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Contributors

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[Extracted from the ANNALS AND MAGAZINE OF NATURAL HISTORY for
January 1848.]

Observations on the Development of the Medusæ. By JOHN REID, M.D., Fellow of the Royal College of Physicians of Edinburgh, and Chandos Professor of Anatomy and Medicine in the University of St. Andrews*.

[With two Plates.]

THE following observations were made upon three colonies of the larvæ of a *Medusa*. One of these was procured on the 15th of September 1845, and the other two on the 11th of July 1846, adhering to the lower surface of stones in pools near low water mark. The stones were of a size which readily permitted them to be conveyed home, where I have kept them up to the present time. The mode I have followed in keeping these animals alive is this. The stones to which they adhere are placed in vessels of considerable size, supplied daily with water fresh from the ocean, and the animals fed once or twice weekly with small morsels of mussels, which they readily swallow. The first of the three colonies consisted of between thirty and forty individuals, and the largest was between two and three lines in length; the individuals composing the other two colonies were more numerous and of somewhat larger size.

After I had completed my examination of the structure of these animals I discovered that they had been described by Sars, first under the generic name of *Scyphistoma*, and afterwards as the larva of the *Medusa*†.

Many of the larvæ increased much in size several months after I took them home, and the body of one that I measured was $\frac{1}{3}$ rd of an inch in length and $\frac{1}{3}$ th of an inch in diameter; another was $\frac{4}{12}$ ths of an inch in length and $\frac{9}{12}$ ths of an inch in circumference.

* These observations were laid before the Literary and Philosophical Society of St. Andrews at the Meetings of the 4th of May 1846 and the 5th of April 1847, and abstracts of them were printed in the 'Transactions' of the Society, and reprinted in Nos. 118 and 131 of the first series of this Journal.

† Annales des Sciences Naturelles, tom. xvi. p. 321, 1841.

As every part of their body is contractile, they can assume a great variety of forms. The more common of these are represented in Pl. V. figs. 1, 2, 3, 4 and 5. Though almost all of them are throughout of a grayish white colour, a few presented spots or patches of a purple colour, which were sometimes observed to disappear and reappear in the same individual. The tentacula are generally from twenty-two to twenty-seven in number, and when fully expanded are three or four times the length of the body. In one that I measured the body was $\frac{4}{24}$ ths of an inch, and the tentacula $\frac{12}{24}$ ths of an inch in length; in another the body was $\frac{2}{24}$ ths, and the tentacula $\frac{8}{24}$ ths of an inch in length. The mouth is very dilatable and varies much in shape, but is most commonly quadrangular. When fully expanded it forms a round aperture occupying nearly the whole of the disc (fig. 5); at other times its margins or lips are elongated and approximated so as to form a considerable quadrangular projection (fig. 2 *b*). Its more common condition perhaps is that represented in fig. 3 *a*.

The four round, equidistant and slight depressions placed between the mouth and margin of the disc are represented in fig. 2 *a*.

The body and tentacula of the larva are composed of two distinct layers, an internal and external. The internal layer chiefly consists of nuclei and nucleated cells (Pl. VI. fig. 19) of various sizes, some of them containing a large number of nuclei; while the external is chiefly composed of a structureless substance with numerous minute nuclei disseminated through it. Numerous nearly elliptical and oval capsules (filiferous capsules), having a long thread or filament coiled up in the interior of each, are fixed upon the outer surface of the external layer, and in much smaller number upon the inner surface of the internal layer, where it lines the internal cavity or stomach. These capsules are most abundant upon the external surface of the tentacula. Fig. 20 is a highly enlarged view of a small portion of one of the tentacula, showing the filiferous capsules attached to its outer surface. These filiferous capsules vary much in size, but the largest are generally of a uniform size, nearly of an elliptical form, and about $\frac{1}{2000}$ th of an inch in their largest diameter (Pl. V. fig. 8). Several of these, detached in examining portions of the larva under the microscope, had burst open at the smaller end, and the spiral thread projected through the opening and was uncoiled (fig. 9). In the entire capsule a rounded and narrow column passes from the smaller end, beyond which it slightly projects, in the direction of its longest diameter, nearly to its other extremity; and this column, to which the spiral thread is attached, protrudes from the interior of the capsule when it bursts. I have never observed these filaments projecting from the capsules when adhering to the surface of the body, unless when subjected to pressure, but it is difficult to use the

more powerful object-glasses necessary for distinguishing these, without compressing more or less the part under examination.

