seen from above, are dotted with white. Above it is olive-green, shining, with the scutellum, suture of elytra, and sub-apical tubercles more coppery. The lateral margins of the elytra, especially beyond the middle to the apex, have a broadish margin of transverse strigose rugosity. The pygidium is finely strigose, the strigæ arranged semicircularly. The posterior coxal plates have shallow oval punctures arranged obliquely. The mentum is pale greenish luteous. The femora are olivaceous; the tibiæ dark green, with orange hairs; the tarsi greenish black."

The following is the description of the species in this museum:—

Coptomia mutabilis, sp. n.

C. olivaceo-viridis, nitidissima; elytris regione scutellari nigro-cyaneo tincto, lateribus dimidio apicali striato-punctatis; pygidio lævi (♂) vel parce punctato (♀); antennis, tibiis tarsisque rufo-piceis.

Long. 11 lin., lat. $6\frac{1}{4}$ lin.

A broad highly polished species, with extremely fine punctuation on the thorax and some obscure lines of punctures on the elytra in the female. The deep-blue shadow around the scutellum varies in extent according to the direction in which the light falls. The pygidium has a few punctures scattered over the surface in the ♀. The lateral margins of the abdomen, seen from above, are dotted with white. The male has the 2nd, 3rd, and 4th segments impressed in the middle. The posterior coxal plates are nearly smooth, with two or three fine punctures only. The pubescence on the chest and legs is nearly black.

Hab. Antananarivo (*Rev. R. Joy*), Fianarantsoa (*Rev. W. Deans Cowan*).

XVII.—*Notes on the Embryology of Sponges.*

By W. SAVILLE KENT, F.L.S., F.Z.S., &c.

[Plates VI. & VII.]

ALTHOUGH the independent investigations of Metschnikoff*, Carter†, Oscar Schmidt‡, F. E. Schulze§, and, more recently, Barrois||, have, as a result, necessitated an important

* Metschnikoff, *Zeitschr. wiss. Zool.* Bd. xxiv. p. 1, 1874.

† Carter, *Ann. & Mag. Nat. Hist.* vol. xiv. pp. 321 & 389, 1874.

‡ Oscar Schmidt, *Zeitschr. wiss. Zool.* Bd. xxv. 2 Suppl., Nov. 1875.

§ F. E. Schulze, *Zeitschr. wiss. Zool.* Bd. xxv. 3 Suppl., Dec. 1875.

|| C. Barrois, *Ann. des Sc. Nat.* tom. iii. 1876.

modification of Prof. Haeckel's original interpretation of the so-called ciliated larvæ or reproductive gemmules of sponges, we can by no means be said to be in possession of an exhaustive knowledge of the histiological or developmental manifestations of these remarkable bodies. Our apprehension of the morphological affinities of the sponges as a class, again, assisted only by the dim and deceptive light derived from this same imperfect knowledge of these reproductive gemmules, is, as a natural consequence, encompassed by a still more perplexing mist of doubt and obscurity. Animated with the desire of contributing, however slightly, towards a more full and accurate comprehension of the true nature and affinities of that organic group with which these debatable structures are associated, I propose here to place briefly on record the results of an extended personal investigation of these special sponge-elements, paying attention more particularly to those phenomena observed which appear so far to have escaped the observation of the authorities just named.

As a preliminary introduction, it is scarcely necessary to remark that this embryological question is here approached from a direction diametrically opposite to that selected, with but one, if any, exception, by all of the before-mentioned investigators. These latter, although differing slightly among themselves in their individual interpretation of the structural elements of the so-called sponge-embryos, agree with one another, and, so far with Haeckel, in according to these bodies, and, *pari passu*, also to the adult sponges, the existence of two or more distinct cellular layers. This concession necessarily, and by these authorities avowedly, carries with it the inference that sponges are true tissue-forming Metazoa, and, at any rate, more nearly related to the simplest tissue-forming Coelenterata than to the Infusoria or other typical Protozoa. Mr. Carter even commits himself so far, though perhaps not intentionally, to this metazoic interpretation as to continually make use of the terms "ectoderm" and "ectodermal layer" in his account of sponge-development. In accordance with the views adopted by myself, which are identical with those held by the late Prof. H. James-Clark, and as explained by me at some length in last January number of this Magazine, the sponges are compound colony-building collar-bearing flagellate monads, exhibiting neither in their embryological nor in their adult condition phenomena that do not find their parallel among the simple unicellular Protozoa, from which group, as a necessary consequence, this identity being established, they cannot consistently be held separate. The so-called "ciliated embryos" or "larvæ" of the various sponge-forms, following

the same view, are regarded by me as the equivalent, not of a single body or person, but as a special aggregation of innumerable individuals to which collectively the title of "compound ciliated gemmules" or "swarm-gemmules" may be most appropriately applied. The chain of evidence supporting this decision, constructed out of the ample data yielded by the investigations of the several specialists mentioned, collated with my own in the same direction, may now be submitted.

