. The extremity of this prolongation presents in *Tubularia larynx* and some other species the appearance of delicate striæ (probably fibres) radiating for a short distance from its central point (Pl. XXI, fig. 6)—a peculiar structure which might easily lead to the belief that an aperture was here present. The appearance of an aperture, however, I believe to be entirely deceptive. In this state it escapes from the gonophore, a circle of very short tentacles having first become developed round the mouth in some species (*T. indivisa*, fig. 16); while in others (*T. larynx*, fig. 24) the oral tentacles do not make their appearance until after the escape of the embryo. After continuing free (Pl. XX, fig. 4, Pl. XXI, fig. 6) for a period, the side opposite to the mouth becomes ultimately developed into a cylindrical stem, which soon clothes itself with a perisarc and fixes the young *Tubularia* to some neighbouring object (Pl. XX, fig. 5, Pl. XXI, fig. 7). After the escape of the embryo, or even during its development within the gonophore, the remains of the plasma may still throw off portions (Pl. XXIII, fig. 24 *g'*), which become developed, in a similar way, into free actiniform embryos. To such embryos the name of *actinulæ* may be given, in order to distinguish them from the *planulæ* of other hydroids.[4]

[1] "Recherches sur l'Embryogénie des Tubulaires," p. 37, pl. 1, in 'Nouv. Mém. de l'Acad. Roy. de Bruxelles,' tom. xvii, 1844.

[2] "On the Development of *Tubularia indivisa*," 'Trans. Micr. Soc.,' 1853, p. 28.

[3] Allman, "On *Tubularia indivisa*," 'Ann. Nat. Hist.,' July, 1859.

[4] Prof. H. J. Clark has given a detailed account of the development of the gonophore and ovarian plasma in Tubularia ("Tubularia not Parthenogenous," 'American Journal of Science and Arts,' vol. xxxvii, Jan., 1864). I cannot, however, accept in all points his interpretation of the appearances presented in the microscopic investigation of these parts. He regards as the true ova certain very minute cells which are visible in the gonophore while yet in a rudimentary state, and which would seem to be those described above as composing the very young tissue of the plasma. Notwithstanding, however, a certain resemblance of these cells to ova, I cannot so regard them. They cannot be followed through any of the changes which characterise the development of a true ovum; they

The generative process in the freshwater *Hydra* offers some striking resemblances to that just described in *Tubularia.* Usually towards the end of autumn, but occasionally even in spring, peculiar tubercles may be seen budding from the body of various species of *Hydra.* They are produced chiefly towards the anterior end of the body. I have especially examined them in *Hydra vulgaris.* They are here of a conical form, and when mature have their apex perforated by a short canal, through which the contents of the tubercle escape. These contents are then seen to be active spermatozoa of the usual form, and the tubercle must be regarded as a male gonophore.[1] Its external wall consists of a single ectodermal layer, and its cavity is traversed by a process of the endoderm, which, at least in the younger stages, extends from the base to the summit of the gonophore, where it remains for some time united to the ectodermal wall. Between this axile process of endoderm, which plainly corresponds to a spadix, and the outer wall of endoderm, the spermatogenous plasma is developed. The entire plasma has the appearance of being divided into longitudinal masses, as if by septa, which pass from the outer wall to the axile spadix. It increases in maturity as we examine it from the base towards the summit of the gonophore, the reproductive elements being still enclosed towards the base in their generating cells, while towards the summit they may be seen as free active spermatozoa, ready to escape through the perforation which is now found in the summit of the gonophore for their exit.

But, besides the spermatogenous tubercles, there also occur, usually on the same specimen, others which, instead of containing spermatozoa, have their cavity occupied by a peculiar cellular plasma, destined to give origin to ova. Their position on the body of the *Hydra,* in every specimen which has come under my observation, was at the proximal side of that part of the animal which carries the spermatogenous tubercles. They form rounded elevations, with a broad base of attachment, and are of less defined form than the others. They seem to be produced by a simple separation of the ectoderm and endoderm of the *Hydra,* with the plasma interposed between the two membranes. They certainly correspond to the female gonophore of other hydroids, but they

simply constitute a portion of the general tissue of the plasma, as well as of the masses which are subsequently detached from it in order to become developed into actiniform embryos. As stated above, however, it is possible that the nucleated cells (Pl. XXIII, fig. 22) which make their appearance at a somewhat later period represent germinal vesicles.

Claparède ('Beobacht. über Anat. u. Entwickel. wirbelloser Thiere an der Küste von Normandie,' 1863, p. 2) also takes a different view of the development of *Tubularia* from that given above. His observations were made on certain minute organisms which he found swimming in the open sea, and which are undoubtedly the actinula-stage of some species of *Tubularia.* He compares them to small medusæ, the body of the actinula representing the umbrella, and the long tentacles the marginal tentacles of the medusa, while that portion which is subsequently to become developed into the stem of the *Tubularia* is viewed by Claparède as corresponding to the manubrium—the mouth of the future *Tubularia,* with its circle of short tentacles, being developed on the summit of the umbrella. Claparède believes that he had found an aperture in the extremity of that portion which is to become the stem, and he has apparently been thus led to interpret this part as the manubrium of a medusa. I have little doubt that Claparède has been here deceived by the peculiar structure described above, and which might easily lead to an error of interpretation.

[1] We owe to Ehrenberg the original determination of the nature of these bodies. His account of them is given in the 'Mittheilungen aus den Verhandl. der Gesellsch. Naturf. Freunde in Berlin,' 1838, p. 14.

present little or no trace of a spadix; and if this ever existed, it must have been depressed at an early stage by the ovarian plasma, which now lies upon an even floor of endoderm.

The contents of these bodies consist in an early period of development of minute spherical cells distributed through a semifluid granular blastema, and generally exhibiting a distinct nucleus. As this cellular and granular material increases in volume, we find it becoming broken up into detached masses. These masses vary much in size and form; they frequently present a very irregular outline, with projecting lobes and processes of no definite or permanent shape. At a somewhat later period some of them burst through the confining wall of ectoderm, and then usually remain for some time in the form of irregularly spherical bodies, attached to the external surface of the gonophore, as if by the adhesive properties of their constituent blastema.

The escaped masses may usually be seen to be themselves composed of an agglomeration of smaller masses, reminding us of a segmented vitellus; but I am, nevertheless, not prepared to regard this complex condition as a true vitelline segmentation. Further, no appearance of a germinal vesicle or spot can at any time be detected in any part of the ovarian plasma, and yet I believe we should not be justified in denying to the masses which have become detached the significance of true ova.[1]

Beyond this point my observations have not extended, but other observers have described the liberated masses as enveloping themselves with a tough membrane, which in some species would seem to develop over its surface peculiar forked spines. On the rupture of this membrane its contents become directly developed into an actiniform embryo, which gradually assumes the form of the adult Hydra.[2]

The resemblance between the embryonic development in Hydra and that in Tubularia is thus very close; indeed, it is impossible not to regard them both as presenting the same essential modification of the reproductive process—a modification whose most striking feature shows itself in the formation of an actinula instead of a planula.

I have had no opportunity of studying the genus *Myriothela* of Sars; but from the observations of Mr. W. P. Cocks, who was the first to meet with this remarkable hydroid genus on the British shores, as well as from those of Mr. Joshua Alder, it would appear that actiniform embryos closely resembling those of *Tubularia* are the immediate result of the development of the ovum.

Several years ago M. Van Beneden described and figured a *Coryne*-like hydroid from the coast of Belgium, and assigned to it the name of *Syncoryne pusilla*, under the belief that it was identical with the original *Coryne pusilla* of Gaertner.[3] In this determination M. Van Beneden was wrong; but his hydroid possesses special interest from the nature of its gonophores, which are described as giving origin to actinula-like bodies, whose form is compared by the Belgian

[1] Rouget, who has examined with much care the reproductive system of Hydra ('Mém. de la Soc. de Biologie,' tom. iv, 1852, p. 387), compares these masses to a Graafian vesicle rather than to a true ovum.

[2] Pallas, 'Karakteristik der Thierpflansen,' p. 53; Ehrenberg, 'Abhandl. der Berl. Akad.,' 1836, p. 115, taf. ii Laurent, 'Froriep's Neue Notizen,' No. 513, p. 101; and 'Nouveaux Recherches sur les Hydres d'eau douce, Voyage de la Bonite,' 1844. See also 'On the Generative System of *Hydra*,' by Prof. Allen Thomson, *loc. cit.*, and Hancock, "Notes on a Species of *Hydra* found in the Northumberland Lakes," in the 'Annals of Natural History,' vol. v, 1850; and more especially Ecker, 'Entwickelungsgeschichte des Grünen Armpolypen,' Freiburg im Breisgau, 1853.

[3] Van Beneden, 'Embryogénie des Tubulaires.'

zoologist to that of a cuttlefish with four arms. Taking for granted that there is here no error of observation, the obvious interpretation is that Van Beneden's hydroid affords an example of development from an actinula instead of a planula.

This is a very important character, and one which, notwithstanding the general resemblance of the trophosome to that of a *Coryne*, must remove the hydroid into a new genus, to which the name of *Actinogonium* may be given.

3. *Significance of the Medusa in the Life-Series of the Hydroid.*

In our attempts to determine the significance of the sporosac, and the part it plays in the life of the hydroid, no difficulty is encountered, for its entire history, from its origin to the fulfilment of the purpose it is destined to serve in the economy of the hydroid, passes uninterruptedly before our eyes, and proves it to be a true generative zooid, giving origin in some cases to spermatozoa, in others to ova, whose development, as we have just seen, may be followed, and we are thus enabled to trace back the hydroid in an unbroken series through the egg from which it is developed, and the sporosac in which this egg originates, to the hydroid trophosome from which the sporosac buds.

The cases in which a similarly unbroken chain can be traced back through the free generative bud or planoblast are naturally far less frequent, for in the majority of cases the planoblast does not produce its generative elements until a considerable time after it has become free, and has undergone more or less change of form as it continues to develop itself in the open sea; and it is very seldom that we can succeed in rearing the free medusa, in the confinement of our tanks, up to the period when it shall attain to sexual maturity, either directly, as in the gonocheme, or indirectly, as in the blastocheme.[1] We thus, then, almost always lose absolute evidence of identity in both gonocheme and blastocheme, when presented at two distant periods of their lives; and there is in such cases, necessarily, an interruption in the series of continuous observations.

Some uninterruptedly continuous observations, however, have been made, and we now know of various instances in which the generative elements have been detected, either in the walls of the manubrium or in special sexual buds developed from the gastro-vascular canals, in medusæ which have been themselves traced to hydriform trophosomes; while in others, though the free medusa in which the eggs or spermatozoa have been found have not been traced by *direct* observation to a trophosome, their resemblance to forms which have been so traced is so close as to justify us in assigning to both a similar origin.[2] There thus remains no longer any doubt that the significance of the medusa in the life-series of the hydroid is in all essential points identical with that of the sporosac; and the assertion here made applies to both gonocheme and blastocheme, with this difference alone, that in the latter the generative elements are not produced directly, but only

[1] In the *Siphonophora* the opposite condition is prevalent; for here the gonophores, even such as present the more complete medusal or phanerocodonic form, usually become loaded with ova or spermatozoa before they detach themselves from the trophosome.

[2] I have elsewhere brought together all the known instances in which medusæ, whether gonophores or blastochemes, traceable to trophosomes, have been observed to develop generative elements. See 'Report on the Reprod. Syst. in the Hydroida,' p. 411, &c.

through the intervention of its sexual buds. We are thus brought up to an important point in the developmental history of the Hydroida, and are enabled to enunciate the following fundamental proposition:

THE FIXED PLANT-LIKE HYDROIDA GIVE ORIGIN TO SEXUAL BUDS, NOT ONLY IN THE FORM OF CLOSED SACS (*the sporosac*), WHICH DEVELOP WITHIN THEM THE GENERATIVE ELEMENTS; BUT ALSO IN THAT OF A MORE SPECIALISED FORM OF BUD, WHICH BECOMES A FREE (RARELY FIXED) MEDUSA, AND THIS ULTIMATELY ATTAINS EITHER DIRECTLY (*the gonocheme*) OR INDIRECTLY (*the blastocheme*) TO SEXUAL MATURITY, AND PRODUCES OVA OR SPERMATOZOA.

But the point to which we thus arrive does not present us with the entire life-series of the medusa-producing hydroid, for the important question still remains, What is the result, immediate and remote, of the development of the ovum produced by the medusa? and how far does this development correspond with that of the ovum produced in a sporosac without the intervention of a true medusiform bud?

A considerable number of facts bearing upon this question have also been accumulated; and the development of the ovum formed in the medusa has been traced, with more or less minuteness, by various observers, so that we are now enabled to present the terms which were still wanting to complete the life-series of the hydroid.

As the observations which have thus aided in completing our knowledge of hydroid development are of great importance in the present inquiry, it will be necessary to give here some account of those cases in which the development of the egg of the hydroid medusa has been satisfactorily traced.

Dujardin[1] observed that a remarkable little medusa, which he described under the name of *Cladonema*, was developed as a bud from a hydriform trophosome, to which he gave the name of *Stauridium*. He had noticed the production of eggs by his *Cladonema*, and had also seen young *Stauridia* developed from these eggs, though the planula stage seems to have escaped him.

Krohn,[2] having placed in a jar of sea-water some mature specimens of Dujardin's *Cladonema*, observed that after a time they had deposited eggs, which adhered to the sides and bottom of the vessel. Soon after deposition, the segmentation of the yolk commenced; and in about forty-eight hours after the beginning of the cleavage the ovum had become changed into a free-swimming ciliated infusorium-like embryo (planula).

This embryo was successfully watched by Krohn through all the subsequent stages—the disappearance of its cilia, the fixing itself to the sides of the jar, its conversion into a little circular disc, the growth of a short column from the centre of the disc, and its final conversion into a hydroid, identical with the *Stauridium* from which Dujardin had originally seen the *Cladonema* thrown off. To Dujardin and to Krohn are thus due the first grand observations by which the whole circle of hydroid development, in the case of a free phanerocodonic gonophore, has been completed.

[1] Dujardin, 'Ann. des Sc. Nat.,' ser. iii, vol. iv, 1845, p. 273.

[2] Müller's 'Archiv,' 1853, p. 420, tab. xiii.

Gosse[1] has seen the medusa described by Forbes under the name of *Turris neglecta,* discharge from the generative mass formed in the walls of its manubrium ciliated planulæ, which, after some time, fixed themselves to the glass, and became elongated into adherent, branched, stolon-like bodies, which threw up a perpendicular stem, on whose summit a circle of four tentacles was developed, and the whole became thus changed into a *Clava*-like hydroid.

Strethill Wright[2] subsequently watched the development of the ovum in this same medusa. His observations agree with those of Gosse, but he has succeeded in tracing the development a step further; for he saw the tentacles increase in number by the growth of others behind those first formed, giving by their scattered disposition a still more *Clava*-like appearance to the hydroid, while he also noticed the formation of a chitinous periderm which clothed the creeping stolon.

Gegenbaur[3] describes the development of the egg in a medusa, which he names *Lizzia Köllikeri.* He has seen the segmentation of the vitellus, and the formation of a ciliated planula, which, after enjoying for a time its locomotive existence, loses its cilia, fixes itself to the side of the vessel, expands one extremity into a disc of adhesion, elongates the rest of its body into a cylindrical stem, which after clothing itself with a chitinous polypary, develops a mouth upon its free extremity, and just below this throws out a verticil of tentacles, while the expanded base becomes extended into short stolon-like prolongations.

The development of the ova in another medusa, named by Kölliker *Oceania armata,* was also observed by Gegenbaur.[4] He traced the segmentation of the vitellus, the formation of a ciliated planula, the fixation of the planula, and its development into a stolon-like body; but beyond this point his observations were not carried.

Wright[5] noticed the occurrence of numerous planulæ which had made their appearance in a vessel in which he had placed some isolated specimens of *Thaumantias inconspicua,* Forbes. He believed that these planulæ were produced by the *Thaumantias,* and he saw some of them fix themselves to the sides of the vessel and develop a lobed disc of attachment. From this disc arose a stem, which after developing from its summit a hydranth closely resembled the *Campanularia raridentata* of Alder.

In the *Zygodactyla (Æquorea) vitrina* of Gosse, Wright[6] also observed free ciliated planulæ to escape from the generative bodies, and, after fixing themselves to the sides of the vessel, become developed each into a hydroid, with hydranth, hydrotheca, and perisarc, bearing, as he informs us, a close resemblance to the *Laomedea acuminata* of Alder.

Alexander Agassiz[7] has followed the development of the egg in two forms of hydroid medusæ—*Melicertum campanula,* Esch., and *Tima formosa,* Agass. In both he has seen the formation of the ciliated planula, the fixation of the planula, and its gradual conversion into a young campanularian trophosome.

[1] 'A Naturalist's Rambles on the Devonshire Coast,' 1853, p. 348, pl. 13.

[2] 'Edinb. New Phil. Journ.,' July 1859, pl. 8, f. 1.

[3] 'Generationswechsel,' 1854, p. 23, pl. ii, figs. 1-9.

[4] *Loc. cit.*, p. 28, pl. 2, figs. 10—16.

[5] 'Micr. Journ.,' vol. ii, new ser.

[6] 'Micr. Journ.,' vol. ii, pl. iv, figs. 1—6.

[7] 'Illustrated Catalogue of the Museum of Comp. Zool. at Harvard College,' No. II, pp. 115 and 134.

I have myself traced the development of the egg of a *Tyaropsis* as far as the planula stage; but though the planulæ continued to live in my jars for some weeks, they ultimately perished without passing into any further phase of their metamorphosis.

The class of observations here enumerated enable us to complete the circle of hydroid development, and justify us in the enunciation of a second proposition, which, taken along with the former one, will express the entire life series of the hydroid:

THE OVA OF THE MEDUSIFORM BUD UNDERGO, LIKE THOSE OF THE SPOROSAC, A CONTINUOUS DEVELOPMENT, BY WHICH THEY BECOME TRANSFORMED INTO HYDRIFORM TROPHOSOMES, WHILE THESE TROPHOSOMES ULTIMATELY GIVE ORIGIN, BY BUDS, TO MEDUSÆ IDENTICAL WITH THOSE FROM WHOSE OVA THE TROPHOSOME WAS DIRECTLY DEVELOPED.

It will be further seen, from the facts now stated, that the earliest stage of the hydroid trophosome is always free and locomotive, and that it shows itself under one or other of two types. One of these types is presented by the great majority of the HYDROIDA, and has been described above as the *planula* of Sir J. G. Dalyell; the other occurs in the genus *Tubularia*, and apparently also in *Myrothela*, *Hydra*, and *Actinogonium*, and has been already described under the name of *actinula*. Every hydroid, if we except such forms as may be proved to pass to the medusal condition directly from the egg, thus commences its free existence either as a planula or an actinula.

Direct Development of the Medusa from the Egg.—In by far the majority of cases in which the development of the hydroid has been successfully traced, the life series of the individual has presented a non-sexual hydra-like form, interposed between the ovum and the directly or indirectly sexual medusal form.

Against the absolute universality of this law, however, certain observations have been adduced, as tending to show that in some cases a direct development from the egg to the medusa takes place without the intervention of a non-sexual trophosome. There is no reason why this should not be so, and yet a careful examination of the cases adduced in support of it will render it evident that most of them afford no evidence which can be relied on as conclusive in favour of the direct development of the medusa from the egg.[1]

It is chiefly among the Æginidan and Geryonidan medusæ that cases believed to afford evidence of direct development have been observed. The first observation bearing immediately on this question is due to Johan. Müller,[2] who captured, on several occasions in the sea, at Marseilles and Nice, a minute free-swimming hydroid. It was of an oval form, about half a line in its longer diameter, ciliated over its entire surface, with two tentacle-like processes near one end, and having at the opposite end an opening which led into a central cavity.

Müller considers this little animal to have been developed directly from the egg, and from its resemblance to a peculiar two-tentacled medusa which he obtained in considerable abundance at Nice, he believes himself justified in regarding it as one of the stages in the development of this

[1] Among the DISCOPHORA a single case also of direct development has been made known; that, namely, of *Pelagia*, a medusa which has been shown by Krohn to be developed from the egg without the intervention of a *Scyphostoma* or polypoid form.

[2] Müller's 'Archiv,' 1851, p. 272.

medusa, into which he supposes it to pass by direct metamorphosis. He refers it to the genus *Æginopsis*, Brandt, and names it *Æginopsis Mediterranea*, Müll. Müller does not seem to have obtained any specimen of his *Æ. Mediterranea*, so far matured as to present traces of the generative elements; but his observations have been in this respect supplemented by Kölliker,[1] who afterwards obtained the same species at Messina in a sexually mature state.

Now, we cannot overlook the fact that Müller has not, in the above case, traced his ciliated hydroid through a continuous series of developmental phases into the adult form of *Æginopsis;* and, without denying the probability that the ciliated bitentacular hydroid is really the larva of the *Æginopsis*, we cannot regard this relation as absolutely proved, while there is no evidence whatever that the ciliated form is the immediate result of the development of an ovum. Indeed, its remarkable resemblance to the singular generative zooid of *Dicoryne* (see above, p. 31) would seem to show the probability of another origin than that by direct development from the egg. Müller, led apparently by the analogy of the planula-stage of the *Hydroida*, considers the ciliated condition of the surface as affording evidence of such a direct development; but the fact that the *Dicoryne*-zooid is also richly ciliated over its whole surface shows that this argument goes for nothing.

Kölliker[2] found in the stomach-cavity of a ten-tentacled Æginidan medusa, captured in the sea at Messina, and described by him under the name of *Eurystoma rubiginosum*, a number of small organisms resembling medusæ in various stages of development, and which he believed he could follow from stage to stage until he found them assume the form of a sixteen-tentacled medusa. To this last, which also belongs to the family of the *Æginidæ*, he gives the name of *Stenogaster complanatus*.

The great difference between these two medusæ appears to Kölliker sufficient proof that the one could not have been produced by the other, and he regards the young stenogasters as having been swallowed by the *Eurystoma*. He views, however, the young *Stenogaster*, exhibiting as it does, various steps in a metamorphosis from a very early stage, as affording evidence of the direct development of *Stenogaster* from the egg. It is, nevertheless, plain that there are no more valid grounds for such a conclusion in this instance than in Johan. Müller's case of *Æginopsis*, while Fritz Muller's case of *Cunina Köllikeri*, as well as the cases described by Gegenbaur and by Keferstein and Ehlers, and the more recent observations of Haeckel, all of which are cited above (p. 83), suggest the probability that the stenogasters noticed by Kölliker originated as buds from the *Eurystoma*.

Other instances which have been adduced as affording evidence of direct development from the egg without the intervention of a trophosome have been already referred to as cases where the medusa passes through a series of metamorphoses before arriving at its adult state. They are M'Crady's case of *Cunina octonaria*, Fritz Müller's of *Liriope cathariensis*, and Haeckel's of *Glossocodon eurybia* and *Carmarina hastata*, all of which, from the very imperfect state of development in which the earliest stages of the medusæ present themselves, have been regarded by their describers as instances of direct development from the egg, though there is no positive evidence of such an origin; and, lastly, there is the instance afforded by *Trachynema*, the ciliated condition of whose youngest discovered stage has led Gegenbaur to consider it also as a case of

[1] 'Zeit. für wissensch. Zool.,' 1853, vol. iv, p. 327.

[2] Ibid.

direct development, though, as we have already seen, the analogy of the *Dicoryne* gonophore is sufficient to show that no conclusion of the kind can be based on such a character.

Though the cases thus adduced afford no absolute proof of the direct development of the medusa from the egg, some recent observations leave us no longer in doubt as to the reality of this phenomenon. The observations alluded to have just been made by M. Mecznikoff of St. Petersburgh, who has traced the development of a *Cunina* as well as that of a *Geryonia* continuously from the egg. In the case of the *Cunina*, a ciliated planula is immediately developed from the egg, and the planula becomes gradually changed—in a way very similar to that already described by M'Crady—into the form of the medusa. In the *Geryonia* there is no ciliated planula, and the medusa form is here attained immediately by the development of the ovum.[1]

Besides these cases of undoubted development from the egg without the intervention of a hydriform trophosome, both of which occur in a group of medusæ of peculiar and exceptional conformation, an instance has been published in which, if the appearances be correctly interpreted, we have in the hydroid medusa of the ordinary type a case of direct development from the ovum. For our knowledge of it we are indebted to Claparède,[2] who obtained on the west coast of Scotland a species of *Lizzia* whose manubrium is described by him as loaded with eggs, some in an early stage, with the germinal vesicle and germinal spot still visible, while others appeared to contain an embryo in various stages of development. Similar ova, with the contained embryo, are stated to have been found floating free in the sea.

Claparède informs us that the embryo, while still confined within the vitellary membrane, presented all the features of a young medusa: from the centre of the bell-shaped umbrella there depended a thick-walled manubrium, whose cavity extended itself into four radiating gastrovascular canals, which ran in the substance of the umbrella, and opened at the margin into a circular canal, while round the margin were to be seen the rudiments of eight tentacles. Claparède's observation on the development of the embryo did not extend beyond this point; it is clear, however, that but slight changes were now needed to convert it into the form of the parent *Lizzia*.

This observation of Claparède has not been confirmed, and it is quite possible that the appearances here interpreted as ova in various stages of development are in reality only buds. A very young bud might be easily mistaken for an ovum, and in a medusa, by no means remotely allied to that described by Claparède, buds occur in an exactly similar position, and might easily give rise to an erroneous interpretation of their nature. (See woodcut, fig. 36.)

[1] For a knowledge of these facts I am indebted to M. Mecznikoff, who allowed me not only to inspect his drawings, but to examine his animals in the progress of their development. M. Mecznikoff's observations necessitate some modification of a statement made in an earlier part of the present work (see p. 23), and already printed before they came to my knowledge.

[2] 'Zeit. für wissen. Zool.,' 1861, p. 401.

4. *Relation between zooidal and embryonal multiplication in the* HYDROIDA; *Polymerism and Heteromorphism; Genetic succession of zooids.*

Having now examined the various modes, whether zooidal or embryonal, by which multiplication is effected in the HYDROIDA, it remains for us to see how the two forms of reproduction are related to one another, and how they are associated in the complex phenomenon which constitutes the life of the hydroid.

From all the facts which the study of the HYDROIDA has made apparent, we may regard it as certain that however long zooidal multiplication may continue, this is not sufficient for the perpetuation of the species, but that a period must at last come in the life of the hydroid when, by an act of true sexual reproduction, new individuals are produced for the indefinite extension of the species through time.

These facts find their expression in a remarkable law originally propounded by Chamisso, when he made his memorable discovery of the true genetic relation between the solitary *Salpæ* and the associated chain-like colonies of these animals; though it was reserved for Steenstrup, by correlating with Chamisso's discovery, not only the genetic phenomenon of the Hydroida, but also various analogous phenomena observed in other members of the animal kingdom, to give a wider comprehensiveness and a more definite enunciation to the law henceforth known as the law of "alternation of generations," an expression originally employed by Chamisso himself when describing the genetic phenomena of Salpa. It is true that Steenstrup's mode of stating his law of alternation of generations was destined to undergo some modification, but it has, nevertheless, received in all essential points abundant confirmation, and will explain, in a way which it alone can do, a host of phenomena which would otherwise have appeared isolated and exceptional.[1]

The law of alternation of generations manifests itself wherever it prevails, in the fact that every act of embryonal development is followed by one or more acts of zooidal development, which invariably conduct us to an ovum in which embryonal development, followed by zooidal development, again occurs, and the entire series becomes thus repeated.

Now, the various series expressing this alternation of sexual with non-sexual development exhibit among the HYDROIDA different degrees of complication, which will be more easily understood if we attempt to present them in the somewhat technical shape of formulæ.

Let t be the trophosome, and g the gonosome then—

$$\text{I.}\quad \underbrace{t+g} \times \underbrace{t+g} \times \underbrace{t+g} \times \quad . \quad\quad . \quad . \quad \&c.$$

will be the general expression for the genetic succession in the life of the hydroid, the sign $+$, indicating succession by zooidal development, and $\times$ by embryonal.

[1] The true significance of the facts on which the law of Alternation of Generations is founded, was for the first time clearly pointed out by Dr. Carpenter. See 'Brit. and For. Med.-Chir. Rev.,' vol. i, Jan., 1848, p. 183, &c.

