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VI. *Researches on the Structure and Homology of the Reproductive Organs of the Annelids.*

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ALTHOUGH several distinguished comparative anatomists have done much by their labours to elucidate the general organization of the Annelids, the reproductive system of organs in this class has been little, if at all, investigated. On this account the author of this memoir is tempted to lay before the Royal Society the results of a systematic series of researches on this subject, on which he has been, for some years, laboriously occupied. These researches conveniently arrange themselves under two leading divisions.

The first will include a merely anatomical description of the chief or typical varieties of form and structure which these organs are found to exhibit in the leading genera of the class; while the second will embrace a brief statement of such homological views as the ascertained facts with respect to their structure, form, and anatomical relations may appear to warrant.

As the organ upon which always, in some part or other of the body of the Annelid, the office of reproduction devolves, is frequently in other parts diverted to other purposes, and modified in outward characters, it will prevent circuitousness of expression if at the outset a name be adopted, under which, whatever its place, size or form, this organ may be generically distinguished.

Under the appellation of the "segmental organ*," accordingly, it is proposed to describe that viscus upon the basis of which, under several striking variations of place and figure, are always ingrafted the true generative structures. By way of a general historical introduction, the author will content himself with the following citation from the recently published lectures† of Mr. HUXLEY, exhibiting the state of knowledge on this subject at the date of its publication, July 23, 1856. "The genitalia of the typical Annelida are *excessively simple in their structure;* indeed, *special reproductive organs* can hardly

* This is an unobjectionable title; it implies no theory, it simply states the fact that the organ is repeated more or less regularly in the segments of the body. No other organ in the body of the Annelid is "segmental;" every other organ is continuous throughout the body. This is the case with the alimentary, the nervous and the vascular systems. The feet are not "organs." Indeed, so intimate in an anatomical sense is the relation between the segmental organ and the foot, that in the development of the embryo Annelid they constitute one system. The hollow bases of the feet are so frequently the depositories of the generative products, that they may be regarded as bearing the same relation to the segmental organ as the uterus does to the ovaries of the Mammal.

† Medical Times and Gazette, 1856-57.

be said to exist in most, *the generative products being merely developed* from *some part* of the walls of the perivisceral cavity into which they eventually freely float, making their way out in a manner which is not quite understood at present; probably through some temporary or permanent apertures at the bases of the parapodia."

From this passage it is obvious that by the most recent expounders of the science of comparative anatomy, it is formally asserted that in the Annelida "special reproductive organs can hardly be said to exist." It will afterwards appear that the facts to be related in this memoir conduct the anatomist to a widely different conclusion.

A brief and special historical introduction will be prefixed to each department of the subject.

By this arrangement references to the researches of other observers will be much facilitated.

The families of Annelids selected for examination will be placed in juxtaposition, more on account of an affinity of type presented by the "segmental organ" than in deference to any other principle of classification.

The Naidea, Lumbricidea, Hirudinea, Terebellidæ, Nereidæ, &c. will on this ground be taken in the order in which they are named.

Naidea.—In his Report* on the Annelids, the author made the following statement with reference to the segmental organ in the genus *Nais*: "The *whole* reproductive system is limited by DUGÈS to the glandular mass which is so readily observed about the anterior third of the body, whereas in reality this only constitutes *one segmental unit*, more developed only than those which are repeated in every ring of the body." Although in the present memoir the author will avail himself of the opportunity to correct certain inaccuracies committed in his "Report" with respect to the interpretation there given in relation to the segmental organ in *Nais*, he will only at present observe, that in 1852 he drew attention to the fact that the generative structures were developed upon one, two or more of the segmental organs common to almost every ring of the body.

To M. DUGÈS the segmental organs, as distributed throughout the two posterior thirds of the body, were unknown. No special description of them has been given by any subsequent anatomist. It is doubtful whether the genus *Nais* is included by LEYDIG in his recent memoir†, "Ueber den Bau und die systematische Stellung der Räderthiere," while incidentally referring to the family of the Lumbricidea. Whether this be the case or not, the author is not acquainted with any special account of this organ in this group of Annelids.

The following description is drawn entirely from his own researches:—

In the freshwater *Naides* the segmental organ is readily examined. A few individuals should be selected and placed between two slips of glass, slightly compressed, and thus viewed as transparent objects.

* Transactions of the British Association, 1852.

† Zeitschrift für Wissenschaftliche Zoologie, 1855.

Nais serpentina may be taken as the type of the genus. In this species the segmental organ is very readily studied in consequence of the softness and transparence of the integuments. Two of these organs are present in every ring of the body, one on either side of the intestine. (Fig. 1 A, B, Plate VI. indicates the system of one segment; at A the organ is shown in its perfect state, at B in outline.) Each organ (A & B) commences (or if the course of the contained current be considered, *ends*) in a single external orifice (*a*). For some distance from this attached end (to (*e*)) the organ bears a single tube, the figure being tape- or band-shaped, and the walls thick. From this point (*e*) to (*f*), a point not far from the free extremity, the band carries a double current, one tending towards and the other out from the general cavity. This is only apparent; it arises from the agglutination of two portions of the ciliated tube. If this part were examined alone, it might be concluded that the entire organ was double, bearing a double current, one going in and the other setting out from the general cavity. This apparent double current in the mid-portions of the organ proves a source of extreme perplexity to the observer. By careful observation it may be distinctly seen that both at the attached portion (*e*) and the free floating portion (*f*) the band is small and the current single. It will now be understood that the double currents, setting in opposite directions, which are seen when the middle third of the tube (*i*, *g*, *h*) is in focus, result from the folding of the tube upon itself. Insignificant as this point may seem, it involves in truth the important questions whether the segmental organ be single or double, whether it carries one current or two, whether in fact it consists of a simple siphon leading out of the general cavity, or of a complex apparatus adapted at once to excrete and to renew the chylaqueous fluid. The solution of this problem involves great care and patience.

At its free internal extremity (A, *b*), this organ is held in a determinate position by means of bridles of delicate threads fixed at (*d*). This arrangement is one of great interest, since the free open end (A, *b*) is thus held in a fixed position, one in which it can never become obstructed. By the action of the large and vigorous cilia (A, *b*), a strong current of fluid is drawn into this open mouth (see arrows, fig. 1, A). At a short distance from this extremity, which is itself trumpet-shaped, the tube undergoes a remarkably bulbous enlargement (*c*). Here the interior bore or channel is also dilated. The walls are thick and muscular, and capable of suddenly closing and again of expanding; a rhythmic movement, which no doubt is intimately connected with the power of this organ to discharge the chylaqueous fluid. This contractile property resides indeed in the parietes of the entire organ. It is a highly irritable structure. At one moment it may be seen relaxed, outstretched and floating in the cavitary fluid, at the next coiled or shrunk up into a minute ball; while in this latter state of contraction, the current of the cilia-driven fluid coursing in the interior is entirely stopped. As soon as the tube relaxes, it goes on again, and so on. Thus the normal action of the tube is dependent upon the cilia by which the bore is lined, the *irregular* action being due to an irregular contractile movement. From the form and structure of the trumpet-shaped extremity, from the setting of the ciliary currents at the mouth and at the base of the tube, it seems

beyond the possibility of doubt that the organ *in this ordinary* state subserves the function of discharging externally the fluid contained in the general cavity of the body. This fluid must necessarily escape *in body* through the tube. This organ does not appear to be endowed with any selective power over the principles or elements of which the fluid is composed. It conveys externally the entire body of the nutritive fluid, *leaving behind only the corpuscles.* This is a fact which is capable of being brought in a direct manner before the mind and under the eye of the physiologist. Around it there crowd many suggestions. It proves that in this comparatively exalted class of animals, the process of secretion, in one case at least, is accomplished by a mechanism comparatively rude, viz. by the direct, unchanged siphonic discharge (outwardly) of the body of the nutritional fluid.

The segmental organs in *Nais* cannot convey externally either the normal corpuscles of the chylaqueous fluid, or the spermatic products; these bodies are by many times too large to traverse the bores of the tubes. [But in this genus neither the ova nor the spermatozoa are at any time found in the general cavity.] They cannot convey a current of water from without to within, from the exterior into the perigastric chamber. This would be contrary, directly opposed, to the ciliary motion within the tube, which sets from within outwards.

They cannot belong, as suggested by LEYDIG, to the mechanism of the respiratory act. It is contrary to all analogy to suppose with him that they are *the* agents of the expiratory act. The inference that they are simply discharge-tubes to the chylaqueous fluid, does not necessarily imply that they are renal in office, as suggested by several authors. The preceding description applies only to the segmental organ in *Nais serpentina*, as it is distributed throughout that part of the body of the worm which is behind the reproductive mass.

In other species of this genus the same organ occurs under characters more or less modified.

In *Nais filiformis* it (fig. 2 *g*, *g*) is not so tape-like or flattened as in *N. serpentina.* The trumpet-end is differently fixed in the cavity. The tube in its mid-portion is also dissimilarly coiled. The attached end (*h*) is more muscular; the free enlarged extremity (*g*) is more elongated; but in this species, as in *N. serpentina*, the organ consists of a *single* tube, beginning internally in an expanded ciliated extremity, floating freely in the general cavity, and terminating in a thickened dilated portion, in which in an especial manner is seated a strong muscular power. In *N. proboscidea* it is formed after the pattern of that of *N. serpentina.* It is, however, more bulbous at its free extremity, and more cord-like in figure. A further variety occurs in *N. parasita.* In *N. pusulosa* (mihi) (not uncommonly found, at certain seasons, in the finest sand of the sea-shore), another modification occurs in the form and structure of this organ.

It remains now to investigate the claims of this organ in a new and hitherto unthought-of relation, namely, in that bearing in which it connects itself with the generative or reproductive structures.

It is by far the most important bearing of this subject. It has not been hinted at by any preceding observer.

In *Nais*, and, as will be afterwards shown, in *Lumbricus*, it may be readily demonstrated that one, two, or possibly more of the "segmental organs" on either side of the body undergo a remarkable increase of size and variation of form.

In *Nais* it often happens that only one of these organs on either side is thus involved (fig. 2 a, a^2; compare a, a^2 with g, g, f in the same figure). At some seasons, however (especially one in which the weather has continued for some time warm and dry), individuals of *Nais filiformis*, *N. proboscidea* and *N. serpentina* may be found in which two organs on either side have undergone a marked generative development. This was remarkably the case in *Nais filiformis* in the summers of 1850–51*. Four organs (two on either side) were then constantly found in an enlarged and modified condition. The two anterior were developed into sacculi, in which were lodged arrow-shaped lemnisci or intromittent organs. During the present year, while conducting many hundred examinations, no single individual of the same species could be discovered in this condition. The two organs in the ring immediately in front of the genital segment have this year exhibited the ordinary or undeveloped state. It is therefore evident that only two segmental organs, the one being developed into the male and the other into the female moiety of the reproductive system, are *necessary* to the generative maturity of the individual. The anterior organs may or may not experience a special growth. When this has happened, they are accessory, not essential in office.

The two segmental organs (fig. 2 a, k and a^2, o) which form the basis of the reproductive masses (i, o), are observed even on first view to be similar in general outline to those which are repeated in every ring of the body (g, g). But on minute comparison, they will be found in reality to be identical with the latter, differing only in size and in the shape of some of their parts. The dilated portions (a, a^2) correspond in the most obvious manner with the equivalent parts (h) of the other organs. The umbrella-like extremities (k, e) (which are the same in form on the ovarian and testicular sides) are seen at once to be the counterpart of the free ciliated ends (g, g) of the ordinary organs.

* This condition is correctly represented in pl. viii. fig. 72, appended to my Report on the British Annelida[1]. I hope I may be permitted in this place to observe that, between the results of my recent and those of my former investigations on the reproductive system of the Annelids, there is no essential difference as far as the latter were carried. The following passage proves that I then suspected that the generative segmental organs were only modifications of the non-generative:—"A comparison between the familiar figures of Dugès and those which are published for the first time in connexion with this memoir, will enable the physiologist at once to perceive that the *whole* system is limited by Dugès to the glandular mass which is so readily observed about the anterior third of the body, *whereas in reality this only constitutes one segmental unit, more developed only than those which are repeated in every ring of the body*."—*Loc. cit.* p. 264. The results of my subsequent inquiries, which it is the purport of this paper to state, enable me now to contribute very materially to a better knowledge of the anatomy and physiology of this part of the Annelidan organization.

[1] Transactions of the British Association, 1851.

The latter are more pear-shaped; the former more umbrella- or fan-like. This difference of figure, it will be afterwards proved, does not involve a difference of function.

The intermediate ciliated tubes (*j*, *d*) are specially distinguished only for their great length and thickness. In all, the cilia at the free floating extremity of the organ beat in such a manner as to raise a current setting strongly *into* the organs, and out of the body of the animal. This fact is worthy of note. It proves that neither the ova nor the sperm-cells can escape through or along these ciliated tubes into the cavity of the body, supposing that in this Annelid, as in many others, they were destined at some time to find their way into this chamber. But the author has convinced himself, by recent observations, that this never takes place in this genus. The general cavity is not used at any time, or under any circumstances, for the purpose of incubation.

The ciliated tubes of the generative organs, it must therefore be inferred, fulfil the same office as those of the ordinary segmental organs; that office is undoubtedly to discharge externally the fluid of the perigastric cavity. The current thus raised, in the case of the special organs, serves also subsidiarily to convey outwards the generative products. The wider bore, more vigorous cilia, and stronger currents, are well adapted in *them* for this purpose*.

It is of great importance to place beyond dispute the mode in which the generative masses (fig. 2 *i*, *b*) occupying the special segments are related to the ciliated tubes (*j*, *d*). The first impression is that there must be some connexion between them; else why the enormous growth of the tubes in the reproductive ring, as compared with those of other parts? The demonstration of this point is attended with great difficulty. The rolling of the animal under view, and the density of the integuments, preclude a clear inspection; but it may be constantly seen that the ovarian mass (*c b*) moves to and fro *with* the dilated portion of the tube (a^2). It is impossible to *see* the opening by which the ova arrive in the interior of this part (*l*) (*utriculus*) of the tube; that they DO get there is, however, certain, for they have been actually seen therein on several occasions by the author, as shown at fig. 2 a^2. From this portion of the tube they escape by the external orifice.

It was the discovery and the clear definition of this important anatomical fact, which first convinced the author that he was justified in deducing from this arrangement the final conclusion, that *the ovarian and testicular masses in* NAIS *did not constitute detached and independent viscera, but that they were structures which were evolved from, or ingrafted upon, a segmental organ, specially modified for this purpose.*

This conclusion has been since arrived at by several different modes of observation.