The initial term or starting-point of the so-called ciliated sponge-embryo is generally recognized as consisting of a small unicellular *Amœba*-like unit possessing the faculty of locomotion from place to place by the protrusion of lobate pseudopodia after the manner of a typical *Amœba*. The diameter of the smallest of these initial units averages the 3000th part of an English inch, its appearance corresponding with that given at Pl. VI. fig. 2. From this most minute size these initial factors occur in every gradation to the dimensions of about the 200th part of an inch, under which larger proportions a spheroidal quiescent state is assumed and the first metamorphosis commences. This is effected by the symmetrical cleavage or duplicative division transversely and longwise, first into two, then successively into four, eight, sixteen, thirty-two segment-masses, and so on, of the entire spheroidal protoplasmic mass. The final result of this continued process is the production of a spherical aggregation of minute rounded units or segment-spheres, agreeing, to all appearance, with the morula derived from the segmentation or cleavage of the ovum of all ordinary higher animals or Metazoa. Figs. 3 to 8 of Pl. VI. serve to illustrate the leading phases of this transformation. According to Mr. Carter the foregoing process of cleavage takes place within a hyaline investing envelope; but the existence of such a structure is not confirmed by the investigations of Haeckel, Barrois, or myself. The next characteristic phase, universally conceded, is the assumption by the morula-like body of a more or less ovate outline, accompanied by the clothing of the entire peripheral surface with long vibratile cilia or flagella. This peripheral surface viewed superficially presents under high magnification a tessellated aspect, each minute polygonal area of this tessellation representing the external or exposed surface of one only of the innumerable segments into which the primary unicellular body has been divided. Pl. VI. fig. 9 represents such a superficial view, the cilia round the margin of the organism, for the sake of perspicuity, being alone introduced. Focusing a little deeper, so as to bring into clear view the

centre of the entire body, which is thus seen as though in longitudinal section (Pl. VI. fig. 10), it will be found that the constituent cellular units or segment-masses have assumed an elongate conical contour, gradually tapering from the exposed peripheral border: the same being united by their posterior extremities, and closely adpressed to one another throughout their lateral extent, they, as it were, in fact, radiate from a common centre. Under these same conditions it is clearly shown that a single cilium originates from the centre of the peripheral border of each of these elongate units, and from its great proportional length may be more correctly designated a flagellum. Increasing in size, it is next found that these elongate units become separated posteriorly, leaving a central ovate or spherical cavity in the common body, while at the same time a short hyaline cup-like expansion develops around the base of the flagellum. This stage is represented in fig. 11 of the same Plate, and is also admitted in Barrois's drawings, and, with some slight modification, in those of Haeckel also. Upon this last there now, however, succeeds a phase which so far has apparently been overlooked by other observers, though it has been encountered personally in association with numerous sponge-forms, and constitutes, in fact, in accordance with the views here adopted as to the nature of these organisms, a natural sequence to the preceding. The aspect now presented is delineated at Pl. VI. fig. 12—the gemmule at this point of the development, as will be at once recognized, consisting of an ovoid aggregation of closely joined collar-bearing units in no way differing individually from the typical collar-bearing sponge-monads or spongozoa of which the adult sponge-body is composed. Each separate unit of this ovoid mass is at this stage of its existence a perfect individual collar-bearing monad, taking in an independent food-supply, which it captures with its collar of adhesive circulating sarcode in a manner similar to that already described by me of *Monosiga gracilis* and other free collar-bearing monads, in the last January number of the 'Annals'*. The morphological identity of the individual units of the sponge-embryo or gemmule with those of the independent monads alluded to becomes at once patent on placing side by side, as I have done at Pl. VI. figs. 13 and 14, the simple flagellate and adult collar-bearing condition of an independent freshwater monad,

* Mr. Xenos Clark, of the San-Francisco Microscopical Society, from whom I have just received a very complimentary acknowledgment of my recognition and support of his father's, the late Prof. H. James-Clark's, discoveries and theory concerning the nature of sponges, has very appropriately compared this sarcode-circulation of the hyaline collar as discovered by me to the action of an "endless revolving belt."

Monosiga angustata, S. K.*, with an isolated unit or zooid from the sponge-gemmule in the same simply flagellate and collar-bearing states. But for the accompanying explanation, indeed, the two might be interpreted as representing slightly varying individuals of the same specific type. Borrowing a simile from the vegetable kingdom, this matured and liberated sponge-gemmule presents now, as it swims through the water, a structural composition broadly corresponding with that of *Volvox globator*. The organism, as a whole, is propelled by the vibratory movements of the associated flagella; while, in the same manner, each unit of the compound body, viewed separately, exhibits that relationship towards *Monosiga* and other independent collar-bearing monads which is borne by those of *Volvox* with reference to such solitary types as *Disselmis* or *Chonemonas*. Sooner or later, the sponge-gemmule having transported itself, by aid of the concerted action of the countless vibratile flagella, to a spot suitable for attachment, the collars and flagella of the separate monads are retracted, and the organism becomes fixed, usually by one extremity, to the chosen fulcrum of support. An exuded veil of sarcode or syncytium is now poured out, hiding the monads from superficial view, and the transformation of the gemmule into a typical sponge-stock, as already detailed by Mr. Carter (*l. c.* p. 334 *et seq.*), is speedily effected.