It is very seldom, however, that the trophosome consists of only a single zooid. Such rare instances are presented by *Corymorpha*, and by certain allied forms whose trophosomes never become developed into a colony of mutually dependent hydranths, and I believe it better to regard the hydrorhizal fibres here as elsewhere in the light of mere extensions of the hydrorhizal base rather than in that of proper zooids—a view supported by their mode of development in the primordial hydranth. In almost every other case, on the contrary, the hydranths composing the trophosomes become greatly multiplied by budding; and in this respect *Hydra* affords no exception, though here the trophosome, by the subsequent detachment of the buds, may become restored to its original condition of a simple hydranth.

Still less tendency is there in the gonosome to present an absolutely simple condition. Indeed, the gonosome is perhaps never limited in its normal state to a single zooid, and we frequently find hundreds and even thousands of zooids entering into the composition of this portion of the hydroid colony.

But the zooids of which the colony is thus composed, whether in its trophosome or its gonosome, may not only be numerous, but may also *vary in form*. Those, indeed, which constitute the trophosome are always of a different form from those of the gonosome. In the trophosome it is rare to find any other form of zooid than that of the proper hydranth. In *Hydractinia*, however, there is associated with the ordinary hydranths the peculiarly modified ones, whose spiral form confers upon the trophosome of this genus so striking a feature; while the nematophores of the *Plumularidæ* can scarcely be regarded otherwise than as special zooids, whose morphological differentiation from the other zooids of the colony is carried to an extreme.

While the type of *heteromorphism* or variety of form among the zooids is fixed for every species, the *polymerism* or simple multiplication of the component zooids is indefinite, and varies with the age, perfection of nutrition, &c., of the individual.

If we specialise the general expression already given (I), so as to make it directly applicable to particular cases of heteromorphic succession in the life of the hydroid, we shall obtain the following formulæ, where *h* is used for hydranth, *bls* for blastostyle, *blch* for blastocheme, *gph* for gonophore :

II. BINARY. $$\underbrace{h + gph} \times \underbrace{h + gph} \times \quad . \; . \; . \; . \; . \; . \; . \; . \quad \&c. \quad \textit{Corymorpha.}$$

III. TERNARY. $$\underbrace{h + bls + gph} \times \underbrace{h + bls + gph} \times \quad . \; . \; . \; . \; . \; . \quad \&c. \quad \textit{Dicoryne.}$$

IV. QUATERNARY. $$\underbrace{h + bls + blch + gph} \times \underbrace{h + bls + blch + gph} \times \quad . \; . \quad \&c. \quad \textit{Campanularia}$$

These formulæ present three types of heteromorphism. In II the heteromorphism is binary (woodcut, fig. 40), in III ternary (woodcut, fig. 41), in IV quaternary (woodcut, fig. 42).

But the hydranth may and does in almost every instance—either directly or through the medium of the common basis or hydrophyton—repeat itself indefinitely by budding before the

FIG. 40.

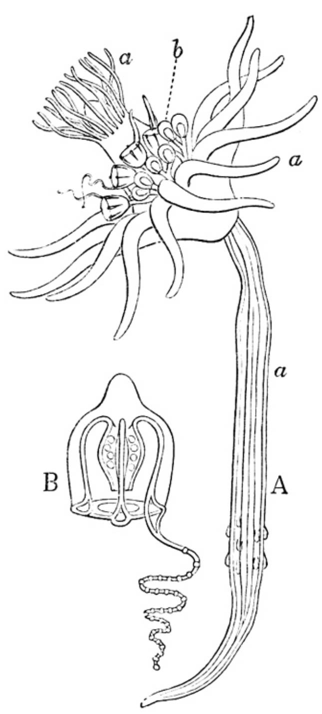


Diagram of *Corymorpha*.

A. An entire colony, consisting of two forms of zooids. *a a a*, the trophosome, consisting of a single hydranthal zooid; *b*, the gonosome, composed of many medusiform zooids.

B. A single zooid of the gonosome after having become free and attained to sexual maturity.

FIG. 41.

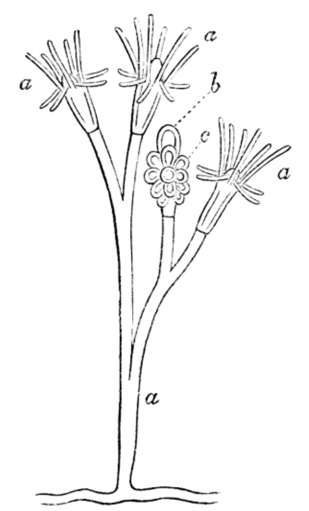


Diagram of *Dicoryne*. Colony composed of three forms of zooids.

a a a a. The trophosome, composed of numerous hydranthal zooids; *b c*, the gonosome, composed of two forms of zooids, namely, *b*, blastostyle, and, *c*, gonophores.

FIG. 42.

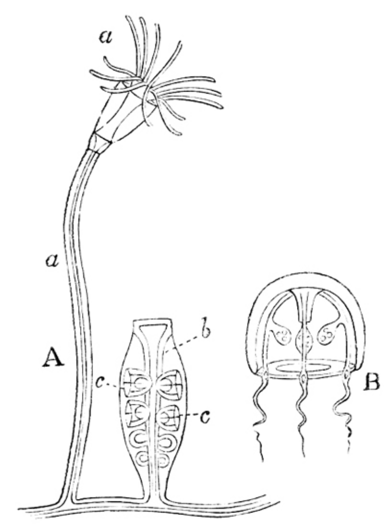


Diagram of *Campanularia*. Colony composed of four forms of zooids.

A. Portion of a colony, with trophosome and gonosome. *a a*. Trophosome, showing one of the hydranths of which it is composed ; *b c*, gonosome, composed of three forms of zooids, namely, blastostyles, blastochemes, and gonophores ; *b*, blastostyle ; *c*, *c*, blastochemes.

B. A blastocheme, which has become free and attained to maturity, showing the gonophores springing within it from the radiating canals.

time arrives when an element of the gonosome is to be budded off ; and a series of homomorphic zooids may thus introduce themselves (woodcut, fig. 41) into the heteromorphic succession, as expressed in the following formula :

$$\text{V.}\ \underbrace{h+h+h+\ \ .\ \ .\ \ \&c.+bls+gph}\times\underbrace{h+h+h+\ \ .\ \ .\ \ .\ \ \&c.+bls+gph}\times\ \ .\ \ .\ \ \&c.$$

where the hydranth becomes indefinitely repeated in the formula of ternary heteromorphism (III) given above, and the same will apply to each of the other two types of heteromorphism.

Now, in all these cases the succession from the primordial nutritive zooid to the ultimate generative zooid or gonophore admits of being expressed in a continuous line ; but one or more of the zooids of the trophosome may emit buds which will diverge from the direct line of succession, and which may then either form the starting point for another similar line of succession, or may be destitute of all power of continuing the succession of the zooids. Thus (woodcut, fig. 43) the primordial hydranth, or any of its derivative hydranths, may repeat itself by a bud which will diverge from the direct line, produce other zooids by gemmation, and thus start off a new series, as expressed in the following formula:

$$\text{VI.}\quad \underbrace{h\left\{\begin{array}{l} h+h+h+\quad .\quad .\quad .\quad \&c. + bls + gph \\ + \\ h+h+h+\quad .\quad .\quad .\quad \&c. + bls + gph \end{array}\right\}}\times h \left\{\;\right\} \times \quad .\quad .\quad \&c.$$

And this state of things may also repeat itself indefinitely, giving rise to an indefinite number of collateral series, diverging from one another and from the primary axis of succession.

FIG. 43.

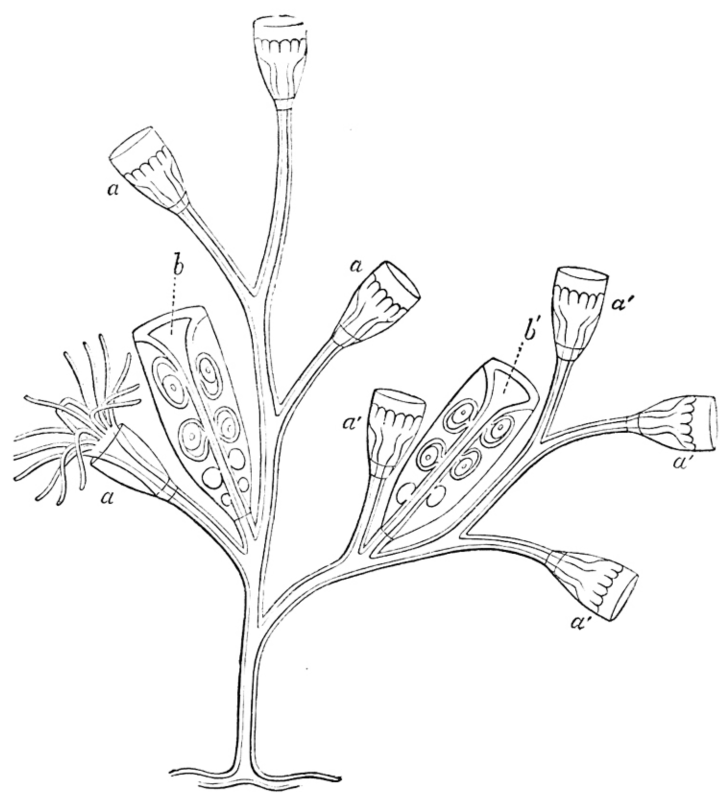


Diagram of *Laomedea*.

a, a, a, a. Hydranths belonging to the primary or direct line of succession; *a', a', a', a'*, hydranths belonging to a secondary or diverging line of succession; *b*, blastostyle of the primary line of succession, bearing gonophores and surrounded by a gonangium; *b'*, blastostyle, with gonophores and gonangium of the diverging line.

As already said, however, the diverging zooid may have no power of continuing the succession. Thus, the spiral hydranth of *Hydractinia* is not intercalated in the direct succession of zooids. It is a diverging zooid, like that which starts off the collateral series in Formula VI, but one which never gives rise to buds, and is therefore incapable of either continuing or originating a new succession.[1]

The following formula, where h' is the spiral hydranth, will express the place and power of this zooid in *Hydractinia:*

$$\text{VII.}\quad \underbrace{h\begin{cases}+\,bls+gph\\+\,h'\end{cases}}\times\underbrace{h\begin{cases}+\,bls+gph\\+\,h'\end{cases}}\times\quad.\quad.\quad.\quad.\quad.\quad\&c.$$

The case expressed in Formula VI is the simple one where only the last hydranth in the succession of buds composing a period is supposed to give origin to a bud of the gonosome. But any other hydranth in the succession may just as well bud off a member of the gonosome, which may thus form a collateral gonosomal axis. This, which is by far the most usual case, is what is actually represented in the diagrams (see figs. 41, 42, 43). The axis, however, thus formed will be necessarily definite, and will contrast in this respect with the indefinitely extended axis of the trophosome, while it will differ from the diverging bud, h' in VII, by the fact of its having the power of repeating the colony by sexual reproduction, while h' has no power of reproduction either sexual or non-sexual.

This condition may be expressed by the following formula, in which not only the last hydranth of the period gives off a bud of the gonosome, but the primordial hydranth itself emits a collateral gonosomal axis:

$$\text{VIII.}\quad \underbrace{h\begin{cases}+\,h+h+h+\quad.\quad.\quad\&c.\;+\,bls+gph\\+\,bls+gph\end{cases}\!\!\Bigg\}}\times h\,\Big\{\;\Big\}\times\quad.\quad.\quad\&c.$$

Besides the particular cases now given certain other modifications of the plan of gemmation will at once occur to any one who has made the Hydroida a subject of study. Those here adduced, however, will serve to convey a sufficiently adequate idea of the more important features in hydroid gemmation. It is thus, by the combination of heteromorphic and homomorphic multiplication, and of direct and diverging series indefinitely repeated, that the animal attains to the condition of those wonderful complex colonies which impress themselves so strongly on the mind of the observer.

So also the gonosome may present, not only a heteromorphic, but a homomorphic multiplication of zooids. In no case, however, so far as I am aware, does any zooid of the gonosome repeat itself by homomorphic gemmation, except in some comparatively rare instances of budding in the Medusa; for though the homomorphic repetition of zooids may be in the gonosome, as in the trophosome, carried to a great extent, it is almost always the result of budding from a zooid of a different form. Thus, the blastostyle never emits buds destined to repeat its own form, and this form, however frequently repeated in the gonosome, is always budded off from the hydranthal element in the trophosome, its own buds, however numerous, being always heteromorphic with itself.

It is a universal law in the succession of zooids that no retogression ever takes place in the series. In other words, no bud ever becomes developed into a zooid which is of a different

[1] The bifurcation occasionally observed in the spiral hydranth of *Hydractinia* is evidently abnormal, and cannot be regarded as contradicting the above statement.

form from the budder, and has, at the same time, preceded it in the line of succession. Thus, true hydranths are never emitted either by blastostyle, blastocheme, or gonophore; and to this law the peculiar gemminate hydriform bodies which are found on the summit of the female blastostyle in certain species of *Halecium* form no exception; for though closely resembling true hydranths, they appear to have a different signification, contributing rather to the generative functions of the hydroid, while they have no power of continuing the succession either in a direct or collateral line like the proper hydranths of the trophosome.

Now, a glance at any of the formulæ given above renders it evident—1. That between every two acts of true generation there are interposed one or more acts of non-sexual multiplication. 2. That the heteromorphic elements in each recurring period of the succession are invariably connected with one another by a non-sexual and not by a sexual genesis. 3. That the type of heteromorphism exactly repeats itself after each true generative act.

A still further fact, however, is apparent in all the cases here adduced, namely, that a certain number of zooids, incapable of attaining to sexual maturity, and hence becoming multiplied only by zooidal reproduction, occur in every succession. To the universality, however, of this principle, Haeckel regards the case of the *Geryonidæ* already referred to (p. 82), as affording an exception. He has found Geryonidan medusæ swimming freely in the open sea, in such an early stage of their development, that he believed them to have been produced by the direct development of an ovum, and yet these medusæ have been traced by him into a condition which he regards as that of sexual maturity, in which state they not only produce generative elements, but give origin, by heteromorphic budding within the stomach, to Æginidan medusæ (*Cuninæ*), these *Cunina*-buds also attaining to a condition of sexual maturity.

These facts are regarded by Haeckel as presenting an entirely new type of genesis—a type totally different in its fundamental principles from the phenomena hitherto included under the head of "Alternation of Generations;" and, believing a new term to be needed for it, he proposes to distinguish it by the designation of "Alleogenesis." It is worth while to inquire how far Haeckel is borne out in this mode of viewing the phenomena of Geryonidan development.

Admitting that Haeckel is right in regarding his Geryonidan as developed directly from the egg without the intervention of a non-sexual trophosome, I am by no means prepared, as I have elsewhere[1] stated, to take for granted the proper sexuality of this medusa. On the contrary, I am still disposed to consider the sexual pouches of the radiating canals as truly zooidal developments corresponding, notwithstanding their flattened leaf-like form, to the more prominent pouches developed on the radiating canals of such forms as *Obelia;* so that, in accordance with this view, the Geryonidan medusa would be a true blastocheme. If this be so, then the non-sexual character of the Geryonidan must be admitted, and a non-sexual element will thus become intercalated in the series, even though the hypothesis of a non-sexual hydriform trophosome be given up. Haeckel, it is true, referring to my view of the zooidal nature of the sexual pouches of *Geryonia*, argues against it, and states his conviction, from personal examination of these pouches, that they are simple lateral dilatations of the canal, with the generative products developed out of the epithelium of their walls.[2]

[1] 'Ann. and Mag. of Nat. Hist.,' 1865.

[2] Haeckel, 'Die Familie der Rüsselquallen, Vorwort,' vii.

Against the direct testimony of so able and conscientious an observer as Haeckel, I should not consider myself justified in insisting on a hypothesis which I have had no opportunity of verifying by direct examination; but yet I can scarcely avoid seeing that Haeckel's description of the structure of these pouches is in some points favorable, rather than contradictory, to my view; thus the currents of nutritive fluid which he has observed flowing in ramified channels through the mass of the ova appear to me to be explicable only on the admission that these currents are contained within a ramified spadix, for the supposition that the generative elements are directly bathed in the fluid of the gastro-vascular canals is so completely at variance with the analogy of these parts in all the other HYDROIDA, that we can scarcely bring ourselves, without very strong evidence, to accept it. If we admit the presence of a true spadix penetrating the pouch, and surrounded by the ova or spermatozoa, we have all the parts needed to establish a detailed homology between the leaf-like pouches of *Geryonia* and the prominent sacs of *Obelia*, and these last are, without any doubt, true zooids, strictly homologous with the sporosacs of *Clava*.

It is more difficult to recognise a zooidal origin in the generative pouches of the *Cunina* which Haeckel has shown to be produced as a bud from the *Geryonia*, and there seems no reason why we should not, with Haeckel, regard the *Cuninæ* as truly sexual medusæ. What may be the subsequent history of these *Cuninæ*, is as yet entirely unknown; and until this shall have been determined, the significance of Haeckel's beautiful discovery of the relation between the Geryonidans and Æginidans must remain but partially recognised.

In the genetic phenomena of the Hydroida, so far as these have been accurately determined, one fact stands out in prominent relief, and its recognition is of great importance in enabling us to perceive the true import of these phenomena, and the mode in which they are associated in the life of the hydroid. I again refer to the fact that in every hydroid the groups included between every two acts of embryonal development (the groups connected by horizontal brackets in the above formulæ) are exactly similar in the nature and succession of their heteromorphic elements, —in other words that the life series of the hydroid may be represented by definite groups of zooids exactly repeated after each generative act.[1] It is plain, too, that each of these groups —which we may conveniently designate as the "periods" of the series—exactly corresponds to the "individual" which constitutes the proper logical element of the *species* in animals which do not present the phenomenon of alternation, the period here repeating itself by true generation, and this repetition continuing itself indefinitely like a circulating decimal, so as to represent the indefinitely extended life of the *species*, while the life of the *individual* is expressed by each period singly. It is further evident that the conception of the individual involved in the above view is in no respect invalidated by the fact that one or more of its zooidal elements may become free, and enjoy an independent existence.

For the views of Hydroid individuality, embodied in the above paragraph, we are indebted to Prof. Huxley, who first assigned to our conception of the biological individual its proper limits when he defined it as "the total result of the development of a single ovum" — a most important determination by which alone the genetic phenomena of the *Hydroida* can be properly understood and brought into comparison with those of the higher animals. At the same

[1] The mere *number* of zooids in two or more of these groups may of course vary, depending as this does on the accident of abundant or deficient nutrition and the like.

time it must be borne in mind that it is "the individual" in the somewhat technical sense of the component of a *biological species* which is to be here understood, and that individuality, in its more ordinary acceptation, cannot be excluded from our conception of the life-series of a hydroid. In this sense every zooid has an individuality of its own—an individuality, however, of a very different kind from that which characterises the successively repeated *groups* of zooids constituting the individuals which logically make up the biological species.

The hydranth normally continues the axis in the hydroid colony, just as the leaf-bud in the plant continues the vegetable axis; the gonophore, on the other hand, has no power of continuing the axis, and constitutes the terminal zooid in each "period" of the series, just as the flower-bud stops the elongation of the axis in the plant. This analogy, however, must not be pushed too far, for while the hydranths and gonophores are simple zooids, the leaf-buds and flower-buds are complex associations of the corresponding element of individuality in the plant.

The normal order of succession of the buds in the trophosome is from the proximal to the distal end of the hydrosoma, so that the older buds are met with towards the base or hydrorhizal end of the main stem and branches, the younger ones towards the summit. In the gonosome, on the other hand, the order of succession is sometimes towards the distal, sometimes towards the proximal end of the axis. In the calyptoblastic genera the order of succession of the sporosacs or blastochemes is invariably from the distal towards the proximal extremity of the blastostyle, on which, in these genera, they are always borne. When a blastostyle is present in the gymnoblastic genera, the gonophores succeed one another, sometimes (*Hydractinia echinata*) from the proximal towards the distal end of the blastostyle, sometimes (*Dicoryne conferta*) from the distal towards the proximal. In *Tubularia* their succession is from the distal towards the proximal end of the common peduncle, which is more or less developed in the various species of this genus, and the same order of succession occurs in *Corymorpha*.

Where no special gonosomal axis is developed the succession is usually from the proximal to the distal extremity of the branch (*Bougainvillia, Perigonimus*), thus corresponding to that of the zooids of the trophosome. Sometimes, however (*Syncoryne, Gemmaria*), it is from the distal to the proximal.

We have thus, then, in the gonosome of the Hydroida, as in the inflorescence of plants, both a centripetal and a centrifugal order of succession. It is possible, however, that irregularities may occur, and that a new bud may be abnormally emitted at the distal side of a centrifugal series, or at the proximal side of a centripetal one, so as to disturb in individual cases the normal sequence of the zooids.

Some further points admitting of comparison with the inflorescence of plants may be noticed in the gonosome of such hydroids as possess a special gonosomal axis. In *Tubularia indivisa* (Pl. XX, fig. 2, 3), and in the male colonies of *Tubularia larynx* (Pl. XXI, fig. 1) the gonophores are—like the flowers of a raceme—carried on short pedicels along the sides of a long common peduncle which springs from the body of the hydranth (woodcut, fig. 44). Their order of development, however, is centrifugal, or from the distal to the proximal extremity of the peduncle, so that the whole group may be compared to a reversed raceme. In the female colonies of *Tubularia larynx* (Pl. XXI, fig. 2, and woodcut, fig. 45), and in *Corymorpha nutans* (Pl. XIX, figs. 1 and 3), the pedicels become branched, with a similar order of development which thus gives us the compound reversed raceme or cyme.

The reversed spike, or spike with a centrifugal development, shows itself in such forms as *Dicoryne conferta* (Pl. VIII, fig. 1, and woodcut, fig. 41); while in *Laomedea* (woodcuts, figs. 18 and 43), *Obelia*, woodcut, fig. 19), and other calyptoblastic forms, we have a reversed spike

Fig. 44.

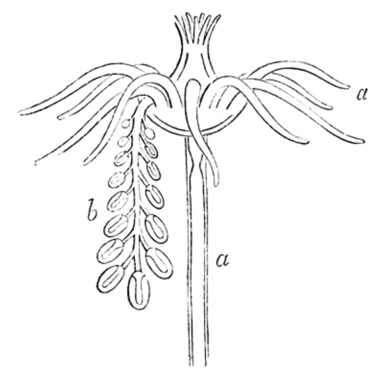


Diagram of *Tubularia indivisa*.

a, a. Hydranth with its stalk; *b*, shortly stalked gonophores, borne on a common peduncle, and increasing in maturity from the proximal to the distal extremity of the peduncle.

Fig. 45.

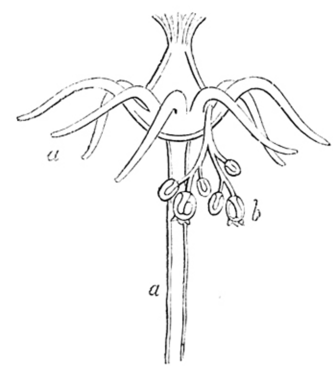


Diagram of *Tubularia larynx*—female.

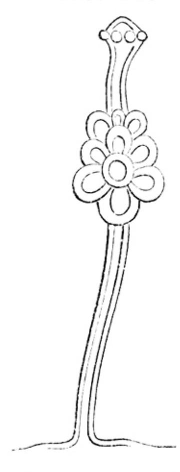
a, a. A hydranth with its stalk; *b*, gonophores, attached by short stalks to a common branched peduncle, and increasing in maturity from the proximal to the distal extremities of the branches.

surrounded by the gonangial sheath, and, were it not for its centrifugal development, strongly recalling the spadix with its spathe in the inflorescence of an araceous plant.

In certain proliferous medusæ (woodcuts, figs. 36 and 37) the buds are borne on the manubrium with a centripetal order of development, thus giving us, according as the buds are sessile or pedunculated, the true spike or the true raceme.

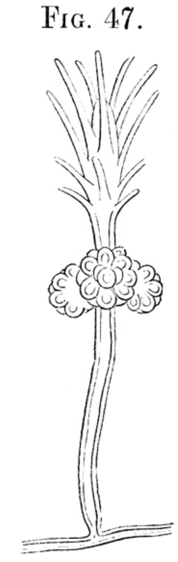
In *Eudendrium* (Pls. XIII and XIV) the male gonophores are disposed in an umbel with the axis, in some cases prolonged beyond it, while in others there is no extension of the axis beyond the depressed portion which carries the gonophores. Though we cannot here recognise any difference in the order of development among the gonophores composing the umbel, we are probably justified in assuming this order to be, as in the true umbel, a centripetal one; for in the female colonies of most species, such as *Eudendrium ramosum* (Pl. XIII, fig. 3), the gonophores are separated from distance to distance upon the stem immediately below the hydranth, and here their order of development is plainly seen to be centripetal.

Fig. 46.



Hydractinia. A blastostyle with gonophores clustering round it, and increasing in maturity from the free or distal to the attached or proximal end.

Fig. 47.



Clava. A hydranth surrounded by a verticil of globular clusters of gonophores.

In *Hydractinia echinata* (Pl. XV, figs. 1 and 3, and woodcut, fig. 46) we have the closely approximated gonophores sessile on a blastostyle, and the development centripetal, as in the true spike, while the axis extends beyond it as a naked prolongation, reminding us of the naked prolongation of the spadix in certain *Araceæ*.

In *Clava squamata* (Pl. I, figs. 1 and 3) and in *Clava multicornis* (Pl. II, fig. 1, and woodcut, fig. 47) the gonophores form dense clusters surrounding the hydranth in a sort of verticil. Each cluster consists of sessile gonophores borne on a greatly depressed common peduncle, and thus recalling the form of inflorescence known as a capitulum. The order of development, however, appears to be centrifugal, instead of being, as in the true capitulum, centripetal, and would therefore, perhaps, more truly suggest a comparison with the depressed cyme which constitutes the axillary inflorescence in many *Labiatæ*.

In the comparison just instituted between the gonosome of the HYDROIDA and the inflorescence of plants it will be noticed that, whenever in the HYDROIDA the generative buds are borne upon a special gonosomal axis like the flowers in an inflorescence, the order of succession is far more frequently a centrifugal than a centripetal one. In the calyptoblastic forms, indeed, it is always centrifugal. This is exactly the opposite of what prevails in plants, for here the centripetal forms of inflorescence greatly exceed the centrifugal ones.

We must be careful, however, not to assign to the resemblances which may be noticed more importance than they are justly entitled to. Yet, after setting aside such as are merely superficial and accidental, many still remain which have their origin in certain deep-seated properties. They may be referred to the common phenomenon of gemmation, which, by agamic multiplication in the animal as well as in the plant, gives rise to colonies whose members, in each case mutually dependent on one another, continue to be organically associated into definitely arranged and determinate groups.

V. HISTOLOGY.

Both trophosome, gonosome, and cœnosome have now been considered in their broader morphological features; their morphology, however, cannot be regarded as complete without some further anatomical details, embracing a histological examination of the tissues.

The HYDROIDA possess an exceedingly simple structure. Every hydroid, as we have already seen, is composed of two layers, an ectoderm and an endoderm. Each of these may present in itself various degrees of differentiation, and we can, perhaps, best study the minute texture of the tissues by examining them first in the ectoderm, and secondly in the endoderm.

1. *The Ectoderm.*

General structure of Ectoderm.—In many cases it is impossible to detect in the ectoderm of the mature hydroid any well-defined structure. A homogeneous blastema with granules and scattered nucleus-like corpuscles, and thread-cells more or less thickly immersed in it, are all that the microscope has as yet in such cases succeeded in demonstrating, though a cellular structure of this layer can almost always be observed in the embryo.

Sometimes, however, the ectoderm of the adult hydroid may be seen to be composed of very distinct cells, which can occasionally be isolated without difficulty under the microscope. In *Hydra viridis*, for example, the ectoderm can be broken down under the microscope into spherical cells, in which a nucleolated nucleus may occasionally be detected. These cells are provided with distinct membranous walls, within which is contained a homogeneous vacuolated protoplasm, in which are often immersed secondary nucleated cells, and also in many of them one or more thread-cells.