The testes on the other side bear the same relation to the tube as the ovary on the side just described. The *utriculus* on the one side is represented by the ejaculatory pouch on the other. At present it is beyond the power of science to explain why these organs, in only one or two annuli of the body, should be implicated in the sexual deve-

* The corpuscles of the chylaqueous fluid in *Nais serpentina* are very large and granular: they may easily be mistaken for ova. One clear view of the *true* ova in the ovarian mass will however convince the observer that these corpuscles are not ova, but the normal form,—elements of the chylaqueous fluid.

lopment, while all the rest should remain in abeyance and in the condition of mere "excretionary tubes;" or why the ciliated tube of one side (always the same in every individual) should be changed into the female system, and that on the other into the male. Such is the nature of the *hermaphroditism* of these Annelids. It is symmetrical; the centres of the opposite sexes are separate and distinct; the organs upon which they are respectively developed are homologically identical. The vascular and nervous systems have, however, a special arrangement in each.

This centralized position of the sexual structures is peculiar to the genera *Nais* and *Lumbricus*. In every other Annelid, *Planaria* forming no exception, every segmental organ in the body is enlisted in the office of reproduction.

There is nevertheless some peculiar power resident in the ordinary segmental organs.

Towards the end of the summer these worms (*Naides*) divide themselves by fission, generally into two parts. The normal reproductive masses are always in the anterior half. The tail-half at this time *has no sexual system*; but in process of time two of the ciliated tubes will swell, enlarge in size, and at the same time become more complex in structure. It is evidently the EFFORT in the tail-half to reconstruct itself into a perfect individual. That it does become a perfect individual the author has never been able to prove by his own observations. The fact is here adduced to prove that there does reside in the segmental organ a power which enables it (the conditions being favourable) to transform itself into an ovary or a testis.

The ciliated tubes in various species of *Nais* have of late years been observed and described by several anatomists, *e. g.* by HENLE, UDEKEM, SIEBOLD, LEYDIG, GEGENBAUER and others. No one has hitherto, however, attempted to connect them with the reproductive system.

Lumbricidea.

Anatomists have long been aware of the existence of the "ciliated tubes" of the Lumbricini. By MORREN* they were described as the "Vésicules Aériennes," and as Tracheæ by WILLIS and LEO†. DUGÈS‡ states that they are "toujours remplis d'un liquide aqueux." HENLE supports this view. SIEBOLD§ professes a similar opinion. This distinguished author observes: "The structure of the respiratory system is not less difficult to be understood. In all genera (of Lumbricini) there are, at the commencement and on each side of the intestine, very tortuous canals, which open upon the ventral surface by a narrow orifice near the median line." Then, describing the cilia, he states: "In *Lumbricus* these aquiferous canals are surrounded by a very distinct vascular network, which has a botryoidal aspect from its numerous pedunculated vesicular dilatations, which are filled with blood:" and then SIEBOLD observes: "These canals, thus

* MORREN, 'De Lumbrici terrestris Hist. Nat.' p. 149.

† LEO, 'De Structura Lumbrici terrestris, dissert. inaug.' in 4to, p. 25, 1820.

‡ Consult a paper by HENLE, "Ueber Enchytræus," and 'Archiv für Anat. und Phys., von MÜLLER,' 1837, pl. 6. figs. 7, 8.

§ SIEBOLD and STANNIUS, 'Anat. of Invertebrata,' translated by BURNETT, p. 171.

situated, remind one of the trembling organs of *Rotatoria* connecting the two lateral canals with the cavity of the body." LEYDIG* has adopted and somewhat extended this homological idea of VON SIEBOLD. DE QUATREFAGES has referred to these organs under the title of "Poches sécrétices venant s'ouvrir sur le dos, &c.†" Both HENLE, SIEBOLD, and DE QUATREFAGES confess that, as yet, "*no description or figure has ever been published giving any idea of their complexity.*" GEGENBAUER‡ was the first accurately to describe the internal free, umbrella-shaped, ciliated extremity of this organ in the Earth-worm.

Thus then, in the genus *Lumbricus*, these ciliated tubes have been long known to exist; but as to their minute anatomy and their real function, nothing but confusion and contradiction have prevailed. It should be further understood, that, of the many anatomists who have more or less specially observed and studied these organs, not one has ever hinted (either directly or indirectly) at the relation in which they stand to the reproductive system. But the recent paper of HERING§, on the organs of generation in the Earth-worm, requires a special historical notice. In the course of the succeeding description it will be seen that the author differs from Herr HERING on the following important points:—1st, as to the size and position of the ovaria; 2nd, not only as to the distribution of the so-called *vasa deferentia*; but 3rd, as to the *very fact of the existence* of these ducts under any shape; and 4th, and most fundamentally, as to the connexion between the generative masses and the "segmental organs." To this latter point HERING makes no reference whatever. Lastly, the author is desirous to correct an error into which he himself was drawn while writing his "Report on the British Annelids" for the British Association (1852). By reference to that Report it will be seen that, in the worms examined in that year, the "segmental organs" in every annulus of the body were crowded with a vast multitude of the ova and young of a certain species of FILARIA. By the singular appearance thus caused, the author was induced to regard the *ordinary* segmental organs as in truth nothing but ovaries, looking upon the "central reproductive masses" as having experienced some special and distinctive development. Subsequent and most carefully-conducted researches have convinced him that he then mistook the ova and young of an Entozoon infesting the Earth-worm for those of the animal itself. He was lured into this error in consequence of regarding the *ordinary* segmental organs of the Earth-worm as the real equivalent of the ovarian segmental organ of the Hirudinæ, and not of those of NAIS. And besides, at that time the segmental organ of the Earth-worm was not known in the whole extent of its minute anatomy.

Lumbricus Jordanii‖, in the months of July and August, presents at a short distance

* "Ueber den Bau und den systematische Stellung der Räderthiere," Zeitschrift für Wiss. Zool. 1854.

† Consult pl. 21 bis, Le Règne Animal, &c. 3me grande division, &c.

‡ "Ueber die sogenannten Respirationsorgane d. Regenwurms," in SIEBOLD and KÖLLIKER's Zeitschrift, vol. iv. p. 221.

§ EWALD HERING, "Zur Anatomie und Physiologie der Generationsorgane des Regenwurms," in Zeitschrift für Wiss. Zool. 1856.

‖ This is a minute terrestrial *Lumbricus*. It is found in July and August in the fine loamy earth of gardens. It is NOT the young of the common Earth-worm.

behind, as in the common Earth-worm, a thickened ring or band around the body. It is bounded by abrupt limits, and implicates four or six of the annuli of the body. When this portion of the integument is closely examined, it proves to depend upon an extraordinary development of the cutaneous follicles. On the abdominal aspect of this thickened portion, *suctorial cups* are formed, by aid of which, during the congress of the individuals, mutual contact is maintained; but the generative segments internally *have no relation* with this suctorial ring of integument, nor has this latter part anything to do with the true *genitalia*. It is like the thumb of the Frog; it is simply a provision for the mutual apposition of two individuals. The enlarged follicles of this cutaneous ring discharge also another function; they supply that peculiar glutinous secretion which affords (in such a remarkable manner in the cases of *Lumbricus terrestris* and *L. complanatus*) a protecting capsule to the ova as they escape from the body. This peculiar hypertrophy of the integuments in the region of the reproductive segment occurs also in every species of *Nais*.

Lumbricus Jordanii is a minute worm of pure white colour. The integuments are transparent enough to enable the eye to read the interior organs. The ordinary segmental organs are present, in pairs (fig. 3 A. *m*, *m*), in every annulus of the body; they do not however float freely in the fluid of the general cavity, as in NAIS. They are attached to the side of the intestine by means of threads or delicate membranes, the trumpet-shaped extremity being fixed to a determinate point.

All those organs which are distributed throughout that part which is posterior to the generative segments are in the *ordinary* condition (fig. 3 A. *m*, *m*). The internal end (*j*) of the tube in this worm is figured after a pattern intermediate between that of *Nais* and that of *Lumbricus*. It is less trumpet-shaped than the latter, and more so than the former.

In this little terrestrial Annelid, as in the aquatic Nais, only two segmental organs, one on either side, are specially evolved into the reproductive condition; in other words, only one ring of the body is implicated in this function; bearing in this respect a striking resemblance to the instance of NAIS, and differing no less strikingly from that of the common Earth-worm, in which six or eight pairs of these organs experience this special enlargement. In *L. Jordanii*, as in *Nais*, the generative tubes (fig. 3 A. *a i* and a^2 *e*) are considerably developed when measured by the standard of the ordinary non-generative ones (*m*, *m*). The utricular ends (*g*, *c*) are far more elongated than in *Nais*, but they bear precisely the same relation to the ovarian masses (*b*, *b*) as is observed in the latter. The intermediate tube (*d*) is extremely coiled and elongated; the free ciliated extremity exhibits a distinctive form; it is pear-shaped (*e*, *i*); it is very long, provided with very thick walls; and at the extremity it is furnished with a lip, highly ciliated (*l*), which appears to be adapted to favour the ingress of the chyl-aqueous fluid into the bore of the segmental organ.

By easy manœuvres a clear sight of the reproductive masses may be obtained in all their relations. Under skilfully-regulated pressure, the entire system will burst its

boundaries and float in the neighbouring fluid. It will be observed at once that a most constant and intimate organic connexion exists between the masses (*f*, *g* and *b*, *b*) and the coiled tubes of their respective sides. The ova on the one side, and the sperm-cells on the other, may be actually seen by the eye, on many occasions, rolling to and fro in the *interior* of the dilated portions of the tubes (*a*, a^2).

To this Annelid no further reference will be necessary, since in every particular the sexual system conforms with the type of that of *Nais*. In the young of this worm the ordinary segmental organ exhibits the form shown at fig. 3, B.

It seems to the author that a candid review of the preceding facts must inevitably conduct to the conclusion that, in this species (which is evidently intermediate between *Nais* and the common Earth-worm), the ovaries on the one side and the testes on the other are not only organically connected with, but are ingrafted upon, and developed from, the standard or normal segmental organ.

In the course of his researches the author has accidentally fallen upon other species of Lumbrici, more or less favourable to the study of this question. In *L. Kanii*, mihi, in the young state, the segmental organ may frequently be discovered in a condition highly favourable to the present investigation (see fig. 4 A). In that *annulus* in which the contained ciliated tubes are destined to become the generative organs, the latter appear at first under the character represented at *c* (fig. 4 B). From one side of the mid-portion of the tube (as at *c*, 4 C) may be observed to bulge minute pear-shaped vesicles, filled with a semigelatinous fluid. Regarded as a whole, it is impossible to doubt that this organ is one of the segmental organs. If this be admitted, the conclusion cannot be resisted, that the vesicular outgrowth (*c*) is really the ovary or the testes in process of development. But in the same individual the other and ordinary segmental organs have altogether a different form and structure (fig. 4 A. *a a*, *a*, and B). Thus is adduced another well-attested fact, in confirmation of the view maintained in this paper, viz. that the reproductive organs in *Nais* and *Lumbricus* are in reality nothing but a modification of the "segmental organs" or "ciliated tubes" which exist, in pairs, in every annulus of the body.

Earth-worm.—The anatomy of the reproductive system in the Earth-worm has been made a subject of express investigation by many competent comparative anatomists.

The points in difference between the author and other observers will be indicated as we proceed.

The anatomy of this system in the Earth-worm has ever been held as almost an insoluble enigma. No intelligible clue whereby to unravel the intricate glandular mass has ever been discovered. Without such a clue the problem never can be consistently solved. It is hoped that such a clue or *principle* is afforded in the succeeding account. It rests upon the fact that between the reproductive masses and the ciliated segmental tubes there exists a *necessary* and regular connexion, and that the glandular masses of the adjacent segments are distinct from and independent of one another. A knowledge of this leading principle of arrangement enables the anatomist at once to convert a con-

fused heap of glands into an orderly system of parts, and moreover, to bring the sexual apparatus of this Annelid within the pale of definite homologies.

Every ring in the body of this worm (except a few at the head and tail) contains two segment organs, one on either side of the intestine: they are convoluted, tubular organs, arising from the ventral aspect of the general cavity near the median line, curving upwards round the intestine and terminating in a fan-shaped ciliated extremity, which is bridled to the septum near its dorsalmost edge. Those segmental organs which are situated anteriorly to the gizzard are very much larger and more distinct than those which are placed behind it.

It is desirable in the first place to obtain a clear idea of an ordinary or non-generative segmental organ in this worm. The following description is drawn from minute researches conducted with care by the author himself. Not having seen the original paper of GEGENBAUER* on this subject, he cannot say how far his own account may agree with or differ from that of this anatomist.

The season of the year, the state of the weather, have much to do with the condition in which these organs are found. All the specimens upon which the following examinations were instituted were taken in the months of July and August, from a rich, loamy, highly-cultivated garden soil.

This fact it is material to know, since nowhere, in the ordinary fields and meadows, does this worm attain the same size and plumpness. The generative *nisus* does not seem to reach its climax until the worm has arrived at a certain period of age and fulness of growth, so that, out of 100 specimens examined, only ten or fifteen may be found in that condition which is required for the successful prosecution of these researches. The accompanying illustration (fig. 5) of an *ordinary* segmental organ of an Earth-worm was constructed from dissections instituted on at least fifty individuals: so exceedingly difficult was the inquiry, that only a small fragment of this extraordinarily complex tube (extending from a to a^2, fig. 5) could be traced in each individual. It was found to be impossible to make such a section of the *annuli* as would afford a complete view of the *entire apparatus*. Notwithstanding these difficulties, the following

* *Note, added April 27th*, 1858.—I have just procured that number of the Zeitschrift für Wiss. Zool., for September 1852, which contains GEGENBAUER's paper "Ueber die sogenannten Respirationsorgane des Regenwurms." It affords me the greatest pleasure to find that the description given in the text, and drawn exclusively from my own unaided observations, agrees almost in every minute particular with the description and figures of GEGENBAUER. It is gratifying to find one's self in agreement with so accurate an observer on so extremely difficult a point in minute anatomy. Our concord, however, ceases at this point. GEGENBAUER's account of the complex botryoidal vascular system of the segmental organs of *Lumbricus* is little more than a passing reference. He seems neither to have deciphered its anatomy nor recognized its homological significance. He speaks of the "schleifenförmigen Organe" as intended, in function, to discharge in a direct manner the fluid of the general cavity, and also to furnish a peculiar excretion from their own walls. Although he alludes to the *increased size* presented by these organs, both in *Lumbricus* and in *Sœnuris*, in the segments containing the generative masses, he overlooks completely the *organic connexion* which I have invariably found to exist between the one and the other, and upon which connexion I have attempted in this memoir to explain the homology of the reproductive system of the Annelids in general.

description conveys an exact and faithful account of the anatomical structure and disposition of this marvellous organ.

In *Lumbricus terrestris* the divisions or segments of the alimentary canal posteriorly to the gizzard and proventriculus are very numerous and closely packed. Each "ring" of the body is divided from the adjacent ones by the intervention of membranous partitions, which either completely or partially isolate the fluid contents of each annular space. It is probable, however, that the fluid of the general cavity freely oscillates from one extreme of the body to the other through perforations in the septa.