The internal is considerably thicker and more opaque than the external layer, is of a slightly yellowish colour when it accumulates at any point in greater abundance than usual, and is folded inwards to form the four equidistant projections seen on the surface of the stomach when the mouth is dilated (fig. 5 *a*), and when the body of the animal is slit open and then spread out (fig. 6 *c*). By making a transverse section of the body, the relative thickness of the internal and external layers, and the manner in which the internal is folded to form the four pouches or short canals that project from the internal surface, are very distinctly seen (fig. 7). These four short canals (fig. 7 *a*) terminate at their upper end in another canal, encircling the mouth and placed between it and the margin of the disc (fig. 6 *b*). Into this circular canal the hollow tentacula also open. The inner surface of the circular canal and the tentacula is lined by the internal layer. The four depressions (fig. 2 *a*) placed between the mouth and margin of the disc correspond to the termination of the four vertical in the circular canal. Across the bottom of these depressions, which at first sight look like apertures, a membrane is stretched sufficiently thin to permit readily of the transudation of fluids.

After reading Steenstrup's observations on the structure of these animals*, where he describes four canals,—one in each angle of the extensible membrane surrounding the mouth and forming the lips,—passing from the circular canal already mentioned, and also another circular canal placed in the free margin of the lips, I repeated my examinations; and though I used glasses of very different magnifying powers, and made numerous trials, I could not satisfy myself of the existence of these canals. No doubt four equidistant white lines presenting the appearance of canals are seen, in certain conditions of the extensible lips, running in the positions indicated by Steenstrup; but in some of the numerous forms which the lips assume these lines entirely disappear, and when present they seem to be formed by narrow ridges on the external surface, resulting from the quadrangular shape assumed by the lips. The free margin of the lips frequently presented indications of the presence of a canal, but I could never satisfy myself of its actual existence. In making such investigations, it must be kept in mind, that the internal is readily separated by pressure from the external layer, otherwise we may be led into error. In the almost daily examinations I have made of these animals during the last two years, I never

* On the Alternations of Generations, &c., translated for the Ray Society, pp. 22, 23.

observed the slightest traces of the hollow quadrangular body described by Steenstrup as growing from the lower surface of the cavity or stomach in the body of the animal, sometimes projecting as high as the mouth, and placed in the middle of the stomach, like the clapper in a bell.

The inner surface of the lips and of the stomach, and the external surface of the tentacula and body, are covered with very fine cilia, so that currents of water, unless when the mouth is shut, are constantly passing in and out from the mouth and along the tentacula. The cilia upon the external surface of the body require the use of the higher object-glasses for their detection, and for a long time they escaped my notice.

The colony of larvæ first obtained began to produce buds and stolons about the middle of January 1846, and the other two colonies at the end of July of the same year. With intervals of comparative repose they have gone on reproducing abundantly ever since; so that, notwithstanding they are constantly suffering loss by death and other causes, the number of individuals in each colony has greatly increased. Whenever buds and stolons are formed, they commence by a thickening of the internal layer at those parts, causing a bulging outwards of the external layer. A single bud (fig. 10 *a*), occasionally two buds, grow from the upper surface of the stolon, and these become developed into larvæ in the manner described by Sars. The buds form upon all parts of the external surface, but most frequently near the lower part, of the body. On many of the larger larvæ several buds were seen growing at the same time (fig. 11 *a*). As a bud enlarges it becomes elongated and attenuated at its free extremity, and bends itself downwards to reach the surface of the stone to which the elongated extremity adheres: after this the attached end is gradually separated from the body of the parent. When thus detached, a small opening presents itself at its upper end, its interior gradually becomes hollowed out and cilia grow upon it, and tentacula commence to sprout around the mouth, exactly in the same manner as in the buds formed on the upper surface of the stolons. The outer surface of the buds is also covered with very fine cilia. Several of the buds were found lying loose at the bottom of the vessels in which the stones are kept, probably detached by accident, and these after a time fixed themselves to the surface of the vessels, and passed through their development into larvæ in the same manner as those that adhered for a longer time to the bodies of their parents. One of these detached buds fixed itself at two separate points, and two mouths, each furnished with its own tentacula, were formed at opposite ends of its upper surface. When a bud was developed on a stolon, the connecting part between the bud and the