In some cases in which it is not easy to detect definite structure in the normal state of the ectoderm, this membrane, by a natural hystolytic decomposition after death, will become broken up into very distinct cells (Pl. I, fig. 4).

Palpocils.—Leydig[1] has called attention to the occurrence in *Hydra* of a minute bristle-like projection of the surface over the site of each thread-cell, without having any immediate connection with the thread-cell itself, and Dujardin[2] had already noticed and correctly described similar bodies as existing on the surface of the capitula which terminate the tentacles in his *Stauridium*. Dujardin further compares them to the processes which are emitted by an *Actinophrys* or an *Acineta*. These bodies, however, had been previously noticed by Corda,[3] where they lie over the smaller kind of thread-cell which occurs in the tentacles of *Hydra;* but he erroneously describes them as direct prolongations from the thread-cell, so as to constitute with it a special organ, which he calls an "organ of touch." They have also been examined by Dr. T. S. Wright,[4] who follows Dujardin and Leydig in showing that they are not directly continuous with the thread-cell, and who also maintains their very simple protoplasmic nature. He proposes for them the name of "palpocils." I can entirely confirm the views of Dujardin, Leydig, and Wright with regard to those bodies which I have examined in various hydroids (Pl. IV, fig. 4).

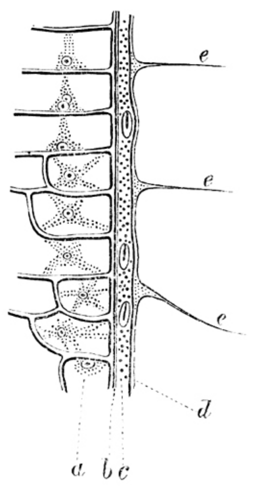
In the marine hydroids a very delicate structureless pellicle can usually be shown to exist for a greater or less extent over those parts which are not covered by the ordinary perisarc. I believe it to be either a simple excretion from the surface of the ectoderm or the result of a metamorphosis of the most superficial portions of this structure. Sometimes, however, the place of this pellicle is taken, at least on the tentacles, by an exceedingly thin layer of a transparent semifluid substance, which seems to possess the properties of sarcode (woodcut, fig. 48). The minute filaments just described as occurring over the site of the thread-cell would seem to be mere continuations of this sarcode layer, which also frequently presents here and there little conical elevations, which have no relation with the thread-cells, and whose summit is continued into a filament of extreme tenuity (woodcut, fig. 48 *e, e, e*). These filaments were first pointed out by Wright, who includes them along with the organs of Corda under the common name of "palpocils."

Leydig is of opinion that there exists over the whole surface of *Hydra*, except the surface of attachment of the foot-disc, a very thin homogeneous cuticle. I am inclined to believe that what Leydig names cuticle is really the sarcode layer, which here, as in the marine hydroids, is continued into the palpocils.

[1] Müller's 'Archiv,' 1854.
[2] 'Ann. des Sci. Nat.,' 1843, p. 370.
[3] Ibid., 2me série, 1837, p. 363.
[4] 'Proc. Roy. Phys. Soc. Edinb.,' vol. i, p. 341.

Fibrillated tissue.—In a great many cases there is developed upon the inner surface of the ectoderm a peculiar tissue, forming an abrupt boundary between the ectoderm and endoderm. It may be well seen in those elongated hydranths which present an extensive surface uncovered by the more or less opaque chitinous perisarc, such as *Clava, Hydractinia,* and *Clavatella,* and in the very contractile body and tentacles of the hydranths of different *Corynidæ,* and in the stem and hydranth of *Corymorpha.* In all these cases it presents the appearance of fine, close, longitudinal and parallel striæ between the ectoderm and endoderm. From the body of the hydranth these striæ usually extend into the tentacles, and may be very distinctly seen in the tentacles of *Coryne pusilla,* where they can be easily traced as far as the terminal capitulum.

FIG. 48.



Part of a tentacle of *Syncoryne pulchella,* showing the superficial protoplasmic layer.

a, Large-celled tissue of endoderm, forming the axis of the tentacle, the cells containing nucleated, and often radiating, masses of protoplasm; *b,* fibrillated layer; *c,* ectoderm, with immersed thread-cells; *d,* superficial layer of protoplasm, which has become extended here and there into *e, e, e,* filaments of extreme tenuity.

I have succeeded in isolating the fibrillated tissue of the large tentacles in specimens of *Tubularia indivisa,* which had been kept some years in spirits. The fibrillated tissue here (Pl. XXIII, fig. 5) consists of two layers, one composed of fibres which take a longitudinal course parallel to the axis of the tentacle, and the other of fibres which take a circular course transverse to the axis. The circular fibres seem to lie externally to the longitudinal, and both form a muscular envelope which is intimately connected with the ectoderm of the tentacle, and comes away with the latter when this is separated from the endoderm.[1]

The fibres thus isolated appear to be tubular, having a diameter of about $\frac{1}{5000}$ of an inch; they are perfectly smooth, but in most cases a very distinct oval nucleus, having a greater diameter of about $\frac{1}{2500}$ of an inch, and with a brilliant nucleolus, may be demonstrated in them. They may sometimes be seen to taper away at each end to a point, when they present the appearance of greatly elongated fusiform cells (fig. 6).

That the fibres thus demonstrated in the Hydroida constitute a true contractile tissue would follow, not only from the analogy suggested by structure, but from the fact of contractility manifesting itself with great intensity in those parts where they are best developed.[2]

[1] In some cases the fibrillated tissue would seem to be more intimately united to the endoderm than to the ectoderm. I have found, at least, that in specimens of *Clava squamata,* which had been preserved in spirits, the ectoderm could be detached, leaving the fibrillated layer still adherent to the endoderm.

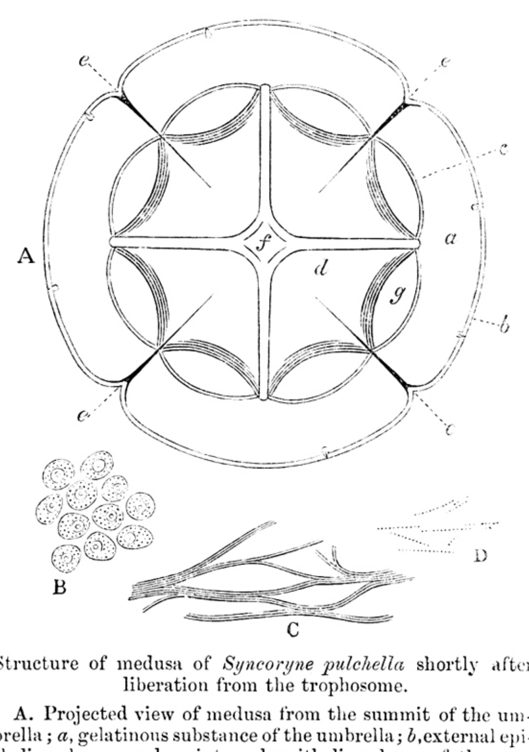
[2] Reichert ("Ueber die contractile Substanz und den feineren Bau der Campanularien," &c., 'Monatsbericht der Akad. der Wissens. zu Berlin,' July, 1866, p. 504) denies the existence of the contractile fibrillated layer whose presence is here insisted on, and maintains that its place is taken by a structureless membrane, to which he gives the name of supporting lamella ("Stützlamelle"), and which he regards as a sort of internal skeleton secreted from the inner side of the ectoderm. He believes that the whole contractility of the hydroid resides in the ectoderm itself, which he says is entirely destitute of cells or cell-constituents. My own observations will not allow me to adopt the views of Reichert.

The fibrillated tissue is largely developed in the umbrella of the medusa, where the fibres are arranged circularly, and where, instead of lying between the ectoderm and endoderm, they are situated on the concave surface of the umbrella, as well as in the membranous velum, of which they constitute nearly the entire substance. We shall examine this tissue in connection with the other structures which enter into the umbrella of the medusa.

Umbrella of medusa.—A remarkable and important modification of the ectoderm is seen in the umbrella of the medusa, where it forms nearly its entire mass, the ectoderm becoming almost wholly changed into a perfectly transparent, elastic, gelatinous-looking substance, traversed by the gastro-vascular canals, which are lined by endoderm.

The following observations on the structure of the umbrella have been chiefly made on the medusa of *Syncoryne pulchella* shortly after its liberation from the trophosome. In this medusa (Pl. VI, fig. 3, and woodcut, fig. 49) the convex surface of the umbrella is covered by a distinct epithelial layer (woodcut, fig. 49 A, *b*) formed of cells (B), containing a nucleolated nucleus, and separated from one another by narrow tracts of homogeneous intercellular substance. These cells appear to consist of simple masses of protoplasm, without distinctly differentiated walls. Under the action of acetic acid they undergo changes of form, becoming elongated oval or fusiform or conical, or even extended into irregular processes, while the protoplasm assumes a more distinctly granular appearance, and the nucleus, with its nucleolus, frequently becomes more evident. Immediately beneath the epithelial layer the proper gelatinous substance (A, *a*) of the umbrella begins. It is transparent, colourless, and elastic, and apparently of the consistence of soft jelly. I have in vain sought for anything like definite structure in it, though Haeckel[1] has shown that in the *Geryonidæ* the homogeneous gelatinous substance of the umbrella is traversed by numerous fine branching fibres in a direction chiefly perpendicular to the surfaces, while the researches of Max Schultze[2] have proved that in the *Discophora* or steganophthalmic medusæ the corresponding part consists of widely separated cells, which send out prolongations from their walls to meet similar prolongations from the neighbouring cells, and with a voluminous intercellular substance, which is composed of a semifluid matter in the meshes of a loose, elastic, fibrous

FIG. 49.



Structure of medusa of *Syncoryne pulchella* shortly after liberation from the trophosome.

A. Projected view of medusa from the summit of the umbrella; *a*, gelatinous substance of the umbrella; *b*, external epithelium-layer, and *c*, internal epithelium-layer of the umbrella; *d*, subumbrellar muscular sac united to the umbrella along the lines of the four radiating canals and along four intermediate lines corresponding to the four meridional furrows *e*, *e*, *e*, *e*, observable on the outer surface of the umbrella; *f*, summit of manubrium.

B. Cells composing the external epithelium of the umbrella.

C. Fibrillated tissue of the subumbrellar muscular sac.

D. Fibrillæ of the muscular sac treated with acetic acid, and viewed under a high power.

[1] Op. cit., p. 166.

[2] Schultze, "Ueber den Bau der Gallertscheibe der Medusen," Müller's 'Arch.,' 1856.

network. Schultze has recognised the close resemblance between this structure and that of certain forms of the so-called connective tissue.

Though I have failed in my attempts to detect structure in the gelatinous portion of the umbrella of those hydroid medusæ which I have examined, I do not desire on that account to insist on its absence. The comparatively small size and soft consistence of most of the hydroid medusæ, and the consequent extreme difficulty of obtaining thin slices fitted for microscopical observation, and freed from the confusing presence of the epithelium and fibrillated layers, throw much greater obstacles in the way of a satisfactory examination of the umbrella of the ordinary hydroid medusæ than what we meet with in the larger and more easily manipulated umbrella of the *Geryonidæ* and *Steganophthalmata*.

Lying immediately on the concave surface of the gelatinous substance of the umbrella, an inner epithelial layer (A, *c*) may under circumstances favorable for observation be demonstrated. It consists of a single layer of cells, and corresponds to the epithelium of the convex surface, but is much more difficult to detect.

The concavity of the umbrella is lined by a sac (A, *d*) which lies immediately upon the inner epithelium layer, and consists of a distinctly fibrillated membrane. The fibres composing it take, when at rest, a circular course parallel to the margin of the umbrella, and are usually in close contact with one another, though occasionally they become separated at intervals, so as to leave numerous fusiform spaces between them (C). They are very fine, measuring about the $\frac{1}{10000}$ of an inch in diameter, and under a high power of the microscope each fibril appears resolved into a single series of corpuscles, a structure which under the action of acetic acid becomes distinct (D). At the margin of the umbrella the fibrillated layer leaves the gelatinous bell and is inflected inwards over the codonostome, so as to constitute the perforated diaphragm or velum.

The fibrillæ of the umbrella and velum, which are thus much more minute than those which have been described in the trophosome, present a marked resemblance to the ultimate fibrillæ of striated muscle; but, instead of being united into fibres, they are spread out into a broad membrane.[1] That the fibrillated layer forms a true contractile tissue, conferring on the medusa those active natatory powers which constitute one of its most striking characters, there cannot be any doubt.

[1] Busk, in a paper full of excellent observations on the structure of some hydroid medusæ ('Trans. Mic. Soc. Lond.,' vol. iii, p. 14), describes the muscular fibres in the umbrella of *Turris neglecta* and in that of a *Thaumantias*-like medusa as "distinctly marked with transverse striæ."

In the swimming-bells of the Siphonophora the fibrillated tissue is very well developed. In a small species of *Diphya*, captured abundantly on the Irish coast, it was easy in very fresh specimens to get a good view of the contractile fibres which are largely developed in the swimming-bell of this Siphonophore. Besides the circular fibres, a longitudinal set seems also to be present. The circular fibres are flattened, and marked with close transverse striæ, which are rendered particularly evident by the application of acetic acid, which also brings out in the walls of the fibre distinct but distant nuclei with contained nucleoli.

According to Haeckel, the fibrillated layers of the umbrella and velum of the *Geryonidæ*, as well as that which invests the stiff tentacles which always exist in the young state of these medusæ, consist of very distinctly striated fibres, while smooth muscle-fibres occur in the walls of the manubrium. He also refers certain fibres and nucleated fusiform cells, which he has detected in the extensile marginal tentacles of these medusæ, to the group of smooth muscle-fibre.

The muscular sac which thus lines the umbrella in *Syncoryne pulchella* is not uniformly adherent to it, and receives its chief attachment along eight meridional lines. Four of these correspond to the direction of the four radiating canals, and the remaining four are so distributed that one lies exactly midway between every two radiating canals.

In medusæ, such especially as have been kept alive for some time in our jars, the muscular sac may be occasionally seen to be separated by a considerable interval from the rest of the umbrella in all the spaces which intervene between the eight meridional lines of attachment, though it still continues closely adherent to these lines (woodcut, fig. 49 A). A few delicate bands may here and there be seen, near the summit of the umbrella, stretching transversely across the spaces between the umbrella and the detached portions of the sac.

It is in this condition that the inner epithelium layer becomes apparent. I have failed to see it as long as the muscle-sac is uniformly in contact with the rest of the umbrella.

An inner epithelium layer has been shown by Haeckel to exist in the *Geryonidæ*. There, however, he describes it as lying on the concave surface of the muscular layer.

In the medusa of *Obelia geniculata* shortly after liberation, the inner epithelium is very distinct, but I have failed in satisfying myself of the existence of a distinct muscular layer in the almost disc-shaped umbrella of this medusa, which, moreover, presents the very exceptional condition of being entirely destitute of a velum. On the other hand, a distinctly fibrillated layer may be seen in the marginal tentacles (woodcut, fig. 59 A *a*), which indeed would seem by their fin-like action to be far more efficient than the umbrella in the locomotion of the medusa.

The inner epithelium consists here of distinctly nucleated cells with narrow intercellular spaces. In many of the cells the nuclei were plainly seen to be in process of division (woodcut, fig. 59 C).

The gelatinous portion of the umbrella thus lies between the two layers of epithelium, and is probably a product of one or both of these layers. In many hydroids the medusa immediately after liberation has this gelatinous portion still thin, but it often acquires great thickness as the medusa advances towards maturity—a phenomenon of which *Bougainvillia* affords a striking example (see Pl. IX).[1]

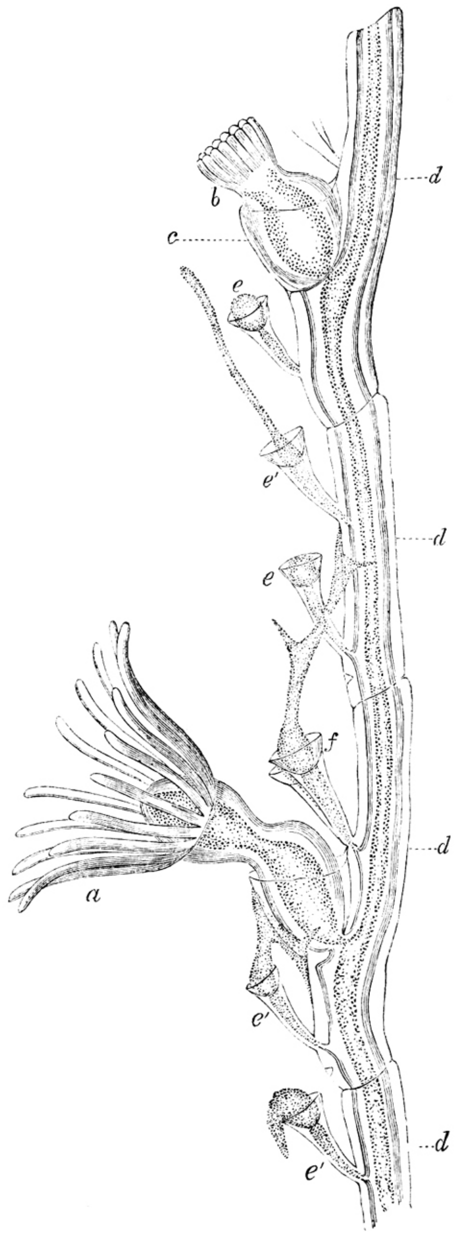
Nematophores.—The general form and relations of the nematophores have been already described (p. 28). The matter which fills the chitinous sheath of the nematophore is a clear semi-fluid substance with scattered granules, and without the slightest trace of structure, but having frequently imbedded in it a cluster of thread-cells. It differs in no respect from the sarcode matter composing the bodies of the *Rhizopoda*, and like it is capable of emitting true pseudopodia. When a specimen of *Antennularia antennina* (woodcut, fig. 50) or *Aglaophenia pluma* (woodcut, fig. 51) is examined in the zoophyte trough of the microscope shortly after removal from the sea, and before it has lost any of its original vigour, the contents of the nematophore-sheaths will be

[1] Haeckel (op. cit.) has described in the umbrella of the *Geryonidæ* certain structures which he has shown to be nearly allied to cartilage, not only in consistence, but in histological composition. This medusa-cartilage forms—1. A ring which runs in the gelatinous substance of the umbrella parallel to its margin, and below the circular canal. 2. Certain rib-like structures (mantel-spangen) which are imbedded in the outer surface of the umbrella, and extend from the margin in a meridional direction for a greater or less distance towards the summit. 3. The rod-like axis of the stiff, solid tentacles.

In all these cases the medusa-cartilage consists of rounded, nucleated, occasionally vacuolated, masses of granular protoplasm, contained in cavities of a clear homogeneous intercellular substance having a cartilaginous consistence.

seen extending themselves in the form of long processes and threads of sarcode, sometimes simple and undivided, sometimes breaking themselves up into branches, sometimes stretching themselves out as free processes into the surrounding water, and sometimes seeming to flow over the surface of the hydrosoma in simple or branching streams; and then again the whole will slowly withdraw itself into its chitinous receptacles, leaving not a trace visible of those wonderfully extensile processes and filaments of sarcode into which it had just before transformed itself. In all this the clusters of thread-cells, when they exist, remain quite stationary, being never carried out with the sarcode in its pseudopodial prolongations.[1]

FIG. 50.



Portion of a ramulus of *Antennularia antennina*, with hydranths and nematophores.

a, Hydranth extended; *b*, hydranth retracted; *c*, hydrotheca; *d, d, d, d*, consecutive segments of the ramulus; *e, e*, azygous or mesial nematophores, with their sarcode contents quiescent; *e', e', e'*, azygous nematophores, with the sarcode contents emitting pseudopodial prolongations; *f*, gemminate or lateral nematophores, with pseudopodial prolongations of the sarcode.

Thread-cells.—The most characteristic elements of the ectoderm are the thread-cells. They occur under various forms throughout the whole of the *Cœlenterata*, and though analogous bodies are occasionally found in some other invertebrate groups, they are nowhere so abundant and characteristic as in the *Cœlenterata*.[2]

The form of the thread-cell varies in different species of hydroids, and even in different parts of the same animal; but it consists essentially of a containing capsule, and a contained filament, which admits under certain conditions of being projected from the capsule (woodcut, fig. 52). The investigation of the thread-cell, with the view of obtaining a knowledge of its structure and mode of action, is one of the most difficult tasks in the anatomy of the HYDROIDA. The minute size, great transparency, and almost entire uniformity of action on the light, of all the parts of these really complex bodies, and the rapidity with which their characteristic function is performed, renders their study one which requires no ordinary patience and practice in microscopical observation, and, notwithstanding the labour which has been bestowed upon them, our knowledge of the thread-cell is by no means in all points satisfactory.

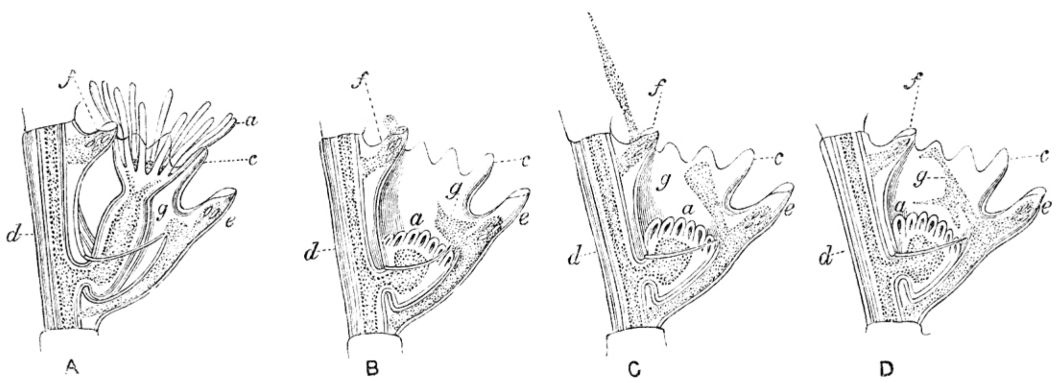
The large thread-cells which occur in the tentacles and body of *Hydra*, or in the capitula which terminate the tentacles in *Coryne*, may be taken as presenting the most usual type of these bodies among the HYDROIDA.

[1] See my "Report on the Reproductive System of the Hydroida," in 'Brit. As. Rep.' for 1863, and a paper "On the Occurrence of Amœbiform Protoplasm and the Emission of Pseudopodia in the Hydroida," 'Ann. Nat. Hist.' for March, 1864.

[2] Among the more recent authors who have studied the thread-cell in the *Cœlenterata*, refe-

If we examine one of the large thread-cells from the tentacle of *Coryne pusilla* previously to its being exposed to the conditions which result in the emission of its filament, we shall find it to consist of an external perfectly transparent oval capsule with rigid walls, and of certain remarkable contents which play an important part in the special function of the thread-cell (Pl. IV, fig. 4). The

FIG. 51.



Hydrothecæ of *Aglaophenia pluma*, with hydranths and nematophores.

A. Hydrotheca, with extended hydranth and with the sarcode contents of the nematophores quiescent. *a*, extended hydranth; *c*, serrated margin of hydrotheca; *d*, segment of the ramulus carrying the hydrotheca; *e*, mesial or azygous nematophore; *f*, lateral nematophore; *g*, lateral aperture through which the mesial nematophore communicates with the cavity of the hydrotheca.

B. Hydrotheca, with retracted hydranth and the sarcode contents of the nematophores emitting pseudopodial prolongations. *a*, retracted hydranth; *c*, margin of hydrotheca; *d*, segment of the ramulus carrying the hydrotheca; *e*, mesial nematophore, with its protoplasm projected in an irregular pseudopodial mass; *g*, through its lateral aperture into the cavity of the hydrotheca; *f*, lateral nematophore, with the commencement of a pseudopodium.

C. Same parts with pseudopodial processes more advanced. *a*, retracted hydranth; *c*, margin of hydrotheca; *d*, segment of ramulus; *e*, mesial nematophore from which a long clavate process, *g*, of protoplasm is projected into the cavity of the hydrotheca; *f*, lateral nematophore from which a long pseudopodium is projected into the surrounding water.

D. Same parts showing different states of extension of the pseudopodia. *a*, retracted hydranth; *c*, margin of hydrotheca; *d*, segment of ramulus; *e*, lateral nematophore with a branching process, *g*, of its sarcode projected into the cavity of the hydrotheca; *f*, lateral nematophore with the pseudopodium entirely withdrawn.

In all the figures a cluster of thread-cells is seen imbedded in the distal end of the protoplasm within the sheath of the nematophore.

capsule is completely closed, and its longer axis is occupied by a membranous tube somewhat wider near the centre than at either end. At one end of this tube, its walls are continuous with those of the capsule, and it is this part of the capsule which usually lies most superficially when the thread-cell is imbedded in the ectoderm; it may, for the convenience of description, be distinguished as the anterior end. The opposite end of the axile tube loses itself in a perfectly transparent mass which occupies nearly the whole of the posterior half of the cavity of the capsule, and in which I have in vain sought for anything like definite structure.

The peculiar phenomena, however, which characterise the evolution of the thread-cell, together with observations upon the structure of the thread-cell in other species, render it almost certain that the apparently homogeneous mass in which the posterior extremity of the

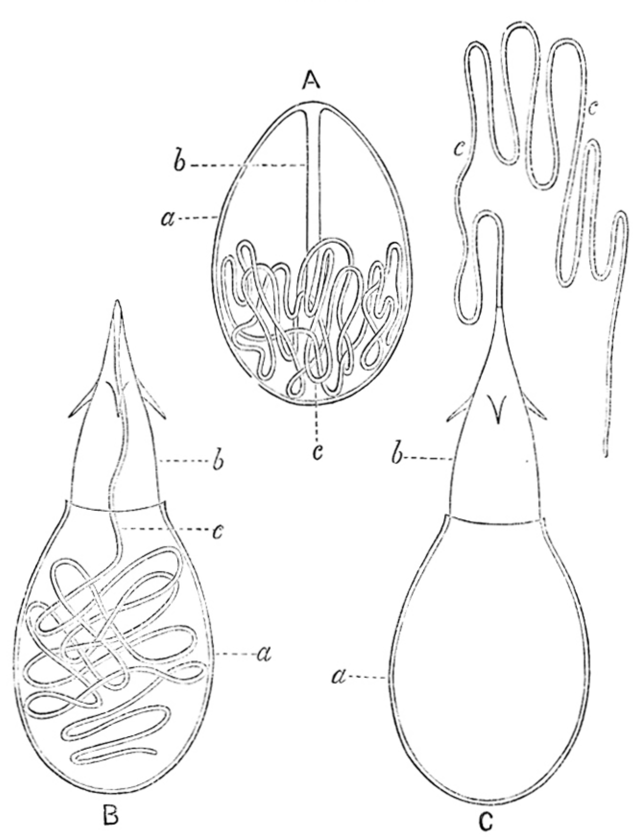
rence may be made to Leidy ("Marine Invertebrate Fauna of the Coasts of Rhode Island and New Jersey," in 'Acad. Nat. Sci. Philadelphia,' vol. iii, 1855), Gosse ('British Sea Anemones,' 1860), Clark (Agass., 'Cont. Nat. Hist. United States,' vol. iv, p. 209), and more especially to Möbius ("Ueber den Bau, den Mechanismus, und die Entwickelung der Nesselkapseln," from the 'Transactions of the Natural History Society of Hamburg,' 1866), who has given us a very full account of these bodies, which he has studied chiefly in *Caryophyllia Smithii*.

axile tube loses itself, is in reality here, as in other cases, a filament rolled upon itself, but of such extreme tenuity and transparency as to render it impossible to distinguish the individual coils.

By carefully adjusted illumination, the whole of the capsule appears to be lined by a membrane of extreme delicacy. The existence of an external capsule distinct from its lining membrane is particularly apparent in the thread-cell after the emission of its contents, for then the outer capsule is seen to terminate by a distinct slightly everted margin round the orifice through which the contents have been expelled (Pl. IV, fig. 5).