In no one of the several phases passed through by this so-called sponge-embryo, as here recounted, can there be said to have been the formation of any distinct membrane produced by the uniting into one morphological whole of the cellular units or segmentation-masses, such as takes place invariably among all Metazoa, each of the separate units of this segmented body exhibiting a totally separate and independent existence. The only presumed metazoic characteristic manifested, indeed, by this ciliated structure is its primary assumption by continual subdivision of a morula-like condition. This moruloid condition, however, can be shown to be common to many undoubted Protozoa as well as Metazoa, the distinction between the two groups depending therefore upon the circumstance whether or not the component segments or blastomeres of this morula-like body maintain a separate existence or become welded into a single continuous tissue or blastoderm. Among those conspicuous instances in which a moruloid condition is exhibited by undoubted Protozoa, attention may be first directed

* An illustration of this and nearly forty other independent collar-bearing monads will be found accompanying an article on these newly discovered organisms, contributed by the writer to the 'Popular Science Review' for April 1878.

to the remarkable form recently described by Prof. Haeckel under the title of *Magosphæra planula*, represented by Pl. VII. figs. 13 to 18, and whose developmental phases correspond remarkably with those of the so-called ciliated sponge-embryo as just described. Placing our data in the same order of succession, we find first the reptant amœboid body, which assumes a rounded quiescent state, and then divides by a similar process of segmentation into a morula or spherical aggregation of rounded corpuscles. These separated segments or blastomeres now spread out on the surface, imparting to it a prismatic or tessellated aspect, as in the sponge-embryo, and further taper backwards and are united to one another posteriorly in a corresponding manner. We have now, indeed, only to add a hyaline collar and single cilium or flagellum to the peripheral border of each unit in place of the several cilia which clothe this region in *Magosphæra*, to produce a morphologically identical organism. What now becomes of *Magosphæra*? After swimming for a considerable while in the open sea, it breaks up or resolves itself into its constituent elements, each separated conical unit shortly afterwards losing or withdrawing its ciliary appendages and assuming an amœboid phase, identical with that from which the spherical colony-form first sprang, and prepared once more to repeat the cycle. A closely similar developmental cycle has recently been shown by Messrs. Dollinger and Drysdale to take place among many of the simple Monadina—an encysted spherical zooid splitting up by longitudinal and transverse cleavage into a morula-like aggregation, each segment of which develops into a distinct individual. My own recent investigations associated with this humble organic group have so abundantly confirmed the results of those of the authorities just quoted that I am inclined to regard this developmental cycle, in conjunction with another, referred to later on, as common to the greater portion of the representatives of the Infusoria Flagellata. The successive phases from the free-swimming monad to the moruloid stage of one of the most prominent types described and figured by the gentlemen last mentioned, in the 'Monthly Microscopical Journal' for January 1874, is reproduced at Pl. VI. figs. 27 to 33, and may be instructively compared with the similar cycle as it occurs in *Magosphæra* and the sponge-gemmules illustrated in the same and accompanying plates. *Polytoma uvella*, which is likewise figured and described by Messrs. Dollinger and Drysdale under the name of the "biflagellate or acorn monad," exhibits the same multiple fission or moruloid mode of reproduction—a fact amply attested even by such early investigators as Ehrenberg, Perty, and Schneider. A remarkable feature presented

by the type last named is, that the flagella remain intact and the animalcule swims actively about while the segmentation of its entire interior substance is progressing.

One specially important factor associated with the developmental cycle of the ciliated sponge-gemmule, that has so far been quite lost sight of, relates to the initial condition of the so-called *Amœba*-like ovum, which by its segmentation develops into the compound structure. How is this presumed ovum produced? Haeckel and his followers regard it as the independent production of an imaginary entodermal tissue. I concede to it the position merely of metamorphosed collar-bearing sponge-monad, which having arrived at mature age has assumed an amœboid phase in a manner precisely identical with that which obtains in *Magospœra* and among many of the simpler free-swimming monad forms just referred to. Such an assumption by the collar-bearing monads or spongozoa of an amœboid state has been personally witnessed over and over again, and is, moreover, amply confirmed, though not with the interpretation here submitted, by Haeckel, Carter, and all other authorities who have concentrated their attention on this organic group. The dimensions furthermore given by Mr. Carter of the smallest ovum-like body observed by him correspond precisely with those of a single collar-bearing spongozoon. As a final link in the chain of evidence it remains to be shown that a parallel mode of reproduction is associated with those independent collar-bearing monads that formed the subject of my last year's communication to the Linnean Society. A single example out of innumerable instances that might be quoted will suffice to demonstrate this fact. The solitary loricated type *Salpingœca fusiformis*, nobis*, represented at Pl. VI. figs. 21-26, exhibits precisely similar phenomena. Commencing first with the typical collar-bearing phase, it next assumes an amœboid condition, then, contracting into a subspherical quiescent state, splits up by symmetrical longitudinal and transverse cleavage into a spheroidal mass of minute segments or blastomeres corresponding essentially with that produced in a parallel manner by the so-called sponge-embryo. The further development of the ultimate segments or blastomeres is likewise identical. The most conspicuous primary transformation of the segmental units consists in both instances of the acquirement of a single flagellate appendage; and this is next succeeded by the growth of the characteristic collar. The only distinction subsisting between the two is, that while the individual units in the case

* Since figured and described by O. Butschli in Siebold and Kölliker's 'Zeitschrift für wissenschaftliche Zoologie' for January 1878, under the title of *Salpingœca Clarkii*.