parent was more frequently absorbed, or at least disappeared, at other times the bond of connection remained; so that occasionally two, three or more larvæ of different or of nearly equal size might be seen growing closely united together at the base, as if one had split itself longitudinally into two or more separate individuals. This chiefly took place when the larvæ were so thickly clustered together that they had not room to spread sufficiently. When the buds were developed into young larvæ, these generally moved outwards from their parents to a small distance, leaving room for those that were to succeed them. This locomotion is generally slow,—one larva that I watched moved $\frac{6}{24}$ ths of an inch in fourteen days,—and is effected by a sliding motion of the attached end over the substance to which it adheres. In this motion the attached end bulges outwards in the direction it is about to take (fig. 12 *a*), and the whole of this end gradually follows, carrying of course the whole of the upper part of the body along with it. More rarely they move more rapidly by pushing outwards a narrow prolongation similar to a long stolon (fig. 4 *a*), which becomes fixed at its further extremity, and the attached end becoming loosened, the whole body is carried onwards by the contraction of the prolonged part. The older larvæ are almost or entirely stationary.

The larvæ, when detached from the surface to which they are adherent, can again fix themselves. I have frequently performed this experiment by placing those detached in separate vessels, and almost always successfully, when care was taken to disturb them as little as possible for three or four days, or longer. A considerable number of larvæ are adhering to the surface of the vessels in which the stones are kept*.

I made several experiments upon the reparative powers of the larvæ. In several the upper half of the body was cut off, and after three or four days its lower or cut end had closed in, and by the sixth day it had attached itself to the surface of the vessel, and shortly assumed all the appearances of an entire larva, sending out stolons and forming buds. Fig. 12 is a representation of the upper half of a larva eight days after it had been cut off. New tentacula, and a new mouth also, after several days presented themselves on the upper or cut end of the lower half. Several were divided longitudinally through their entire length, and when means were not taken to keep the cut edges apart they soon adhered again, and no traces of their division remained. In one divided longitudinally the two portions were kept apart,

* According to Sars, "si on détache violemment ces polypes, il n'y a qu'un petit nombre qui peut se fixer de nouveau, et alors ils n'adhèrent pas si fortement qu'à l'ordinaire; la plupart restent libres au fond du verre."—*Opus cit.* p. 339.

and in each the cut edges approximated and adhered, and two separate animals were thus produced from one.

The larvæ are voracious, and readily seize and swallow univalve or bivalve molluscans, or a crustacean, as large or even larger than their own bodies before they are stretched out, and after retaining them in the stomach, generally for about twenty-four hours in summer and nearly twice as long in winter, they reject them through the mouth. They also not unfrequently swallow one of their neighbours, and its sojourn in the stomach for some time terminates in its digestion and destruction. When they seize a univalve molluscan too large to be swallowed, they retain it firmly embraced in their tentacula, and insert their elongated mouth into the interior of the shell; and in like manner they keep dead articulate animals, or molluscans without shells, too large to be swallowed, in their tentacula for more than a day, and probably extract nourishment from them by acting on their textures by their extensible lips.

The larvæ of the first colony, obtained in September 1845, did not split transversely into young Medusæ in the spring of 1846, as I expected them to do, but continued to produce stolons and buds abundantly. A great number of them had then attained a large size, and many of them presented on their outer surface transverse rugæ, and four pretty deep equidistant vertical grooves, as represented in fig. 13, but none of them presented the appearances now about to be described, indicative of their splitting transversely into young Medusæ. In the beginning of February of the present year, the upper part of the body of some of the larvæ of the first colony became cylindrical, considerably elongated and much diminished in diameter, with thickly-set rings forming at the top. From the circumference of the rings first formed eight equidistant lobes or rays began to grow, the rings increased in size and became of a reddish brown colour, the tentacula gradually wasted away, and in the course of eight days the young Medusæ were beginning to detach themselves in the manner described by Sars. While this was going on at the upper part of the body, the process of elongation and the formation of new rings was proceeding downwards, as represented in Pl. VI. fig. 14, so that thirty or forty rings, each of which was about to become a young Medusa, could be counted on the body of one larva at the same time, and the body in some cases measured three-fourths of an inch in length. At this period the upper part of the body was of the form of an inverted pyramid, and had a distinctly reddish brown colour. As the grooves separating the rings increased in depth, it was observed that the body of the young Medusa above was at last attached only to the upper margin of the lips of the one below. Fig. 15 is a greatly enlarged representation of one of these young