The characteristic action of the thread-cell may be brought into play under the microscope by some force artificially applied, such as the pressure of the compressorium, or the contact of alcohol or acetic acid. This action consists in a sudden change of form, the capsule opening at its anterior end, from which a very remarkable body is at the same time projected with a rapidity which renders it impossible for the eye to follow it in its progress (Pl. IV, fig. 5, and woodcut, fig. 52 B, *b*). When, however, this act is completed, the projected body may be seen to be an elongated sac whose walls are at one end continuous through the opening in the capsule with the membrane by which the latter is lined, and whose opposite end tapers away to a point. Just where this sac begins to thin away towards its point, three rigid spines are fixed in a verticil to the outer surface of its walls, their points being directed backwards like the barbs of an arrow.

FIG. 52.



Diagrammatic Views of the Thread-cell.

A. The thread-cell previous to the emission of its contents. *a*, the double wall of the capsule; *b*, reflected portion of the inner membrane of the capsule-wall, forming the axile tube of the unevolved thread-cell; *c*, the filament lying in complicated coils in the bottom of the capsule.

B. The thread-cell immediately after the first stage of evolution. *a*, the double wall of the capsule; *b*, the barbed sac formed by the eversion of the axile tube; *c*, the filament still lying within the capsule and barbed sac.

C. The thread-cell after the complete emission of the contents. *a*, the double wall of the capsule; *b*, the barbed sac; *c*, the ejected filament.

The projection of the barbed sac does not, however, constitute the whole of the phenomenon presented by the thread-cell under the influence of the force which gave origin to its evolution; for this first act is followed—in most cases instantaneously—by a second, which consists in the projection, from the pointed summit of the sac, of a filament (woodcut, fig. 52 C, *c*) of great tenuity and transparency, which rapidly shoots across the field of the microscope until it attains a length of between thirty and forty times that of the longer diameter of the original capsule; at the termination of the emission, one end of the filament always remains in connection with the free end of the barbed sac. The whole act of evolution is thus completed, and the capsule is now seen to contain nothing but an absolutely colourless homogeneous fluid.

Such are the phenomena presented by the thread-cell in the act of evolution, but the amazing rapidity with which the whole takes place renders it extremely difficult to determine in what the remarkable series of changes now described essentially consists. There can, however, be no doubt that the sudden appearance of the barbed sac is the result of a process of eversion of the membranous tube which in the original state of the thread-cell occupies its axis, and which is formed by the lining membrane of the capsule inverted into itself at its anterior end. The eversion of this tube, by which it becomes freed from the restraint of the capsule, is necessarily accompanied by its sudden expansion and development; and that this is the real nature of the phenomenon in question, receives ample confirmation from what may be witnessed in another kind of thread-cell to be presently described.

It is still more difficult to determine the nature of the act which shows itself in the emission of the filament, than of that which constitutes the emission of the barbed sac. Previously to emission, no trace of a filament can be detected in the thread-cell now under consideration; but, as already said, there can be little doubt that the transparent homogeneous-looking mass in which the posterior part of the axile tube loses itself before its eversion has commenced is nothing more than the filament closely coiled on itself (as shown diagrammatically in woodcut, fig. 52 A).

It is probable that the expulsion of the filament, like that of the barbed sac, consists also in an act of eversion; a view which would of course render it necessary to regard it, notwithstanding its extreme tenuity, as a flexible membranous tube.

It must be borne in mind, that the barbed sac and the filament are in no way continuous with the outer rigid wall of the capsule, but only with the delicate sac by which this is lined. The outer wall opens at its summit by a definite orifice which appears to have been previously closed by a minute lid which is thrown off in the act of evolution, and which may be occasionally seen after the completion of this act adhering in the form of a little disc to the edge of the now expanded orifice, through which the contents of the capsule had been emitted.

Another form of thread-cell which throws light on the structure and action of that just described, occurs also among the HYDROIDA. In *Hydra,* it is in the form of a minute oval capsule, much smaller than the former, and having its cavity occupied by a spirally coiled filament which may be easily seen through its transparent walls. The act of evolution consists in the emission of the filament, but the barbed sac which constitutes so important a feature in the evolved thread-cell of the first kind cannot here be distinguished.

In some other HYDROIDA, the second kind of thread-cell acquires a larger size than in *Hydra.* I have carefully examined it in *Gemmaria implexa,* where it is met with scattered in the ectoderm of the hydranth, and where, from its comparatively large size, it is well fitted for observation. It here consists of an oval capsule (Pl. VII, fig. 9), within which may be seen, previously to emission a long thread, consisting of a straight and a coiled portion. The straight portion crosses the capsule diagonally, and is continuous at one end with the walls of the capsule, while at the opposite end it begins to be rolled up in distinct coils which almost completely fill the capsule. The coiled portion of the thread, however, does not surround the straight portion, but is placed entirely on one side of it, as had been already noticed by Clark in the thread-cells of *Syncoryne mirabilis.*[1]

[1] Clark, loc. cit.

The phenomenon of emission consists here, as in the form of thread-cell first described, of two distinct acts (see Pl. VII, fig. 10). The immediate result of the exciting cause is the projection of a long tubular thread from the anterior end of the capsule. This thread attains the length of about eight times that of the longer diameter of the capsule; and on the completion of its emission one end remains attached to the capsule, while the free end presents a small oval dilatation, behind which the thread is furnished for a short distance with very minute spines, which seem to be arranged spirally on its walls.

The projection of this thread thus constitutes the first step in the evolution of the thread-cell; but it is no sooner completed, than a still finer thread is shot out with great rapidity from its free extremity to a length about equal to that of the first. The whole act of emission is thus completed, and the capsule seems entirely emptied of its contents.

It is probable that the smaller kind of thread-cell in *Hydra* has a structure similar to that now described, though the minuteness of the parts unfits it for a satisfactory demonstration. It is evident, too, that the long thread with its armature of minute spines, whose emission constitutes the first stage in the action of the last-described thread-cell, is the exact homologue of the barbed sac of the first kind, the fine terminal filament in the two being also homologous organs.

The first stage in the emission of the contents of the capsule in the second kind of thread-cell takes place occasionally so slowly, from accidental resistance, that the course of the thread may be easily followed by the eye; and then it will be plainly seen to roll outwards by an act of eversion, reminding us of the mode of extension of the tentacles of a snail. The emission of the finer thread from the extremity of this is, probably, also by an act of eversion; but I have never succeeded in following it so as to obtain direct evidence that it is so.[1]

A fact which has an important bearing on the structure of the thread-cell is the difference of capacity presented by this body according as it is examined in its unevolved or evolved state. It would seem that, in some cases, the capacity of the capsule after evolution is less than it was previously, and then we can understand that no necessity may exist for its emitted contents being replaced by others. In certain cases, however, the total cavity of the thread-cell after the evolution may occupy a space more than double that which characterised it before the commencement of this act. Now, as this occurs in a sac, one portion, at least, of which must consist of a flexible membrane which would yield to any pressure from without not counterbalanced by an equal pressure from within, and as no tendency to collapsing can be detected in the evolved thread-cell, it is plain that, simultaneously with evolution, a fluid must be admitted into it from without,

[1] The observations of Möbius (loc. cit.), made chiefly on the thread-cells of *Caryophyllia Smithii*, have led him to describe the axile tube as consisting of three tubes, included by invagination one within the other. I cannot find direct evidence of this triple invagination in the thread-cells of any of the Hydroida I have examined. It must, however, be borne in mind that the much larger size of the thread-cells of *Caryophyllia* render them more favorable for the determination of structural details; while this view of the axile tube receives support from the fact that the proximal portion of the exserted filament in the thread-cell of *Gemmaria* greatly exceeds in length the straight portion of the unexserted filament; for this portion is the representative, in the non-evolved state, of the proximal portion of the evolved filament, and the difference between the two can scarcely be otherwise explained than by supposing the straight unevolved portion to consist of a tubular filament several times invaginated into itself.

unless we suppose that the cavity of the thread-cell is occupied by a compressible and expansible aëriform fluid. This latter supposition cannot be maintained, and if the former view be accepted, we must either admit the power of rapid imbibition in the walls of the cell, or suppose the presence of some definite opening, not yet detected, through which the surrounding water may gain access to its cavity.

The two forms of thread-cells now described may be regarded as the principal types under which these bodies occur in the HYDROIDA. Of the nature of the force by which the emission of their contents is effected we cannot yet speak with certainty. Everything that has been observed, however, is opposed to the supposition that the act of evolution is a vital one, dependent on the irritability of certain tissues which enter into the structure of the thread-cell. It is far more probable that it is simply physical, depending on the mere elasticity of the parts, and brought into play when the internal structures are mechanically released from the tension in which they had been held during the previous state of repose.

One fact may here be mentioned which is inconsistent with the idea of the evolution of the thread-cell being a vital act; namely, that prolonged immersion in certain re-agents, such as alcohol, will sometimes have no effect in destroying its characteristic properties; for I have seen the thread-cells of hydroids which had remained for months immersed in alcohol retain the power of emitting their contents on the application of some other re-agent, such as acetic acid.

There is reason to believe that, in some cases at least, the thread-cell when brought into use is at the same time forcibly ejected from the ectoderm in which it had been previously imbedded, and not merely drawn out of its berth by its attachment to the prey; and there is no reason why this act should not be referred to an irritability residing in the ectoderm, and receiving its special stimulus from the conditions which rendered necessary the employment of the thread-cell, such as the contact of living prey.

The employment of the thread-cell by the hydroid would, under these circumstances, involve both a vital and a physical act—the vital manifested in the ejection of the thread-cell from the body of the hydroid, the physical in the emission of its contents.

The special purpose fulfilled by the thread-cells in the economy of the animal, and their probable employment as urticating organs, will be considered under the section which treats of the physiology of the HYDROIDA.

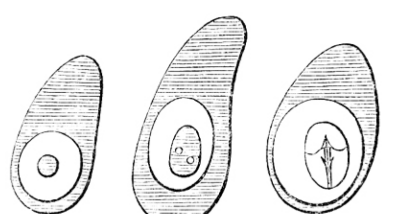
While the thread-cells in the HYDROIDA are entirely confined to the ectoderm and its appendages, they are by no means uniformly distributed in it. It is in the tentacles of both hydranth and medusa that they are usually most abundant; and here we find them either generally scattered through the ectoderm, or distributed through it in knot-like or wart-like or verticellate groups, or collected together in the spherical capitula in which the tentacles of some genera terminate (see Pls. IV, V, &c.). In many medusæ the ectoderm forms, at the base of the marginal tentacles, bulb-like thickenings which are loaded with thread-cells (see woodcut, fig. 56*e*). In many cases, minute thread-cells singly, or in clusters, are scattered superficially in the walls of the umbrella; in the genus *Gemmaria* (Pl. VII) we also find four piriform chambers extending from the circular canal of the medusa into the umbrella-walls, and filled with small oval thread-cells which have the appearance of lying loose within their cavity (figs. 3 and 6); while numerous similar but smaller sacs, filled with thread-cells, may be seen in *Willia* opening into the circular canal, and thence extending in a meridional direction along the walls of the umbrella.

In *Gemmaria* are also found certain remarkable pedunculated sacs which are developed from the marginal tentacles of the medusa, and filled with thread-cells (Pl. VII, figs. 3 and 4). Thread-cells are also, in many cases, specially developed in the nematophores—those peculiar sarcode appendages already described as characterising the family of the *Plumularidæ*.

It is almost certain that the thread-cells are always developed in the interior of proper cells, and they may be frequently separated from the ectoderm with the generating cell still surrounding them.

From observations which I have made on the larger kind of thread-cell in Hydra, it would seem that a portion of the protoplasm of certain ectodermal cells (generating cells) becomes differentiated as a spherical or oval mass which may be seen to occupy a vacuole in the midst of the remaining protoplasmic contents of the cell (woodcut, fig. 53), and in which one or more nuclei are usually apparent. This little mass is to become developed into the thread-cell. It continues to increase in size, and becomes invested by a distinct cell-wall, while its contained protoplasm becomes, in a way which I have not been able to follow, metamorphosed into the proper contents of the thread-cell. After this the now mature thread-cell becomes free by the rupture of the cell in which it had been generated.[1] The development of the thread-cell may thus to a certain extent admit of comparison with that of spermatozoa—a comparison already made by Leuckart—but we are still far from having a satisfactory notion of the origin and mode of development of these remarkable bodies.

Fig. 53.


a b c

Development of thread-cell in *Hydra*.

a. Generating cell of the thread-cell detached from the ectoderm, containing a very pale yellowish protoplasm, from which a small mass has become separated, and occupies the interior of a vacuole, where it looks like a nucleus in a cell.

b. The separated mass of protoplasm has become larger and more oval; two nucleolus-like corpuscles were in this instance apparent within it.

c. A developed thread-cell occupies the place of the protoplasm-mass in the vacuole of *a* and *b*.

To the ectodermal structures also belong the sense-organs—ocellus and lythocyst. These will be considered in the section on the physiology of the Hydroida.

2. *The Endoderm.*

Cellular structure of endoderm—contents of the cells.—The demonstration of a definite structure in the endoderm is much easier than in the ectoderm. Here, indeed, we seldom meet with any difficulty in making out a very distinct cellular composition.

Most usually, two sets of cells may be detected in the endoderm: an external set, with mostly clear, colourless contents, having but few granules; and an internal set, which forms the immediate boundary of the somatic cavity, and contains abundance of coloured granules.

The separation between these two sets of cells is often quite abrupt. In many hydroids those composing the external set are large, elongated, and with their longer axis in the direction of the radius of a transverse section of the hydroid, while those composing the internal set are

[1] Möbius has noticed that in the development of the thread-cells of *Lucernaria* and of certain *Actinozoa* amœboid changes of form are occasionally exhibited by the generating cell. Op. cit., p. 10.

much smaller and more spherical (see Pl. VII, fig. 5). Sometimes, however, the two sets pass imperceptibly into one another without any distinct boundary-line.

In *Hydra viridis*, the cellular structure of the endoderm is very distinct. The contents of most of the cells composing it are here peculiar, and consist of a colourless protoplasm with very definite green corpuscles imbedded in it, and in almost every instance with one and occasionally with two clear vacuolæ excavated in it.[1] It was the occurrence of these vacuolæ which caused Ecker,[2] by overlooking the proper cell-wall, to adopt the erroneous view that the whole tissue of *Hydra* was merely a mass of vacuolated protoplasm.

Among those cells which lie most internally and form the immediate boundary of the somatic cavity in *Hydra viridis*, are many which are destitute of green corpuscles, but contain brown, irregular granules, mostly included in a secondary cell which is itself imbedded in the vacuolated protoplasm of the mother-cell.

The green corpuscles possess a very definite form—a circumstance in which they contrast strongly with the brown granules. They are spherical, and present in their interior a lighter-coloured space which gives them a close resemblance to thick-walled cells. They will be again referred to. (See below, p. 136.)

Along with those cells which contain the green corpuscles, there also occur, especially in badly fed *Hydræ*, others in which the green contents are replaced by smaller spherical but colourless bodies, which are probably the green corpuscles in an undeveloped or transformed condition. Occasionally, also, an irregular mass of brown granules may be seen in the same cell with the green granules.

The cells which thus compose the endoderm of *Hydra* possess but a weak union with one another; they are easily separated by a slight force, and on becoming free immediately assume the spherical figure, without any trace of their having been previously united into a tissue.

No green matter is developed in the cells of any other species of *Hydra*. In *Hydra fusca*, there occur among the cells which form the boundary of the stomach cavity, many which are of an elongated piriform shape, with the broad thick end projecting into the cavity, and with their thin ends imbedded among the others. Within these piriform cells, secondary cells may usually be detected; these are spherical in shape, sometimes having clear colourless contents with a nucleus, while in other cases they are filled with irregular brown granules, and present no evident nucleus. Sometimes the piriform cells contain only free brown granules, while we may also often meet with instances in which, besides the free granules, the same piriform cell will contain the clear nucleated secondary cells, and the secondary cells filled with brown granules. This may be regarded as the typical condition of the same parts in the other HYDROIDA, though it is seldom so distinctly demonstrable as in *Hydra*.

The walls of the somatic cavity are probably in all HYDROIDA, if we except *Hydra*, clothed to a greater or less extent with vibratile cilia. These cilia are remarkably distinct among some of the *Tubularidæ;* while in other cases in which their existence has not been proved by direct observation, the peculiar currents visible in the fluid contents of the somatic cavity leave no doubt that it is to the agency of such cilia that these currents are mainly due. *Hydra* would appear to constitute a solitary exception in the non-ciliated condition of its somatic cavity.

[1] Allman, "On the Structure of *Hydra viridis*," in 'Brit. Assoc. Reports' for 1853.

[2] Ecker, "Zur Lehre vom Bau und Leben der contractilen Substanz der niedersten Thiere," 'Zeitsch. f. wiss. Zool.,' Bd. 1, 1849.

The endoderm of the proper digestive cavity is probably in all HYDROIDA thrown into more or less complicated lobes or ridges, which disappear where this cavity passes into the common cavity of the cœnosarc.

This condition may be well seen in *Hydra fusca*, especially when, as sometimes happens, we have an opportunity of looking down into the stomach of the uninjured animal through the widely open mouth. Numerous ridges may then be witnessed, extending from the walls of the cavity almost to its centre. These ridges are rendered papillose by the projection from their surface of the peculiar piriform cells already described, while the furrows between them are comparatively smooth. I have witnessed a similar condition of the endoderm in the digestive cavity of *Cordylophora lacustris*, *Coryne pusilla*, *Syncoryne eximia*, and many others, where thick, irregularly sinuous and lobulated ridges of endoderm project into the stomach from the inner surface of its walls. A furrowed and lobulated state of the endoderm may also be witnessed in the manubrium of the medusa, and in the spadix of the sporosac of many hydroids.[1]

The hydranth of *Tubularia indivisa* presents a very remarkable condition of its endodermal layer (Pl. XXIII, fig. 1). Immediately within the mouth, the cells containing the coloured granules form a narrow smooth zone of vermilion dots, immediately behind which the surface of the endoderm is disposed in irregularly oval prominent vermilion patches, separated by paler narrow sulci. In tracing these patches backwards, we find that they become smaller and more numerous, gradually resolving themselves into small spots, and ultimately into minute scattered puncta which at the posterior extremity of the hydranth, where its cavity passes into that of the stem, become more densely grouped, and are here arranged in radiating bands of a bright vermilion colour. Along the line where the anterior contracted portion of the hydranth passes into the wider basal portion, the endoderm is thrown into numerous remarkable pendulous lobes of a piriform shape and bright vermilion colour (Pl. XXIII, fig. 2). They consist each of a cluster of very distinct spherical cells, containing vermilion-coloured granules, among which are numerous small clear spherical elements, apparently oil-drops. They present a close resemblance, both in their form and in the nature of their contents, to the zone of gland-like lobes which occupies a very similar position in the interior of the hydranthal zooids of certain *Siphonophora*.

Canaliculation of endoderm.—In some HYDROIDA we have a very peculiar and exceptional condition of the somatic cavity and of its endodermal lining; for while this cavity in most HYDROIDA consists of a simple tube, it is in the cases here alluded to composed of numerous intercommunicating canals.

This condition is well seen in different species of *Tubularia*. The stem of *Tubularia indivisa* for example, presents immediately within the perisarcal tube a continuous layer of ectoderm enclosing the endoderm which extends to the very centre of the stem, and thus obliterates all trace of a central somatic cavity (Pl. XXIII, fig. 7). The place of this cavity, however, is supplied by numerous canals, which are excavated in the endoderm and take a longitudinal course through the stem, occasionally communicating by lateral offsets with one another, and finally all merging in a common central cavity at the base of the hydranth.

In a transverse section of the stem, the canals present a wedge-shaped form, the narrow end

[1] In certain *Geryonidæ* (*Glossocodon eurybia*, *Carmarina hastata*), Haeckel (op. cit.) describes, as gastric glands, peculiar leaf-shaped organs which occur in the inner walls of the manubrium (four in *Glossocodon*, six in *Carmarina*). They are composed of clusters of large cells with dark-coloured contents.

being directed towards the axis, and are seen to be arranged in a single zone at some distance from the centre. They are manifestly simple tubular lacunæ interposed among the cells of the endoderm, and destitute of special walls. They are irregular in size, one of them especially being usually considerably larger than the others; and Agassiz, who was the first to call attention to this difference of size, lays considerable stress upon it, for he regards it as constant, and considers the large channel to represent that which alone constituted the cavity of the *Tubularia* in its young state. I have made many sections of *Tubularia* stems, and have always found the tubes irregular in size, and in most cases one of them considerably surpassing the others, as affirmed by Agassiz. Wright, who first distinctly drew attention to the tubular lacunæ, represents them as of equal size; but his figure must be regarded as merely diagramatic. I am not, however, prepared to assent to Agassiz's view of the origin of the large channel. I believe, on the other hand, that the simple somatic cavity of the young *Tubularia* is represented in the adult by the common chamber at the summit of the stem, into which the longitudinal channels all open. It is only in the free stage of *Tubularia* that its cavity is simple; and immediately after it has become fixed the hydranth is carried upwards by the development of a stem whose cavity exhibits, at the moment it can be detected, the compound character of the adult.

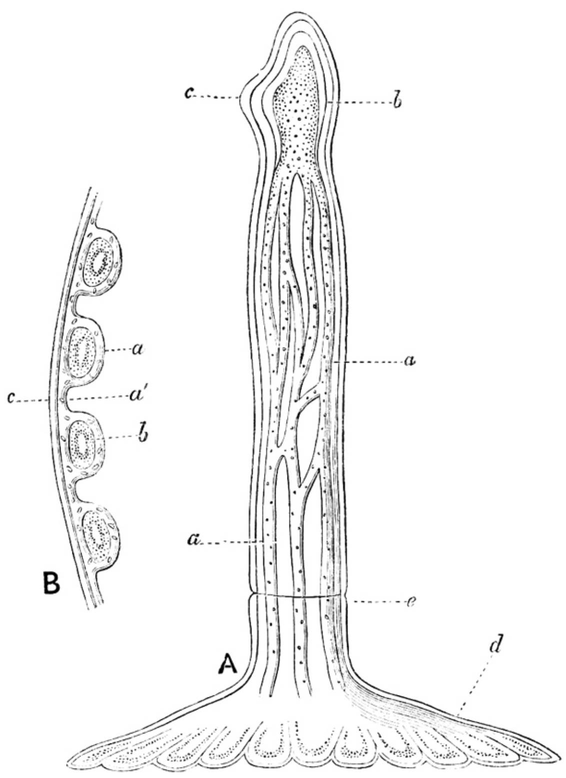
That portion of the endoderm which occupies the axis of the stem consists of large cells of a spherical form, or by mutual pressure more or less polygonal; they are filled with a clear colourless or slightly granular fluid, while the more peripheral portion of the endoderm is composed of small spherical cells containing abundance of minute vermilion-coloured granules; it is in this peripheral portion of the endoderm that the lacunæ are excavated. The walls of the lacunæ are clothed with very long and distinct vibratile cilia.

A structure which in all essential points resembles that just described in *Tubularia indivisa* occurs also in *Corymorpha nutans*, the endoderm of the stem being here, as in *Tubularia*, excavated by longitudinal lacunar canals (Pl. XIX, figs. 1, 6, 7). These canals inosculate here and there with one another; they are much more numerous than in *Tubularia*, but towards the base of the stem they become by mutual coalescence less numerous than in the distal part; they lie just within the ectoderm, and open above into a common cavity in the basal portion of the hydranth. Here the endoderm which forms the floor of the hydranth-cavity rises as a broad conical projection so as to nearly fill the posterior half of the cavity. The axis of this projection is perforated by a narrow canal by which the cavity of the hydranth is continued to the summit of the stem. At this point the canal becomes wider, and receives the longitudinal channels of the stem. The peripheral portion of the endoderm, or that in which the canals are excavated, is composed of small spherical cells with reddish-brown granular contents, while the rest of the endoderm is composed of loose cells with clear colourless contents, and forms a thick pith-like column which occupies the whole axis of the stem. I have not succeeded in detecting cilia in the canals, but, from the very distinct currents which may be witnessed in these canals in the living hydroid, I have no doubt of the presence of cilia here as in *Tubularia*.

The superficial position of the endodermal canals both in *Tubularia* and *Corymorpha* renders them conspicuous without dissection, even to the naked eye, for they give to the stem the appearance of being marked by longitudinal bands from one end to the other.

In *Antennularia antennina* the cœnosarc in the main stems presents also a canaliculated condition, one, however, which differs in some important points from that of *Tubularia* and *Corymorpha;* for, while in the two latter the canals of the stem are mere lacunæ excavated in a common endoderm, the whole cœnosarc is in *Antennularia* broken up into separate tubes, each with its own endoderm and ectoderm, and all surrounded by a common chitinous perisarc (woodcut, fig. 54).

Fig. 54.



Canalliculation of Endoderm in *Antennularia antennina.*

A. Very young hydroid, just after the fixation of the planula and the elevation of the primordial stem. *a*, *a*, the canals of the endoderm, inosculating here and there with one another; *b*, common cavity, formed by the coalescence of the endodermal canals at the summit of the stem; *c*, commencement of a ramulus; *d*, lobed hydrorhizal disc, forming the surface of attachment of the young hydroid; *e*, circular groove, commencement of segmentation in the stem.

B. Part of a transverse section of the adult stem. *a*, ectoderm, and, *b*, endoderm of cœnosarcal canals; *a'*, extension of the ectoderm in the intervals of the canals; *c*, perisarc.

Twenty or more tubes will thus be found in the main stem of a specimen of *Antennularia*. They lie close upon the inner surface of the perisarc, and are connected to one another by an extension of their ectoderm (woodcut, fig. 54 B). In some parts of their course they are straight and parallel; in others, more or less sinuous and reticulated by inosculation. The whole centre of the stem is empty, and has no communication with the somatic cavity, instead of being occupied, as in *Tubularia* and *Corymorpha*, by an endodermal pith-like core, or instead of being, as in most of the Hydroida, occupied by the somatic cavity itself. Very distinct currents may be witnessed in these tubes, especially in the young hydroid, thus affording evidence of the existence of vibratile cilia on their walls.

Endoderm of tentacles.—In the tentacles of the Hydroida, both those of the hydranth and of the medusa, the endoderm usually undergoes a peculiar and important modification. In *Hydra* the tentacles are quite pervious throughout their entire length, while they are lined by a simple continuation of the endoderm of the digestive cavity; but in every other hydroid with which I am acquainted, the endoderm of the tentacles of the hydranth presents a peculiar septate appearance, looking in some cases like a solid core divided by numerous transverse septa into circular discs, and entirely filling up the tube of the tentacles, while in others, though the same septate condition exists, there is still a narrow pervious canal in the axis.

I believe that in all these cases the apparent septa are really the opposed walls of large adjacent endodermal cells which encroach more or less on the cavity of the tentacle, often even to its entire obliteration.

This structure may be well seen in the tentacles of various species of *Corynidæ* (*Coryne pusilla*, Pl. IV, fig. 3, &c.). For some distance from the distal extremity of the tentacle, the cavity is usually entirely obliterated by thin membranous septa which stretch transversely across it. Further towards the base of the tentacle, the septa become less regular, and the obliteration of the tube is now plainly seen to be caused by the large irregular cells of which the endoderm is here composed, and which encroach upon its cavity to such an extent as entirely to fill it; while at a little distance from the base the encroachment of the endodermal cells is usually not so complete, and the cavity of the tentacle, though greatly contracted, still continues pervious, and admits into it fluid with suspended particles from the digestive cavity of the hydranth.

Many of the cells which thus constitute the peculiarly modified endoderm of the tentacle contain a very distinct nucleolated nucleus, round which is generally collected a colourless finely granular protoplasm, which is often kept in connection with the cell-wall by radiating prolongations. A few large coloured granules are also usually contained in the cells. Towards the distal extremity of the tentacle, where the septa are most regular and complete, we generally find a little granular mass collected in the centre of the distal surface of each septum, or else forming a little axile column stretching from septum to septum. These septa, with their intervening chambers, have much the appearance of large cells which stretch entirely across the tube of the tentacle; it is possible, however, that they may be formed by the coalescence of two or more cells from opposite sides, as in the more proximal portions, but here accompanied by the disappearance of their walls in the axis of the tentacle, and the consequent confluence of their cavities.

In some other cases the endodermal cells are not developed to such an extent as to obliterate in any portion the cavity of the tentacle, which thus remains pervious in its entire length; but the large size and regular form of these cells continue to confer on the tentacle a distinctly septate appearance. I have found this condition in the tentacles of *Garveia nutans* (Pl. XII, fig. 6).