of the sponge-product remain bound together in a social cluster throughout their metamorphoses, in *Salpingæca* they are scattered abroad, as shown at Pl. VI. fig. 26, during the immature or unflagellate condition, their development to the adult state being afterwards effected during an attached and solitary condition. The matured collar-bearing spongozoa next throw around them, as already related, a common investing veil of glairy sarcode or syncytium, while the solitary *Salpingæca* builds for itself, by a similar process of exudation, its elegant-shaped protective sheath or lorica*; this at first is also soft and syncytium-like, but acquires an apparently chitinous or perhaps keratose consistence after short exposure to the water. The slight distinction between the two forms under the conditions last described finds its precise counterpart among the higher ciliate Infusoria, as instanced by the solitary lorica-inhabiting types *Cothurnia* or *Vaginicola* as compared with the social genus *Ophrydium*, the innumerable units of which exude around them and inhabit a common mucilaginous domicile. The social slime-dwelling form, *Phalansterium* of Cienkowski (*Monas socialis*, Fresenius), as compared with *Bicosæca* or other simple loricate Monadina, affords again a similar parallel among the more closely related ordinary Flagellata.

The further development to the characteristic adult sponge-form of the attached ciliated gemmule, the collars and flagella of the individual units being withdrawn and replaced by an investing syncytial mantle, has, as already mentioned, been described by Mr. Carter, with relation more especially to the siliceous-spiculed type *Halichondria simulans*, in this same magazine for November 1874. Barrois, again (*l.c.*), has traced these same developmental phases in a similar manner in numerous other sponges, including more prominently *Halisarca lobularis* and *Desmacidon fruticosa*. Among the phenomena connected with this further development, attested to by both these writers, is the early appearance of the spherical ciliate or monad-lined chambers which have received from Mr. Carter the title of ampullaceous sacs. How these chambers originate does not appear to have attracted the attention it deserves. Haeckel, however, has pronounced them to be mere spherical dilatations of the ordinary canals, while Barrois maintains that they make their appearance first as independent structures within the substance of the syncytium, communicating with the canal-system later on. This latter interpretation I am in a position not only to thoroughly indorse, but to further prove that these ciliated chambers are derived by a process

* This sheath or lorica, in order to economize space, is represented in its entirety in only one of the figures illustrative of this species.

of segmentation from a primary reptant amœboid and subsequently spheroidal unit in a manner identical with that already detailed of the free-swimming ciliated gemmules. Plate VII. figs. 1 to 7 serve to illustrate the successive phases of this development of a ciliated chamber as observed by me first in a species of *Halisarca* apparently identical with *H. lobularis*, and since confirmed by the investigation of innumerable other forms. Figs. 1 to 4 exhibit no deviation whatever from the normal process of segmentation producing the moruloid phase of the so-called ciliated embryo; and it is only when the separated units or blastomeres assume their next more characteristic and uniflagellate condition that the distinction becomes apparent. Here, as shown in section at fig. 5, the flagella are developed on the interior instead of the exterior border, and project into a central cavity instead of into the surrounding water. The matured development of the same chamber, in which the individual units or zooids have attained their typical form and characteristic collars, is similarly shown at fig. 7. As will be immediately recognized, it needs merely the eversion of this inward-turning spherical aggregation of collar-bearing monads to produce the typical free-swimming gemmule or so-called ciliated embryo represented by fig. 12 of the preceding Plate. At fig. 8, Plate VII., half a dozen monads from the same mature ampullaceous sac, but more considerably magnified, are delineated; and close to them (fig. 9) is placed, for the purpose of comparison, an example of an independent collar-bearing form, described by me in my monograph of the group under the title of *Desmarella moniliformis*. This type, which occurs somewhat rarely in salt water, forms small chain-like, free-floating colonies of from two to six or eight individuals only. Apart from the explanation here given, it would be scarcely possible to distinguish it from the separated spongozoa of the ampullaceous sac; and it affords another illustration of the close relationship that exists between the sponges and these more simple independent collar-bearing types. Throughout these latter, indeed, when extensively known, types are constantly recurring that manifest in their narrower cycle of existence a correspondence with some isolated developmental phase of the separated zooids of the former.

Although the symmetrically ovate shape, with the collars and flagella of the separate units forming an even and uninterrupted elegant frill-like border throughout the peripheral surface, as delineated at Plate VI. fig. 12, represents what may be accepted as the most typical and characteristic expression of the so-called ciliated sponge-embryo, it will be found