Medusæ immediately after it had separated itself from the body of a larva. A small proportion, probably not above one-sixth or one-seventh of the larvæ, underwent this process of splitting into young Medusæ, and in no case that I observed did it extend through the whole length of the body of the larva; for a portion, often very small, at its attached end did not become ringed (fig. 14 *a*), threw out new tentacula before the young Medusæ last formed were detached, and it continued to live as a larva. Some of the larvæ of the other two colonies obtained in July of the preceding year began to yield young Medusæ about the middle of March, and exactly in the same manner as in the first colony. A fortnight, or more, generally elapsed, after the commencement of the separation of the young Medusæ in a larva, before the process was finished.

The general appearance and habits of the young Medusæ immediately after they have detached themselves from the larvæ have been described already by Sars, but there are various parts of its structure which stand in need of additional elucidation. External to the quadrangular mouth occupying the centre of the lower surface of the body of the young Medusa (fig. 15) are four bifid hollow processes, placed at equal distances from each other, and adhering by the end of their undivided portion to the inner surface of the inferior wall of the stomach (fig. 15 *a*). The inferior wall of the stomach, which forms also the inferior surface of the body, is so thin that at first sight these processes appear to be attached to the external surface. Fig. 16 is a greatly enlarged view of one of these bifid processes. Each of these processes forms two hollow floating tubes, communicating with the stomach or internal cavity by a common orifice (fig. 16 *a*), and having the edges of their external surfaces covered with numerous filiferous capsules (fig. 16 *b*). The stomach is large and extends nearly to the margin of the body or disc. Outside the position of the four bifid processes, and on the lower surface of the inferior wall of the body, there is a circular band, slightly elevated, more granular and opaque than the portion of the body placed within it, having prolongations passing off from its outer edge to the intervals between the eight bifid lobes or rays that spring from the margin of the body, and others along the centre of the lower surface of these bifid lobes, as far as the ocellus placed at the point of bifurcation of each lobe (fig. 15). When the animal contracts the marginal lobes in swimming, this circle becomes narrower, more distinctly defined, and approaches nearer to the mouth. In certain states of the animal the prolongations from the outer edge of this circle to the intervals between the eight bifid rays are longer than represented in fig. 15. When the animal is examined in certain positions and with glasses of

weak power, this circle, and the sixteen prolongations extending outwards from it to the intervals between the rays, and along the lower surface of the rays themselves, assume pretty nearly the appearances represented by Steenstrup as vessels; and as I have been unable to satisfy myself of the presence of any vessels there, I am inclined to believe that he has been misled in this way. I have occasionally observed the appearance of a thread-like nervous circle around the mouth, sending a filament along each of the rays towards the ocelli, on approaching which it bifurcated; but not having been able to make these out at other times, under circumstances that appeared favourable for their detection, I am not prepared to affirm that a nervous system is present.

At the point of bifurcation of each of the marginal lobes or rays there is placed, as Sars has described, a little eminence, hypothetically designated by Steenstrup an ocellus (figs. 15 *c* & 17 *a*). This ocellus forms a mammillary process, consisting of three distinct structures (fig. 17 *a*). The apex is chiefly formed of a considerable number of very minute crystals, and a small part of its base is more opaque and more granular than its larger middle portion. From a greatly enlarged view of the crystals occupying the apex of the ocellus, given in fig. 18, it will be observed that the upper are shorter and thicker than the lower; in fact, while a few of the former are almost as thick as they are long, some of the latter are almost needle-shaped. On fixing the polarizing apparatus to the microscope, it was observed that these crystals depolarized the light. I gave some of the young Medusæ to Principal Sir David Brewster for examination, and he returned me the following report: "The small raised portions of the Medusæ named ocelli consist each of six or more similar parts, each part having the property of depolarizing polarized light. When all the other portions of the animal are absolutely black, the ocelli shine with considerable brightness. Upon turning the Medusæ round in a plane perpendicular to the axis of vision, the individual parts of the ocelli disappear and reappear, according to the angle which their neutral axes (if they have double refraction), or their planes of separation (if they are merely polarizing laminae), form with the plane of primitive polarization. If these raised portions named ocelli are really organs of vision, the probability is that their axis of vision is perpendicular to the general surface of the Medusa."