In the planoblast also the tentacles usually present the same septate appearance as in the hydranth, the endoderm being frequently so developed as entirely to obliterate the tube. Examples of this may be seen in the marginal tentacles of most medusæ, as, for instance, those which constitute the planoblasts of *Obelia dichotoma*, and of *Podocoryne carnea*, as well as in the tentacles of the free sporosac of *Dicoryne*. Those cases, however, in which the tentacle preserves a complete continuity of its tube are much more common in the medusa than in the hydranth. In the medusa, indeed, it is far from uncommon; we find it, for example, in the marginal tentacles of the medusa of *Syncoryne eximia* (Pl. V, fig. 4), *Gemmaria implexa* (Pl. VII, fig. 4), and *Sarsia strangulata* (woodcut, fig. 17), and, according to Haeckel, in the long extensile tentacles of the *Geryonidæ*.[1]

In the bulb-like expansion which usually exists at the base of the marginal tentacles of the medusæ, at the point where the radiating canal meets the circular canal, the endoderm acquires increased thickness, and often forms lobulated projections which encroach upon the cavity, but never obliterate it (woodcut, fig. 56). These projections are usually rich in cells filled with coloured granules, which, like the coloured granules of the digestive cavity, appear to be secreted in secondary cells developed in the interior of mother-cells.

The endoderm lining the remainder of the gastrovascular canals is, on the other hand, entirely destitute of lobes or ridges. It is very thin, and would seem to have a purely distributive function, the fluid contents of the canals being propelled by vibratile cilia which clothe their walls. These cilia may be well seen in *Syncoryne eximia* (woodcut, fig. 56).

[1] Reichert (loc. cit.) maintains the entire absence of the endoderm in the tentacles of the sertularian and campanularian hydranths, while he regards the septate appearance as produced by simple extensions of his "supporting lamella," which, according to him, forms a layer secreted on the inner surface of the tentacular ectoderm. This view, however, is opposed by the structure, which easily admits of demonstration in the tentacles of many tubularian hydroids.

PHYSIOLOGY OF THE HYDROIDA.

In attempting a classification of the various phenomena of hydroid life, we are at once met by the difficulty of arranging them under definite physiological heads. The low grade of specialisation on which the HYDROIDA stand, renders it often impossible to assign to these phenomena a definite physiological significance, and many of the acts which make up the life of such simple organisms can scarcely claim to be referred to one more than to another of the great classes under which the functions of animals are usually distributed.

Notwithstanding this, however, we shall find it convenient to speak of the vital acts of the HYDROIDA under the following heads :—1. Digestion. 2. Circulation, Nutrition and Growth of the Tissues, and Respiration. 3. Secretion. 4. Contractility. 5. Sensation. 6. Phosphorescence. 7. Reproduction. We must, however, keep in mind that these classes do not all necessarily possess the definiteness which characterises them in the higher and more specialised members of the animal kingdom.

1. *Digestion.*

So far as observation has taught us anything regarding the food of the HYDROIDA, we may conclude that it consists mainly of living animals, though Diatomaceæ and other minute free vegetables contribute also to their subsistence. The patient observations of Trembley and the older naturalists on the fresh-water *Hydra* had long ago shown that animals of considerable size, such as entomostraca, and even aquatic larvæ and worms, are seized by the tentacles of this voracious little hydroid, and carried to the mouth, through which they are borne into the cavity of the body; and subsequent observations have proved that in other HYDROIDA the nature of the food and the capture of the prey are in all essential points similar to what has been noticed in the *Hydra*.

It is in this act that the functions of the thread-cells seem to be mainly called into play; and repeated observations have shown that no sooner do the tentacles come in contact with the living prey, than all power of resistance in the latter is at an end; its efforts to escape seem suddenly paralysed, and it becomes an easy victim to the rapacity of its captor.

If the prey be at this stage released from the grasp of the hydroid and placed under the microscope, all the soft tissues of its surface will be found pierced with discharged thread-cells.

Observers are by no means agreed as to the true functions and mode of action of the thread-cells. By most they are supposed to penetrate the tissues of the prey, and those which, like the larger thread-cells of Hydra, are provided with an apparatus of barbed spines, have been described as plunged beyond the barbs into the soft tissues of the victim. Other observers, and more especially Möbius, reject the idea of penetration, and maintain that the thread-cells arrest the motions of the prey by the mere adhesion of the ejected filament.

I believe, however, that it will be found that there is an actual penetration, but not to the extent that is usually insisted on. If some soft body, such as a worm, be brought into contact with the tentacles of a Hydra, the surface of contact may be seen immediately afterwards to be covered with large discharged thread-cells, many of which will be found with the freed end of the barbed sac inserted into it as far as the roots of the barbs. I have never, however, witnessed a deeper penetration than this, and the barbs themselves were never immersed.

I believe that in such cases the action of the thread-cell consists in the sudden ejection of the barbed sac against the tissues of the prey, which, if these be soft enough, allow the point of the sac to penetrate as far as the roots of the barbs. This act is instantly followed by the ejection of the filament, for which the barbed sac has opened the commencement of a passage, and which now worms its way among the tissues, recalling the mode in which the delicate filaments which form the *mycelium* of certain parasitic fungi penetrate the organic structures infested by them.

It is impossible, however, to believe that such effects as follow the action of the thread-cell can be produced by mere mechanical penetration, and the conclusion is irresistible that the penetration is accompanied by the injection of some potent virus which acts by rapidly destroying the irritability of the living tissues, the tubular filament of the thread-cell as it continues to insinuate itself, affording at the same time a channel by which the special secretion of the cell is conducted into the deeper parts of the tissues of the prey.

In judging of the functions of the thread-cells, however, it must not be forgotten that they also occur in parts which preclude the possibility of their being employed as offensive or defensive organs, as, for instance, when they exist, as they frequently do in great numbers, in that part of the ectoderm which is under cover of the hard chitinous perisarc, or when they are included in the interior of cavities which can have nothing to do with the capture of the prey, as in the sac-like receptacles which occur in the umbrella of *Gemmaria*.

Though we have scarcely yet sufficient data to enable us to determine the exact limits of that part of the somatic cavity on which the function of digestion specially devolves, we shall perhaps be justified in considering as such that portion of it which is included within the hydranth, and which is almost always distinguished by its form and by some special structure of its walls from that which belongs to the cœnosarc; while in the medusa the cavity of the manubrium, or at least its basal portion, must also be regarded in a special sense as devoted to the digestive functions of the free planoblast.

When the food has once passed the mouth and entered the cavity of the hydranth, or that of the manubrium of the medusa, it is there subjected to a process of solution. Of the nature of the solvent we as yet know almost nothing. There can be little doubt, however, that it is secreted from the walls of the cavity; and though it must be more or less diluted with water which has obtained admission through the mouth, its action on the food is powerful and rapid. This process is doubtless aided by the motion to which the contents of the digestive cavity are subjected by the contraction of the walls and the vibration of the cilia which clothe them. The soluble and nutritious parts are speedily separated, and the insoluble and non-nutritious *débris* are ejected through the mouth.[1]

[1] Corda ("Anat. Hydræ fuscæ," in 'Ann. des Sci. Nat.,' 1837) has described the body-cavity of Hydra as communicating with the external medium by an orifice situated at the end opposite to the

The product of this process, consisting of the dissolved and disintegrated nutritious portion of the food, mingled with certain materials which it has received from the walls of the digestive cavity, and diluted with water which has been introduced from without, is propelled from the cavity of the hydranth into that of the cœnosarc, or from the manubrium into the radiating canals of the medusa, in order to be distributed to the several tissues. It thus becomes the *somatic fluid*, to be presently considered in its relations to the circulatory functions.

Examined under the microscope, this fluid is seen to be of a very heterogeneous nature. Its basis is a transparent colourless liquid, and in this solid bodies of various kinds are suspended. These consist partly of disintegrated elements of the food, partly of solid coloured matter which has been secreted by the walls of the somatic cavity, partly of cells, some of which have undoubtedly been detached from these walls, though it is possible that others may have been primarily developed in the fluid, and partly of minute irregular corpuscles, which are possibly some of the effete elements of the tissues.

Beyond this point it is plain that digestion cannot be traced as a specialised function, and its phenomena here become coincident with those of circulation.

2. *Circulation, Nutrition, and Respiration.*

Between the phenomena associated above under the general head of digestion, and those which might with equal justice be claimed by circulation, it is impossible to draw any well-marked line of demarcation. The somatic fluid, whose relations to digestion we have been just considering, has relations quite as intimate with circulation; for though in one aspect we may compare it to the chyme or chyle of the more highly specialised animals, in another it admits of just as close a comparison with the blood.

No trace of a differentiated blood vascular system has been detected in any hydroid. The nearest approach to it is that which is presented by the radiating and circular canals of the medusa, and yet these are simple offsets from the digestive cavity.

The place of the blood is taken by the fluid which pervades the somatic cavity, and which consists of the digested food largely mingled with water which has gained admission by the mouth, as well as with certain materials which have been secreted by the walls of the somatic cavity.

The fluid which thus permeates the somatic cavity and extends through all its ramifications must not be supposed to be in a state of rest. On the contrary, it is subjected to constant motion, which manifests itself in currents more or less regular in their velocity and definite in their direction.[1] In some cases the currents present a remarkable definiteness and regularity.

mouth. I have not been able to confirm this observation; and though Leydig ("Ueber den Bau der Hydren," in 'Müller's Archiv,' 1854) and Hancock ("Notes on a Species of Hydra," in 'Ann. Nat. Hist.,' 1850) support Corda's statement, I cannot avoid believing that the orifice in question is accidental.

[1] Cavolini was the first who distinctly noticed the currents of the somatic fluid in the HYDROIDA. He has described them in a campanularian hydroid (Sprengel's 'Cavolini,' p. 56). They were subse-

This may be well seen in the stems of *Tubularia indivisa*, where the contained fluid is distributed in numerous parallel streams ascending through some of the channels which are excavated in the endoderm of the stem of this hydroid, and descending through others. The ascending streams become confluent at the summit of the stem, and from this point the descending streams issue. Every now and then the direction of the streams is reversed, the fluid flowing down the channels which just before carried ascending streams, and flowing up in those through which the streams had previously descended. Here and there the longitudinal channels communicate with one another by transverse branches, and through these branches the fluid may be seen flowing from one longitudinal channel to another. Occasionally the fluid will remain for a short period at rest in one of the channels, while it continues to flow in its ascending and descending streams in the others. The somatic currents of *Tubularia*, however, are by no means always easily seen, and it is only now and then that a specimen occurs, which, from the transparency of its tissues, and the abundance of floating corpuscles in the somatic fluid, presents conditions favorable for observation.

In *Corymorpha nutans*, the structure of whose stem resembles that of *Tubularia indivisa*, similar definite currents may be witnessed; and in *Antennularia antennina*, whose cœnosarc, as already mentioned, is composed of numerous tubes within a common perisarc, currents of an entirely similar kind may be seen ascending in some of these tubes, descending in others, passing over from one to another by intercommunicating branches, and again resting in others, but ready to start off in a fresh stream upwards or downwards while we continue to watch.

It is rare, however, to find the currents of the somatic fluid presenting the regularity and definiteness which characterise them in the instances just mentioned. In those far more numerous cases in which the somatic cavity is simple instead of being composed of separate and distinct channels, the contained fluid may occasionally be seen in a single broad stream flowing through the axis of the stem or branch, then coming to a state of rest and after a short period of repose, starting off anew in a reversed direction. Most usually, however, the movement in such cases, instead of being in the form of a definite current, consists in an irregular commotion in which the floating corpuscles are whirled about in all directions. Within more limited cavities, such as that of the spadix in the sporosac and of young buds in process of development, the motion of the fluid is generally in circular streams, which may be seen coursing round the walls of the cavity and returning into themselves. These streams in the developing bud usually present great activity. A similar disposition of the streams in circular currents may be witnessed in the cavity of the hydranth; but the motion here ought probably to be referred to digestion rather than to circulation, as it does not seem to have any proper distributional office, being most likely specially connected with the preparation of the aliment.

In the gastrovascular canals of the medusa, the currents are very distinct, the transparency of the surrounding tissues rendering it easy to observe them. In all these canals, whether radiating or circular, they constitute simple streams, which in some of the radiating canals may be seen flowing from the proximal towards the distal end, and in others from the distal towards the proximal, and, as it would seem, reversing themselves every now and then in all these tubes. In the

quently described by Lister, who also detected them in the stem of *Tubularia indivisa* ('Phil. Trans.,' 1834). Since then the currents in the somatic cavity of the HYDROIDA have become familiar to every observer of these animals.

circular canal the fluid may also be seen flowing at one time in one direction, and then again in the opposite.

That the motion of the somatic fluid in all these cases is mainly caused by the impulse of vibratile cilia, there can be but little doubt. Dujardin appears to have witnessed these cilia in the stem of his *Syncoryne decipiens;*[1] and in the stem of *Tubularia indivisa*, where the cilia clothing the lacunar channels and their relation to the currents were first pointed out by Dr. T. S. Wright,[2] they are very distinct, and can be demonstrated with the greatest ease in a transverse section of the stem (Pl. XXIII, fig. 7). By carefully applied pressure, I have succeeded in ejecting the spadix in an inverted state through the proximal end of a detached sporosac of *Tubularia indivisa*, when its internal surface being thus exposed, a rich clothing of very distinct actively vibrating cilia has been brought into view (Pl. XXIII, fig. 10).

It must, however, be admitted that in the greater number of hydroids the existence of endodermal cilia has not been proved by direct observation. In most hydroids the tissues are too opaque to afford a view of the delicate cilia which may clothe the cavities, while sections of the stem will afford none of that aid which we obtain from them in *Tubularia;* for the section is accompanied in most other species by a collapsing of the cavity which would necessarily interfere with the action of the cilia and remove them from observation. In every case where a satisfactory view of any portion of the free surface of the endoderm in the Hydroida has been obtained, as, for instance, where the transparency of the tissues is such as to afford no obstacle to a view of the deeper seated parts, this surface is invariably—except in *Hydra*, where cilia appear to be really absent—seen to be clothed with vibratile cilia. Thus, in certain medusæ the cilia may be easily seen vibrating along the walls of the radiating and circular canals.

It is probably, then, a nearly universal fact that the free surface of the endoderm in the Hydroida is ciliated, and that the fluid in contact with this surface is kept in motion by the impulse it receives from the cilia.

It must not, however, be overlooked that the contractility of the walls has its share in this motion. The fluid contained within the gastric cavity of the hydranth may, indeed, be frequently seen to be forcibly expelled from this cavity by its contraction into that of the cœnosarc—the mouth of the hydranth being at the same time kept closed—and then again drawn back into the gastric cavity, when the contraction which had expelled it is succeeded by an expansion.

As every portion of the somatic fluid is thus successively brought in contact with the walls of the somatic cavity, it yields to the tissues by a process of direct absorption the nutriment necessary for their growth and maintenance, and receives from them such portions of their substance as in the performance of their vital functions had become effete.

That the formation and growth of the tissues is intimately connected with cell-formation is rendered obvious by attending to the phenomena which accompany rapid growth among the Hydroida.

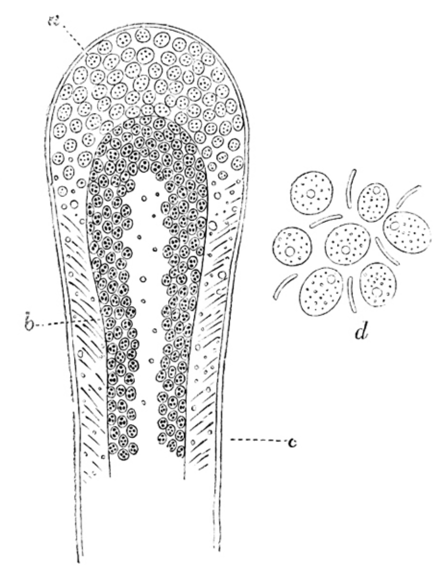
A healthy colony of *Obelia dichotoma* was placed in a jar of sea-water. In a few days most of the hydranths had disappeared, but adventitious branches had begun to be sent out in great profusion from various parts of the surface. These branches elongated themselves with

[1] 'Ann. des Sc. Nat.,' tome iv, 1845, p. 275.
[2] 'Proc. Roy. Ph. Soc. Edinb.,' 1855-56.

astonishing rapidity, in some cases at the rate of three quarters of an inch in thirty-six hours.

The distal extremity of the branch was its growing point, and here it terminated in a slight enlargement which formed a cul de sac, in whose walls both endoderm and ectoderm were distinctly differentiated (woodcut, fig. 55). The somatic fluid penetrated to the extremity of the branch. The ectoderm formed a considerably thicker layer than the endoderm, and was composed of very distinct, nearly spherical cells, with clear granular contents, and with but little intercellular plasma. Numerous slightly curved, cylindrical bodies, resembling undeveloped thread-cells, appeared to lie free in the intercellular plasma, where they were scattered among the true cells.[1] Under the action of acetic acid a distinct nucleus was rendered evident in the ectodermal cells.

FIG. 55.



Growing extremity of an adventitious branch of *Obelia dichotoma*.

a. Ectoderm overlaid by a delicate pellicle of chitine, and composed of distinct cells, where it occupies the growing point; *b*, endoderm; *c*, ectoderm, somewhat removed from the growing point, its cells no longer evident; *d*, some of the cells from the ectoderm of the growing point, treated with acetic acid, more highly magnified, and with thread-cell-like bodies lying scattered among them.

The endoderm of the growing point was also distinctly composed of spherical cells in a very scanty intercellular plasma. The endodermal cells, however, were much smaller than those of the ectoderm, and, instead of the clear contents of the latter, the endodermal cells contained coloured granules.

On following the cells of the ectoderm backwards from the growing point, they were found to become less and less distinct; it was, indeed, plain that they had undergone a metamorphosis, and at a short distance from the extremity no true cells could any longer be detected in the ectoderm, which now presented in a sectional view only an obliquely striated and granular appearance. The endoderm, on the other hand, retained its distinctly cellular structure throughout. The perisarc, which on the proximal part of the branch possessed considerable thickness, showed itself on the growing part as a scarcely perceptible pellicle.

I did not succeed in detecting anything like a process of cell-division in the ectoderm of the growing point, nor could I satisfy myself that the cells became multiplied by endogenous formation of cell-broods within the cavity of the older ones. The appearances were, on the other hand, rather in favour of the direct formation of the cells out of the plasma.

The cells of the endoderm probably originate in the same way, but they appear soon to become ruptured and to discharge their contents into the somatic fluid, which filled the cavity of the growing stem.

In certain other tissues, growth would seem to take place by cell-division. This, at all events, appears to be the case in the epithelium of the umbrella of *Obelia* (see below woodcut, fig. 59, c).

[1] This structure recals that of certain young sponges, with the spiculæ which are to form the skeleton scattered among more or less individualised masses of protoplasm.

The currents described above, as existing in the somatic cavity of the HYDROIDA, serve not only for the distribution of the nutritive fluids among the tissues—an office in which they admit of comparison with the somatic circulation of the blood in the more specialised members of the animal kingdom—but they also contribute to bring this fluid into more immediate relation with the surrounding medium, and thus subserve the function of *respiration*.

No differentiated respiratory organs occur anywhere among the HYDROIDA, and the interchange between the nutritious fluid and the surrounding medium must take place through the general surface of the body, more especially through those portions of it which, not being under cover of the chitinous perisarc, are more directly exposed to the conditions under which such interchange may be effected.

The cilia which cover the external surface of the hydroid when in the stage of planula, as well as those which clothe the free sporosac of *Dicoryne*, and those which occur on certain hydroid medusæ not yet traced to a trophosome, such as *Trachynema*, Gegeng., are probably subservient to respiration as well as to locomotion.

3. *Secretion.*

That distinct secretions are found among the HYDROIDA, and that even special structures are set aside for their elaboration, there cannot now be any doubt.

One of the most marked of these secretions consists of a coloured granular matter which is contained at first in the interior of certain spherical cells, and may afterwards become discharged into the somatic fluid. These cells, as already mentioned, are developed in the endoderm, in which they are frequently so abundant as to form a continuous layer upon the free surface of this membrane. It is in the proper gastric cavity of the hydranth and medusa, in the spadix of the sporosac, and in the bulbous dilatations which generally occur at the bases of the marginal tentacles of the medusa, that they are developed in greatest abundance and perfection; but they are also to be found more or less abundantly in the walls of probably the whole somatic cavity, if we except that portion of the gastrovascular canals of the medusa which is not included within the bulbous dilatations.

In the parts just mentioned as affording the most abundant supply of these cells, they are chiefly borne on the prominent ridges into which the endoderm is thrown in these situations; when they occur in the intervals between the ridges, they are smaller and less numerous.

The granular matter contained in the interior of these cells varies in its colour in different hydroids. In many it presents various shades of brown; in others it is a reddish-brown or light pink, or deeper carmine or vermilion or orange; or occasionally a fine lemon-yellow, as in the hydranth of *Coppinia arcta*, or even a bright emerald green, as in the bulbous bases of the marginal tentacles of certain medusæ. No definite structure can be detected in it; it is entirely composed of minute granules, irregular in form, and usually aggregated into irregularly shaped masses in the interior of the cells. It is to this matter that the colours of the HYDROIDA, varying as they do in different species, are almost entirely due.

The coloured granular matter is undoubtedly a product of true secretion; and the cells in which it is found must be regarded as true secreting cells. These cells are themselves frequently to be seen as secondary cells in the interior of parent cells, from which they escape by rupture, and then falling into the somatic fluid, are carried along by its currents, until ultimately, by their own rupture, they discharge into it their contents.

We have no facts which may enable us to form a decided opinion as to the purpose served by this secretion. Its being always more or less deeply coloured, and the fact of its being abundantly produced in the digestive cavity, might suggest that it represented the biliary secretion of higher animals. This may be its true nature, but as yet we can assert nothing approaching to certainty on the subject: indeed, considering how widely the cells destined for the secretion of coloured granules are distributed over the walls of the somatic cavity, it would seem not improbable that the import of the coloured matter may be different in different situations; that while some of it may be a product destined for further use in the economy of the hydroid, more of it may be simply excretive, taking no further part in the vital phenomena, and intended solely for elimination from the system.

The fluid which acts so powerfully as a solvent on the food which has passed into the digestive cavity, must certainly be also regarded as a secretion. We are ignorant of its exact source, but it is in all probability derived, like the coloured matter, from cells developed in the walls of the cavity.[1]

Under the head of specific secretion must also probably be classed the fluid contents of the thread-cells.

That the remarkable green matter which is contained in the endodermal cells of *Hydra viridis* is a special product of these cells there can be no doubt. Its very definite structure, however, would seem to take it out of the class of ordinary secretions, and place it rather in the same group of products as spermatozoa and thread-cells.

The researches of Cohn[2] have led him to believe that the green colouring matter of Hydra is identical with that of *Euglena*, and with that of *Loxodes*, *Stentor*, and certain other green *Infusoria;* and, further, that in all these cases it is indistinguishable from the chlorophylle granules of certain *Algæ*, especially of *Vaucheria*. He has shown that the green granules in these animals, as well as in a green *Planaria* which he has also examined, present precisely the same appearances under the action of sulphuric acid as those which we witness in the chlorophylle of plants when subjected to the same treatment; for instead of remaining unchanged, or merely becoming charred, the granules, when brought into contact with the acid, pass in a very characteristic way from verdigris-green to a more intense bluish-green, and at last, in solution, become almost blue.

From these facts Cohn concludes that the green matter in the organisms mentioned, at least in *Euglena* and the green ciliate *Infusoria*, performs a function similar to that of the chlorophylle of plants, and he regards it as destined for the excretion of oxygen.

The chitinous perisarc which, to a greater or less extent, invests the surface of almost every hydroid, is perhaps rather a product of metamorphosis of tissue than of true secretion, the most external portions of the ectoderm becoming converted into the perisarc, which increases in thickness by successive additions to the inner surface, these additions giving a distinctly

[1] The cells described by Haeckel as arranged in peculiar leaf-like groups in the stomach-walls for certain medusæ belonging to the family of the *Geryonidæ*, would seem to be destined for the elaboration of some special secretion.

[2] Cohn, "Beitr. zur Entwckel. der Infusorien," 'Zeit. f. Wiss. Zool.,' vol. iii, 1851.

laminated condition to the otherwise absolutely structureless perisarc. To the same class of products belongs the gelatinous-looking investment which envelopes the acrocyst in *Sertularia pumila*, &c. (see p. 50), and in which a distinctly laminated character may frequently be detected.

4. *Contractility.*

The existence of a fibrillated tissue in the HYDROIDA has been already mentioned; and there can be no doubt that this tissue is endowed with contractility, and is the proper seat of the more energetic motions performed by these animals. The act by which the hydranth becomes suddenly retracted when touched is evidently due to the contraction of the longitudinal fibres which are developed on the inner surface of the ectoderm; and the rhythmical and exquisitely graceful movements of the medusæ have their seat in the contractile fibres which are developed on the concave surface of the umbrella and in the velum, and are antagonised by the elasticity of the gelatinous substance which constitutes the chief mass of the umbrella.

It is, indeed, in the motions of the medusæ that we find contractility manifesting itself in its highest degree of intensity among the HYDROIDA. In these beautiful zooids the contraction of the sub-umbrellar fibres necessarily diminishes the cavity of the umbrella, and by thus expelling in a jet a portion of the water which had filled it in its expanded state, causes the propulsion of the medusa in an opposite direction, or that in which the convexity of the umbrella is turned forward, while the relaxation of the fibres immediately following their contraction permits the elasticity of the umbrella to come into play, so that its cavity instantly resumes its original capacity, and receives within it a fresh supply of water, to be again expelled as a propelling force by the energetic contraction of the fibres. The part played here by the velum would seem to consist chiefly in controlling the diameter of the aperture through which the jet of water is propelled from the umbrella cavity.

But contractility is by no means confined to the fibrillated tissue. There are many parts of the HYDROIDA in which no trace of fibres can be detected, and which are yet eminently contractile. Thus the broad four-lobed lip of the medusa of *Obelia geniculata* is remarkable for its mobility and its power of constantly changing its form while under observation, and yet it consists exclusively of a single layer of differentiated masses of protoplasm (membraneless cells) without the slightest trace of fibres.

Ecker has shown that the body of *Hydra viridis* is to a great extent composed of a contractile, semifluid homogeneous substance, agreeing in all essential points with the sarcode matter of the lowest animals. Ecker, however, is wrong in denying a cellular structure to *Hydra*, for the sarcode is not only differentiated into distinct cell-masses, but these masses are included each—in most cases along with certain granular products—within a proper cell-wall. By the rupture of the cell-wall the protoplasm can be liberated under the microscope; and Ecker has seen it then undergoing evident contraction, forming isolated masses, which continually change their shape like an *Amœba*.

There can be little doubt that many of the motions of the HYDROIDA are due to the contractility of this homogeneous sarcode; and while we may refer the sudden retraction of the hydranth when touched to the action of the fibrillated tissue, its subsequent slow extension would seem to be the result of the contractility of the sarcode, probably combined with the general elasticity of the tissues.

I have already shown that the substance which fills the nematophores of the *Plumularidæ* is mainly composed of a similar sarcode, which here, however, is not confined in cells; and it can, therefore, extend itself beyond the surface of the hydroid in the form of long pseudopodia, which will occasionally even branch exactly as in certain *Rhizopoda* (see woodcuts, figs. 50, 51). The remarkable capsules filled with thread-cells, which are borne along the marginal tentacles of the medusa of *Gemmaria implexa* (Pl. VII, fig. 3, 4), are supported on peduncles of extraordinary extensibility. In these peduncles we have also an example of true sarcode identical with that of the *Rhizopoda*. Strethill Wright has also shown that those filiform processes of the ectoderm of the HYDROIDA, which he calls "palpocils," are composed of a true rhizopodal sarcode; and these processes are probably offsets of a very thin sarcode layer, which, as already mentioned, can be seen, in certain cases, to extend over the surface of the hydranth.

Under the head of contractility the phenomena of ciliary motion must also be included. Vibratile cilia, as we have already seen, exist in almost every case on the walls of the somatic cavity, and mainly contribute to the production of the currents so well known in the nutritive fluids of the HYDROIDA; while the planula or early locomotive stage of most hydroids, as well as certain hydroid medusæ (*Trachynema*) and the free sporosac of *Dicoryne conferta*, are provided with an external covering of vibratile cilia.