that different examples of these bodies, derived even from the same sponge, present an extraordinary latitude of variation. Among the most conspicuous and frequent of these variations, is one which, indeed, in certain sponge-forms occurs almost as frequently as the typical one just alluded to; it is represented by Plate VI. fig. 15. The deviation in this example, as will at once be recognized, consists of the distinct character of the component parts of the lower half of the organism, the typical elongate flagellate units which characterize the upper one being here replaced by irregularly spheroidal cells, which are more or less confluent with one another. Grasping at a straw, those committed to the metazoic interpretation of the Porifera have selected this inconstant type for the demonstration of their views respecting the bilaminar or diblastic structure of these bodies. No distinct inner and outer lamina, as first represented, being found to exist, the front flagellate portion is now made to do duty for the exoderm, and the hinder one for the endoderm. The constituent elements of this latter region being found again occasionally retreating into the central cavity of the compound body, this has been accepted as a proof of the invagination of the endoderm and the formation of a primitive "gastræa." The untenability of this interpretation, however, is at once proved by the inconstant occurrence of this type, while in addition it is easy to show that the basal and larger cellular elements are merely modifications or more advanced stages of growth of the smaller frontal ones. Two figures borrowed from Barrois (Plate VI. figs. 19, 20), representing two separate developmental phases of the ciliated embryo of *Halisarca lobularis*, assist in the demonstration of this fact. In the second of these (fig. 20) we find that the cellular units of the lower portion of the body, though abruptly larger than those of the upper one, exhibit the same uni-flagellate character, while in the preceding figure the transition from one to the other is perfectly gradual and uniform. Another figure is given by this authority, derived from the same sponge-type, corresponding with our own fig. 10, but prior to the development of the flagella, and in which the component cells from one end to the other present a precisely similar size and character. Haeckel, again, in his 'Kalkschwämme,' Taf. 4. fig. 6, represents the ciliate embryo of *Ascetta clathrus* as corresponding entirely with my delineation at fig. 9 of that of *Grantia compressa*, the whole peripheral surface consisting similarly of minute even-sized cells, exhibiting in superficial view a tessellated aspect. No distinction whatever is indicated here between the cellular constituents of the anterior and posterior portions of the organism, though at

the same time he delineates an apical aperture and central cavity, the latter lined with a separate layer of so-called endodermal cells, the existence of neither of which is any longer maintained. Still more direct testimony, if needed, in demonstration of the identity of the constituent elements of the upper and lower portions of the sponge-embryo, even where those of the latter one are of considerably larger size, is afforded by Plate VI. fig. 16, in which, as will be seen, the cellular elements of the lower portion exhibit all the characters of the adult collar-bearing zooids or units, while those of the upper part have arrived only at the semideveloped uniflagellate and collarless condition. This interesting example was met with in a calcareous sponge-form common on the Jersey coast, closely allied to Haeckel's *Ascandra pinus*, and having associated with it innumerable other embryos presenting the typical ovate and uniform character delineated in fig. 12. This somewhat abnormal example last described furnishes a complete key to the commonly occurring form delineated at fig. 15, this latter, indeed, representing a slight modification of the same type, in which the zooids of the lower portion have still further outstripped their antipodal companions in the race, losing their collars and flagella, and assuming the passive amœboid state accompanied by a syncytial exudation before these others have so much as developed the first-named structures. Why, in some instances but not in others, this disparity in the degree of growth should exist between the separate units or zooids of the anterior and posterior portions of the aggregate mass is easily explained. On making a suitable section through a sponge-body containing these embryos it will be found that in some cases these bodies are released from their syncytial matrix in their entirety, the zooids under these circumstances developing evenly throughout the periphery, while in others they for a while remain partially immersed within the same. In this latter case the zooids of the two opposite portions naturally develop at a different rate, those appertaining to the immersed one being temporarily retarded in their growth. In many instances indeed it would seem that the most posterior or deeply immersed cellular constituents do not perfect their final subdivision and development into the typical collar-bearing monads until the permanent attachment of the embryo. Mr. Carter has applied to these occasional larger cells at the posterior extremity of the ciliated embryo the title of root-cells, these same, when present, taken collectively, representing the region by which attachment to the selected fulcrum of support is most usually effected. It is a significant fact that, in cutting open or otherwise examining

a young sponge shortly after this first attachment, the ampullaceous sacs in these sponge-forms, when they occur, are confined entirely to the basal region, and are evidently developed from the posterior root-cells.

Although the embryonic form last discussed, and which, from its peculiar contour and aspect, might be denominated the acorn-form, represents the most conspicuous and constantly recurrent deviation from the normally ovate type, innumerable other variations occur, presenting an altogether irregular and unsymmetrical shape. One of these irregular variations is represented at Plate VI. fig. 17, and another at fig. 18. In the latter of these certain of the cellular units have developed their flagellate appendages, while the others present the amorphous rounded form characteristic of those of the lower portion of the acorn type. In the former example a nest- or cup-like shape is assumed, not unlike the basal portion, taken separately, of the acorn variety, and in which the zooids are for the most part fully matured. Other variations might be figured and described without number; those given, however, suffice for the required purpose, that of demonstrating the non-persistency of contour of these so-called embryonic bodies. In addition to variation in contour, these same structures will be found even in one sponge-stock to vary among themselves considerably in calibre, notwithstanding that the component units or zooids exhibit a corresponding phase of development. Some of these bodies are several times larger than others, and contain necessarily a very much greater number of separate units. This non-conformity of the size of these unit-aggregations of like age appears to admit of two constructions. In the one case it seems highly probable that the primitive rounded *Amæba*-like mass from which these compound bodies are developed is built up, previous to its assumption of a quiescent state and subsequent segmentation, through the fusion or coalescence of a variable number of the original and typical collar-bearing zooids with which the sponge-cavities are lined, and in a manner parallel to that of the independent monad form illustrated by Plate VI. figs. 27 to 33, in which sometimes two only and sometimes a much larger number of zooids coalesce and produce by a corresponding process of segmentation a larger or smaller number of daughter zooids or macrospores resembling the parent. The coalescence of two *Amæba*-like sponge-units has been frequently observed; and it is not unreasonable to premise that a similar welding with one another, as in the case of the simpler monad, of a larger number of similar units is