The inner half of the lower surface of the bifid portion of each of the marginal lobes (fig. 17) is thinned off to a sharp edge, bounded externally by a continuation of the ridge running along the middle of the inferior surface already described, so that the bifid portion resembles in form a pair of strong scissors.

A number of larger and smaller filiferous capsules, similar to

those observed in the larvæ, adhere to the outer surface of the young Medusæ; and fine cilia are present on the inner surface of the lips and stomach, and on the outer surface of the four bifid processes floating in the stomach.

Though the normal number of the marginal lobes or rays is eight, yet occasionally they were as few as four and as many as twelve. In a few cases one or more of these lobes were trifid, with an ocellus placed in the cleft of each division.

I was not able to preserve the young Medusæ alive more than twenty days. During that time the lobes or rays had become shorter from the expansion of the body, and in a few, small papillæ were forming in the clefts between the lobes.

A comparison between the observations of Sars and Steenstrup upon the larvæ of the Medusa living in the ocean, and those made upon them while living in the artificial condition described, elicits some facts of considerable interest. According to Sars and Steenstrup, the colonies of these animals living in the ocean split up entirely into young Medusæ each spring, and completely disappear, and new ones are founded in September from the ova of the adult Medusæ; but while living in the artificial state, as was also some years ago remarked by Sir John Dalyell*, a certain number only of the individuals of the colony undergo this process, and that not throughout their entire length; for even a portion of each of those that form young Medusæ by transverse divisions of their substance, continues to live as a larva. The first colony I obtained was seventeen months in my possession before any of the individuals composing it underwent its development into young Medusæ. That the larvæ, even when living in the ocean, are not always formed in autumn and undergo their development into young Medusæ in spring, is evident from the fact, that two of the colonies in my possession were obtained from the ocean in July. Whether these larvæ had been generated the preceding autumn, and continued to live as such up to the time they were obtained from the ocean, or had been generated at some period subsequent to this, it is impossible to determine.

Account of a new Actinia.

Though the *Actinia* I am about to describe has in many respects a close resemblance to the *Actinia chrysanthellum* of Mr. Peach, described and figured in Dr. Johnston's late edition of his work on 'British Zoophytes,' vol. i. p. 220, it yet differs from it suffi-

* Jamieson's Philosophical Journal for 1836.

ciently, at least as far as I can make out, to justify me in regarding it as a distinct species. If this should be confirmed, I would propose to name it *Actinia cylindrica*.

Body elongated, cylindrical, free; tentacula uniserial, submarginal; mouth elongated upwards, forming a conical tube with small processes attached to its margin.

This animal was found in St. Andrew's Bay, by Mrs. Macdonald and myself about two years ago, immediately after it had been thrown ashore during a storm, and it was kept alive for three days. Fig. 21 (Plate VI.) is a representation of the form of the animal of the natural size.

The body is cylindrical and marked by longitudinal lines. The inferior fourth of the body is translucent, more contractile than the upper part, and sometimes assumes nearly a conical form with the apex downwards. The upper three-fourths of the body are opaque and of a faint pink colour. The tentacula are twelve in number, ranged in a single row, smooth on the surface, of a light pink colour, and having their internal or oral surface crossed by four zigzag white lines (fig. 22). They are elongated transversely or flattened from within outwards, and taper towards their free extremity. They were never seen more elongated than what is represented in fig. 21, but as the animal appeared to be languid, it is quite possible they are capable of greater elongation. When contracted to the utmost they formed little conical eminences, projecting outwards and upwards, and were seen to be attached immediately below the outer margin of the disc. Twelve bands of a faint reddish brown colour and adhering along their edges, radiate inwards from the circumference of the disc, converge at its centre, and prolong themselves upwards to form the mouth, or rather the lips. The margin of the lips is surrounded by twelve small processes, six of which are very minute; these processes are of a triangular form and of an orange colour, except at the edges, which are translucent. This prolonged mouth did not always occupy the centre of the disc, but could be directed towards any part of the margin.

The external sac sent strong partitions inwards, the position of which was marked by the longitudinal lines on its outer surface, and in the interstices of these partitions the ovaries were placed. This animal in many respects closely resembles the *Iluanthos Scoticus* of Professor E. Forbes*, and the chief difference between them is found in the structure of the mouth.

* Annals of Natural History, vol. v. p. 180.

EXPLANATION OF PLATES V. and VI.