But whether the segmental spaces be isolated or not, the ciliated organs which they circumscribe are individualized and independent, the adjoining ones having no connexion whatever with one another. The following account is descriptive of all those which are situated posteriorly to the *proventriculus* and the generative region.

This organ is far more complicated in structure in the Earth-worm than it is in any other species of *Lumbricus*. The tube which connects the free extremity (fig. 5 *f*) with the fixed end (a^2) is extremely convoluted, lengthened and thickly intermixed with vessels.

This intermediate tube is divisible into three distinct portions. First, a smooth-walled, minutely diametered membranous part, which extends (from *e*, to *d*) from the umbrella-like termination (*f*) to the camerated or cellular portion (at *d*). This division of the tube is uniform throughout in diameter. It is the smallest and most contracted of the entire tube. It is vigorously ciliated in its interior bore. The ciliary current sets from the free end (*f*) in the direction of the fixed end (a^2). The next division of the tube extends from the termination of the smooth membranous part (at *d*) to the commencement of the third stage (at *i*). This portion is not ciliated. The walls bulge out into lateral cells. This part of the tube appears to split into two, which unite again, as is the case in the corresponding organ of the Rotifera. Such an arrangement is not, however, represented in the accompanying figure (5); for it is only apparent (*d*, *i*).

The segmental organ in this portion is inextricably blended and matted up with blood-vessels (although in the figure, for the sake of clearness and simplicity, the vessels are omitted). From its peculiar structure and extreme vascularity, this part may be regarded as typically indicating the true seat of the process of ovogenesis, as it occurs in the segmental organs of other Annelids.

The fourth division of the tube stretches from the end of the celled portion (*i*) to the commencement of the muscular part (*j*). This again is strongly ciliated. In function it is evidently exclusively expulsatory. Its walls are thick and contractile. The last, outermost or dilated portion (*b*), bounded internally by the smooth-walled division (*j*) and externally by the attached end (a^2), is however the most striking and remarkable part of the whole apparatus. It is almost invariably, in the months of July, August and September, crowded with the ova and the young of a certain species of Nematoid Entozoon (5, *k*), which might readily be mistaken for the ova and the young of the Earth-worm itself. Although formerly deceived by the appearance presented by these Entozoa, a

critical study of their structure has convinced the author that they are not the young of the Earth-worm, but individuals belonging to the genus *Filaria*.

This dilated muscular portion of the segmental organ is not ciliated internally. But its walls are capable of contracting vermicularly or peristaltically.

The *vascular system* connected with the segmental organ receives a special development. In *Nais*, however, this is not the case.

During the past summer, 1856, the author was so fortunate as to discover five or six specimens of Earth-worm very large, the ordinary segmental organs of which were precisely in the condition illustrated in fig. 5, in which the vascular system had acquired an extraordinary degree of development (*g g* and *h h*). The vessels connected with the ciliated tubes of the ordinary as well as with those of the generative segments were on these occasions found to be in this remarkable state. This botryoidal condition of the vessels has been cursorily alluded to by SIEBOLD and GEGENBAUER. It is not present in every individual and on all occasions. It is in some way connected with the condition of sexual maturity. That this is the case the author has assured himself by a great number of most careful dissections. Sometimes the vascular system of the segmental organ is in a state of almost entire abeyance. When present under the most evident circumstances (as in fig. 5), it may be described as consisting of three parts. First, of two or three large trunks (*n*, *g*, *m*), which curve upwards from the ventral to the dorsal trunks. These vessels form thus a *framework* by which the slender ciliated tube (*a*, a^2) is held vertically *in situ*, they themselves being vertically disposed.

Between the primary vertical trunks extends a vast multitude of secondary branches (*l*, *l*), which further subdivide to form a dense plexus of smaller vessels (omitted in the figure for clearness' sake), in the meshes of which the ciliated tube (*a*, a^2) is entangled. It is the presence of this mass of vessels which renders it so extremely difficult to trace the coils (*d*, *i*, *j*) of the tube. This reticular plexus, in a more or less pronounced form, is much more frequently present than that curious portion of the vascular system next to be examined.

As already stated, in the Earth-worm, at certain seasons and conditions of growth, a dense mass of florid blood is attracted to, and held in the region of the segmental organs. It is contained at these times, not in ordinary cylindrical vessels, but in capacious lateral cæcal branches, terminating in large bulbous pear-shaped extremities (*h*, *h*). Now this portion of the vascular apparatus of the organ evidently constitutes a *special provision*. What is its purpose? It is not fitted in any way or in any sense to aërate the contained fluid.

In virtue of a contractile power with which the bulbous extremities are endowed, not only are they adapted to attract towards, and detain in the neighbourhood of the segmental organ a large extra supply of blood, but they are also fitted to exercise a supplementary power to drive into the plexus of capillaries which more immediately embraces the coils of the ciliated tube an extraordinary supply of blood. Does not this definition at once suggest the inference, that therefore at certain seasons and under

certain conditions of growth some *extraordinary* function devolves upon the tube itself? else why this exceptional condition of the vessels? On this point the author does not at present wish to pledge himself to any particular doctrine, not even to the opinion which he ventured to express in his Report in 1851, or the opposite. All he is desirous to state is that this periodic afflux of an extraordinary quantity of blood to the region of the *ordinary* segmental organs, in the Earth-worm, seems to indicate that under the constraining influence of certain exceptional conditions they may experience a generative activity. On no occasion, however, has he been able to *prove* this by the discovery of the presence of the real ova and young of the worm itself. But in support of this view the question may be asked, if the "ordinary" segmental organ were designed merely and exclusively to drain off, in an *unselecting* mechanical manner, a given quantity in a given time, of the chylaqueous fluid, does it not seem incomprehensible that so highly organized, such a completely constructed apparatus should have been provided to execute a purpose so simple? This latter is undoubtedly its purpose in *Nais*, and accordingly the organ is reduced to the characters of a simple non-vascular tube. It cannot be the expiratory half of a respiratory apparatus, as supposed by LEYDIG; such a supposition is opposed to all that is known of the mechanism of respiration in the invertebrated animals. If it be designed to fulfil the office of an excretory gland, it may be said that by its *open* internal mouth it may eliminate, *in body* and directly, the chylaqueous fluid, while, from its peculiar connexion with the vascular system, it could only remove the contents of the latter by the normal cell-agency method of membranous secretion.

Accepted in this latter sense, they may be said to discharge a renal function. In relation to the fluid contents of the vascular system, these organs may be said to be capable of exercising a *selective* influence in virtue of some property resident in the membranous walls of the vessels and tube. But such selective property cannot be said to reside in the cilia with which the trumpet-shaped extremity of the tube is armed. They act on the cavitary fluid simply mechanically. If, therefore, the segmental organ stands in the relation of a kidney to the blood proper, it is scarcely possible that it can do so in relation to the chylaqueous fluid, unless we admit the maxim that the simpler the fluid, the simpler is the anatomical construction of the solid organs designed to react upon it.

These botryoidal appendages to the vessels of the segmental organ do not appear to exist in *Nais*, or if they do, they are so small as to be invisible even under a high power; if they do not, it is a point of difference between the structure of the part in *Nais* and *Lumbricus*.

In parting with this subject, the reader's attention is particularly drawn to the analogy which exists between the botryoidal or pear-shaped cæcal appendages which project laterally from certain of the vessels of the segmental organ of *Lumbricus* and those vascular tufts and pouches (hereafter to be described) of the segmental organs of *Arenicola*, *Terebella*, and those of the Nereid family.

The Sexual System of the Earth-worm, *Lumbricus terrestris*, appears, on a superficial inspection, to consist of an inextricably confused mass of ovaria and testes, bound to and centred in a particular region of the body without rule, law, or intelligible order*. But the results arrived at by the numerous anatomists who have laboured on this subject are still more confused and contradictory. Sir E. Home, Dugès, Meckel, Hoffmeister, De Quatrefages, D'Udekem, and lastly, and more especially and recently, Meissner and Hering, amongst many others, may be named in this category. They have bequeathed to us no consistent account of the reproductive organs of this worm. These organs have proved a puzzle to anatomists of every age; and they are so to this day, notwithstanding the meritorious researches of those whose names have been mentioned.

The author is fully impressed with the difficulties which beset the investigation. He has not therefore ventured upon conclusions with respect to the subject in dispute, without great care, caution and labour.

He now believes, however, that he has seized the true clue which will conduct the patient dissector to a complete and satisfactory solution of this long-vexed problem.

He will proceed at once to state the results of his own researches, indicating in notes the points whereon he differs from other observers.

The dissection of the Earth-worm requires great manipulative skill and experience. The animal should be pinned down (with the back upwards) to a cork-bottomed vessel. The posterior half of the body may be cut off as unnecessary for our purpose. By means of a curve-scissors a longitudinal incision should then be made along the dorsal median line. The point of the instrument should run in the hollow axis of the intestine. The integuments should then be pinned down and slightly stretched. A gentle stream of *fresh water* should now be allowed to fall on the worm thus opened. This will carry away the contents of the intestine, and float the delicate parts without arresting ciliary action. If the operation thus far has been carefully performed, the object is ready for examination. The eye should be first carefully carried along the septa, or the membranous partitions between the annular chambers. It will be seen that these membranous septa, when clearly traced out by the aid of the handle of the scalpel, divide with great regularity the reproductive masses into *segmental groups*. This point implicates a principle of great anatomical importance. It establishes this fact, viz. that the *contents* of each ring or annulus are *distinct from, and structurally independent of*, those of the adjacent rings or annuli†.

It countenances the idea of the zooidal individuality of each annulus. An annulus in the generative region is a perfect organism in its nervous, hæmal, visceral, fluid and reproductive parts, not, however, an hermaphrodite organism.

* See plate 21 bis, in the volume "Sur les Annelides," 'Règne Animal,' which is taken from the dissections of *Lumbricus trapezoides* by De Quatrefages.

† Lest the dissector who undertakes to repeat these researches should be led hastily astray, it is here proper to explain that it is meant only those parts which take their *origin* in the individual segments, not those masses which by growth swell beyond the dimensions of *several* annuli.

At this stage of the dissection, it may be easily observed that each segmental space has its own distinct and independent ciliated tube.

On further examination it will be seen that it is around the bases or attached ends of these tubes that the reproductive masses cluster.

The ovarian and testicular masses are definitely bounded by the dissepiments (*j*, *j*, *j*). The roots of these bodies are always situated within the space of its own segment; but the *body* of the larger glands (as *c* and *i*) may from their size extend across several segments.

These few leading statements explain the *principle* on which the sexual system of *Lumbricus* is constructed. (Fig. 6 represents the entire system in the condition of its greatest development.)

Before proceeding to the minute dissection of these parts, the position of the thickened collar, so prominently observed on the external surface, with respect to that of the generative masses within, should be particularly noticed. It will be seen to be placed, by several segments, behind these masses. This thickened ring is bounded by sharp borders before and behind. It involves six or eight annuli of the integuments. On its abdominal surface two suctorial cups are observable. It is most certain that these cups are not perforated at the bottom; they cannot therefore be, as supposed by some anatomists, the outlets of certain tubes within*. They are in truth designed only to hold the individual in apposition during the generative congress. That there is no organic connexion between these cups and the reproductive masses, may be further proved by carefully examining (internally) (previously dissecting away the intestine) the condition of the ciliated tubes in the intervening segments. They are not developed like those in the generative segments; they belong to the class of the "ordinary" segmental organs. These intervening annuli are not crossed in this worm, as described and figured by HERING in *Lumbricus agricola*, by the vasa deferentia and oviducts. In fact they are altogether excluded from, and beyond the limits of the reproductive segments.

Now, in studying the visceral contents of each ring within the limits of the generative region, it will be best to proceed from behind forwards.

The dissector thus comes first upon the largest and most prominent (fig. 6, *i*, *i*) of all the generative masses. They are testes. This can only be proved by the examination of the products contained within them, under the microscope. They have a white, glittering, oily colour. In figure they are intestiform, the coils, of which there are two or three, being tied together by means of a mesentery. The capsule consists of a proper membranous tunic, and is seen to be thinly supplied with vessels when carefully floated and suspended in water; these two testicular masses, which lie across and fill up several

* The distance internally between the tegumentary ring and the generative masses is represented by EWALD HERING (Zeitsch. f. W. Zool. Nov. 12, 1856) as traversed, in *Lumbricus agricola*, by the oviducts and *vasa deferentia*. The most carefully repeated dissections have convinced me that neither of these ducts exist in *Lumbricus terrestris*. If they have no existence in this species, it is highly probable that HERING has been led into error in describing them in *Lumbricus agricola*.

rings, may be traced with perfect clearness to comparatively narrow peduncles (*g*, *g*). These peduncles, when minutely and successfully dissected out, will be found to connect themselves intimately with the *roots* of the ciliated tubes or *special* "segmental organs" of the same annular spaces. If now the peduncles and the attached tubes be cut away by a curved scissors as near as possible to the abdominal surface, and then placed on a glass slide so as to admit of being examined under the microscope, it will be discovered that the tube and peduncle of the testicular mass run into one another (as shown in fig. 7 *a*, *b*, *c*) and that the outlet (*d*) is common to the peduncle (*a*) and the ciliated tube (*b*). This outlet cannot be detected on the external tegumentary surface of the animal; it is far too minute and closely contracted. No orifice can be discovered even in specimens preserved in spirits. But its position may be clearly ascertained by the position of the attached extremity, internally, of the ciliated tube. The confluence of the peduncle of the testes and base of the ciliated tube is a fact of great homological value. It proves that the generative gland is an outgrowth from, and organically the development of the "segmental organ."

It is a fact which brings the generative system of this worm, hitherto so incomprehensible, within the rule which governs the formation of this system in the Annelida in general*.

The two ciliated tubes, one on either side, which are contained in this testicular ring, differ in no respect whatever from those (fig. 5) of the non-generative rings, but in that of size. They are considerably larger than the latter, so much so as to be quite visible to the naked eye.

The botryoidal vascular appendage (fig. 5, *g g*) exhibits the same character. The tubal portion (*j e*) is only more densely coiled and complicated. The umbrella-shaped extremity is very large, and the cilia act with great force. Neither HERING, DE QUATREFAGES, nor GEGENBAUER allude anywhere in their writings to the fact, which is so significant in a homological sense, of the increased size of the ciliated tubes of the generative segments in *Lumbricus*.

Before proceeding to investigate the contents of the second (from behind forwards) generative ring, it is material that the dissector should convince himself that in the first ring nothing connected with the reproductive organs is contained but the testes and the ciliated tubes just described. No ducts crossing the space can be discovered, no ovaries or sacculi of any description.