sometimes effected*. The abnormal and, in some instances, prodigious comparative size of the amœboid masses from which the ciliated embryo is developed admits, however, of a second interpretation. As shown by Haeckel in many of his illustrations (a portion of one of which, representing his *Ascaltis cerebrum*, is here reproduced, Plate VII. fig. 12), the external border of the amœboid mass is invested by a continuous and even layer of the normal flagellate monads. Now it has been demonstrated by me in my communication on this same subject to the Linnean Society last year, and has since been confirmed by repeated subsequent observation, that the amœboid particles or cytoblasts stationed within the substance of the syncytium, and which later on, under normal conditions, assume the typical collar-bearing form, receive their sustenance through the flagellate types, which, having filled themselves to repletion, pass all additional supplies, arrested by the hyaline collars, through their own bodies into the syncytium, where the same are at once seized by the amœboid particles. By a similar process it is not improbable that certain of these large amœboid masses, as indicated in the figure quoted, represent ordinary cytoblasts or imperfectly developed flagellate zooids, upon which the task of conversion into the ciliated swarm-gemules specially depends—to which end they are, as it were, specially fed and fattened up by the superincumbent flagellate units. The falling-off or diminishing amount of the food supply might, under these conditions, arrest at any stage the further development of these amœboid masses, causing them to enter upon their final transformations at different epochs of growth, which would thus sufficiently explain the variable calibre of the ciliated bodies produced by subsequent segmentation†.

From the account now submitted of the developmental manifestations of the so-called ciliated sponge-embryo it is clearly evident that we have here represented merely a mode of increase, for a special purpose, by multiple fission, differing in no essential manner from that common to *Magosphaera* and

* Haeckel further describes and figures the coalescence of numerous individuals into one homogeneous amœboid mass of his simple monad form *Protomyxa* as a prominent feature in the developmental cycle of that type.

† That this suggested interpretation does not in any way militate against the conception of the unicellular and Protozoic nature of the essential Spongozoa is sufficiently demonstrated from the fact that among certain colony-forming higher ciliate Infusoria, and notably the genus *Zoothamnium*, special zooids are at times developed for a closely parallel object, and attain, in comparison with the ordinary units, an equally disproportionate size.

the independent collar-bearing types, such as *Salpingoeca*, and the majority of the Infusoria flagellata. That these bodies cannot in any way be compared with the true ova of the ordinary Metazoa is demonstrated not only by their inconstant form and character, disassociated also with any act of spermatic fecundation, but from the fact that the segmentation of the primary unit gives rise to a morula-like aggregation, which does not develop by the fusion of its constituent particles or blastomeres into a single germ-lamella or blastoderm, but into a number of distinct and independent unicellular zooids or units. The Metazoic interpretation of the nature of sponges, as grounded upon the developmental manifestations of these same bodies, must likewise as a consequence be abandoned, or otherwise be extended to the simple Monadina, Radiolaria, and Catallacta, which produce a similar morula-like segmentation-mass, thus leaving the Protozoa in possession only of little more than an empty title. The true nature and significance of the so-called ciliated embryos of the sponge, while not reconcilable with the proposed Metazoic interpretation, becomes clearly intelligible on collating these organisms with the unicellular Protozoa. Regarded from this position, the identity of the ovate aggregation of separate units which constitute the so-called sponge-embryo with the similar aggregation of units of the segmented monad, afterwards separated and dispersed as swarm-spores, is made apparent. This sponge-embryo is in this manner demonstrated to be merely an aggregation of swarm-spores held closely bound to one another throughout the process of development. It may therefore be appropriately denominated a "swarm-gemmule," whose mission it is in its aggregate condition to lay the foundation of a composite sponge-stock similar to the one which gave it birth, and in a manner identical with that individually effected by each motile swarm-spore of the solitary monad.

As a final demonstration of the Protozoic nature of sponges, the multiplication of these organisms by the production of countless infinitesimal spores after the manner of the typical Monadina has been determined. This spore-formation is brought about through the assumption by the matured collar-bearing zooids of a quiescent encysted state, accompanied or not by the fusion of two individuals. The spores produced by the breaking up into almost invisibly minute particles of the entire protoplasmic substance of the encysted zooids are liberated in the substance of the syncytium; and within this matrix each spore develops again through an amœboid or cytoblastic and then simply flagellate phase to an adult collar-bearing unit. This multiplication of the typical sponge-

monads or Spongozoa by the means of spores represents the constant and normal manner in which the growth and extension of the sponge-colony is effected—the aggregated masses of individuals or swarm-gemmules, liberated only at certain periods, representing a special development for the more extensive dissemination of the species. The subject of spore-formation, associated with the reproduction of sponges, has been already adverted to in my contribution to the 'Annals' in January last, and is entered into at considerable length in my communication made in June 1877 to the Linnean Society. Pending the publication of these more abundant details, figs. 19 to 25 of Plate VII. accompanying this article will assist to illustrate some of the more conspicuous phenomena that accompany this method of reproduction.

I gladly avail myself of the present opportunity of recording my most grateful acknowledgments to the Government-Grant Committee of the Royal Society, who, by their liberal award to me of a grant of £50, have placed at my disposal those instruments of precision not otherwise accessible, but absolutely requisite for the accurate determination of the ultimate structure and affinities of the group of organisms discussed in this communication.

Channel-Islands Zoological Station,
St. Heliers, Jersey, June 21, 1878.

EXPLANATION OF THE PLATES.