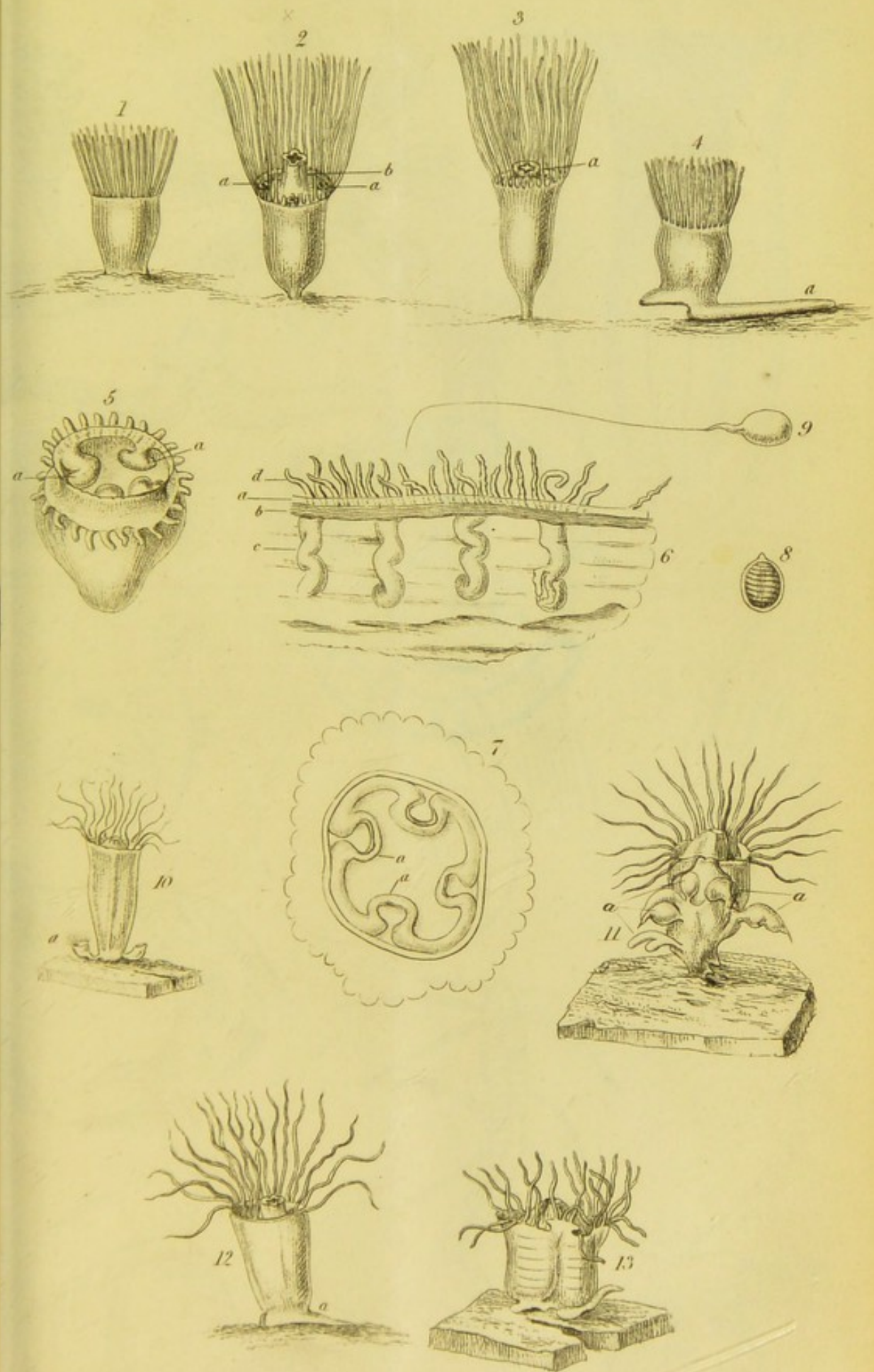
PLATE V.

- Figs. 1, 2, 3, 4 and 5.* Representations of the more common forms assumed by the larvæ.
- Fig. 6.* A larva slit open and stretched out to show the four vertical canals, and the manner in which they terminate in the circular canal: *a*, extensible lips; *b*, circular canal; *c*, four vertical canals; *d*, tentacula considerably shortened by their contraction.
- Fig. 7.* Transverse section of the body of a larva to show the manner in which the four vertical canals are formed: *a*, vertical canals.
- Fig. 8.* Filiferous capsule entire.
- Fig. 9.* Filiferous capsule burst and the spiral filament uncoiled.
- Fig. 10.* Larva throwing out stolons, from one of which a bud is springing.
- Fig. 11.* Larva having several buds growing from its surface.
- Fig. 12.* Upper half of a larva eight days after it had been cut across.
- Fig. 13.* One of the forms assumed by some of the larvæ.