There is therefore every reason to believe that the viscera bounded by the septa of this ring are distinct and independent, and wholly unconnected with those of the adjacent rings, and that they communicate externally by separate ducts whose openings are within the limits of this ring. This ring, then, is exclusively dedicated to the male organs. In this particular it differs from the generative annulus in *Nais*, in which the

* In the excellent paper already referred to, HERING speaks in several places of the *constant connexion* between the "schleifenförmigen Organe," ciliated tubes and the ovaries and testes. But the mere proximity, of which he speaks, is very different from the view maintained in the text.

segmental organs of opposite sides of the same ring become developed into opposite sexual parts (ovaries and testes*).

The second generative *annulus* in the order mentioned is exclusively ovarian. The greatest care should be taken to float well the delicate septa in order to define distinctly the annulus. Having done this, it will be easy to prove that the mass (*f*) and the base of the ciliated tube (*i'*) run together, and become blended into one structure.

The most minute dissection fails in the attempt to isolate the duct which, it may be supposed, leads from the ovary. When the gland is cut out deeply in connexion with the ciliated tube, it is found to surround this tube as shown at fig. 8; so intimate is this connexion, that it is certain that (as in the case of the testes and tube in the segment behind) the gland and the tube must have a common outlet. The ovary is considerably smaller than the testes. Its capsule is more dense and vascular, and its interior structure is much more thickly supplied with blood. The vessels in the structure of the ovaries have a peculiar arrangement; they run parallel with the lobuli of the gland, a dense capillary plexus being formed between the larger trunks.

The ciliated tubes of this ovarian annulus do not differ in size or structure from those of the testicular annulus. It is therefore impossible to tell why on the one an ovary should be ingrafted, and on the other a testis†.

In the common Earth-worm the second, third and fourth generative segments (fig. 6 *d*, *e*, *f*) are ovarian. Each ovarian segment is anatomically only a repetition of the other; all are constructed upon the same plan. Some slight difference in the size and position of the glandular masses may be observable; there is none in their ultimate relations.

The fifth segment (from behind) of the generative rings is again testicular. In general and minute structure this segment is precisely the same as the first. At this point

* In the plate copied from his MS. and published in the grand edition of the 'Règne Animal' (vol. Annelides, pl. 21), De Quatrefages indicates the most posterior of the generative masses in *Lumbricus trapezoides* as the testes, the anterior group being the ovaries.

† Ewald Hering, in his account of the ovaries in *Lumbricus agricola*, describes and figures the ovaria as occupying the *hindmost* of the generative segments. "Durchschneidet man jetzt den Darm an der beschriebenen Stelle, so erscheinen die Ovarien unter der Loupe als zwei flache, ovale oder birnförmige, in einen mehr weniger langen Faden auslaufende Scheibchen, die an die vordere Scheidewand des dreizehnten Segments ungefähr 1 Mm. von der Mittellinie, 0. 5. Mm. von der Bauchfläche mit ihrem breiten Ende angeheftet frei in die Leibeshöhle hineinragen, so dass ihre Fläche der Bauchfläche parallel geht. Da an derselben Stelle jederseits auch das Schleifenförmige Organ befestigt ist, so isolirt man das Ovarium am besten, wenn man jenes fasst und beide nebst dem angrenzenden Theile des Septums herausschneidet. Auf einem Gläschen ist es dann leicht weiter zu isoliren. *Stets findet man den flimmernden Trichter des schleifenförmigen Organs an der Basis des Ovariums angeheftet.*" *Loc. cit.* Judging from his figures as to the real character of what Hering here describes as the ovaria, and guided by what is so perfectly and clearly demonstrable in *Lumbricus terrestris* (a species synonymous with his *Lumbricus communis*), it appears beyond doubt that this observer has mistaken some other structures for the true ovaria. Hering's account differs as widely from the statements and figures of De Quatrefages, with respect to the ovaria of an allied species, as they do from my own.

the reproductive rings terminate anteriorly, so that the first and the last segments in this region are testicular, the three intermediate ones being ovarian.

The ovaria of *Lumbricus* are much more transient in duration than the testes. The latter in a certain condition are always present at every season of the year; the former only in the summer months. The ova, while yet in the ovaria, are beautifully clear transparent cells. In August and September they seem to consist of nothing but germinal vesicles; afterwards appear the germinal SPOTS, and then the rudimentary vitellus. It is at a subsequent stage, just before their extrusion from the body, that they become covered with a cocoon or characteristic capsule, each capsule containing many ova. This capsule is a compound of chalk and *mucus*. The source of the chalk has never yet been described. In the median line between the ovaria there are situated two or more glandular bodies (fig. 6 *l*, *l*), the contents of which under the microscope prove to consist of nothing but carbonate of lime*.

Both in the ovarian and testicular segments, there are sacculi attached to the bases of the segmental organs, which in the former case serve as receptacles for the ova (*vitellaria*), and in the latter as receptacles for the semen. In one case the ova acquire their calcareous capsules; in the other the sperm-cells become developed into active spermatozoa. These membranous sacculi have long been known to anatomists. They were described in the author's Report (1854) on the Annelids, in the Transactions of the British Association.

The preceding account embodies a brief outline of the author's researches into the reproductive organs of the Annelids.

They justify the following general conclusions:—

1. That the ovaria and testes in *Lumbricus terrestris* (vel *communis*) are centralized together in one special region of the body.

2. That the ovaria and testes are situated in *different annuli* and attached to different "segmental organs."

3. That the segmental organs of the male and female annuli are identical in shape, size and structure.

4. It follows that the ducts leading from each ovary and testis, being identified respectively with the ciliated tubes of their own rings, open externally by distinct orifices. This conclusion, if true, renders it impossible that HERING'S observations can be correct.

At this place it is interesting to inquire what can be the meaning of the increase of size which takes place in the ciliated tubes or "segmental organs" which are limited to the generative region, as compared with those of the ordinary segments of the body.

* The egg-capsules of *Lumbricus agricola* have been well described by Dr. GEO. MEISSNER (Zeitsch. f. Wiss. Zool. 14 Sept. 1854). He observes, "Der Regenwurm legt, wie bekannt ist, Eierkapseln. Diese sind bei den verschiedenen Arten von verschiedener Gestalt und Grösse; die Grössten sind die citronenförmigen Kapseln des *L. agricola* (vielleicht," he observes, "mit Ausnahme derjenigen des *L. gigas*, DUGÈS, die ich nicht kenne). In jeder Eierkapsel befinden sich in der Regel mehre Eier oder Dotter in einer milchweissen zähen Flüssigkeit suspendirt," &c. &c. He does not, however, allude to the chalk-secreting glands.

The first impression is, that they must be connected with the reproductive masses; but in what way and what physiological sense? It has already been demonstrated that the ovaria and testes respectively, in their several segments, are anatomically developed from the ciliated tubes. But this fact throws no light upon the use of the tubes themselves. Is it possible that they can act as the conduits by which the generative products are conveyed into the perigastric cavity? No, it is *not* possible, for the cilia by which the tubes are lined act in the reverse direction, tending rather to carry outwards, and that with great force, any body that may perchance be thrown into the channels of the tubes. This fact is sustained by another fact, viz. that in *Nais* and *Lumbricus* neither the ova nor the sperm-cells have ever, under any circumstances, been discovered in the general cavity of the body. On these and other grounds it is then probable that the augmented size of the ciliated tubes in the "generative region" may be ascribed to two causes: 1st, to the fact that they are the roots from which the ovarian and testicular masses arise; and, 2nd, that by means of their open ciliated ends, they may effect the discharge of a larger quantity of the cavitary fluid from the segments in which they are situated; and the more rapid elimination of this fluid from this region is most probably concerned in the more energetic nutrition characteristic of the generative segments*.

Hirudinei.—The segmental organ in the Leech tribe exists under very readily demonstrated conditions. Two genera of this family will be here selected for the purposes of illustration, viz. the common officinal Leech (*Sanguisuga medicinalis*), and the Sea Leech (*Albione muricata*).

The method to be observed in the dissection of these Annelids is the same with that recommended in the case of *Lumbricus*.

After pinning the *common leech* down carefully to the trough and opening the body by a longitudinal incision along the dorsal aspect, pinning down again the integuments, the whole stomach and its diverticula must be minutely picked away. The dissection should be repeatedly washed with very gentle streams of fresh cold water, in order to remove the blood which obscures everything. The object being thus carefully cleansed and then floated in water, a full and complete view of the segmental ovarian and the median testicular systems will present itself. It is most important that at this stage the anatomist should well and clearly instruct himself as to the relative extent and relative anatomical places of these two systems.

The one consists of a bilateral series, of extremely delicate floating pearly membranous organs, equalling in the number of their *pairs* that of the annuli marked on the integuments.

* In a paper in MÜLLER'S Archiv, 1844, on the genitalia of *Lumbricus terrestris*, H. MECKEL remarks that there are three pairs of testes with sacculi and three pairs of ovaries, the latter being intimately joined to the former. This statement seems to show that the results arrived at by MECKEL closely correspond with the description contained in the text. They do so only as regards the distribution of the masses of the ovaries and testes. To MECKEL, however, the existence of the ciliated tubes was unknown, nor does he suspect the importance of the septa in separating the ovaries and testes into segmental independent groups.

The other, more medianly situated, and bilateral also, consists of two series (one on either side) of spherical white little bodies, tied together by an intermediate thread, which unite at a common point anteriorly.

A third element should be noticed, namely, the small *sacculus* which, immediately behind the anterior mass of the united testes, lies also on the median line.

Now the first of these three systems of organs has been described as belonging to the reproductive system by no other writer than the author of this paper*.

By Dugès they have been described as the Respiratory Sacculi; by De Quatrefages, in *Hirudo vacca* and other species of this genus, as the "Poches secrétrices latérales avec leur cœcum," and by Leydig simply (in *Nephelis*) as the analogues of the ciliated tubes of the Rotifera; by Müller, Meckel, Siebold, and Milne-Edwards and others, as the "internal branchiæ" or aquiferous vessels. Not one of these distinguished anatomists appears at any time to have discovered the existence of *ova* in these variously designated organs. No suspicion, therefore, as to their ovarian character, could have existed. Gegenbauer and Leydig are the only physiologists who have caught even a glimpse at their true homology. Thus stands at the present time the question as to the history of the reproductive system and of the segmental organs in the genus *Hirudo*. It must be confessed that much information remains to be acquired. The author hopes that the following contribution will go far to supply this admitted desideratum.

The testes and the copulative median pouch have hitherto been regarded as constituting the entire reproductive apparatus of the Leech family. The vermiform processes appended to the fundus of the pouch have been described as the ovary, and the pouch itself as the uterus. It will now be demonstrated, for the second time, that this idea with respect to the ovarian system of this family, involves a very complete and radical error.

It may be desirable to commence by admitting, that the minute membranous organs, which in the Hirudinei exist in pairs (one on either side of the stomach) in each ring of the body, are the equivalents or homologues of the ciliated tubes or segmental organs, as already described in *Lumbricus* and *Nais*†.

* In my Report to the British Association in 1851, I described at length the anatomy of the reproductive system of the common Leech. As no reference whatever has been made to that description by any subsequent writer (see the last edition of Dr. Carpenter's 'Principles,' &c., Professor Owen's 'Lectures on the Invertebrata'), except Mr. Rymer Jones ('Animal Kingdom,' last edition, 1856), in this country, I resolved to apply myself during the past two summers to the renewed investigation of the subject. The result is that I have again and again, in every essential respect, demonstrated the correctness of my first account. Some of these demonstrations have been recently witnessed by Dr. Carpenter and Mr. Busk. An error or two of minute detail and of interpretation, as contained in the original report, are corrected in the improved description given in the text. In one important respect, however, the reproductive system of the Leech, although descriptively resolved, was utterly incomprehensible to me in a homological sense, for I had not then discovered that the ovaria (and their appendages) of this Annelid are really the equivalents of the ciliated tubes of *Lumbricus* and *Nais*.

† As the following passage from a recent paper by Leydig ("Ueber den Bau und die systematische Stel-

But notwithstanding this morphological affinity, a remarkable difference obtains between the segmental organs of the Hirudinei and those of Lumbricini, as will afterwards appear.

In Hirudo officinalis and Albione muricata *every segmental organ in the body is not only an excretionary instrument for the discharge of the cavitary fluid, but is also an ovary**.

lung der Räderthiere," Zeitsch. f. Wiss. Zool. 1854), represents the present state of knowledge on this subject, it is here transcribed:—"Der beschriebene Respirationsapparat der Rotifera hat, vom morphologischen und histologischen Standpunkt aus angesehen, die grösste Aehnlichkeit mit jenen organen, welche bei *Lumbricinen* und *Hirudinen* als Athmungsorgane gelten. Auch bei ihnen kommen geschlängelte und genäuelte Röhren vor mit hellem Lumen, die sich entweder ohne Blase nach aussen öffnen (z. B. *Clepsine*) oder vorher in eine contractile Blase münden (z. B. *Nephelis*). Nach innen mündet der Kanal mit einer erweiterten und bewimperten Oeffnung in die Leibeshöhle aus. Ich sehe in diesem Endstück der Röhren das Analogon der 'Zitterorgane' der Räderthiere und auch die Wimperrichtung geht bei den Anneliden nach einwärts in den Kanal. Eine schöne Darstellung von der innern Mündung des Respirationskanal beim Regenwurm gibt Gegenbauer, und wie ich schon an einem andern Orte (Müller, Archiv, 1852) ausgesprochen, so bin ich der Ansicht, dass das 'arabeskenförmige Organ der *Nephelis* und das rosettenförmige Wimperorgan der *Clepsine*,' worauf auch bereits Gegenbauer angespiel that, nichts weiteres sind, als die Endstücke der Respirationskanal dieser Hirudineen. Von gleicher Bedeutung halte ich die eigenthümlichen 'pantoffel- und füllhornförmigen organe' der *Synapta digitata* welche Joh. Müller (Archiv, 1852) aufgefunden und deren feine Cilien ebenfalls nach einwärts schlagen." Leydig then proceeds to argue in favour of the *respiratory function* (!) of these organs, opposing the ideas of Gegenbauer, Bergmann and Leukart, who in *Lumbricus* attribute to the ciliated tubes the office of kidneys.

It should be here stated, that in 1852 (Annal. des Sc. Nat. t. 28. p. 175) De Quatrefages, although unacquainted with the real minute anatomy of these organs, yet hints at the analogy between those of *Lumbricus* and *Hirudo*. "Les poches latérales des Sangsues, évidemment analogues aux canaux tortueux des Lombrics, ont été considérées, soit comme des organes de respiration (Dugès et quelques autres anatomistes), soit comme des organes de secrétion devant fournir, plus particulièrement que d'autres glandes, la mucosité qui enduit le corps de l'animal. J'ai embrassé cette dernière opinion," &c.....And he embraces this opinion knowing the views which I had then published, for he observes, "M. Williams Médecin anglais, qui a publié un rapport fort étendu sur l'Anatomie des Annélides, vient d'émettre une opinion toute nouvelle. Il regarde ces poches et ces canaux comme faisant partie des *organes reproducteurs femelles* des Sangsues et des Lombrics." It will be seen that, with respect to the female system of *Lumbricus*, the results published in this paper differ in some points from those given in my Report, to which De Quatrefages alludes. My former and my recent researches differ, however, only in this particular, that whereas I formerly described every "segmental organ" in the body as an ovary, more extended study has convinced me that under normal circumstances in the *Earth-worm* only a few of these organs become developed into ovaries. In the Common Leech and the Sea-leech the *entire lateral series* of the segmental organs of the body, I still maintain, are ovarian.