5. *Sensation.*

Of late years several observers have believed themselves successful in demonstrating a nervous system in the HYDROIDA, while others have refused to admit the existence of a differentiated nervous system in these animals, and consider the arguments which have been adduced in favour of its presence as resting upon imperfect or incorrectly interpreted observations.

The advocates for the existence of a specialised nervous system in the HYDROIDA all agree in regarding as its principal part an apparent filament with ganglion-like enlargements, which may be seen running in the form of a ring round the margin of the medusa just below the circular canal. Agassiz maintains the existence of such a ring-like cord, and assigns to it the function of a nerve-ring, in *Sarsia*, *Tiaropsis*, *Staurophora*, and *Bougainvillia*; M'Crady in *Eucheilota*; Fritz Müller in *Tamoya*, a genus belonging to the family of the *Charybdæidæ*, as well as in *Liriope* and *Cunina*, true hydroids;[1] and Leuckhart in a medusa which he refers to Gegenbaur's genus *Eucope*; while Hensen also admits the presence of a nerve-ring in the *Eucope* of Gegenbaur. But by far the most complete description we possess is that by Haeckel,[2] who has studied the structures in question

[1] The hydroid structure of the *Œginidæ*, in which *Cunina* is included, must follow, from the remarkable observations of Haeckel on the structure of *Cunina* and on its genetic relations with the Geryonidan Medusæ.

[2] Haeckel, op. cit.

with great care in certain medusæ belonging to the family of the *Geryonidæ*, more especially *Glossocodon* (*Liriope*) *eurybia* and *Carmarina hastata*, where it would appear that they are very conspicuous, and well fitted for examination.

According to Haeckel the nervous system in the *Geryonidæ* consists of a very slender ring-like cord, which runs round the margin of the umbrella immediately below the circular canal, and under each marginal vesicle swells into a ganglion. From these ganglia filaments are sent off, one along the course of each radial canal as far as the stomach, and one to each of the tentacles, while another penetrates the marginal vesicle in order to undergo within it a peculiar distribution. In the system thus constituted he believes that he has succeeded in demonstrating nerve-elements. The nerve-cells of the nervous ring are contained in the ganglia only; in the intervening portions the ring presents merely a longitudinally striated appearance.

While with Haeckel's very detailed description we should hardly be justified in denying the existence of a marginal nerve-cord with ganglia in the *Geryonidæ*, I am by no means prepared to attribute a similar significance to the cord-like structure which may be seen running round the margin of the umbrella in other medusæ (Pl. XVI, fig. 8, and woodcuts, figs. 58 and 59). I have in several cases carefully studied this part of the medusa, and have arrived at the conviction that in all these the apparent cord is only the ectodermal layer, which lies immediately upon the distal side of the circular canal, and constitutes the extreme margin of the umbrella, presenting, when viewed along the plane of the codonostome, the appearance of a chord. In the medusa of *Campanularia*, which Gegenbaur refers to his genus *Eucope*, and in that of *Obelia*, which he includes in the same genus,[1] I have no doubt as to this being the true interpretation of the supposed nerve-cord, while the structures assumed to be ganglia are only thickenings of the ectoderm at the points which give attachment to the *lithocysts* or sense-capsules, to be presently described.

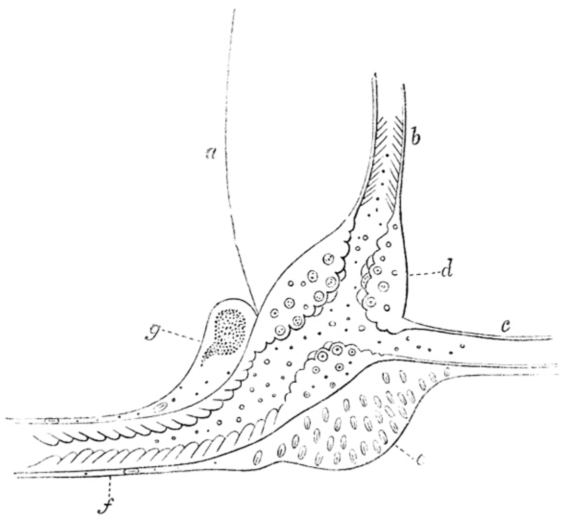
Besides the structures to which the significance of a nervous system has been thus assigned, certain bodies which have been long known and regarded by common consent as organs of sense, hold a prominent place in many hydroids. They occur only in the medusæ, and are of two kinds—the *ocellus* and the *lithocyst*.

The Ocellus.—The ocellus consists of a little mass of pigment, forming a well-defined coloured spot, in some species black, in others vermilion or deep carmine. In most cases (Pl. V, fig. 3, Pl. VI, fig. 3, and Pl. IX, fig. 8) no other structure can be detected in the ocellus; but sometimes (Pl. XVII, fig. 5, and Pl. XVIII, fig. 6) a transparent, refracting body may be seen immersed in the pigment mass. The ocellus is always situated in the walls of the bulbous dilatation which exists at the root of the marginal tentacle of the medusa (woodcut, fig. 56), where it lies very superficially, being imbedded exclusively in the ectoderm, while a

[1] The genus *Eucope* was founded by Gegenbaur for certain small medusæ which are known to be the planoblasts of campanularian hydroids. He subdivides his genus into a deep-belled and a shallow-belled section—sections, however, which differ from one another by characters which are at least of generic value. The deep-belled forms are the planoblasts of the true *Campanulariæ*, while those with shallow bells are the planoblasts of another campanularian genus (*Laomedea* of authors, in part), and had already been described by Péron and Lesueur, under the generic name of *Obelia*. *Eucope*, as a generic appellation, must therefore be suppressed in favour of the older names of *Campanularia* and *Obelia*, by which the deep-belled and shallow-belled forms must be respectively designated.

thin layer of the latter passes over it so as to separate it from direct contact with the surrounding water. In *Tyaropsis* alone does a similar definite pigment mass occupy a different position. In this genus it is situated not at the root of a tentacle, but at the base of a lythocyst, in the interval between two neighbouring tentacles (woodcut, fig. 57). I cannot, however, regard the pigment-shot in *Tyaropsis* as the equivalent of the ocellus in other medusæ; for besides its connection with the lithocyst rather than the tentacle, it is imbedded in a thickening of the endoderm of the circular canal instead of being, as in the true ocellus, an exclusively ectodermal structure.

FIG. 56.



Part of the umbrella-margin, with basal bulb of marginal tentacle, in *Syncoryne eximia*.

a. Umbrella wall; *b*, distal extremity of a radiating canal;—vibratile cilia may be seen clothing its walls; *c*, part of circular canal; *d*, endoderm of bulbous dilatation of base of marginal tentacle;—it is thrown into prominent lobes, which project into the cavity of the bulb; *e*, cushion-like thickening of ectoderm loaded with thread-cells; *f*, marginal tentacle; *g*, ocellus, imbedded in a thickening of the ectoderm.

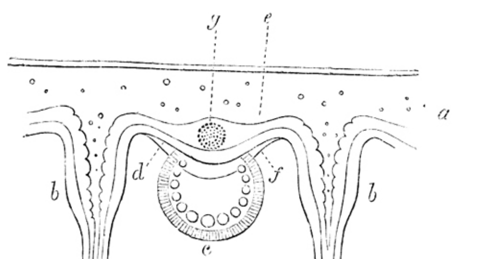
When the pigment of which the ocellus is composed is examined under a high power of the microscope, it is seen to possess a more definite structure than the granular coloured matter which is secreted in the walls of the somatic cavity. The ocellus is, in fact, composed of an aggregation of very minute cells, each filled with a homogeneous coloured matter. Such, at least, is the structure of the ocellus in *Syncoryne eximia*, and it is probable that in other cases a similar structure may be demonstrated.

As just said, a transparent body, capable of refracting the light, may be sometimes seen immersed in the pigment. A very distinct refracting body, of a lenticular shape, has been described by Quatrefage as imbedded in the outer side of the pigment in *Eleutheria*. In the nearly allied *Clavatella* I have found a minute, spherical, transparent, and refracting body imbedded in the same way in the pigment of the ocellus (Pl. XVIII, fig. 5); and Krohn and Claparède had already made a similar observation. It is, however, here of soft consistence; it seems to be easily broken down, and I have occasionally failed in detecting any trace of it. A similar refracting lens-like body may be seen in the ocellus of *Cladonema* (Pl. XVII, fig. 6). In every other case with which I am acquainted the ocellus consists merely of a mass of pigment-cells, without any structure which can serve as a refracting medium, unless the transparent layer of ectoderm which is continued in front of it may be regarded as contributing to the functions of the ocellus by its refractive action on the rays of light. In *Eleutheria* and *Clavatella*, indeed, the ectoderm presents at this spot an abruptly prominent convex surface, which Quatrefage has compared in *Eleutheria* to a cornea.

We have no means of forming anything like a certain conclusion as to the proper function of the ocellus. The universal presence of a definite pigment, and the occasional occurrence of a refractile, lens-like body, have suggested a comparison with an organ of vision, and against the justice of this comparison no sufficient argument has been yet adduced.

The Lithocyst.—Like the ocellus, the lithocyst is invariably developed on the margin of the umbrella. It consists of a transparent, mostly spherical capsule, within which are contained one or more transparent refractile concretions generally of a spherical or oval form. In *Cunina* alone among the HYDROIDA the concretions are, according to Haeckel, in the form of crystals, the usual condition of the analogous bodies in the *Discophora* or steganophthalmic medusæ. In most cases there is but one of these bodies in each capsule. Sometimes, however, they are more numerous. In *Tima Bairdii* the number varies from four to twenty in different lithocysts of the same specimen. In *Tyaropsis* they are arranged in a regular crescent parallel to the distal wall of the capsule, as Agassiz has pointed out in a North American species of this genus, and as I have myself found in a *Tyaropsis* from the Scottish coast (woodcut, fig. 57), in which I have counted about thirteen concretions in each capsule.

FIG. 57.



Part of the umbrella-margin of *Tyaropsis scotica*.

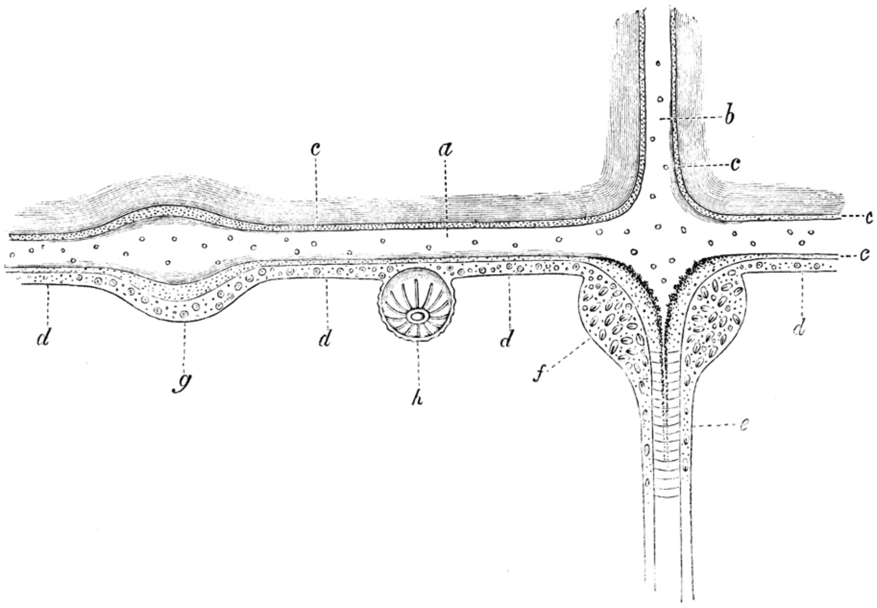
a. Circular canal; *b, b*, marginal tentacles; *c*, lithocyst; *d*, ectoderm of distal side of circular canal; *e*, endoderm; *f*, projection of the ectoderm, lying at the inner side of the lithocyst; *g*, ocelliform spot, imbedded in the endoderm of the circular canal.

The concretions offer resistance to pressure; and, according to Gegenbaur, would seem to consist of carbonate of lime in an organic basis, which retains the form of the original body after the mineral matter has been removed by acid. The mineral constituent is, according to Haeckel, a phosphate of lime in the *Geryonidæ*. At least, it here dissolves in acids without effervescence. The concretions, in every case, are quite motionless, and never lie free in the capsule.

A careful study of the lithocysts in two very common hydroids—*Campanularia Johnstoni* and *Obelia* (*Laomedea*) *geniculata*—has rendered apparent the following facts, which may probably be regarded as representing, in all essential points, the usual structure of these bodies among the HYDROIDA.

In *Campanularia Johnstoni* there are eight lithocysts which alternate with the eight marginal tentacles of the medusa; each lithocyst (woodcut, fig. 58*h*) is immersed for a little way in the cord-like structure, which forms the extreme margin of the umbrella, and which sends a very delicate extension of its substance over the whole of the free surface of the lithocyst. It consists of a spherical transparent and structureless vesicle or capsule, the greater part of whose cavity is occupied by a soft spherical pulp, in whose distal pole, or that opposite to the point of attachment of the vesicle, there exists a deep well-defined excavation; and within this, but not entirely filling it, is the spherical highly refractile concretion. In the pulp itself I could detect no trace of structure, but when seen in profile it has a slightly wavy outline, possibly occasioned by a special layer which intervenes between it and the walls of the capsule. Its surface is marked by twelve or fifteen delicate striæ, which take a meridional course at exactly equal distances from one another. Towards the distal pole they all terminate distinctly on the margin of the excavation, and may be thence traced to within a short distance of the opposite pole, though I have never been able to follow them exactly to it. The striæ generally appear light-coloured when contrasted with the darker intervening spaces. It is often difficult to detect any trace of them, but with a high power and carefully adjusted illumination they frequently appear with great distinctness, more especially under the action of dilute acetic acid.[1]

FIG. 58.



Part of the Umbrella-margin in the Medusa of *Campanularia Johnstoni.*

a, cavity of circular canal; *b*, cavity of a radiating canal; *c*, *c*, *c*, *c*, endodermal lining of radiating and circular canals; *d*, *d*, *d*, *d*, ectoderm forming the extreme margin of the umbrella; *e*, ectoderm of marginal tentacle; *f*, thickened ectoderm at the base of the tentacle loaded with thread-cells and directly continuous with *d*, the ectoderm of the umbrella-margin; *g*, marginal ectoderm thickened where it lies over the spot from which a new tentacle is to spring; *h*, lithocyst.

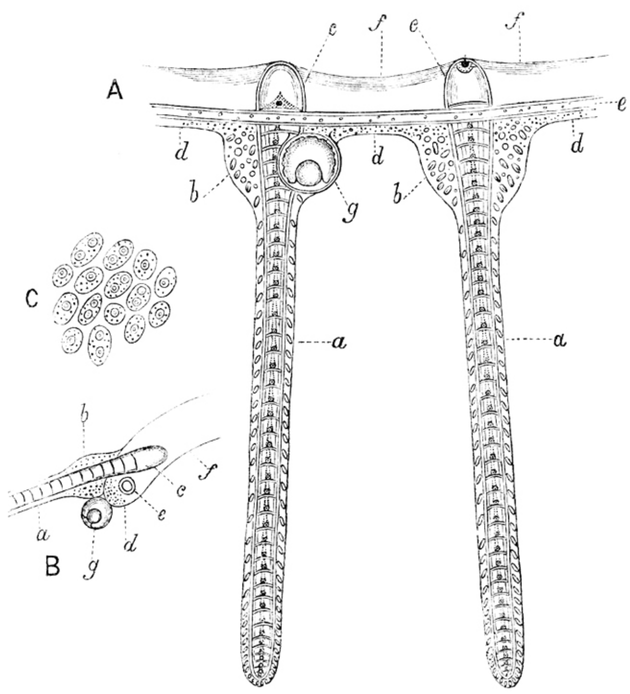
In *Obelia geniculata,* the lithocysts are also eight in number, two being situated in each of the four interradial spaces (woodcut, fig. 59 A *g*, and B *g*). They are sessile on the cord-like margin of the umbrella,and are placed each at the subumbrellar side of the base of a tentacle, but not exactly in its meridian plane. The structure of the lithocyst resembles that just described in *Campanularia Johnstoni*, consisting, like it, of a spherical capsule with a contained pulp, which nearly fills it, and which is excavated at the distal pole of the capsule into a cavity in which is the spherical refracting concretion. I could, however, obtain no distinct evidence of the meridional striæ visible in the lithocyst of *C. Johnstoni*.[2]

[1] Busk appears to have noticed these striæ, for in a paper which he read before the Microscopical Society of London ('Trans. Mic. Soc. Lond.,' vol. iii, p. 22), and which gives the most complete account of the lithocyst we had possessed up to the time of its publication, the author describes "an indistinctly fibrous, radiating appearance," which might sometimes be detected in the more external parts of the contents of the lithocyst in a *Thaumantias*-like medusa.

[2] Keferstein and Ehlers ('Zoolog. Beiträge,' p. 88, pl. xiii, fig. 4) describe the *Eucope polystyla* of Gegenbaur, which is, however, really an *Obelia*. They give a good figure of the lithocyst, but they mistake the cavity in which the concretion is contained for a peduncle projecting into the capsule from its distal wall, and carrying the concretion on its summit. A similar mistake seems also to have been made by Fr. Müller ("Ueber die Randbläschen der Hydroidenquallen," in Max Schultze's 'Arch. f. Mic. Anat.,' 1865, vol. i, p. 143), in his account of the lithocyst of an allied Medusa.

In most cases no definite structure can be detected in the walls of the external capsule. In an undescribed species of *Tyaropsis*, however (*Tyaropsis scotica*, woodcut, fig. 57), these walls are composed of very distinct prismatic cells, lined with a finely granular layer, which immediately invests the pulp and the zone of concretions imbedded in its surface, and I have noticed a similar structure in another medusa allied to *Thaumantias*. Gegenbaur has pointed out the existence of a layer of polygonal cells, which lines the capsule in one of the *Geryonidæ*, an observation which has been confirmed by Haeckel in other members of this family; and in the medusæ of *Campanularia* and *Obelia* described above there is indication of a special lining of the capsule.

Fig. 59.



Medusa of *Obelia geniculata*.

A. Part of the umbrella-margin. *a*, *a*, marginal tentacles; *b*, *b'* thickened ectoderm at the base of the marginal tentacles; *c*, *c*, large cell forming the proximal extremity of the marginal tentacle where it is plunged into the gelatinous substance of the umbrella; *d*, *d*, *d*, ectoderm forming the extreme margin of the umbrella; *e*, circular canal; *f*, *f*, gelatinous substance of the umbrella; *g*, lithocyst.

B. Meridional section of umbrella-margin. *a*, marginal tentacle; *b*, thickened ectoderm at base of marginal tentacle; *c*, large cell forming the proximal extremity of marginal tentacle; *d*, ectoderm of extreme margin of umbrella; *e*, circular canal in transverse section; *f*, gelatinous substance of umbrella; *g*, lithocyst.

C. Structure of epithelium clothing the inner surface of the umbrella. In several of the cells the nuclei have undergone division.

Hensen, in his remarkable memoir on the auditory organ of the Decapod Crustacea, describes the lithocyst of a medusa, which he refers to Gegenbaur's genus *Eucope*, and maintains that the concretion is connected to the walls of the capsule by a bundle of very fine hairs ("auditory hairs").[1] This observation of Hensen, however, has not been confirmed by other investigators, and I consider it almost certain that the meridional striæ described above have given rise to the appearance which Hensen has mistaken for hairs.[2]

[1] "Studien über das Gehörorgan der Decapoden," 'Zeit. für Wissensch. Zool.,' vol. xiii, p. 355, note.

[2] The lithocyst has been studied with great care by Haeckel (op. cit.) in *Glossocodon eurybia* and *Carmarina hastata*, Geryonidan Medusæ which, from their large size, offer special facilities to the observer, though they belong to a peculiar type, and their lithocysts, as described by Haeckel, present features which differ in many points from the structure which, as we have already seen, these bodies present in *Campanularia* and *Obelia*.

In the Medusæ which form the subject of Haeckel's observations the lithocyst is completely included within the gelatinous substance of the umbrella-margin. It is described as a transparent sphere seated on the upper side of a ganglion of the nerve-ring. Its walls are formed of a homogeneous membrane lined with a pavement epithelium, and it is filled with what appears to be a watery fluid, into which projects from the upper free wall of the capsule a clear spherical body, attached to the wall by means of a broad short stalk, and containing within it one or more small, concentrically laminated concretions.

Within the capsule, on its base, there is seated a cushion-like body, apparently in immediate con-

The lithocysts are almost always freely exposed to the surrounding water upon the margin of the umbrella. In *Glossocodon* and *Carmarina,* however, they are entirely included within the gelatinous substance of the umbrella. They are usually sessile, but are occasionally (*Cunina*) borne upon a distinct peduncle; they generally occur in the interval between two marginal tentacles. In *Obelia,* however, they are situated on the inner side of the base of a tentacle.[1]

The distribution of the lithocysts on the umbrella margin is at first always symmetrical, and their number is equal to or a multiple of that of the radiating canals. It is only in certain cases in which the lithocysts become very numerous, as, for example, in *Tima,* that this numerical law ceases to be apparent.

We know as little of the function of the lithocyst as we do of that of the ocellus. Consisting as it does of a capsule and contained concretions, it presents a structure which has been compared with that of certain organs which are met with in the mollusca and in the crustacea, and which have in both these groups been generally regarded as organs of hearing, and a similar function has from analogy been attributed to the lithocyst. The analogy, however, is by no means so close as to justify us in attributing an auditory function to the organs in question, while their structure would seem to indicate a relation to light at least as intimate as to sound.[2]

nection with the ganglion of the nerve-ring. It is composed of roundish and fusiform cells, and Haeckel regards it as a nervous ganglion. On each side it is prolonged into a flat, longitudinally striated, band-like cord, which is evidently composed of close parallel fibres, and which he considers to be a nerve of sense. These two sense-nerves, after passing up like meridian lines on the walls of the capsule, unite at the opposite pole. Here the fine fibres which compose them appear to become interwoven into a cord, which, after forming the stalk of the spherical body which immediately encloses the concretions, passes into its interior. Haeckel regards this body as a second internal ganglion. It appears to be a round vesicle, containing within it a mass of small, closely aggregated cells. In the midst of these cells are the concretions, consisting of a calcified organic basis, the organic matter being apparently united with phosphate of lime. He is unable to satisfy himself as to the mode in which the fibres of the sense-nerves terminate within the spherical body, though he believes it probable that their extremities are in connexion with the cells existing in the interior of this body.

Haeckel's interpretation of the various structures which he thus finds in the interior of the lithocyst, and regards as ganglia and nerve-cords, may be open to criticism, though it must be admitted that it is not easy to offer any very satisfactory view of them. The two supposed sense-nerves which he has observed running in two opposite meridians on the inner side of the wall of the capsule will suggest a comparison with the meridional striæ described above, as apparent on the central pulp of the lithocyst in *Campanularia.*

[1] In *Oceania octona* and *O. turrita,* Forbes ('Monograph') describes a cavity at the base of each tentacle, just below the ocellus, and having within it a vibrating mass. He regards this cavity as a lithocyst, with its contained concretion. A recent opportunity of examining the *O. turrita* of Forbes has convinced me that what Forbes took for a lithocyst is only a dilatation of the gastrovascular system, with its contents set in motion by the vibratile cilia of the walls, a suspicion which had already been entertained by Busk and by Gegenbaur.

[2] The visual functions of the lithocyst, though maintained by Agassiz, Fr. Müller, and partly also by Haeckel, who is inclined to attribute to them a double function of sight and hearing, has been by no one so well supported as by Busk ("On the Anatomy of a Species of Thaumantias," 'Trans. Mic. Soc.

The two forms of sense-bodies now described are never associated in the same species, and the case of *Tyaropsis*, as already shown, affords no exception. It has been already stated, as a nearly universal rule, that the ocelli are confined to the true sexual medusa or gonocheme while the lithocysts are found only in the blastocheme. Exceptions to this rule, however, are afforded by *Thaumantias*, as limited by Gegenbaur, which, though a blastocheme, has ocelli instead of lithocysts, and by *Staurophora* and *Laodicea*, which are also blastochemes, though, according to Agassiz, the ocellus takes the place in them of the lithocyst. On the other hand, *Goodsirea*, Wright, has, according to Wright's observation,[1] lithocysts instead of ocelli, though it is a true gonocheme. *Melicertum*, another blastocheme, is, according to Agassiz, also very exceptional, for neither lithocysts nor ocelli are found in it.

The ocellus, however, is by no means so constantly present in the gonocheme as the lithocyst is in the blastocheme, many planoblasts, with the other characters of the gonocheme, having no definite pigment spot, though the bulbous expansion at the base of the tentacles, with its contained coloured matter, has in such cases been frequently confounded with a true ocellus.

Touch.—Analogy would lead us to regard it as probable that sensitiveness to touch resides in all parts of the surface of the HYDROIDA—such parts, at least, as are not under cover of a thick perisarc. It would seem, however, that this sensitiveness is in a special degree conferred upon the tentacles of both hydranth and medusa. The slightest contact of the tentacles of the hydranth with a foreign body not destined to be appropriated as food, will frequently be followed by the instant contraction of the entire hydranth, accompanied, in the calyptoblastic hydroids, by retraction within the hydrotheca, an action which is plainly subservient to the safety of the animal by causing its withdrawal from sources of injury. The ordinary contact, however, of pabulum with the tentacle, excites only the prehensile functions of one or more tentacles, and is not accompanied by any general contraction of the hydranth. In like manner the marginal tentacles of the medusæ instantly contract on being touched. We are not, however, obliged to conclude that these acts are necessarily accompanied by consciousness on the part of the hydroid. Like many other apparently conscious acts in the animal economy, they may be purely reflex and automatic.

Corda and Wright have described as organs of touch the minute bristle-like bodies to which the latter has given the name of palpocils (see above, p. 107). Haeckel[2] has also described as organs of touch certain long fine and stiff hairs ("Tastborsten"), which he has observed in *Cunina*, and which Gegenbaur[3] and Keferstein and Ehlers[4] have observed in *Œgineta;* they are developed from the epithelium lying over the ganglion-like swelling on which the lithocyst is seated in these medusæ;

Lond.,' vol. iii, p. 22), who adduces in favour of this view the action of the lithocyst on polarized light, when the concretion exhibits a well-defined black cross, indicating, as he believes, a gradually decreasing density from the centre to the circumference, and pointing to a close resemblance between these bodies and the crystalline lens of higher animals. Evidence of the sensibility of the hydroid planoblasts to light is found in their habit of congregating on the light side of the jar in which they may be confined. I have noticed, on the other hand, that the planulæ of *Plumularia pinnata*, in which, however, nothing like sense organs exist, avoid the light, always crowding towards the dark side of the jar.

1 'Edinb. New Phil. Journ.,' July, 1859.

2 'Die Familie der Rüsselquallen,' p. 137.

3 'Versuch eines Systemes der Medusen,' p. 266.

4 'Zoologische Beiträge,' p. 94.

while Häckel has found similar hairs arranged in three verticils upon the knob-like extremity of the tentacle in another medusa, *Rhopalonema umbilicatum*. It is probable that in attributing to these various structures a specially developed sense of touch, their true function has been assigned to them; but it must, at the same time, be admitted that we have no direct evidence of their real purport in the economy of the animal.

6. *Phosphorescence.*

Among the most remarkable faculties possessed by the HYDROIDA is the power with which many of them are endowed of emitting light—a power which, like contractility and sensation, ought, perhaps, to find its place among the functions of irritability, as it appears to be always manifested in obedience to the action of a stimulus.

If a healthy colony of *Obelia dichotoma*, for example, be irritated in the dark by being roughly touched, a beautiful pale-white light will be seen for an instant to flash along the branches. Here the power of emitting light would seem to reside exclusively in the trophosome, and I have sought for it in vain in the free planoblasts of this hydroid, where one might, *à priori*, expect to find it.