PLATE VI.

- Fig. 1.* Typical spongozoon or collar-bearing monad of the calcareous sponge-form *Grantia compressa*, $\times 1000$ diameters. *n*, endoplast; *c.v*, contractile vesicle.
- Fig. 2.* The *Amœba*-like body from the same sponge-form, out of which by segmentation the swarm-gemmule or so-called ciliated embryo is produced—which may represent either a typical sponge-monad, as at fig. 1, that has withdrawn its collar and flagellum, and assumed an amœboid phase, or a similar monad in its undeveloped and cytoblastic state.
- Figs. 3–8.* Successive developmental phases of the swarm-gemmule of the same sponge, commencing with the assumption by the last-named amœboid body of a spheroidal form, and terminating in the production of a morula-like aggregation of segment-masses or blastomeres.
- Figs. 9, 10.* The characteristic form of the swarm-gemmule when liberated from the syncytium of the parent sponge, viewed at fig. 9 superficially and at fig. 10 in optical section; the segment-masses of the preceding morula-like body have assumed a conical shape, radiating from the centre to the periphery, each of the same bearing in the centre of its exposed or distal border a single cilium or flagellum. $\times 350$ diameters.

- Fig. 11.** Optical section of a portion of a still further advanced condition of the same swarm-gemmule, in which rudimentary collars have been developed around the distal flagella; through the enlargement and expanding outward of the cellular constituents a central cavity is now possessed by the common body.
- Fig. 12.** The fully matured condition of the same swarm-gemmule, which is now shown to be an ovate aggregation of typical collar-bearing monads similar to that represented at fig. 1, and of which the parent sponge-stock is essentially composed.
- Fig. 13.** Separated monads from successive developmental conditions of a similar swarm-gemmule, that at *a* possessing a flagellum only, and the other, *b*, being provided with its characteristic collar, contractile vesicle, and endoplast.
- Fig. 14.** Adult and immature conditions of a solitary collar-bearing flagellate monad, *Monosiga angustata*, S. K.,—*a* representing the collarless and immature one, *b* the adult form, and both exhibiting a remarkable correspondence with the similar developmental phases of the isolated sponge-monads given in the preceding figure. $\times 2500$ diameters.
- Fig. 15.** An irregularly-formed acorn-shaped swarm-gemmule from the same sponge, in the anterior part of which the monads have not yet developed their collars, while at the posterior end the collars and flagella have been withdrawn, and the separate monads, coalescing laterally with one another, accompanied by the exudation of a syncytial film, have produced an amorphous amœboid mass.
- Fig. 16.** Another example of an "acorn-shaped" swarm-gemmule from the same sponge, in which the disparity of development between the constituent monads of the anterior and posterior halves is not so considerable; those of the latter present the characteristic adult collar-bearing form, while those of the anterior portion possess as yet only single terminal flagella.
- Fig. 17.** An irregular nest-shaped swarm-gemmule from the same sponge, composed of adult collar-bearing monads.
- Fig. 18.** An abnormal and entirely unsymmetrical swarm-gemmule from the same sponge-form, in which the constituent monads exhibit the two phases of development presented at fig. 15.
- Figs. 19, 20.** Two swarm-gemmules of *Halisarca lobularis*, in the first of which the as yet immature and unflagellate monads correspond with each other in size, while in the second those of the lower portion are considerably more developed (after Barrois).
- Fig. 21.** Adult monad of the solitary collar-bearing loricate type *Salpingoeca fusiformis*, S. K. (The lower portion of the lorica, to save space, has been omitted, but is represented in its entirety at fig. 26.) $\times 2000$ diameters.
- Fig. 22.** The same monad, having withdrawn its collar and flagellum, assuming an amœboid state.
- Figs. 23–25.** Successive phases following upon the amœboid condition of the same animalcule, corresponding with those illustrated by figs. 3–8 of the sponge-monad, and terminating in the production of a similar morula-like aggregation of segment-masses or blastomeres.
- Fig. 26.** The segment-masses or blastomeres of the preceding morula-like body becoming separated from one another, and issuing from the parent lorica as simple flagellate monads or swarm-spores; these subsequently become attached, and grow to the adult state.
- Fig. 27.** An adult individual of Messrs. Dollinger and Drysdale's "hooked monad" (*Heteromita uncinata*, S. K.).

Fig. 28. Two individuals of the same species about to coalesce.

Figs. 29–33. Illustrating the coalescence or fusion of four individuals of the same type, followed by the production of an irregular amoeboid mass, which finally resolves itself by a process of segmentation, and in a manner identical with that of the sponge-monad and solitary collar-bearing form last figured, into a corresponding morula-like body, the constituent units of which are finally liberated as minute zoospore-like bodies which grow to the parent form. *Figs. 27 to 33*, representative of this type, are reproduced from Messrs. Dollinger and Drysdale's figures.

PLATE VII.

Fig. 1. *Amœba*-like corpuscle or zooid of *Halisarca lobularis*, out of which, by repeated segmentation and differentiation of the cleavage-masses, the characteristic spherical ciliated chambers or "ampullaceous sacs" are constructed. $\times 400$ diameters.

Figs. 2–4. Various phases of this process of segmentation, terminating at *fig. 4* in the production of a morula-like aggregation of rounded blastomeres.