It appears, therefore, that to Gegenbauer is due the merit of having first suggested the analogy between the segmental organ of *Clepsina* and *Nephelis* and that of the Earth-worm. This suggested analogy has been further extended by Leydig. By neither of these observers, however, has the slightest allusion been made to the connexion which exists between these organs and the reproductive system in these Annelids.

* I have made very numerous examinations on species of *Clepsina* and *Nephelis* which inhabit the pools of this neighbourhood (Swansea), with a view to ascertain whether the "*arabeskenförmige*" organs, as described by Leydig in these genera, contain ova in every ring of the body, as in the Common Leech and Sea-leech, or whether only a few of these organs, as in *Nais* and *Lumbricus*, experience an ovarian development, the rest remaining in the condition of mere excretionary tubes. But, in consequence of the extreme

The tube (fig. 9 *d h*, Plate VII.), which in the case of the segmental organ of the Common Leech, proceeds from one limb (*n*) of the organ and terminates in a spherical membranous vesicle (*l m*), is evidently the counterpart of the ciliated extremity of the segmental organs of *Nais* and *Lumbricus*. Both open into the cavity of the body. In the Leech, however, neither the vesicle, nor the tube into which it is prolonged, is ciliated; but, in lieu, they are highly contractile. The vesicle is the respiratory *sacculus* of DUGÈS. It does not, as DUGÈS contends, communicate externally by an orifice in the integuments, but internally with the cavity of the body as just stated. The tube which supports this vesicle arises from that limb of the segmental organ which contains the ova in the least developed condition (fig. 9 a^2. *n*, *c*). It is probable, therefore, that the chylaqueous fluid which this tube is designed to discharge, flows throughout the entire extent of the organ from the point of entrance (*n*) to that of exit (*a*), before it escapes externally. In this course the fluid may afford the materials of nourishment to the ova (in the direction of the arrows) as they travel from one limb to the other of the looped organ, and this is the more probable, as the proper tunic of the organ is very scantily supplied with blood-vessels.

The organ itself in the common leech (fig. 9) may be described as a looped tube, the limbs (*a*, a^2) of which, returning upon themselves, and one invaginating the other, open externally at the same point. These organs form two series, one on either side of the stomach. They are external to the stomach and to the testicular series. There are therefore (as in *Nais* and *Lumbricus*) two of these organs in each ring of the body. This fact is of morphological value, for the testes bear no relation either in number or position to the *annuli* of the body. The organs stand vertically *in situ*, the ends (*a*, a^2) being attached to the abdominal surface, and the *fundus* (*b*) floating upwards near the roof of the containing chamber.

In order to the further examination of these delicate organs they must now be cut out, as closely to the abdominal surface as possible, by means of small curved scissors. They should then be floated in water on a glass slide, covered by a thin slip and placed under the microscope. If the organs have been successfully dissected out, it will be seen that one limb (a^2) is broader and more transparent than the other (*g a*). In the former limb (a^2) the ova (*k*) are merely pellucid cells, consisting exclusively of the germinal vesicle and germinal spot. In the latter limb (*g a*) the ova (*j*) have acquired their full complement of vitellus. At this stage they exhibit a flattened ovoid form. This fact affords a demonstration as to the course taken by the ova in their passage from the ovary (*f* a^2) properly so called, towards the exterior. The seat of the true ovary is marked by the plexus of vessels (*f*). By the ovary is meant that part of the apparatus in which the ova are formed, that part which is endowed with the peculiar power of ovogenesis. In relation to this special centre, all the rest of the organ may be characterized

density of the integuments, it was impossible to obtain such a view of the internal parts as would justify any conclusions on the subject. These organs in *Clepsina* are stated by LEYDIG to be ciliated. No cilia can be discovered in any part of their structure, either in the Common Leech or in the Sea-leech.

as the oviduct, but it is also a *vitellarium*. The tubular limb (*g a*) is entirely devoid of vessels. No part whatever of the segmental organ in the common leech is ciliated. In this particular it strikingly departs from that of *Nais* and *Lumbricus*. This observation applies also to the segmental organ of *Albione*. It is of great homological importance to note, that in *Hirudo* and *Albione* (fig. 10), and *probably* in all the genera of this family, the segmental organ is made the uterine receptacle of the ova as they are being thrown off from the ovary. *This is not the case in any other family of Annelids that the author is acquainted with, except the Aphroditaceæ and Glycera alba.* In *Nais* and *Lumbricus* the sperm- and germ-structures, as has been explained (figs. 6, 7, 8), are accumulated by the side of, or as an appendage to, this organ. In other Annelids, as will be afterwards explained, other deviations from this mode of storing the generative products occur. It follows therefore that, in the Leech tribe, the *ova* at all events at no time reach the cavity of the body. This may be one reason why in this family the perigastric cavity is so much contracted, and the contained fluid so reduced in volume.

In *Albione muricata*, several specimens of which the author has examined with great care, the female system exhibits precisely the same characters as that of the common leech. In *Albione* the *annuli* are not so close and numerous; consequently the *ovaria*, which are synonymous with the segmental organs, are not so close and numerous as they are in the common leech.

They are much larger, broader, and more evident than those of the latter Annelid.

The months of July, August, and September should be selected for the examination of this worm. When opened, after the manner already explained in the case of the common leech, the whole interior of the body, from the head to the tail, will be found to be lined by what appears to the naked eye to consist of a bright pink-coloured flocculent lining membrane. But when detached in pieces and placed under the microscrope, its real composition becomes evident.

The pink tint is due to the colour of the vitellus of the ova, and the membrane-like appearance of the whole arises from the union and apposition of the individual ova-laden segmental organs. Successfully individualized, these organs in *Albione* (fig. 10) will be found to present the same outline as those of the Leech. They are looped, horseshoe-like tubes. They are utero-ovarian as in the Leech. *Albione* differs from the Leech in two important organic facts. In *Albione* the cavity of the body is wide and spacious; in the Leech it is contracted and numerously bridled.

In *Albione* the blood vascular system is in a rudimentary stage; in the Leech it is highly developed. The ovarian limb, therefore, in the former is not vascular as in the latter.

This completes an outline of the account which the author has to offer of the *female system* of the Hirudinei:—how universal in extent and distribution, compared with that which has hitherto been received as the utero-ovarian apparatus in these Annelids!*

* In the grand edition of the *Règne Animal*, the female system in *Hirudo vacca* (see pl. 24, fig. 1, p. 213) is figured and described as consisting of a single pouch, the uterus (with its appended vagina) and two

It is noteworthy, that in the entire family of the Hirudinei the female or ovarian system preponderates considerably in size and extent of distribution over the testicular, whereas in *Nais* and *Lumbricus* the male and female moieties of the reproductive parts exhibit very nearly equal proportions. In the Hirudinei the ovaria are beyond all doubt identified with the lateral series of the segmental organs. It will be afterwards inquired how far it is correct to consider the testes as also one or more of these organs modified after a different model*. Leeches are hermaphrodite; but, although the male and female parts are present in each individual, and since there is no internal communication between these two parts, the union of two different individuals is necessary to impregnation: the individual is not fertilized by its own sperm-fluid, but by that of another.

The *male system* of the *Hirudinei* is well known to anatomists. As to its descriptive anatomy, the author has nothing now to add. He is desirous only to offer a few observations with respect to its homology.

In speaking of the ovaria it should have been stated that they are all of equal size and development. It is however a fact of singular morphological interest to note that in that particular *annulus* at which the testicular series converges, or that from which they arise, *the ovaria are wanting*. Now it is only necessary to suppose that the two segmental organs normal to this particular *annulus*, instead of obeying the rule applying to all the others, experience a special growth and expansion, giving rise, not to *ovaria*, but to highly developed and systematically distributed *testes*, and the morphologist is at once furnished with the key by which he may unlock the mysteries of this most complex and hitherto incomprehensible system of organs. In fact the two series of testicular organs, proceeding from (or converging in a penis at) one median point, represent two segmental organs, united at the mid-line and modified into this special system of parts. But all this is accomplished, not by the introduction of a new structure or

glandular appendages called ovaries. De Quatrefages thus adopts and confirms the account given many years before by Dugès of the female system of *Hirudo officinalis*. The male system in *Hirudo vacca* is correctly described by De Quatrefages. The true feminine organs he has completely overlooked. The same charge is to be preferred against this anatomist with reference to the descriptions given by him of the reproductive organs of *Hirudo branchiata* (see his "Mémoire sur le Branchellion de D'Orbigny," Annal. d. Sc. Nat. 1852). He observes: "Les organes génitaux femelles sont d'une extrême simplicité. Ils consistent *en deux longues poches renflées* en masse, dont les canaux excréteurs se renflent légèrement vers le tiers postérieur de leur trajet, et se réunissent en un seul sur la ligne médiane vers le milieu de l'intervalle qui sépare le septième et le huitième ganglion." Thus is described by De Quatrefages the female system of this leech. He here evidently mistakes the median copulative pouches for ovaria, between which and the latter there is nothing in common. In the same volume of the 'Annales de Sciences Naturelles,' De Quatrefages figures and describes the reproductive organs of *Albione muricata*. In this instance this author has not only altogether overlooked the real ovarian organs, but the true testicular series has also altogether eluded his observation!

* In my Report on the Annelids, 1851, I was led to the mistake of believing that each ovary communicates directly with each testis by means of a duct, thus permitting of an internal impregnation of the ova. This duct is however, I am now convinced, as Professor Owen (see last edition of his Lectures on the Invertebrata, 1855) has pointed out, a branch from the median vessel which goes to supply the segmental organ.

viscus, but by the skilful adaptation of a normal organ. By this simple morphological view an intelligible principle is suggested, by the light of which the most anomalous organs are reduced to a rule of consistent homology. The testes are arranged on the same plan in *Hirudo officinalis*, *H. vacca*, *H. branchiata*, and *Albione*. In all they take their origin from two segmental organs, the pair belonging to the same ring. According to this interpretation the testes of the Hirudinei are as naturally referable to the segmental organ as those of *Lumbricus* or *Nais*. In the latter the developed glands keep within the limits of the *annuli* from which they originate. In the former they extend over a considerable portion of the body. Both are traceable to the same roots.

*Terebella**.—The segmental organ in *Arenicola* will be taken as the type of the structure and function of this viscus in the family of the Terebellidæ. With these organs in the common Sand-lug every comparative anatomist, in a general sense, is familiar; on laying open the cavity of the body they appear at once under the character of vascular pouches or sacculi. By CUVIER, MILNE-EDWARDS, and every other anatomist, they have been correctly described as the true organs of reproduction. To this conclusion all have been alike driven, since no other organs in the body could be discovered to which such functions could reasonably be imputed.

This is literally all the information that we possess at the present time with respect to the generative system of this and the allied genera of Annelids.

It may well be asked how far does this information carry the philosophic anatomist? It is in truth of little value. It conveys no homological idea. It implies no general principle. It does not connect the reproductive system of this genus with that of any other Annelid. It establishes no system.

It cannot be disputed that organs so important as the generative, must in the very nature of things be subjected to the governance of a morphological law of more or less extended application. Abrupt transitions and exceptions are impossible.

There is no difficulty in proving that the reproductive system of *Arenicola* is a direct continuation of that which has already been described in the Lumbricidæ, Naidæ, and Hirudinei. The morphologist thus rises, step by step, accumulating proof upon proof of the *unity* of the segmental organ in the several families of Annelids as they are being successively examined.

In *Arenicola piscatorum* (common Sand-lug) there are six lateral pouches which, in healthy specimens, during the months of July and August are in a condition of extreme vascularity. They are quite visible to the naked eye, by their bright red colour. The minute structure of these pouches can be studied by carefully dissecting them from their attachments to the abdominal wall of the cavity and placing them under the microscope.

* Under this head the genus *Arenicola* is included, on the ground of the close anatomical resemblance which exists between its segmental organs and those of *Terebella*. The former is classified as a Dorsibranchiate, and the latter as a Cephalobranchiate Annelid, terms apparently descriptive of wide differences. Beneath this exterior difference there lie however the strongest proofs of intimate relationship of structure in some of the most important organs of the body.

One of them thus viewed is shown at fig. 11. It consists of a simple sac, or bag, the distal fundus of which (*c*) is cæcal. The interior cavity (*m*) throughout the upper three-fourths, from *d* to *c*, is a single undivided space. The attached extremity is formed into two very distinctly marked channels or tubes (A *b*), the interior of which is lined by cilia which beat in opposite directions. In the glandular tube (*a* A) the ciliary current sets towards the cavity of the organ (*m*); in the simple tube (*b* B) it sets out from this cavity (as indicated by the arrows). Although this organ has long been known to anatomists, this peculiar looped formation has never been recognized. The lining membrane is everywhere covered by ciliated epithelium. In the fundus the current leads up on one side, and down towards the outgoing limb on the other. The two limbs (A *b*) by which the organ is tied to the wall of the perigastric chamber are not similarly formed. The ingoing limb exhibits a more glandular character; its walls are considerably thicker and more richly supplied with blood than those of the other. About the middle of its course it enlarges into a round gland-like body (*l*), the axis of which is perforated by the tube. This gland is subdivided into parallel lobuli, the vessels being specially and peculiarly distributed. It is therefore not a simple bulging of the tubular leg of the organ. It is a special structure, destined to perform a special office, which will be afterwards explained. The exact mode and the place, in which this ingoing limb of the organ begins, is a point of essential importance to determine. As long as the author's investigations were confined to full-grown specimens, necessitating the part to be cut out in order to be examined, he found it impossible to solve this point. It was only after having discovered young *Arenicolæ* in a suitable condition, that he was enabled to prove by direct demonstration that it commenced in an *external* orifice (A^b) on the abdominal surface of the animal. If this limb opened directly into the general cavity, it would be the exact equivalent of the ciliated trumpet-shaped extremity of the segmental organ of *Nais* and *Lumbricus*. The ciliary current in this limb (A^b, A) would then consist of the cavitary fluid; but as this limb opens externally, the ingoing current which it serves to convey can consist only of sea-water.