PLATE VI.

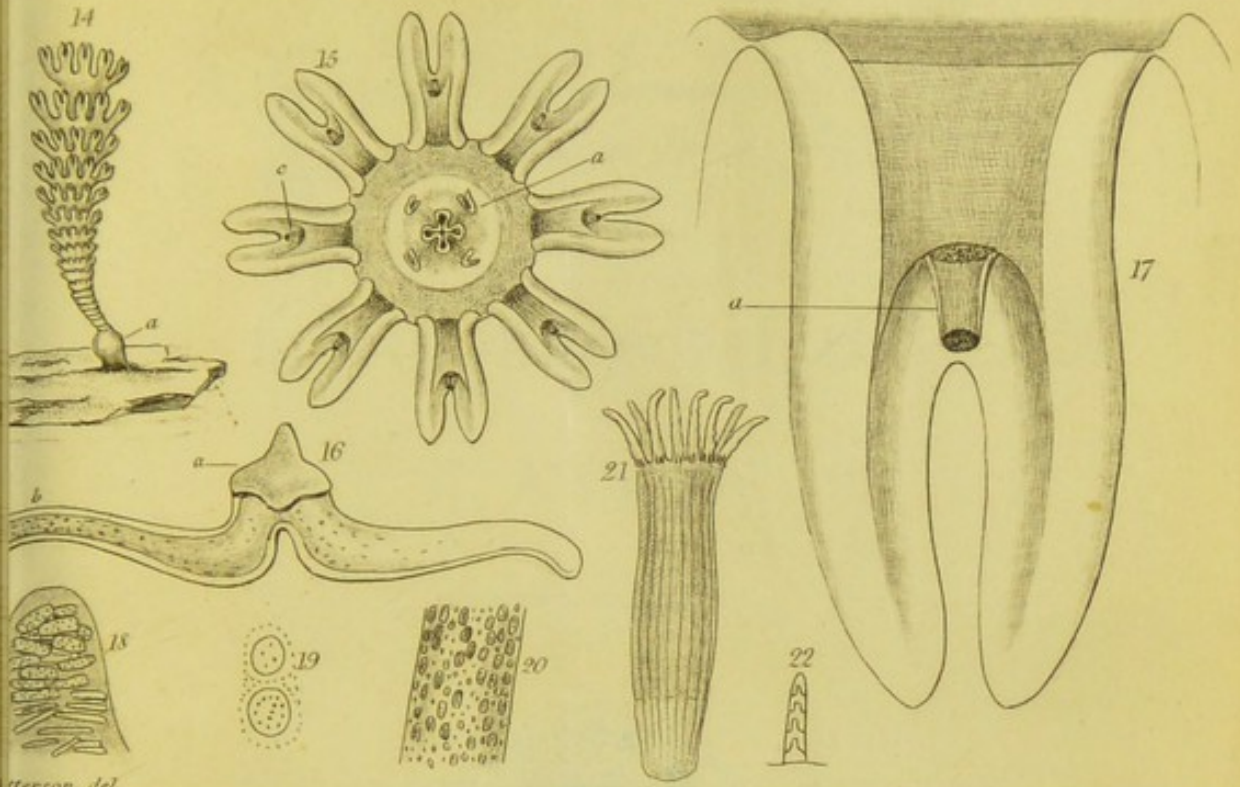
- Fig. 14.* Larva in the process of splitting into young *Medusæ*.
- Fig. 15.* Lower surface of one of the young *Medusæ* after its separation from a larva: *a*, one of the four bifid processes in the stomach; *c*, ocellus.
- Fig. 16.* Greatly enlarged view of one of the bifid processes in the stomach.
- Fig. 17.* Greatly enlarged view of one of the eight marginal rays or lobes: *a*, ocellus.
- Fig. 18.* Greatly enlarged view of the crystals in apex of ocellus.
- Fig. 19.* Two of the nucleated cells and several of the nuclei that enter so abundantly into the structure of the internal layer, as seen when a portion of this layer is detached.
- Fig. 20.* Small portion of a tentaculum, highly magnified, to exhibit the filiferous capsules adhering to its outer surface.
- Fig. 21.* Representation of *Actinia cylindrica* of the natural size.
- Fig. 22.* Oral surface of one of the tentacula.