Fig. 5. The succeeding developmental phase of the ampullaceous sac of the same sponge, as seen in optical section. The segment-masses have now spread out upon the surface and assumed a conoidal form, each of the same bearing apically a long lash-like flagellum, which projects into the common spheroidal cavity.

Fig. 6. An example of about the same age, focussed superficially, in which the segment-masses, while considerably separated from one another, are held together by the hyaline or syncytium-like wall of the body of the "sac," upon the inner surface of which their apices project.

Fig. 7. A fully matured ampullaceous sac of the same sponge, as seen in transverse optical section, and in which the previous conical, uniflagellate segment-masses have developed into typical collar-bearing sponge-monads or Spongozoa. The eversion of this matured monad-chamber is alone required to produce a structure essentially corresponding with the "swarm-gemmule" represented at *fig. 12* of the preceding Plate. $\times 800$ diameters.

Fig. 8. A few individual units or sponge-monads from the preceding figure, further enlarged: *n*, nucleus or endoplast; *c. v*, contractile vesicle.

Fig. 9. A colony of the independent, free-swimming, collar-bearing monad *Desmarella moniliformis*, S.K., which occurs in chain-like aggregations of from two to as many as eight individuals, with which the separated sponge-monads in the preceding figure essentially correspond. $\times 1000$ diameters.

Fig. 10. Sporocyst-like bodies found associated with a siliceous sponge-form (*Halichondria*, sp.). $\times 600$ diameters.

Fig. 11. Detached fragment of a siliceous sponge (*Halichondria*, sp.), showing at *a* an ampullaceous sac in its semideveloped or moruloid condition, at *bb* two amoebiform bodies emitting pseudopodia, and which after assuming a quiescent or encysted state, develop through the cleavage of their substance into ampullaceous sacs. *sy*, syncytium. Several typical adult sponge-monads or Spongozoa are shown at *c*.

- Fig. 12.* Portion of the cavity of a calcareous sponge (*Asclatis cerebrum*, Hkl.), showing at *a* the internal lining of characteristic flagellate cells, and at *b* a swarm-gemmule in its earlier amœboid and unsegmented state. (After Haeckel.)
- Fig. 13.* An isolated zooid of *Magosphæra planula*, Hkl., derived from the dismemberment of the adult spherical colony form.
- Fig. 14.* A similar zooid with the cilia retracted and presenting an amœboid aspect.
- Figs. 15 & 16.* The preceding amœboid zooid, having in the first instance assumed a quiescent or encysted state, and in the second become divided by cleavage into four spherical segment-masses or blastomeres.
- Figs. 17 & 18.* Two adult colony-spheres of *Magosphæra planula* developed in a moruloid manner from a continuation of the cleavage process of the preceding type, the first viewed superficially, and the second in optical section. In the latter instance the union of the separate zooids with one another by their slender posterior extremities is made manifest, the colony presenting under such conditions a close structural correspondence with the swarm-gemmule of the sponge, illustrated by figs. 10 & 11 of the preceding Plate. Both consist of similar unit-aggregations, the separate zooids in the case of *Magosphæra* having numerous terminal cilia, and in that of the sponge-gemmule a single cilium only. (Figs. 13–18 after Haeckel.)
- Fig. 19.* A separated sporocyst with spores from a calcareous sponge, *Leucosolenia botryoides*, Bow.
- Fig. 20.* An intraspicular area of *Leucosolenia botryoides*, consisting of a thin film-like expansion of structureless sarcode or syncytium, in which are immersed collar-bearing sponge-monads in an encysted state; these, as at *a*, are laden with spores, while, as at *b*, these spores have been liberated and scattered within the syncytium by the dissolution of the cell-wall of the encysted monads or sporocysts. These liberated spores gradually develop through an amœboid phase into typical collar-bearing monads, and fill up the intraspicular loculi, as shown in the succeeding figure. An exceedingly minute triradiate spicule is shown at *sp*, developing within the substance of the syncytium. $\times 600$ diameters.
- Fig. 21.* A similar intraspicular area of the same sponge, in which the typical collar-bearing monads have increased to such an extent as to completely line it in a continuous pavement-like manner; the collars of the individual monads, so as not to interfere with the general view, are represented only along the upper margin, and as single instances in the two pores marked *p*.
- Figs. 22–24.* Spore-capsules or sporocysts of a siliceous sponge (*Hali-chondria*, sp.) derived from the encystment of the ordinary collar-bearing monads. At fig. 24 the sporocyst is bursting and setting free its countless granular spores.
- Fig. 25.* Spherical cluster of spore-like bodies from a species of *Hymeniacidon*. These are at first enclosed within a membranous sporocyst, and afterwards, falling asunder, become distributed throughout the substance of the syncytium. $\times 500$ diameters.

Saville-Kent, William. 1878. "XVII.—Notes on the embryology of sponges." *The Annals and magazine of natural history; zoology, botany, and geology* 2, 139–156.
<https://doi.org/10.1080/00222937808682401>.

View This Item Online: <https://www.biodiversitylibrary.org/item/81237>

DOI: <https://doi.org/10.1080/00222937808682401>

Permalink: <https://www.biodiversitylibrary.org/partpdf/63381>

Holding Institution

Smithsonian Libraries

Sponsored by

Smithsonian

Copyright & Reuse

Copyright Status: Public domain. The BHL considers that this work is no longer under copyright protection.

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.