It is of great interest to inquire, What can be the purpose of this inflowing stream of the exterior sea-water? Is it intended to replenish the fluid contained in the cavity of the body? If so, this organ in *Arenicola* performs an office which is precisely the reverse of that which devolves upon it in *Nais* and *Lumbricus*. But it is certain that the fluid thus introduced into the cavity of the organ (*m*) is driven out again, in whole or in great part, by outwardly-acting cilia through the limb (*b* B). That this second or outgoing tube *also opens externally* (B^b), can be distinctly seen by the eye (in young specimens properly arranged for the examination). The water-current, therefore, which is driven into the organ at the limb (A), is driven out again almost entirely at the limb (B): none, if any part at all, penetrates into the cavity of the body. Now there is no doubt upon the author's mind, although he has never been able actually to demonstrate the fact, that this outgoing leg (*b*) of the looped organ (A, B) not only communicates directly with the exterior, as at B^b, but also, by means of a

lateral process (*n*), *opens into the cavity of the body*. It is by this last process that the ova in the female and the sperm-cells in the male reach the perigastric chamber. As far as the commencement of this lateral process, the generative products are conveyed by the cilia-excited water-current already explained; but how they are made at this particular point to turn towards *n*, the opening leading into the perigastric chamber, instead of escaping externally with the water-stream through B, can only be explained by ascribing to this spot a vital sphincteric selective office. The only link that is wanting in the chain of evidence proving that the ova *are formed in* and then pass out from the segmental organ into the perigastric chamber, is just the opening from the former into the latter. The ova in the female and the sperm-cells in the male are abundantly and constantly found in the fluid of the general cavity, and the author has repeatedly, in the series of observations which he has instituted upon this subject, actually seen, in large crowds, the *ova* in the outgoing limb (*b* B). The ova at this point consist of clean pellucid germinal vesicles. The vitellus has not yet appeared. After they have sojourned for some time in the general cavity, the latter begins to show itself. Now although the author, in consequence of the peculiar difficulties of the subject, has never been able to demonstrate clearly the mode by which the generative products pass from the segmental organs into the perigastric cavity, he is compelled to believe that this passage is made, from *the fact* that the ova, at one stage, are actually seen *in the segmental organ*, at another, *in the general cavity of the body*. To complete the chain of evidence it is only necessary to *demonstrate the mode* in which they escape from the one place into the other. The segmental organ is the true ovary in the female and the true testes in the male. It is not difficult to prove this proposition. The ingoing limb of the organ (as far as the point *d*) is a highly *glandular* structure; its vessels are densely packed and specially arranged; its walls are thick and stromatous; at its mid-point (*l*) is a noted glandular development. From the vascular system of this gland proceeds the great vascular organ stretching from g^2 to g^1.

To the one side of this great vascular system there are appended peculiar cæcal pouches (*e e*); from the other (*f f*), a dense capillary plexus. This vascular appendage is the morphological equivalent of the blood-system connected with the ovogenetic limb of the segmental organ of the Leech (*f*, fig. 9), and of the botryoidal apparatus of vessels (*h h*, fig. 5) connected with the segmental organ of *Lumbricus*.

It is impossible that this most singular system of vessels can discharge any other function than the following: viz. (*a*) it is the receptacle of an extra supply of blood to an organ susceptible of periodical expansion; (*b*) it excretes something from the blood-proper into the cavity of the segmental organ (*m*), which is essential to the further development of the generative products. In *Arenicola* it is quite certain that the ova and sperm-cells pass through the last stage of their development in the perigastric chamber. How they escape out of this chamber has never yet been proved *.

* Rathke and Grube have argued that *Arenicola* is androgynous. De Quatrefages, however, from his knowledge of the development of the spermatic particles, has long recognized the existence of separate

It now remains to show that the segmental organ of *Arenicola*, the minute anatomy of which has been just described, is the homologue of the segmental organ of *Nais*, *Lumbricus* and *Hirudo*.

If the partition (*d*, fig. 11) which separates the two rudimentary limbs (A, B) of this organ were carried a little higher in the direction of the fundus (*c*), the entire organ would be converted into *a tube*, which, if one end of it opened into the cavity of the body, instead of communicating externally, would correspond precisely with the *ciliated* tubes of *Nais* and *Lumbricus*. But sufficient of the tubular character is presented by the structure of this organ to connect it indisputably with its homologues in *Nais*, *Lumbricus* and *Hirudo*. In all it is a *looped* organ; in all it is the basis of the reproductive system; in all there passes through its axis a current of fluid, the design of which is to transport the generative products, either into the cavity of the body or externally. The difference is only in the mode in which the tube is folded upon itself.

It is here of importance to remark that this is the *first Annelid* we have encountered, in which the cavity of the body has been employed as a receptacle for the generative products. The segmental organ being still the true generative apparatus, a change of anatomical arrangement became obviously necessary, in order to adapt it to the novel condition just stated.

Terebella.—The segmental organ in the genus *Terebella* (fig. 12) occurs under a form and character which ally it in the most direct and intimate manner with that of *Arenicola*. *T. nebulosa* is an elegant Annelid. It is large enough to admit of dissection. In the summer months the blood-vascular system is highly developed, the branchiæ are brightly florid, and the segmental organs (when the worm is opened) present an intensely vascular appearance.

Dissected in the usual mode, removing with care the alimentary canal, it will be seen that a series of curved elongated sacculi (of which fig. 12 are two specimens) exist on either side of the ventral median line. They extend throughout the setiferous portion of the body (in this family it may be called the thoracic), and seem to be as numerous as the largest setiferous feet, which in *T. nebulosa* are sixteen in number.

Although the identity of the segmental organ of *Terebella* and that of *Arenicola* is so evident as to admit of no doubt, yet there are between them several differential features.

In *Terebella* the organ is more deeply divided by the partition (fig. 12 A. *j k*) between the limbs than it is in *Arenicola*, a fact which approximates it more nearly to *a tube*.

The vascular appendage (*h*, B) is also differently placed. In *Terebella* it is in con-

sexes in *Arenicola* and *Terebella* (Comptes Rendus, xvi. 1843); but long before this, Stannius had concluded that the sexes were separate in *Arenicola*, from the fact that in different individuals the contents of the general cavity of the body were different (Müller, Archiv, 1840). Stannius also observes that the parent sperm-cells leave the segmental organ (his testes) before the formation of the spermatozoa, which are found only *in the cavity of the body*. Krohn, in *Alciopa*, confirms this fact (Wiegmann's Archiv, 1845). Put the great mistake committed by Krohn, Frey and Leuckart is, that they assert that in *Arenicola*, *Alciopa*, *Nereis*, *Syllis*, *Sabella* and other Annelids, the *ova* and the spermatozoa "*are developed free in the general cavity*...!!"

nexion with the ingoing limb, in *Arenicola* with the body of the organ. This circumstance with still greater emphasis points to the ingoing limb (*f m*, B) as the seat of the ovogenesis; indeed the entire dark half of the organ (*m f*) may be correctly called an ovary. The limbs of this organ in *Terebella* have precisely the same anatomical relations as in *Arenicola*. The ingoing leg (*f m*, B) (*f f j*, A) commences in an *external* orifice (*d* B, *c* A), and therefore carries *water*, as in *Arenicola*. This water traverses the organ as indicated by the arrows at A, fig. 12.

The outgoing limb (*k c*, A) is formed after the model of the corresponding part in *Arenicola*. The main channel opens externally (at *c*). A secondary tubular process (*e*) leads into the general cavity; it serves to convey into the latter the ova or sperm-cells, as they are conducted to this spot by the ciliary epithelium which lines the interior of the organ (A).

It will be seen that one half (*f m*, B, fig. 12) of the segmental organ in *Terebella* is highly vascular and glandular, and that the other half (*n n*, B) is simply excretory and membranous. This distinction marks also the offices of these halves respectively. The peculiarly evolved vascular system is connected only with the ovarian or spermatic half, the other half being simply the oviduct or *vas deferens*, according to the sex.

In the male and female *Terebella* the segmental organs are precisely the same in number, size and structure. It is only possible to distinguish the sex by the microscopic examination of the morphotic elements contained in the segmental organs and in the general cavity of the body. In the female they are ova, in the male they are sperm-cells, or spermatozoa in both situations.

The general cavity in *Terebella*, as in *Arenicola*, acts as a reservoir in which the generative products complete the last stage of their development. In the female it is a *vitellarium*, in the male a *vesicula seminalis*.

The segmental organs in *Terebella* differ in number in different species; in none do they differ in minute structure. In *T. nebulosa* this organ is segmentally repeated sixteen times; in *T. conchilegia* only six times (in other words, it is only present, in pairs, in six segments); in *T. multisetosa* twenty-four times; in *T. cirrata* about eighteen times; in *T. parvula* only three times. In all it is constructed on the type of that of *Arenicola*.

Between the genus *Terebella* and that of *Arenicola*, as regards the reproductive system, there prevails *apparently* one striking difference. In the former the anatomist discovers a large glandular mass, extending from the head along the median line to some distance in the direction of the tail. This gland-structure coincides internally with the smooth, foot-like, dense tegumentary structure observable in every species of *Terebella* on the thoracic half of the abdominal aspect of the body externally.

It has been described, by Cuvier, Milne-Edwards, De Quatrefages, Grube, Stannius and others, as the testes.

At one time the author of this paper also put upon these parts a similar construction; he has however since convinced himself that they have nothing to do with the system of the testes, nor do they aid in any way in the process of reproduction.

They are present alike in the male and in the female. In structure they consist of follicles filled with large fatty particles, differing most widely from the true sperm-cells. The office of this median glandular mass is undoubtedly to supply the lubricating and cementing fluid by which the animal forms and moulds its tube.

The testes in the male *Terebella* are the lateral pouches or true segmental organs, as in the female they are ovaria. In this genus, as in *Arenicola*, the generative products in both sexes are early introduced into the general cavity, in the fluid of which they rapidly become developed.

In concluding his remarks upon the Terebellidæ, the author is anxious to recapitulate one or two points. That the lateral pouches are the real reproductive organs is certain from these facts:—

At a particular season they are crowded with ova (in the female) and sperm-cells (in the male). These products respectively are less developed than those contained in the general cavity; but as to their being one and the same bodies in the two places, there is no doubt. Next, there is the negative evidence of the absence of any other organ in the body entitled to be called a genital apparatus. And thirdly, there is the incontrovertible proof, derived from the structure and segmental position of the organ, that it is the homologue of that part in the Hirudinei in which the ova are formed and afterwards lodged throughout the entire period of their intra-maternal life. The segmental organ of the Terebellidæ, as will be afterwards proved, bears a most intimate analogy to that of the Sipunculidæ amongst the Echinoderms.

Sabellidæ and *Serpulidæ*.—The system of the segmental organs in these families presents several peculiarities. In the true Terebellidæ these organs were found to be restricted to the thoracic or anterior portion of the body. In the genera *Sabella* and *Serpula* the case is reversed; they are absent in the thoracic and present only in the abdominal portion. They are far more numerously repeated in these families than in the Terebellidæ. As formerly stated, the ova and sperm-cells in the latter escape into and float freely in the general cavity of the body. This is not the case in *Serpula* and *Sabella*. Although the generative elements escape out of the channel of the organ (fig. 13, *a d b*) (probably at *c*), they do not pass into the free space of the perigastric chamber, there to float about, as in *Arenicola* and *Terebella*. They are bounded by a delicate membrane or bag (as represented in the case of *Chloræma*, fig. 23 *e e e*), the cavity of which is intersected by vessels and areolar tissue, and filled with a glutinous fluid, quite unlike the chylaqueous fluid, by which the ova are fixed and tied together, generally into rows. To what part of the ciliated tube (*a d b*, fig. 13) in *Sabella* it is attached, it is impossible to determine with exactness; but that it is not the ovary, but only a receptacle for the ova, will be afterwards shown to be highly probable, from the conditions under which it occurs in *Chloræma* and some Nereids.

In *Sabella* and *Serpula* the organ is the same in figure and structure. It is a looped tube (fig. 13), the fundus of which (*d*) is dilated, as compared with the two limbs; with one, the ingoing limb, is connected a dense tuft of looped vessels (*f*, *g*, *e*). The interior is highly ciliated.

In every species of *Sabella* and *Serpula* examined by the author, the sexes have been seated on separate individuals. In the majority of species the ova (*h*) have a bright pink colour. The female, by this mark, may be readily distinguished from the male, the colour of which is brownish or greenish*. From these statements it follows that the segmental organ in *Sabella* and *Serpula* are *permanent viscera*, and not temporary formations, as affirmed by De Quatrefages. In fact, it is a mistake to suppose that the process of ova- and sperm-development, *in any Annelid*, is limited to a month or two in the year. Ova in an immature state are found in the bodies of the youngest as of the oldest. This fact proves that the structures by which the ova are generated must be permanently present.

The preceding account of the segmental organs of the Sabellidæ and Serpulidæ has been drawn from an examination of the following species:—*S. alveolata*, *S. vesiculosa*, *Leucodore ciliatus* (very favourable for this purpose), *Amphitrite auricoma*, *Sabella à sang vert*, *Sabella hospita* (mihi). Of the Serpulidæ the author has only studied with care the following species:—*S. triquetra*, *S. contortuplicata*, *S. lactea*. In all the Sabellidæ and Serpulidæ the segmental organ is present in every ring of the body, except the thorax and the caudal appendage.

The Nereid group.—Under the head of the Nereid group, for the purposes of this memoir, several families of "errant Annelids" will be included. Of the reproductive organs of this group nothing whatever is known. No comparative anatomist has even suspected the existence of the "segmental organ" in any one of the members. Stannius, Kölliker and De Quatrefages, and probably other microscopic observers, have indeed established the fact that the ova and the spermatozoa are found on separate individuals. Hence has been inferred the diœcious character of this group. Not one single observation has ever been made by any of these observers as to the character of the reproductive organs themselves. The author begs therefore to offer the succeeding description as drawn exclusively from his own researches.

In every Nereid, the ciliated, looped, horseshoe organ to which the author has applied the name of the "segmental organ," exists without a single exception.

The demonstration of this organ in *Nereis margaritacea* is attended by great difficulty. It can only be accomplished either by the tedious process of placing annular *sections* of the body under the microscope, or by the discovery of a young specimen at that age at which the integuments are transparent; and then it is only in the region of the tail of the worm that the ciliated organ becomes visible to the eye. In *N. margaritacea* it

* Stannius and De Quatrefages have already pointed out the fact that the sexes were seated on separate individuals in the *Sabellidæ*; but it is evident from the following passage, that De Quatrefages has altogether overlooked the real ovaria and testes of these Annelids, and mistaken for them the masses, attached to them, of the ova and sperm-cells. He says in his essay, "Sur les Hermelliens" (Ann. d. Sc. Nat. 1848, t. 10. p. 46): "Le testicule consiste en une sorte de trame aréolaire d'une ténuité extrême, qui part de l'aponévrose médiane," &c. . . . "L'ovaire est en tout semblable au testicule." De Quatrefages then states that these organs are temporary, and, after the ova and the sperm-cells pass into the general cavity, they disappear through atrophy. It will be seen how entirely the results stated in the text differ from those published by the French naturalist.

consists of a tube, highly ciliated, both ends of which communicate with the *exterior*. The ingoing limbs (fig. 14, *d d*) are situated in the immediate neighbourhood of each dorsal foot. The outgoing limbs (*b b*), considerably longer and more tubular than the former, open externally to the median side of the root of each ventral foot. The cilia by which this horseshoe tube is lined are highly vigorous, capable of supporting a powerful current. Thus much is quite certain*, that this current arises externally and terminates externally. It can consist, therefore, only of the exterior element. The current of the element thus excited can only traverse the organ itself. It cannot enter into the perigastric chamber. But it can, as will now be shown, convey outwards the generative products along the outgoing limb. And this, as evidence accumulates, will appear as the true function of this water-current.