On the other hand, in species of *Thaumantias* and allied forms which I have met with swimming in the open sea, and which are almost certainly planoblasts liberated from some trophosome as yet unknown, the luminosity was very striking and beautiful. In these medusæ, when an individual confined in one of my jars was touched in the dark, the whole umbrella-margin became instantly lighted up by a multitude of luminous points. The luminosity was entirely confined to the margin of the umbrella, and, indeed, might be seen to have its exclusive seat in the bulbous bases of the marginal tentacles.[1] These phosphorescent hydroid planoblasts must be regarded as one of the chief sources of the luminosity of the sea.

In some of the most brilliantly phosphorescent hydroid trophosomes, the luminosity presents a singular intermittence, the light appearing, when the hydroid is touched, to *palpitate* in a very beautiful way over the surface. Its duration, however, is very transitory; within a few seconds it will have entirely vanished, and will then need a repetition of the stimulus to call it forth. After a few such repetitions the power seems to exhaust itself, and rest for some time is needed before it can be again excited.

The vapour of alcohol exerts a very marked influence on the emission of the light. On exposing a campanularian trophosome to alcoholic vapour, given off at a temperature of about 70° F., I was surprised to find that not only was a brilliant luminosity called forth, but that the light had acquired a persistence very different from its usual transitory manifestation. It continued, indeed, for about five minutes while held over the vapour, after which, though still exposed to the vapour, it gradually faded away.

It must be here borne in mind, however, that the action of the stimulus in the experiment

[1] Busk ('Trans. Mic. Soc. Lond.,' vol. iii, p. 22) has described the luminosity of a Thaumantias-like medusa, in which he also found the seat of the light to be confined to the marginal tentacular bulbs.

with the alcohol is continuous, while the mechanical stimulus exerts itself only for a moment. A stimulus presenting a closer parallelism with that of the alcohol is afforded by contact with atmospheric air. I have always found that the hydroid, when suddenly removed from the water into the air, becomes brilliantly luminous at the moment of the change of medium; the luminosity here, however, as in the case of simple mechanical stimulus, lasts only for a few seconds, notwithstanding the continuous action of the atmosphere on the animal. After its disappearance the vapour of alcohol will again call it forth, accompanied by the persistence which characterises the application of this stimulus.

Many hydroids, however, are destitute of phosphorescence. It does not exist in the fresh-water *Hydra*, and I have never witnessed it in any gymnoblastic form; while among the *Calyptoblastea* it would seem that only some are endowed with it. Observations, however, are still wanting on this point, and phosphorescence will doubtless yet be found in species in which it is not at present known to exist.

Of the immediate source of the phosphorescence we know scarcely anything, and though in some other phosphorescent animals it would seem to reside in a special luminous secretion we have no evidence of such a secretion in the HYDROIDA. Its dependence here on the operation of a stimulus would remove it from simple physical luminosity, such as may result from a process of slow combustion or from insolation. It may, it is true, be asserted that the immediate result of the stimulus is to excite the formation of a luminous secretion, but in the absence of all evidence of any such secretion this explanation cannot be accepted. The luminosity would here seem rather to be, like electricity in other cases, the direct accompaniment of certain vital actions.[1]

7. *Reproduction.*

The reproductive faculty, whose exercise gives rise to the calling into existence of a new being, belongs properly to the department of Physiology, while development, or the successive changes of form which this being undergoes, is a subject of Morphology, and has been already treated of in its proper place under that head.

Reproduction in the HYDROIDA may be either sexual or non-sexual; the sexual showing itself in the production and fertilization of the ovum, the non-sexual in the production of buds and in fission.

[1] Some observations which I have made on the luminosity of *Beroe* have brought out the somewhat unexpected result that the faculty of emitting light is not possessed by these animals at all times during the twenty-four hours. It does not exist in the presence of daylight, and *a previous seclusion of the animal for some time in darkness* is always necessary for its manifestation (see 'Proc. Roy. Soc. Edinb.,' 1862, p. 519). I have no reason to believe that this is the case with the HYDROIDA, though I have made no observations which can here be regarded as decisive. It certainly is not the case with *Noctiluca*, one of the most vividly luminous of animals, and one well fitted for observation.

a. Sexual Reproduction—Generation.

Comparison of the Sexes in the Hydroida.—The existence of differentiated sex in the HYDROIDA was first announced by Ehrenberg,[1] who maintained that the so-called "egg-capsules" in *Coryne*, *Sertularia*, &c., had the significance of special fertile animals, to which he gave the name of females, while he regarded the ordinary hydranths as the sterile individuals of the colony.

With this announcement we may date a well-marked era in the history of progressive discovery among the HYDROIDA; for it is to the happy conception of Ehrenberg that we must refer the more philosophic views which within the last few years have so greatly advanced our knowledge of the structure, functions, and relations of these animals.

The celebrated German micrologist, however, did not grasp the full meaning of the facts of which he had thus so nearly given us the exact interpretation; for he regarded the central column (blastostyle) of the gonangium in *Sertularia* as the equivalent of the central diverticulum (spadix) in the gonophore of *Coryne*, while he viewed the gonophores borne on the sides of the blastostyle in *Sertularia* as merely eggs equivalent to the true eggs contained in the gonophore of *Coryne*.

The doctrine of the sexual differentiation of the HYDROIDA was confirmed by Lovén in a remarkable memoir, originally published in the 'Transactions of the Royal Swedish Academy' for 1835, and thence translated into Wiegmann's 'Archiv.'[2] In this memoir Lovén gives an account of those singular extracapsular medusiform gonophores which are described above (p. 57) under the name of "meconidia;" he found them in a Campanularian hydroid (*Gonothyrea Lovéni*, Allm.), and recognised in them their true sexual function. He also describes the occurrence of medusi-form gonophores in two species of *Syncoryne;* and having observed that in the gonophores of one of these species the cavity of the umbrella was filled with ova, he distinguishes them from mere organs, and regards the gonophores in both instances as special female animals.[3]

Naturalists had now not only become familiar with the presence of true ova in the HYDROIDA, but they saw in the portions of the colony set aside for their production something more than mere organs. No one, however, had as yet discovered any trace of spermatozoa; Ehrenberg at this time makes no mention of a male element, while Lovén calls the nutritive polypites male, and in this view of their nature falls behind Ehrenberg, who more truly names them sterile or sexless individuals.

[1] 'Corallenthiere, Abhandl. der Königl. Akad. der Wiss. zu Berlin,' 1832.

[2] 'Beiträge zur Kentnniss der Gattungen *Campanularia* und *Syncoryne*, Wiegm. Arch.,' 1837. Erster Band, S. 239.

[3] It may here be noticed that Wagner had already (Isis, 1833, § 256, tab. xi) found medusa-like gonophores, filled with ova in a hydroid which he names *Coryne aculeata*, apparently a species of *Podocoryne;* but, not being aware of the doctrine of Ehrenberg only just announced, the exact significance of these bodies escaped him.

The doctrine of the sexuality of the HYDROIDA now waited only for the discovery of the male element in order to receive its complete development. This discovery was made by Ehrenberg, who, in 1838, pointed out the real nature of certain conical tubercles which at particular seasons are developed on the body of the freshwater hydra, and had been by previous observers regarded as a peculiar disease to which this animal was supposed to be subject, but which were now shown by Ehrenberg[1] to be true spermatophorous capsules, while a further and important step in this direction was made by Krohn, who a few years afterwards announced that he had, in the *Pennaria Cavolinii*, Ehren., found certain receptacles similar in form to the ovigerous ones long ago described by Cavolini in the same remarkable hydroid, but containing spermatozoa instead of ova. Similar observations were made on *Tubularia indivisa* and on *Eudendrium racemosum*, as well as on *Aglaophenia pluma* and the *Sertularia* (*Eudendrium?*) *missenensis* of Cavolini, in all of which Krohn succeeded in detecting spermatozoa.[2]

It is now certain that every species of hydroid gives origin to male and female zooids (or, in case of such medusæ as may be directly developed from the egg, to male and female sexually generated individuals), one destined for the production of ova, the other for that of spermatozoa. The separation of the sexes in distinct generative zooids, or in distinct individuals of a sexually generated offspring, is thus absolute and universal among the HYDROIDA. In by far the greater number of cases the separation is carried even further than this; for we scarcely ever meet with male and female gonophores in the same colony. As an almost universal rule, then, the HYDROIDA are diœcious; in other words, every colony is unisexual.[3]

Some few cases of a monœcious condition, however, occur. This has been noticed by many observers in the freshwater *Hydræ*,[4] where, indeed, it is the most usual condition. I have found it also in *Plumularia pinnata*, which sometimes carries on the same stem both male and female gonophores, and Hincks has observed it in some other sertularian hydroids.[5] In *Dicoryne conferta* too there may generally be found, among the dense forest of stems with which this hydroid invests the surface of univalve shells, some stems carrying male and others female gonophores. Each stem, however, carries gonophores of one sex only, though it would seem that both male and female stems are united by the creeping stolon into a common colony. In *Hydractinia*, on the other hand, whose habit is entirely similar to that of *Dicoryne*, we never meet with the two sexes in a common colony; perhaps even never investing the same shell.

Origin of the Generative Elements.—Throughout the whole of the HYDROIDA the generative elements originate between the endoderm and ectoderm, and, with one exceptional condition to be presently described, are always formed in the walls of an organ strictly homologous with the manubrium of a gymnophthalmic medusa.

[1] 'Mittheil. aus den Verhandl. der Gesellsch. naturf. Freunde in Berlin,' 1838.

[2] Krohn, "Einige Bemerkungen und Beobachtungen über die Geschlechtverhältnisse bei den Sertularinen," 'Müller's Archiv,' Jahrg. 1843, S. 174.

[3] Krohn had already noticed that, in all the species examined by him, the male and female gonophores were borne on separate colonies (loc. cit., p. 181).

[4] See especially Prof. Allen Thomson "On the Coexistence of Ovigerous Capsules and Spermatozoa in the same Individuals of *Hydra viridis*," in 'Proc. Roy. Soc. Edin.,' No. 30, 1845-47.

[5] 'Quarterly Journal of Science,' July, 1865, p. 409, note.

This organ forms the axile diverticulum in the young adelocodonic gonophore, and the manubrium of the sexual medusa, while it is represented by the entire sexual zooid which buds from the radiating canals in the blastocheme or non-sexual medusa.

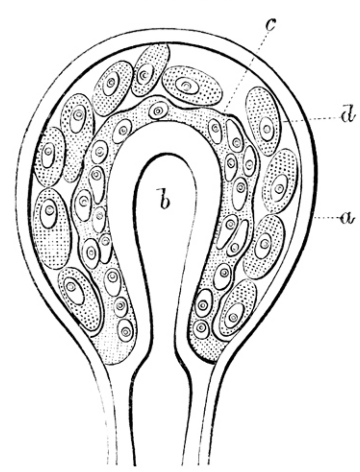
It is not at first easy to say whether the generative elements have their proper origin in the ectoderm or endoderm of this body, as in most cases they can be merely seen filling the space between these two membranes, which become more and more separated from one another as the included mass of ova or spermatozoa increases in volume.

From some favorable observations, however, which I have succeeded in making on certain species of hydroids, I have convinced myself that the true origin of the ova and spermatozoa is to be found in the endoderm, while the ectoderm serves merely as a confining and protecting sac until such time as the generative elements acquire sufficient maturity to allow of their liberation, which always takes place by simple rupture or absorption of the ectodermal sac.

Thus, in the gonophores of the male colonies of *Sertularia polyzonias* the spermatogenous tissue may be seen filling the entire space between the long cylindrical axile spadix and the surrounding walls of the gonophore. In most specimens it may be easily seen that the spermatogenous mass is far from being of uniform maturity throughout; for while towards the axis of the gonophore it is still very immature, the mother-cells being here distinctly visible with the ultimate spermatic cells within them, we find that towards the periphery it consists of free active spermatozoa. The youngest portion of the mass is thus that which is still in contact with the spadix or endodermal portion of the gonophore, while the oldest portion is situated externally, being in contact with the confining ectoderm—a condition which would be scarcely possible if the ectoderm, rather than the endoderm, gave origin to the spermatic cells.

A state of things exactly parallel to this may be seen in the female gonophores of *Coryne pusilla*, in which, moreover, the actual formation of the ova may be satisfactorily traced. At an early period in the development of these gonophores, the large thick spadix may be seen to be surrounded by a granular plasma, throughout which numerous minute nucleated cells are scattered (woodcut, fig. 60). These cells I regard as the germinal vesicles and spots of the future ova, round which no distinctly differentiated vitellus can as yet be detected. In a more mature stage of the gonophore, while the same peculiar tissue continues to invest the spadix, the peripheral portion of this tissue may be seen to be thrown off in the form of undoubted ova, consisting each of a germinal vesicle and spot precisely similar to those observed in the more central portion of the mass, but now with a portion of the common plasma differentiated round each germinal spot in the form of a a very definite vitellus. When the gonophore has attained complete maturity, the whole of the plasmatic mass, with its immersed nucleated cells, has become metamorphosed into fully formed ova.

Fig. 60.



Young Sporosac of *Coryne pusilla*, showing certain early stages in the formation of the ova.

a, Outer wall (perigonium) of the sporosac; *b*, cavity of spadix; *c*, plasma, investing the spadix, and having imbedded in it the germinal vesicles of the future ova; within the germinal vesicles are seen the germinal spot and the *punctum germanitivum*; *d*, fully formed ova, in each of which a portion of the common plasma has become differentiated as a vitellus round the germinal vesicle.

I have spoken above of an exception to the all but universal fact that the generative elements originate between the ectoderm and endoderm of a body homologous with the manubrium of a naked-eyed medusa. The exception referred to consists in the origination of ova in the blastostyle, as may be seen in *Sertularia pumila* and one or two other species of *Sertularia*.

In *Sertularia pumila* a solitary gonophore of the ordinary form, and containing in the usual way ova or spermatozoa, originates, as in other cases, by a bud from a blastostyle. In the female colonies, however, nucleated spherical bodies, in no way distinguishable from young ova, are found in the walls of the blastostyle itself, between whose ectoderm and endoderm they seem to lie (woodcut, fig. 21, *k*). I have not succeeded in satisfactorily tracing the destination of these bodies; but I have reason to believe that the true gonophores bud forth from that part of the blastostyle in which the nucleated bodies occur, and that these, as young ova, pass from the blastostyle into the budding gonophore, where they would then naturally occupy their normal position between the endoderm and ectoderm of an organ representing the manubrium of a medusa, destined to undergo there a further development before being discharged into the acrocyst, which, as we have already seen, exists in this species. Each gonophore, after having performed its duty as a receptacle, in which certain intermediate stages of development take place, would seem to disappear, and be succeeded by another, which in a similar way receives its young ova from the blastostyle on which it buds.[1]

b. Non-sexual Reproduction.

Gemmation.—As already said, non-sexual or agamic reproduction may manifest itself in the HYDROIDA either by budding or by fission. There is scarcely any part of the external surface of a hydroid which may not give origin to a bud, though the actual conditions which determine the formation of this bud are entirely unknown. Buds capable of becoming developed into one or other of the various forms of zooids, which make up the hydroid colony, may be emitted by the hydranth, by the hydrocaulus, or by the hydrorhiza. In the gonosome we find that not only does the blastostyle give origin to buds destined to take part in the generative functions, but that the medusæ themselves have the power of emitting buds from various parts of their surface. The form and development of these buds have already been considered in the morphological section of the present Monograph.

As an almost universal fact the bud, from whatever part of the hydroid it is emitted, has its somatic cavity in open communication with that of the budder, so that the common somatic fluid passes freely from the one into the other. Cases, however, have been recorded (see above, p. 82) in which certain Æginidan medusæ would seem to give origin to buds from the *internal* surface of the manubrium. It is possible that there may be here some error of observation, and, though

[1] Bodies, undoubtedly of the same nature as those here described, but without any indication of a nucleus, are figured by Agassiz in an American species, which he regards as identical with the *Sertularia pumila* of Europe (op. cit., pl. xxxii, fig. 9). They had also been already described by Lindström (op. cit.).

we owe the statement to able and trustworthy inquirers, it is yet to be desired that we had further verification of a fact so much at variance with the phenomena of gemmation as presented elsewhere among the HYDROIDA.

It is rarely that the medusa has been noticed to emit buds simultaneously with the production of ova or spermatozoa. Instances, however, are on record in which the sexually mature medusa has also multiplied itself by budding. This has been observed by Busch[1] in a medusa which he refers to the *Sarsia prolifera* of Forbes, and in which the basal bulbs of the tentacles gave origin to medusa-buds, which were coexistent with the presence of generative elements in the walls of the manubrium; by Krohn[2] in the medusa of *Clavatella*, which he has seen to be loaded with ova at the same time that medusa-buds were emitted from the margin of its umbrella; and by Sars,[3] who in a blastocheme (*Thaumantias multicirratus*, Sars) saw medusæ budding from the radiating canals simultaneously with the existence of the convoluted generative pouches.

No multiplication by budding has ever been noticed in the sporosac, a zooid which, it is to be borne in mind, is almost from its first appearance engaged in the production or protection of the generative elements.

Fission.—Though budding thus constitutes a highly characteristic and all but universal phenomenon among the HYDROIDA, multiplication by spontaneous fission is, on the other hand, rare and exceptional. Kölliker[4] observed a process of true fissiparous multiplication in a medusa (*Stomobrachium mirabile*, Köll.) obtained in abundance at Messina. The fission always commenced by a vertical division of the manubrium, which thus became doubled; and this stage of the process was followed by a similar division of the umbrella, separating the animal into two independent halves. The process, however, did not stop here, but was followed by a further division of each of the two first-formed segments into two others, by a fission at right angles to the direction of the first; while Kölliker's observations led him still further to conclude that the process does not terminate with even the second cleavage, but, on the contrary, that it still goes on, the animal continuing to multiply itself by frequent acts of fission.

Developed generative bodies were not observed in *Stomobrachium mirabile*, and Kölliker is of opinion that this medusa is only the young of another (*Mesonema cærulescens*, Köll.) found in the same seas, and in which no division takes place, but in which well-developed generative sacs occur along the course of the radiating canals.

But besides this case of fissiparous multiplication in the medusa I am enabled to give a very well-marked and interesting one which I met with in the trophosome of an undescribed campanularian hydroid (woodcut, fig. 61), to which I have assigned the name *Schizocladium ramosum*.[5]

I have not as yet met with this hydroid more than once. It is a profusely branched form, with its trophosome having much resemblance to that of *Obelia dichotoma*; but as no gonosome

[1] Busch, 'Beobacht. über Anat. u. Entwick. einiger wirbellosen Seethiere,' p. 1, pl. i, fig. 1.

[2] Krohn, 'Wiegmann's Archiv,' 1861. In the gemmiferous specimens of the *Clavatella* medusa examined by myself, there were no visible generative elements.

[3] Sars, 'Bescrivelser.'

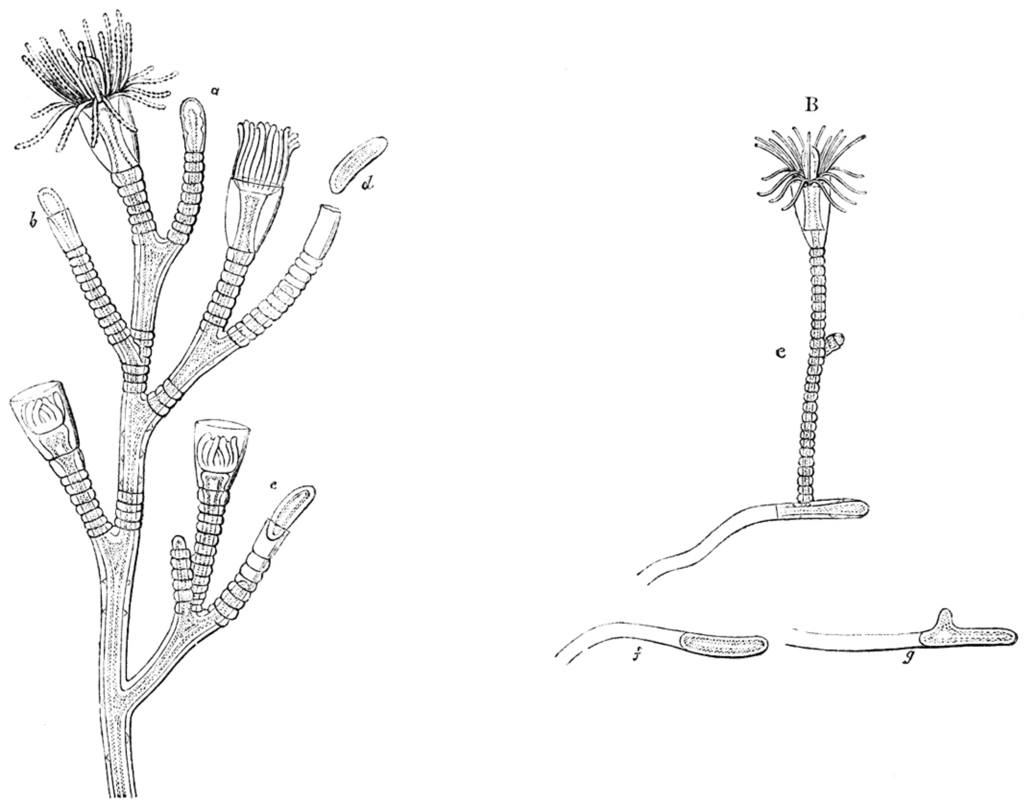
[4] 'Zoologische Beiträge, 1861.'

[5] "On a Mode of Reproduction by Spontaneous Fission in the Hydroida." 'Reports of Brit. Assoc. for the Advancement of Science,' 1870.

was present in any of the specimens collected, its exact systematic position cannot now be more than provisionally assigned to it.[1]

Besides the ramuli which here, as in the hydroids generally, support the hydranths, others are developed in abundance from all parts of the hydrocaulus. These (A, *a*) commence just like

FIG. 61.



Schizocladium ramosum, showing reproduction by spontaneous fission.

A. Part of an adult colony magnified about six diameters. *a*, One of the fissiparous ramuli, still entirely invested by the chitinous perisarc; *b*, a fissiparous ramulus, in which the contained cœnosarc has extended itself beyond the distal extremity through the ruptured perisarc; a constriction (the commencement of fission) has begun to show itself in the cœnosarc of the ramulus where still covered by the perisarc; *c*, the fission is completed, and the separated portion is escaping from the distal extremity of the ramulus; *d*, the separated portion has entirely disengaged itself, and has become a free frustule in the surrounding water.

B. Gemmation of the hydroid from the free fission frustule. *f*, The free frustule, after having excreted a mucous tube, from which it has partly withdrawn itself; *g*, a bud has begun to be emitted from the side of the frustule; *e*, the bud has become developed into a hydranth with its hydrotheca and hydrocaulus, and the young trophosome has begun to complicate itself by the emission of a branch.

the ordinary ramuli as offshoots from the hydrocaulus, and consist, as usual, of a continuation of the cœnosarc invested by a chitinous perisarc. Unlike the ordinary branchlets, however, they never carry a hydranth, but are destined for the multiplication of the colony by a process of spontaneous fission.

After the entire ramulus has attained some length, the contained cœnosarc continues to

[1] It is quite possible that in *Schizocladium ramosum* spontaneous fission never occurs simultaneously with true sexual generation.

elongate itself. In doing so it ruptures the delicate pellicle of chitine which closes the extremity of the ramulus, and extends itself quite naked into the surrounding water.

It is now that the process of fission commences. A constriction takes place in the cœnosarc at some distance below its distal extremity, and in the part still covered by the chitinous perisarc (*b*). The constriction rapidly deepens, and ultimately cuts off a piece (*c*), which slips entirely out of the perisarcal tube and becomes a free zooid (*d*), while the surface of disseveration soon heals over, and the axial cavity of the free frustule becomes here as completely closed as at the opposite end.

The detached segment is now about the $\frac{3}{100}$ of an inch in length, and strikingly resembles a planula in all points except in the total absence of vibratile cilia. It attaches itself by a mucous excretion from its surface to the walls of the vessel, and exhibits slight and very sluggish changes of form. It now slightly advances along the surface of support, withdrawing itself from the first-formed portion of the excretion, which remains behind as a tube of great tenuity, adhering to the sides of the vessel (*f*).

In tracing the further history of the frustule it was found that this never directly developes a mouth or becomes transformed into a hydranth. After a time a bud springs from its side (*g*), and it is from this bud alone that the first hydranth of the new colony is developed.

The bud which thus becomes developed into the primordial hydranth remains attached to the fission-frustule, which forms for it a sort of hydrorhiza, but which would seem ultimately to perish and give place to true hydrorhizal filaments. In the mean time the primary bud emits others (*e*), and a complex branching colony is the result.

The fission-frustule thus admits of a comparison with the free medusiform element of other hydroids, with which it agrees in never becoming directly developed into a hydriform trophosome, but from which it differs in the very important fact of taking no part in the true generation of the hydroid, and in giving origin to a new colony only by a non-sexual multiplication.

The fissiparous multiplication of *Schizocladium* would seem to throw light on the nature of certain bodies which made their appearance in a jar containing living specimens of *Corymorpha nutans* (see Plate XIX, figs. 12—14). These bodies presented a close resemblance to the fission-frustule of *Schizocladium*, and were seen to become developed into hydranths, which it is almost certain ultimately repeat the form of the adult *Corymorpha*. Their origin was, at the time I noticed them, very enigmatical, but I now regard it as highly probable that they are produced by a process of spontaneous fission from the filaments which are emitted towards the base of the stem in the *Corymorpha*. They would seem, however, to differ from the fission-frustules of *Schizocladium* in becoming *directly* developed into a trophosome.

The decapitation and successive renewal of the hydranths, referred to above (p. 69) as occurring in various species of *Tubularia*, may be compared with the phenomenon of fissiparous multiplication just described. In the decapitation of *Tubularia*, however, the separated hydranth is not destined to undergo any further development; it has matured its sexual buds, and has accomplished all the objects of its existence before being cast off, and it then perishes, to be replaced by another.

The decapitation of *Tubularia* admits of a still closer comparison with the formation and detachment of discs (*ephyræ*) from the hydriform stage (*scyphostoma*) of *Aurelia* and other *Discophora*. Here, however, the discs into which the *scyphostoma* breaks up by a process of transverse division which has its equivalent in the budding, by which the sexual zooids are formed from the hydriform trophosome of the HYDROIDA, are destined to undergo further development and enjoy an independent existence like that of the hydroid planoblasts. But notwithstanding this difference the analogy is still close and interesting; for the more simultaneous occurrence of the transverse constrictions which result in the formation of a pile of discs before their ultimate detachment in the *scyphostoma* has but little significance; while, as we have already seen, the hydranths successively produced and detached from the stem in *Tubularia*, are formed not by a process of budding, but by one of metamorphosis which shows itself in growth with change of form in the distal extremity of the stem in this hydroid,—a mode very similar to that by which the successive terminal discs or *ephyræ* are developed from the *scyphostoma*.

PLATE I.

Clava squamata.

Fig.

1. A male colony magnified. The hydranths are seen, some fully extended, others in various states of contraction.

2. The same, natural size, attached to a piece of *Fucus nodosus*.

3. A cluster of female gonophores.

4. A portion of the hydranth-walls, after having undergone natural histolitic decomposition, very much magnified. The ectoderm is seen to the left, resolved into minute cell-like elements, limited externally by a delicate structureless pellicle, and separated from the endoderm by a layer of fibrillated (muscular) tissue. The endoderm is breaking up into large spherical cells.

5. A male gonophore. The spadix is surrounded by the spermatic mass.

6. A female gonophore. A single ovum, with its germinal vesicle and germinal spot, lies on one side of the spadix, which it has pushed out of the axis of the gonophore.

7—11. Development of the embryo.