In the examination of the more minute structures figured above, a one-eighth of an inch object-glass made by Powell and Leland, and a one-fourth of an inch object-glass by Smith and Beck, were employed.

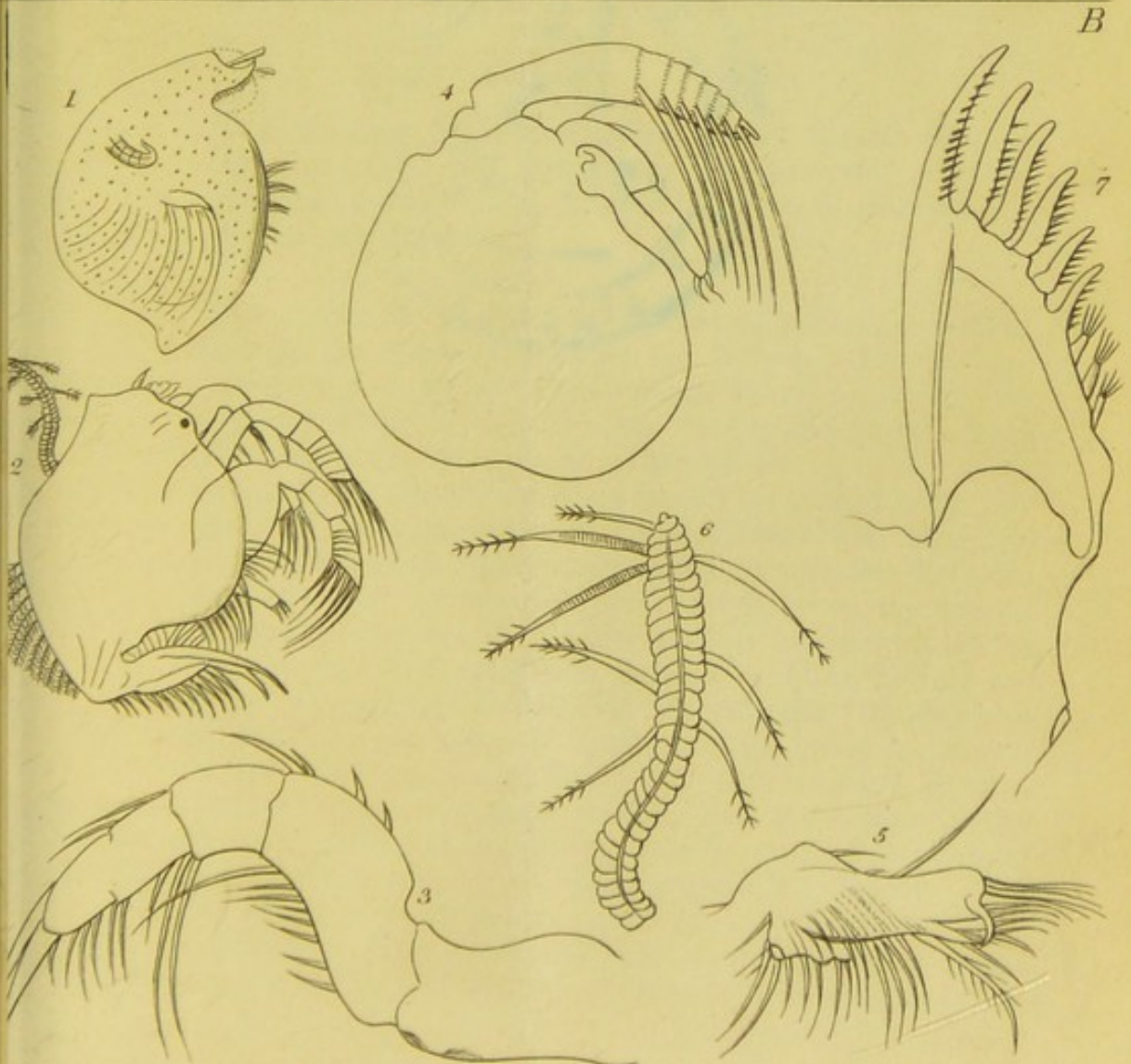


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