With the short, broad, ingoing limb is intimately connected the tuft of cæcal vessels (*e e*, fig. 14) to which, in other Annelids, reference has already so often been made. Now if the demonstration could be pushed no further than this point, it would confessedly be difficult to connect this horseshoe ciliated tube, and its associated tuft of vessels, with the true reproductive function. But it is capable of proof that the ova in the female, and the sperm-cells in the male, escape, although in some undetermined mode and by some undemonstrated passage, from this organ into the complexly areolated tissue (shown at fig. 15 *e i a g*) which fills the chamber of the pedal appendages. From various observations the author is persuaded that this tissue is *a development from the segmental organ* (at fig. 16, a single cirrus filled with this ovarian tissue (*d*) and its blood-vessels is figured), and that in size and vascularity it is proportionate to the stage at which the contained germinal elements have arrived†.

In the Nereid group generally the female is much larger than the male. This difference is very striking in *N. lamelligera* and *N. renalis*. The cephalic extremity of these worms is entirely destitute of the "segmental organ." This is also remarkably the case in *Nephthys Hombergii*. The nervous chord in this œsophageal region is highly developed in all the Nereid group.

This feature of structure is also very prominent in the Ariciadæ‡. The segmental organ in this family is limited in its distribution to the two posterior thirds of the body. The ova- and sperm-bearing masses (fig. 17 *a h c* and *a h c*) exhibit the same relation

* In *Spio vulgaris* and *S. coniocephala* I have enjoyed the advantage of demonstrating this fact to Mr. Busk and Dr. Carpenter.

† Until I came to study the generative system of the Annelids, I always looked upon the florid and brightly vascular elements of the feet as specially designed to fulfil a *respiratory function*. I am now convinced that, if this purpose is fulfilled at all, it is only so incidentally. The great and paramount office of these specially developed parts of the vascular system is to supply the means of growth to the generative organ. It is now almost certain that what Milne-Edwards has called the "branchial hearts," in the Eunicidæ, are sacculated developments of the vessels designed to supply the reproductive system.

‡ The drawings which accompanied the original draught of the present paper to the Royal Society, included carefully executed figures of four species of *Aricia*, viz. *A. Cuvieri*, *A. Owenii* (mihi), *Janira crinigera* (mihi), and *Janira illecta* (mihi).

to the ciliated tube as that which has already been explained in the Sabellidæ and *Nereis*.

These Annelids present a favourable opportunity for determining the question whether the large masses (fig. 17 *a c* and *a c*) of ova which in the female *apparently* occupy the perigastric chamber, are really IN that cavity, or are contained in the areolæ of a delicate stromatous tissue as already described in *Nereis*, *Sabella* and *Serpula*. Well-defined and repeatedly conducted observations have convinced the author that the latter, and not the former, is the case. In the Ariciadæ especially, it may be observed that the peculiarly areolated tissue in which the ova are contained is distinguishable into two parts, one of which is densely and intimately connected with the blood-vessels (see fig. 16; fig. 17 *c h*), the other forming a mere utricular receptacle to the generative elements (fig. 17 *a*, *a*; fig. 15 *e*). There is no doubt that that portion (fig. 17 *c h*; fig. 16 *d b*) which is ultimately bound up with the vascular system, is designed to supply a fluid secretion, *from the blood-proper*, which is necessary to the further growth of the generative products. This illustration confirms what has been constantly observed during the foregoing descriptions, that the blood-proper system in the Annelids is much more intimately connected with the process and the organs of reproduction than the chylaqueous fluid. This important fact implies evidently a difference of vital and chemical composition in these two fluids. The higher fluid is used for a higher purpose, the lower for a lower. The segmental organs in the Ariciadæ occupy the floor of each annular compartment (as shown in fig. 17 *i j* and *i j*).

The genus *Nerine*, first defined by Dr. JOHNSON, affords by far the most favourable conditions for the study of the segmental and reproductive systems of any of the Nereid families. The coast near Swansea is inhabited by three species of this genus (viz. *N. vulgaris*, *N. comocephala*, *N. beata* (mihi). The last, and unfortunately the rarest, is beyond comparison the best adapted for the purposes of the present investigations. In this elegant worm the entire apparatus (as represented in fig. 18 *a b c* and *a b c*) may be readily and clearly defined by the eye. It is here quite easy to demonstrate the connexion between the ciliated tube (fig. 19 *a b*) and *the appended mass* (*c c c*) of the germinal products. This mass fills completely the hollow bases of the foot and the entire chamber of its own segment. *It embraces* the ciliated tube (*a b*). It is evidently a part of the latter; and yet in the most transparent specimen (*Nerine beata*, mihi) it is utterly impossible to define how the germ-products escape from the tube (*a b*) into the mass (*c c c*). But the author is most anxious to draw especial attention to the fact of the presence of this ovarian or sperm-mass (according to the sex) in constant and visible association with the ciliated looped tube. It serves to reflect light upon the association of the same parts in specimens in which the demonstration is necessarily obscure. It illustrates *the principle* contended for in this paper, that the "segmental organ" is the true and real source of the generative products; in other words, that the latter are THE organs of reproduction; the masses appended to the latter, hitherto mistaken by DE QUATREFAGES for ovaria and testes, themselves being only the utricular or spermatic receptacles of their products.

There is no discoverable difference between the segmental organ of *Nerine* and that of *Nereis*. The ova are very distinctive and characteristic, however, in the former.

The segmental organs are very largely developed in the genus *Eunice*. The blood-vascular system is here highly developed. The branchiæ, which carry the blood-proper exclusively, are closely connected with these organs. The same trunks supply the cæcal tufts of the latter and the straight capillaries of the former. All the Euniceadæ are diœcious. The female is nearly twice as large as the male during the height of the reproductive season. Although they *appear* to be in the free cavity of the body, it is quite certain that the generative products do not move to and fro in the fluid of that cavity. They are contained in a delicate areolar structure, which serves to limit the products of each segment to its own proper chamber. The ciliated tube and its appended vascular tuft (fig. 20 *c*) can only be demonstrated by transverse vertical sections of the body; sometimes, and by a pure accident, a most complete view of the segmental organ (*a e b*) may be obtained by this method. It is a far more saccular and prominent organ in *Eunice* than in *Nereis* and *Nerine*. The fundus (*e*) shows a union of the two limbs as in *Terebella* and *Arenicola*, and as in the latter, the vascular, ovarian or ingoing leg is of a denser structure and darker colour than the outgoing limb (fig. 20 *a*), which is long and tubular*. There is every reason to believe that in the allied genera of *Lycidice*, *Aglaura* and *Œnone*, the segmental organs coincide in structural type with the standard of that of *Eunice*. They are, however, less vascular than in the latter. All the genera of this family are diœcious.

In the genus *Syllis* the segmental organ, which cannot by any manœuvre be directly demonstrated, is most probably correctly represented in its minute and general anatomy by that of *Psamathe* FUSCA, a closely allied genus. Once recognized in this Annelid, there is no difficulty in readily demonstrating the entire characters of the segmental organs. The integuments covering the roots of the feet are perfectly transparent. Within the hollow of each foot a beautifully looped, extremely delicate, slender, membranous, ciliated tube (fig. 21, *a b c*) may be discerned, corresponding in every essential particular with the looped ciliated tube of *Nerine*.

But what is of special interest in this case is, that the appended glandular yellowish mass (*e e*) in the female, which spreads irregularly into the hollow bases of the cirri and setiferous feet, can be most distinctly traced into organic connexion with the ciliated tube, and with that limb (*a*) of the loop, of which the vessels are most developed. During the constant movement of the little worm while under examination, it may be distinctly observed that the ova- or sperm-bearing mass *moves in constant connexion with the ciliated tube*. So exquisitely delicate is the entire apparatus, and so minute are the ova, that it is quite impracticable to trace them in their passage from the "mass" into the tube. Since however this fact has been observed, beyond doubt, in other Annelids, and since it is supported by the analogy of everything that is now clearly known with

* The dissections upon which rest the statements in the text, were made upon *Eunice gallica* (MILNE-EDWARDS), *E. sanguinea*, and *E. Harrassii* (M.-E.), which are common on the shores around Swansea.

respect to the reproductive organs of the Annelids in general, the conclusion may safely be drawn, that in escaping from the body the ova take the course of one of the limbs of the ciliated tube*.

Cirrhatulus Lamarckii is a common worm on the coast of the Bristol Channel. It may be readily found in every stage of growth. The region of the tail, in some specimens, at a certain (young) age is quite transparent. It is then easy to obtain a view of the segmental organ (fig. 22 *a c b*). In this worm, as in the Nereids generally, the *ova* are not retained within the segmental organ as in the Leech tribe; they escape into a dependent tissue which fills the chamber of the annulus in the mature individual. It is provided with its own specially disposed vascular apparatus (*d*). Its position in the chamber of the segment is vertical. The ends of the loop are situated closely together. In general figure the organ is intermediate between that of *Terebella* and that of *Nerine*. The sexes in *Cirrhatulus* are situated on separate individuals.

The author has made numerous attempts to arrive at a correct knowledge of the segmental organ in *Glycera alba*, an Annelid which is remarkable for the entire absence of the blood-vascular system. He has been able to do little more, in consequence of the dense character of the tegumentary structures, than to prove the presence of the organ. It has been observed by De Quatrefages, but never anatomically defined. It is an irregularly looped organ, destitute of a vascular tuft, and *unciliated*. In another particular it is remarkable: the ova in the female are retained within the proper limits of the membranous walls of the organ itself, after the type of the ovarian segmental organs of the Hirudinei. This fact the author has proved repeatedly by direct observation; but it may also be established negatively. The branchiæ are capacious hollow processes, communicating in the most open manner with the perigastric cavity. The fluid of the latter circulates freely in the former. In this branchial fluid the ova are never observed.

In looking back over the preceding description of the segmental organs of the Nereid group, it is impossible to resist the belief that, notwithstanding the numerous varieties of size, figure, position, structural peculiarities, mode of the looping of the ciliated tube, the place and method by which it is connected with the mass of the generative products, and other diversities, in one and all the genera, it is beyond all doubt *the same organ*. If the identity of the organ in the several groups of this family be admitted, then the homology between the Nereid type of the segmental organ and that of the other families of Annelids already referred to in this memoir, must also be admitted. This conclusion is one of great importance and novel interest. It simplifies a question which, up to this moment, has proved as complex and perplexing as any problem in comparative anatomy. It affirms that hitherto, and in the typical families of Annelids examined, the anatomist has discovered only *one essential organ*, under manifold varieties of form, upon which is ingrafted the reproductive system.

* By reference to a paper by De Quatrefages in the Annales des Sciences Nat. 1854, on the development of the spermatozoids in *Torrea vitrea*, it will be seen that in no single particular are the results of my researches on the genus *Syllis* confirmatory of the statements which he has made.

Let us now proceed to trace the segmental organ throughout other and still more remarkable variations of type, preserving nevertheless its homological identity.

De Quatrefages has devoted a separate memoir* to the publication of the results of his researches into the organization of the family of the Chloræmea (of Dujardin). His investigations seem to have been most elaborate, and yet De Quatrefages has been entirely misled in reference to the reproductive system of this family. He thus expresses himself:—"Je n'ai rien vu dans les Chlorèmes qui pût être regardé comme un organe reproducteur, ce qui tient sans doute à l'époque de mes observations, qui, par deux fois, ont eu lieu en automne. Toutefois je ne puis croire encore avec M. Costa que les sexes soient réunis, soit chez les Chlorèmes, soit chez un genre quelconque de cette famille. Les organes que ce naturaliste à regardés comme des testicules occupent exactement la même position que les glandes salivaires que j'ai décrites, et sont représentés par l'auteur lui-même comme tenant à l'œsophage. De nouvelles observations bien précises me paraîtraient donc nécessaires. Dans le cas où le fait annoncé par M. Costa viendrait à être confirmé, il en résulterait que les Chlorémiens devraient entrer dans le groupe des Annelés dioïques où ils représenteraient les Annelides tubicoles, comme les Lombrics et les Naïs représentent les Annelides errantes."—*Loc. cit.* This is all that occurs in the special memoir of the French anatomist with respect to the reproductive system; such an account can hardly be said to be either consistent or intelligible. But De Quatrefages himself admits that new observations, *bien précises*, on this subject are necessary. The author of this memoir hopes that this desideratum will now be supplied.

Chloræma Dujardinii is very frequently met with on the Welsh coast of the Bristol Channel. If the principle be conceded that the segmental organ, with its associated germinal masses, of this Annelid, may be received as expressive of a law applicable to the entire class, points of clear morphological meaning will now be placed beyond the possibility of controversy. In order to verify by observation the facts now to be narrated, it is necessary that specimens in a suitable condition should be examined at two different seasons, viz. in May and June, and in August and September. In the individuals examined during the former months, the fact will most certainly and easily be established, that the ova in the female, and the sperm-cells in the male, are most clearly and distinctly contained *within* the membranous limits of the segmental organ†. In those observed later in the season (August and September), the state of things delineated in fig. 23, Plate VIII., will almost constantly be noted; viz. that in which the ovules and sperm-cells have escaped from the segmental organ and accumulated in large irregular masses (A *e e e*, female) (B *d d*, male), which float in the fluid of the general cavity, but which are bounded by a distinctly limiting membrane. This membrane it is which prevents the germinal products from entering directly into the free space of the perigastric chamber; and observation proves that at no stage of their development do

* Ann. d. Sc. Nat. tom. xii. 1849.

† Amongst the original drawings which accompanied this paper to the Royal Society, were two illustrating the conditions referred to in the text.

they enter into this chamber. In this particular the Chloræmea fall in with the rule which prevails without exception throughout the great group of the Errant Annelides. Recognizing the parallel tubes (A *b* and *ff*, and B *b*) as the true segmental organs, and remembering the demonstrated facts, that at one time the germinal products are actually to be seen within these tubes, and that at another they hang in masses externally around them, the truth of the proposition contended for in this memoir is established, that the segmental organs are in the female the true ovaria, and in the male the true testes. But careful homological study is required, in order to convince one's self that the primary and secondary looped tubes of the Chloræmea are in truth the morphological representatives of the ciliated segmental tubes of the Nereid families. In the Chloræmea these tubes are *not* ciliated, either within or without. This is a distinctive peculiarity, which allies them with those of the Hirudinei. But they stand alone and without example amongst the other Annelids in this feature, viz. that the *three* looped organs (*ffc*, A) on either side are connected together by means of intermediate tubes. The anatomical conditions in the male (B) and the female (A) are precisely the same. The same description applies to both.