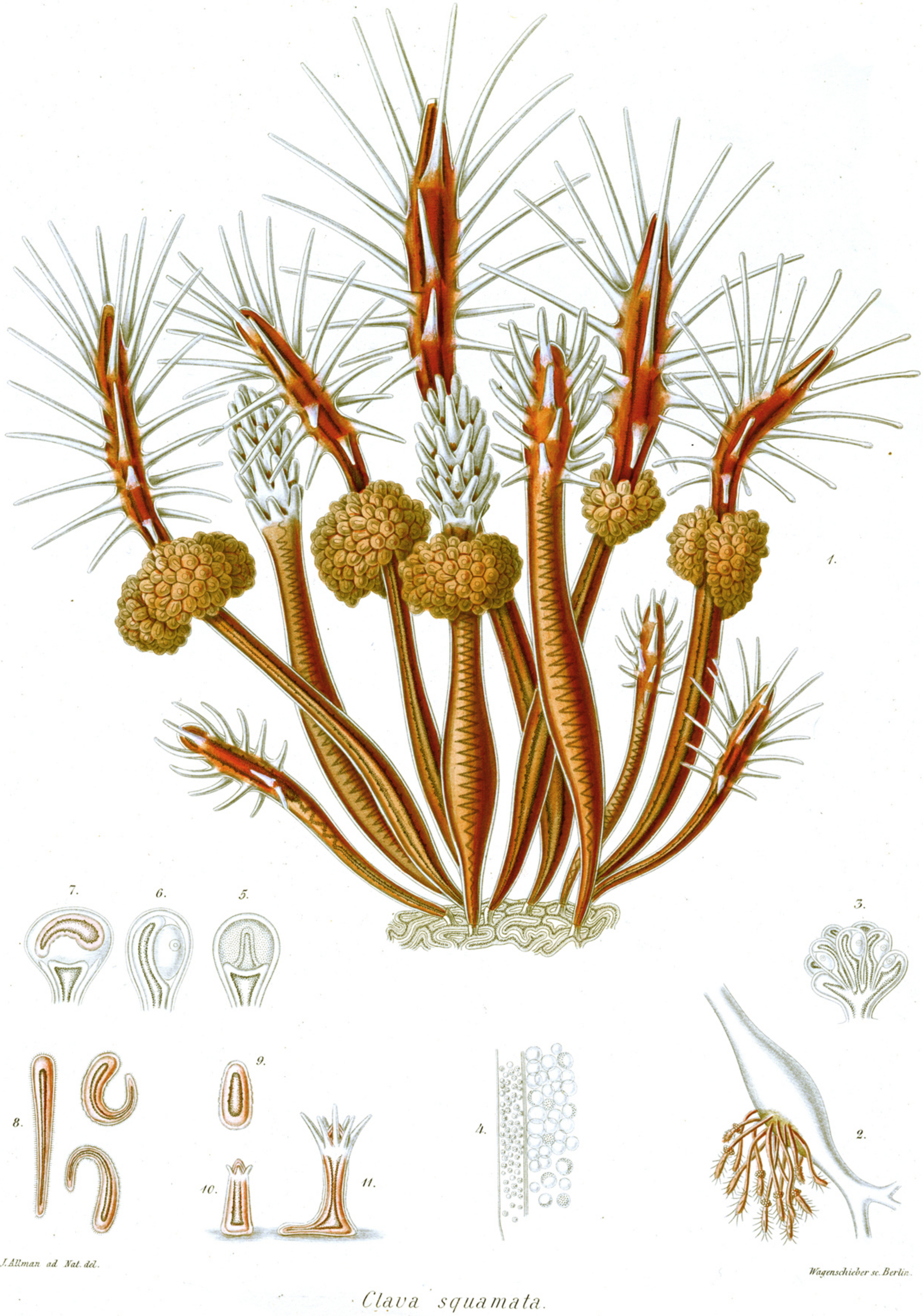
7. The embryo still confined within the walls of the gonophore, from which it is ready to escape into the surrounding water.

8. Embryos liberated as ciliated planulæ from the gonophores. They are drawn in various positions which they are in the habit of assuming, and may be seen either fully extended or more or less bent upon themselves.

9. The planula, after it has lost its cilia and has become contracted longitudinally preparatory to fixing itself.

10. The planula after it has become fixed and has developed a single verticil of tentacles.

11. The young *Clava* still further developed. A second verticil of tentacles has been emitted at the proximal side of that first formed, the tentacles of the second verticil alternating with those of the first; a stolon has begun to be emitted from the base.



G. J. Allman ad Nat. del.

Wagenschieber sc. Berlin.

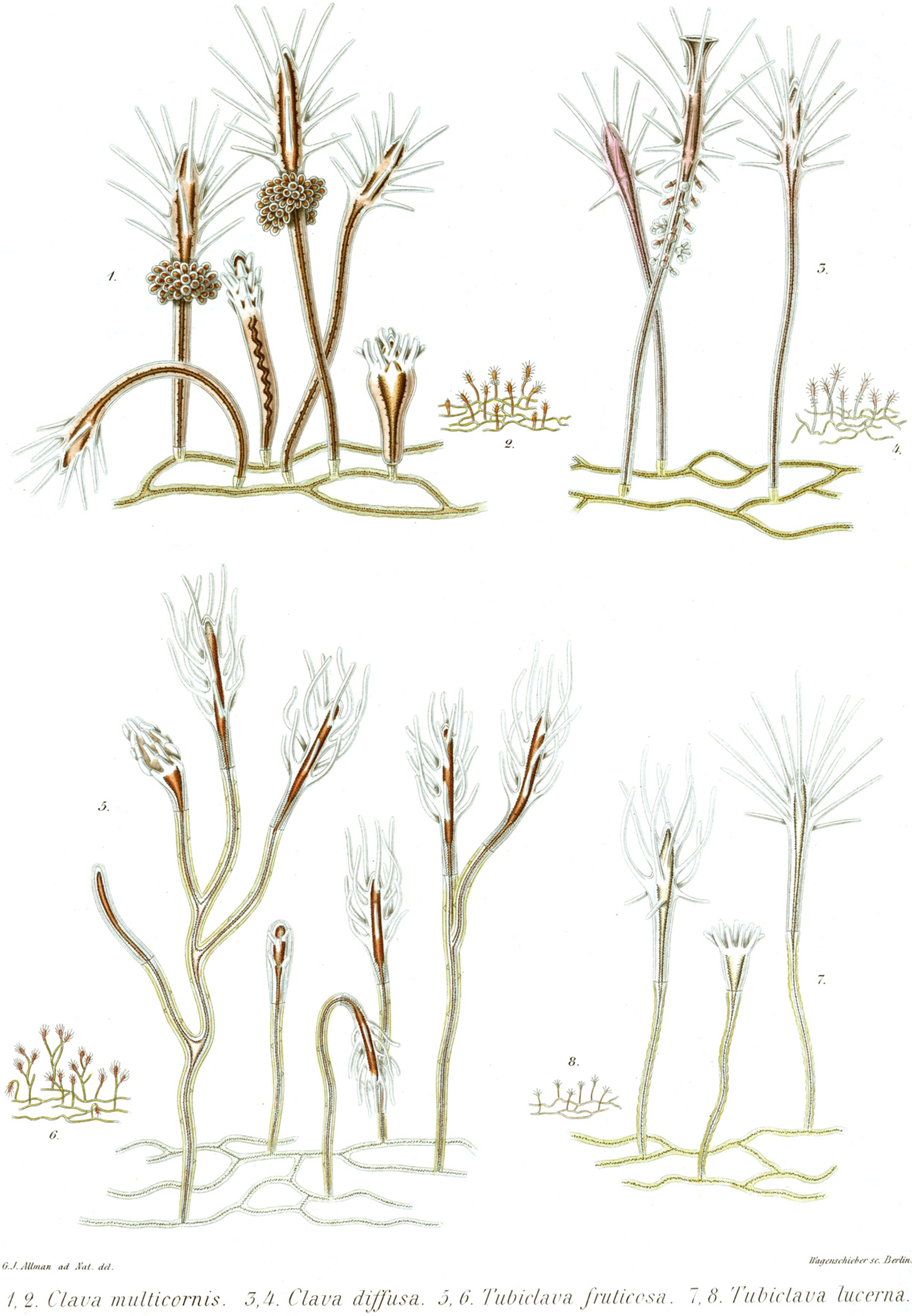
Clava squamata.

PLATE II.

Clava multicornis, Clava diffusa, Tubiclava fruticosa, Tubiclava lucerna.

Fig.

1. *Clava multicornis,* magnified.
2. The same, natural size.
3. *Clava diffusa,* magnified.
4. The same, natural size.
5. *Tubiclava fruticosa,* magnified.
6. The same, natural size.
7. *Tubiclava lucerna,* magnified.
8. The same, natural size.



G. J. Allman ad Nat. del. Wagenschieber sc. Berlin.

1, 2. *Clava multicornis.* 3, 4. *Clava diffusa.* 5, 6. *Tubiclava fruticosa.* 7, 8. *Tubiclava lucerna.*

PLATE III.

Cordylophora lacustris.

Fig.

1. Portion of a female colony, magnified; *a*, very young gonophore; *b*, gonophore more advanced, containing ova, which are embraced by the branches of a ramified spadix, and have their germinal vesicles distinct; *c*, gonophore still further advanced; the ramifications of the spadix have disappeared, and the segmentation of the vitellus has been completed in the ova; *d*, further stage of development, in which the ova have become planulæ, and are ready to escape from the gonophore; *e*, the gonophore has become ruptured at the summit, and the ciliated planulæ are escaping into the surrounding water.
2. A colony of *Cordylophora lacustris*, of the natural size, attached to the under surface of a piece of floating timber.
3. A male gonophore, the spermatic mass embraced by the ramifications of the spadix.
4. The distal portion of a male gonophore still more magnified: *a*, external chitinous investment, showing layers of deposition; *b*, ectotheca; *c*, endotheca; *d*, ramified spadix embracing the spermatic mass.
5. Planula much magnified, in two different states of contraction. Its interior is occupied by a large cavity, and an ectoderm and endoderm are distinctly visible in its walls.
6. The planula after it has lost its cilia and has become fixed.
7. Further stage of development, in which the distinction between stem and hydranth has become apparent, and a verticil of four tentacles has begun to be developed from the hydranth, while the stem has excreted a delicate chitinous perisarc.
8. The young *Cordylophora* still further developed; the tentacles are still in a single verticil, but have increased in length, and the hypostome has become prominent.
9. Mature spermatozoa; in the group to the left the heads are still enclosed in the generating cell.

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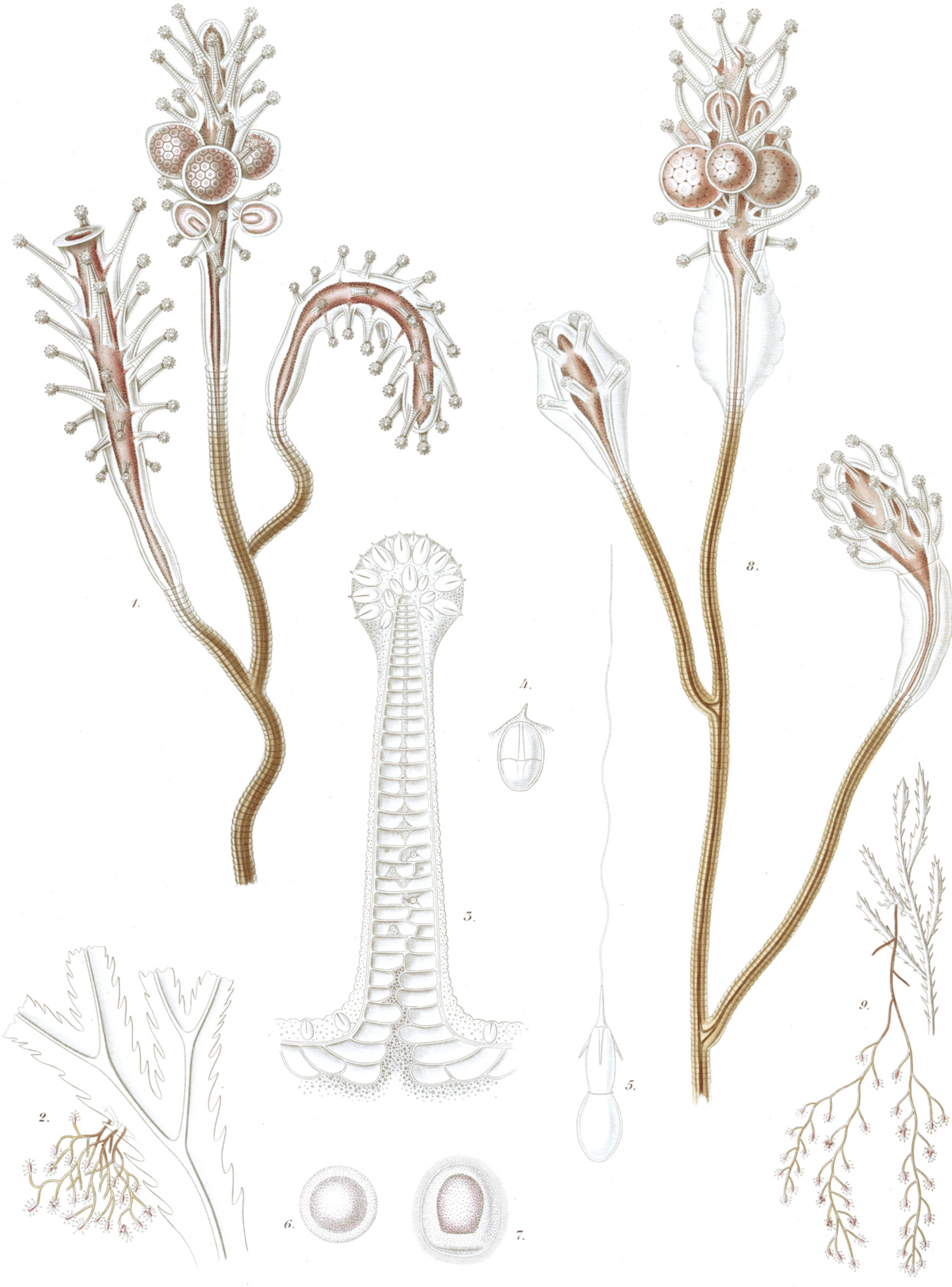
Cordylophora lacustris.

PLATE IV.

Coryne pusilla, Coryne vaginata.

Fig.

1. Portion of a female colony of *Coryne pusilla*, magnified.
2. A colony of *Coryne pusilla*, natural size, attached to a piece of *Fucus serratus*.
3. A tentacle of *Coryne pusilla*, very much magnified, showing its chambered endoderm and its capitulum loaded with thread-cells.
4. A thread-cell from the capitulum before the emission of its contents, and with the superficial portion of the ectoderm in which it is imbedded carrying a palpocil.
5. A thread-cell from the capitulum after the emission of its contents.
6. Mature ovum of *Coryne pusilla*, as it appears just after liberation by the natural rupture of the gonophore. In this stage the germinal vesicle becomes visible under compression.
7. Planula of *Coryne pusilla;* the cilia are very long. A peculiar striated area is visible towards one end.
8. A portion of a female colony of *Coryne vaginata.* At the left a hydranth-bud is seen, entirely enveloped in a delicate sac-like extension of the perisarc.
9. A colony of *Coryne vaginata*, natural size, attached to a piece of *Cystoseira*.



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1_7. Coryne pusilla. 8, 9. Coryne vaginata.

PLATE V.

Syncoryne eximia.

Fig.

1. A portion of a colony magnified, the hydranth to the left, loaded with planoblasts.

2. A colony, natural size.

3. A planoblast shortly after liberation, very much magnified; and, as it appears, with its tentacles extended when floating passively in the water.

4. Terminal portion of a marginal tentacle of the planoblast, showing its continuous axial tube, and its ectodermal spherules loaded with thread-cells.

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Syncoryne eximia.

PLATE VI.

SYNCORYNE PULCHELLA, SYNCORYNE FRUTESCENS.

FIG.

1. *Syncoryne pulchella*, magnified.
2. The same, natural size.
3. A planoblast of *Syncoryne pulchella*, shortly after liberation, as it appears while floating passively in the water.
4. *Syncoryne frutescens*, magnified.
5. The same, natural size.
6. Planoblast of *Syncoryne frutescens*, shortly after liberation.

Pl. VI.

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1_3. *Syncoryne pulchella.* 4_6. *Syncoryne frutescens.*

PLATE VII.

Gemellaria implexa.

Fig.

1. A portion of a colony, magnified.
2. A colony, natural size, attached to a piece of rock.
3. A planoblast shortly after liberation, as it appears while floating passively in the water, very much magnified. The tentacular appendages are seen with their peduncles in various states of extension.
4. A marginal tentacle of the planoblast still more enlarged, and with the appendages entirely retracted.
5. Longitudinal section of a portion of the hydranth showing histological structure: *a*, ectoderm with imbedded thread-cells; *b*, muscular layer; *c*, external large-celled layer of endoderm; *d*, internal or glandular layer of endoderm immediately surrounding the somatic cavity.
6. One of the clavate sacs filled with thread-cells from the umbrella-margin of the planoblast.
7. A thread-cell from the capitulum of a tentacle previous to evolution.
8. The same after evolution.
9. One of the large thread-cells from the ectoderm of the hydranth previous to evolution.
10. The same after evolution.

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Gemellaria implexa.

PLATE VIII.

Dicoryne conferta.

Fig.

1. Portion of a colony enlarged. The sporosacs are borne upon blastostyles, which spring, some from the hydrocaulas, and some from the hydrorhiza.
2. A colony of the natural size, spreading over a shell of *Buccinum undatum*.
3. The female locomotive ciliated sporosac, shortly after liberation from its ectotheca, as it appears when swimming. It is viewed at right angles to the plane of its two tentacles.
4. The same viewed in the plane of the tentacles.
5. The male sporosac still enclosed within its ectotheca.
6. The same after liberation from the ectotheca, as it appears when swimming.
7. Longitudinal section of a female sporosac made at right angles to the plane of the tentacles, and viewed under slight compression.

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Dicoryne conferta.

PLATE IX.

BOUGAINVILLIA FRUTICOSA, BOUGAINVILLIA RAMOSA, BOUGAINVILLIA BRITANNICA.

FIG.

1. *Bougainvillia fruticosa*, magnified.
2. The same, natural size, attached to the under surface of a piece of floating timber.
3. A planoblast of the same, just after liberation, and in the act of swimming away from its trophosome.
4. The planoblast floating passively in the water.
5. *Bougainvillia ramosa*, magnified.
6. A colony of *Bougainvillia ramosa*, natural size.
7. A planoblast of *Bougainvillia ramosa*, shortly after liberation, as it appears while floating passively in the water.
8. Mature planoblast (*Bougainvillia Britannica*), drawn from a specimen captured in the open sea. This planoblast has not yet been referred with sufficient certainty to its trophosome.

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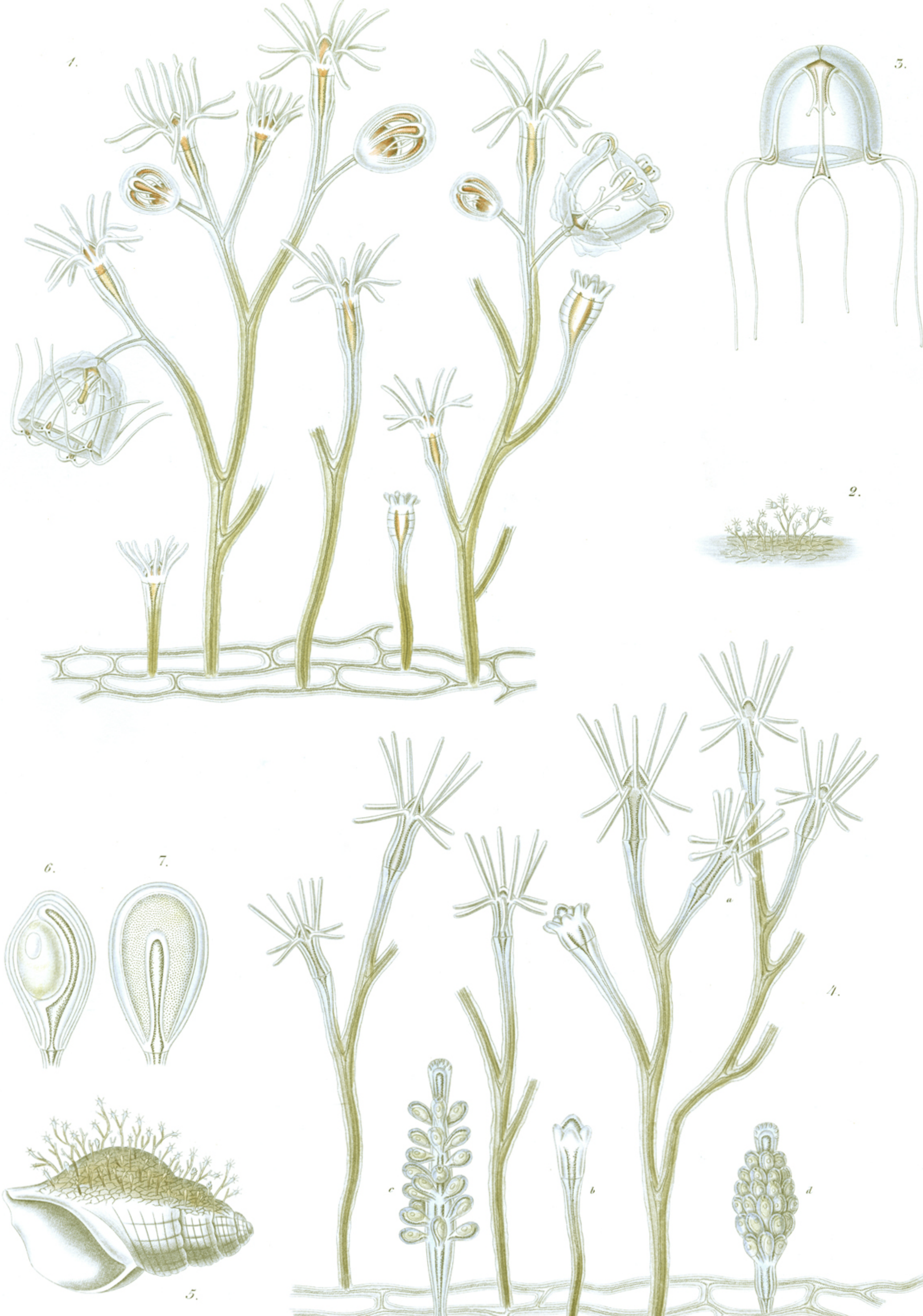
1_4. *Bougainvillia fruticosa.* 5_7. *Bougainvillia ramosa.* 8. *Bougainvillia Brittanica* (*medusa*).

PLATE X.

BOUGAINVILLIA MUSCUS, HETEROCORDYLE CONYBEAREI.

FIG.

1. *Bougainvillia muscus*, magnified.
2. The same, natural size.
3. Planoblast of the same, shortly after liberation.
4. *Heterocordyle Conybearei*, magnified: *a*, hydranth, in which the tentacles have assumed a clavate form as the result of contraction; *b*, young hydranth; *c*, blastostyle extended with its sporosacs; *d*, the same contracted.
5. A colony of *Heterocordyle Conybearei*, natural size, spreading over a *Buccinum* shell.
6. Female sporosac of same.
7. Male sporosac of same.



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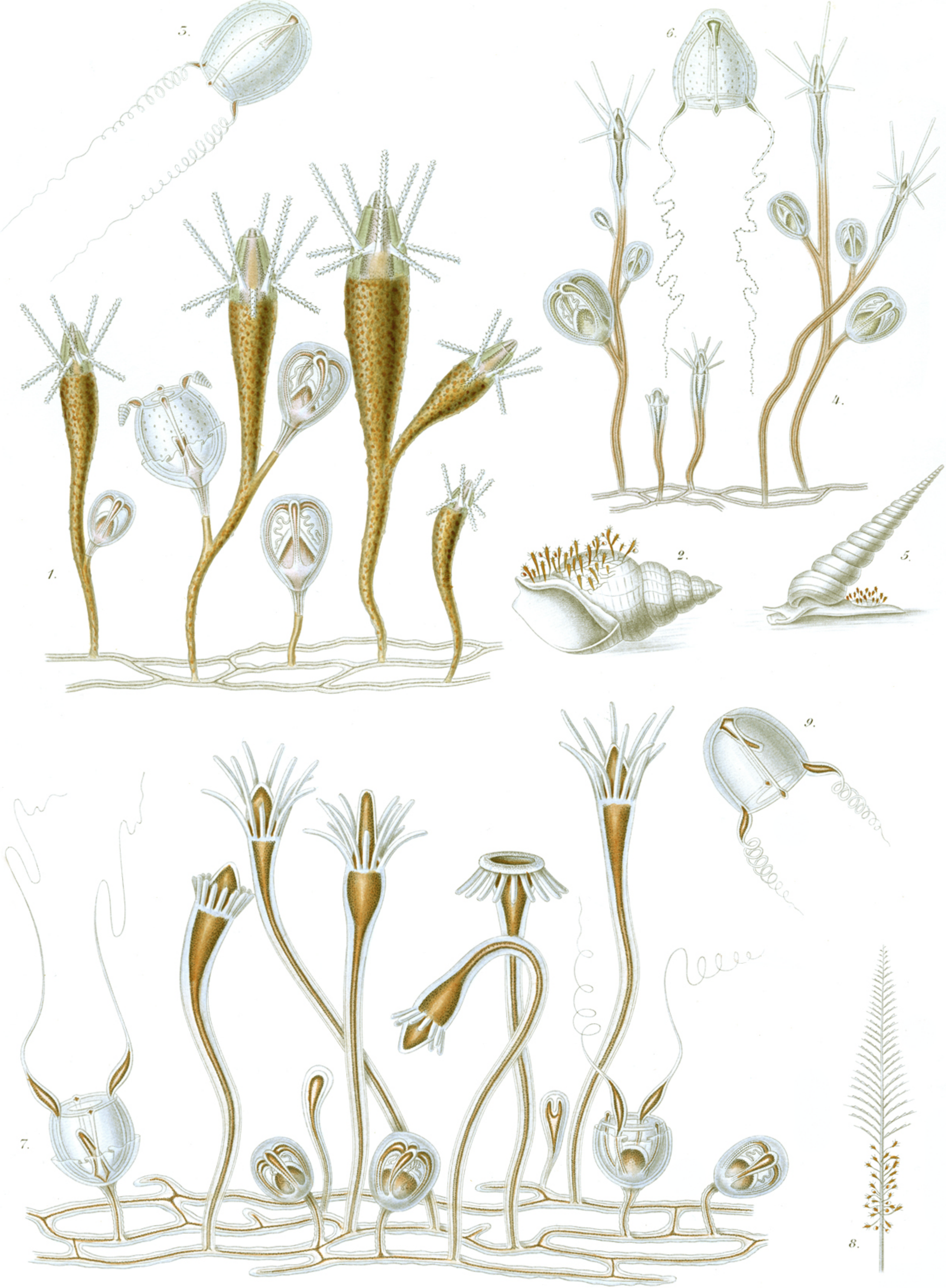
1_3. *Bougainvillia muscus.* 4_7. *Heterocordyle Conybearei.*

PLATE XI.

PERIGONIMUS VESTITUS, PERIGONIMUS MINUTUS, PERIGONIMUS SERPENS.

FIG.

1. *Perigonimus vestitus*, magnified.
2. The same, natural size, extending over the surface of a *Buccinum* shell.
3. Planoblast of same, shortly after liberation, and in the act of swimming.
4. *Perigonimus minutus*, magnified.
5. The same, natural size, attached to the operculum of *Turritella communis*.
6. Planoblast of same, shortly after liberation.
7. *Perigonimus serpens*, magnified.
8. The same, natural size, on a fragment of *Plumularia*.
9. Planoblast of the same, shortly after liberation, and seen while swimming.



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1_3. *Perigonimus vestitus.* 4_6. *Perigonimus minutus.* 7_9. *Perigonimus serpens.*

PLATE XII.

BIMERIA VESTITA, GARVEIA NUTANS.

FIG.

1. *Bimeria vestita,* magnified.
2. The same, natural size.
3. An ultimate ramulus of same, carrying a male sporosac, much enlarged, to show the structure of the sporosac with its ramified spadix.
4. *Garveia nutans,* magnified.
5. The same, natural size.
6. Distal portion of tentacle of same, much magnified.
7. A female sporosac of same, much magnified: *a,* ectotheca invested by a delicate chitinous pellicle; *b,* mesotheca; *c,* endotheca; *d,* rudimental radiating canals in the proximal portion of the mesotheca.
8. A male sporosac of same.
9. Spermatozoa of same. The mode in which the head of the spermatozoon is occasionally curved upon itself is here seen.
10. Planula of same.
11. Young of same, developed from the planula.

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1_3. *Bimeria vestita.* 4_11. *Garveia nutans.*