The worm being properly arranged for observation under the microscope, it may be seen that at the base of the cephalic tentacle, on either side, there appear the ends of two independent tubes (fig. 23, *a*, *b*). The smaller one (*a*) is invaginated or embraced by the larger (*b*). The smaller is very much darker (in the female) in colour than the larger. This colour is due to the vitellus of the ova. The larger one is pellucid and colourless, and filled (in May and June) with ova in a very immature condition. By this distinction of colour the entire organ may be traced backwards in the direction of the tail of the animal. At a short distance is discernible a second bulge (*c*) in the transparent half of the tube. From the centre of this bulge or dilated portion there proceeds a secondary tube (*f*), which, forming a short loop (*j*), returns upon itself, and ends by a similar tube in the longitudinal tube (*a a*). The second lateral loop is formed in the same manner. The third and the last (*c a*) is formed by the union of the two long ducts (*b c* and *a a*). The limbs (*f*, *f*) of the secondary processes have at the points of their origin (*c*, *c*) an external communication, but the returning or dark-coloured limbs, which end in the horizontal duct (*i a*), have no such external communication. They open outwardly only at the extreme cephalic termination (*a*); all the loops, however, by some means or other, are enabled to discharge their contents into the appended masses (*e*, *e*, *e*), which correspond with the former in number and position.

Now if the connecting tubes (*k*, *k*) which unite the secondary loops (*fj*, *fj*) did not exist, the analogy between the latter and the normal or standard segmental organ of the Nereid group would be at once admitted; but the presence of intermediate ducts, which unite all the secondary parts into one system, involves apparently the morphology of the chloræmacean organ in difficulty and doubt, and withdraws it from the chain of that series which, up to this point in the class, has been found to consist of links uninterruptedly connected and reciprocally related.

This doubt arises from a superficial and not from a real dissimilarity. Each loop is evidently a correct representative of a segmental organ. In *Chloræma Dujardinii* (fig. 23) there are only three of these loops; in two new species* discovered by the author they amount to four and six. The Chloræmea are allied to the Terebellidæ in this particular, that the segmental organ is limited to a few of the thoracic segments. It is absent in the abdominal. The Chloræmea resemble the Nereids and Sabellidæ in this respect, that neither the ova nor the sperm-cells, at any time, are introduced into the free cavity of the body. No special expansion of the blood-vascular system occurs in connexion with the apparatus of the segmental organs. The blood in every species is green.

The *Nemertine Annelids* were described some years ago by De Quatrefages, as presenting a singular anomaly in the structure and disposition of the generative system. In the genera *Lineus*, *Borlasia* and *Nemertes* he gave an elaborate account of the alimentary organ, which in these genera so prominently occupies the axis of the body, under the title of the "ovarium." In his "Report on the Annelids," in 1851, the author contended, in the strongest terms, that the ovarium of De Quatrefages was in truth "a great alimentary cæcum;" observing that "at short distances, along the whole line of the body, on either side of the great 'cæcum,' membranous sacculi existed in the intervals between the lateral pouches of the alimentary tube, *on which sacculi undoubtedly* the office of reproduction devolved." This description has recently, in all its details, been adopted by an English writer on Natural History, without one word of acknowledgment.

The following statement is based upon observations far more extensive, numerous and *skilled*, than those upon which the original "Report" of the author rested. Examined by itself, and without the guiding ideas suggested by the preceding history, it would have been quite impossible to have unriddled the mystery of the reproductive or segmental system of the Nemertidæ. So slippery, and dense, and untransparent are the integuments, so completely does the great alimentary cæcum fill up the "cavity of the body," and so intimate and frequent are the connective bridles between its lateral cæca and the integuments, that no original demonstration of any value could have been arrived at. Having seized the clue, and knowing what to look for, the demonstration of the true segmental organs becomes certain and easy.

They correspond in number, not with the cæca of the alimentary canal, but with the *annuli* of the body. The marks of these *annuli* are not written on the exterior tegumentary surface; they are distinguished only by the transverse septa which internally cross the cavitary space at regular intervals and parcel it into segmental chambers. In each of these chambers are lodged two segmental organs, one on either side of the median line. In the female they contain ova; in the male, sperm-cells. There is only one species amongst the numerous members of this family in which it is possible to *demonstrate* the segmental organs *in situ* and as transparent objects under the microscope, viz. in *Polia quadrioculata*; it is a semitransparent flesh-coloured worm. Sometimes, by a

* Drawings of which were forwarded to the Royal Society with the original MS. memoir.

happy accident, individual specimens are met with, in which the *ova*-bearing segmental organs can be most clearly and distinctly seen. In the other genera of the Nemertidæ dissection is necessary.

The segmental organs of the Nemertidæ coincide in shape, place and structure with the *ovarian* or *female series* of the Hirudinei in these respects. In the female they are utriculo-ovarian, they retain within their own limits the ova, they observe the Annelidan type of the horseshoe or looped figure, and they are co-numerous with the true segments of the body.

The male system, in every respect, is the precise correlate of the female. There is no analogy between the *male* organs of the Nemertidæ and those of the Hirudinei. In the latter a special segment is devoted to the male apparatus, and the individuals are hermaphrodite; in the former, the sexes are seated on separate individuals; the entire series of segmental organs in each sex respectively being converted into ovaria and testes. As the vascular system is little developed, it sends no special branches to the segmental organs.

The discovery of the real generative parts in the Nemertidæ enables the naturalist to determine their true affinities in the class. It is evident that to place them under a common title of Turbellaria in contact with the Planariea, is to ignore altogether the existence of the organs of reproduction, for in this respect they are separated from the Planariea by a very wide interval. The latter are monœcious, the former dicœcious. Nor is there the slightest analogy in the plan of structure upon which the alimentary system is formed.

These two groups are joined together by only one common character, and that the most superficial, namely, by the ciliated integuments. The author proposes, therefore, to separate the Nemertina or the cestoid Annelids from the true Turbellaria, synonymous with the order Planariea, under which order he includes only the tribes *Cryptocœla*, *Dendrocœla* and *Rhabdocœla*. These latter are united by a striking similarity of structure; all are hermaphrodite, in all the reproductive organs are formed on one common type.

Although the organization of the Planariea has long been known to anatomists, there remain to be noticed several points of morphological novelty. No attempt has ever been made to connect the generative viscera of this family with those of the typical Annelids. In the characters of these organs, the Planariea, on a superficial view, appear to be irreconcilably separated from all the normal Annelids. A deeper insight into the homology of these parts will, however, most certainly enable the philosophic anatomist to recognize in them none other than a modification of the typical segmental organ which, under many variations of outward form, has now been traced almost throughout the entire class of the Annelida.

The generative organs of the Planariea consist *apparently* of two parts, viz. of a central male sacculus (fig. 25, *b*) with its dependent cæca, and of a central female sacculus (*c*) with its complex system of appended canals (*d d* and *f f*). Thus it seems that

the universal rule which requires that the segmental organs should observe a bilateral and symmetrical arrangement in all Annelids, is entirely set aside in this case. This anomaly will be found, however, rather to corroborate than to violate this morphological principle.

The male system (*b*) is in truth composed of two distinct segmental organs, fused into one sacculus in the median line. The female system (*e*) is also composed of two distinct segmental organs, blended like the male into one vagino-utricular pouch in the median line.

This simple view of the case resolves all difficulties. If the *four* constituent organs stood apart from each other and in their normal anatomical positions, they would at once be seen in their true morphological relations. But these relations are not the less real, albeit they are rendered the less obvious by the fusion of the two opposite organs.

The testes (*e e*, fig. 25) are two long unbranched cæcal appendages; the ovaria (*d d*, *f f*) constitute a widely-distributed and complexly-branched system of cæcally-ending canals, all meeting at the utricular centre (*c*). No part, either of the male or female system, is ciliated. The ova are at all times contained within the limits of the tubuli (B); they never fall into the general cavity of the body. In this particular the segmental organs of the Planariea agree with those of the Hirudinei and Aphroditaceæ. It should here be noted as remarkable, that this is the first occasion on which the anatomist has observed a *branched structure* in the segmental organ. It foreshadows that formation which will be immediately described in the corresponding organs of the Aphroditaceæ. The looped or horseshoe-like character is now surrendered. But although this type of structure is lost, *the homological identity of the organ itself is unquestionably preserved.* Thus far, then, the history of the reproductive system of the Annelida has proved to rest on a natural and consecutive series of individual demonstrations, following one another in an order of obvious and necessary sequence.

We now approach the last link in the Annelidan chain. It surpasses all the others in interest; it enables the morphologist to state that the exception proves the rule; it is hoped that it will bring within known analogies systems of organs which hitherto have been regarded as irreconcilable anomalies. This remark could scarcely until now have been made with reference to the segmental organs of that class, of which, indeed, *nothing whatever* was known.

The author is not aware that any light whatever has been thrown, by any former anatomist, upon the nature and structure of the generative and segmental system of the Aphroditaceæ.

When he commenced his researches on this subject, he had to grope through perfect darkness. He could draw no light from anterior investigations; no anatomist had ever before recognized the generative organs of this family under any shape. The problem to be solved, therefore, was not simply to *discover* the true organs upon which the function of reproduction devolved, but, being known, to bring them within the sphere of established homologies.

The family of the Aphroditadæ comprehends the genera *Aphrodita*, *Polynoe*, *Pholoe*, *Sigalion* and *Spinther* (JOHNST.).

They are all more or less common on the coast of the Bristol Channel. In all, the system of the segmental organs is reducible to one typical standard. The sexes are seated on separate individuals.

The anatomical position of the segmental organs involves questions, the morphological meaning of which (as will subsequently be discussed) extends far beyond the limits of this family of Annelids.

Let us take for type the condition of these organs as they exist in *Aphrodita aculeata*. In order to arrive at a correct estimate of the reproductive system of this Annelid, specimens of both sexes should be examined in the spring, and again in the autumn. A good example of a female Aphrodita being obtained, the dissection should thus be proceeded with:—Pin the animal down to the trough with the back upwards. Open it by a longitudinal incision extending from the tail to the head. The incision should cut through the scales, felt and integuments, in order to lay open the spacious perigastric chamber. The integuments should be now carefully stretched and pinned down to the sides. The interior is now exposed. Let the dissection be then gently floated in salt water. The entire alimentary system and a considerable portion of the segmental system will be now rendered perfectly and distinctly recognizable. At this stage the parts will present exactly the appearance exhibited in fig. 26, in which a network of minute tubes or threads (*d d*, *b b*, *c*) seem to twine around and embrace the diverticula (*a*, *a*, *a*) of the alimentary canal *. From the gastric end of the proboscidiform œsophagus (*e*, fig. 26) to the tail, the digestive cæca (*a*, *a*) are co-numerous with the feet, into the hollow bases of which they are inserted.

In proceeding to the second stage of this dissection, the entire alimentary system must be taken away, and with it, necessarily, a considerable portion of the reproductive network. If this part of the proceeding be delicately and successfully performed, a perfect view will have been obtained of the attached ends (*a*, *b*, *a*, *b*, fig. 28) or roots of the branched segmental organs (A, B). These roots will be found to equal the alimentary cæca in number, and therefore that of the feet which are situated posteriorly to the proboscidiform œsophagus. They appear under the character of pyriform tubuli (*a*, A, *a*, B), commencing or ending in a single external orifice (*a*, *a*). Internally they are lined by a ciliated epithelium, the cilia being large, dense, and acting with great force and vigour. The current raised by these cilia sets up on one side and down on the other (see arrows). The ciliary epithelium ceases at the point where the primary branches (*b*, *b*) divide. All the rest of the organ (from *b* to *c*) is *unciliated*, and filled with the reproductive products. This portion is elaborately branched (at A *d* is shown a small portion, magnified, of the female organ, at B *d*, of the male),—the branches, as formerly stated, twining round the diverticula of the stomach. No microscopic object can

* Both the number of the alimentary diverticula and that of the embracing segmental organs have been very much reduced, for the sake of distinctness, in this figure.

be more beautiful than a portion of this tubular network (taken from the female organ). The individual tubes are bridled (A *e*) on one side, and glandular (A *d*) on the other. A similar structure is exhibited by the male tubes (B *d*).

The author thinks it probable that if the roots or attached ends (*a*, *a*, fig. 28) of these organs could only be followed through the integuments to their extreme outlets, they would be found to divide into two limbs, an ingoing and an outgoing; a fact which would account for the clearly divided ciliary currents, as they are seen in the dilated portions (A, B) of the organs (see arrows). If this fact of the bifurcation of the tube were clearly determined, there would be no difficulty whatever in connecting the segmental organs of *Aphrodita* with their homologues in the typical Annelids. In the absence of *proof* upon this point, however, they must be described as commencing in a *single tube*, the internal extremity of which divides into a numerous system of branches. None of these branches communicate openly with the general cavity of the body. It is therefore probable that these organs are exclusively dedicated to the office of reproduction. They seem unfitted to discharge any subsidiary function.

Now there are several features in the history of the segmental system of *Aphrodita*, which irresistibly suggest certain definite inferences as to its morphology. In the first place, the individual organs are segmentally or annularly repeated; in the second, they constitute a symmetrical bilateral series. They arise from either side of the median ventral line. They float in the fluid of the perigastric cavity (accidentally tangled around the gastric cæca). The ova in the female, and the sperm-cells in the male, are seen with perfect clearness *in the interior* of their branching tubuli. The significance of these facts cannot for a moment be disputed. If there be any basis of truth or fact in the science of comparative anatomy whereon to rest the doctrine of equivalent forms (morphology), it cannot be denied that the branched segmental organs of *Aphrodita* are only another example, under the guise of an unusual variation, of the typical segmental organ as now described in the Annelids in general.

In *Sigalion*, *Pholoe* and *Polynoe*, this system occurs under precisely the same characters as those just indicated in *Aphrodita*. If there be any difference, it is marked only by the number and complexness of the branches (fig. 27 A, B).

The blood-vascular system in all the Aphroditadæ is almost, if not entirely wanting; upon this special point the author has instituted numerous and careful observations. In no instance whatever amongst this family has he ever succeeded in detecting the faintest trace of a blood-vascular system, except in *Pholoe inornata*. In this little Aphrodite a vessel may be seen, carrying a colourless fluid, in contact with and parallel to the ventral nervous chord, slowly undulating with pulsations. Practically this fluid-system is wanting in the Aphroditadæ; it can therefore play no part in the generative functions. As will be subsequently shown, this fact, added to a mass of others, will compel the morphologist to admit a close zoological affinity between the aberrant Annelids and the Asteriadea and Echinidea among the Echinoderms.

This completes the anatomical history and morphological relations of the segmental system of organs in the class Annelida.

It now remains to speak of the leading points thus established. The demonstration has been long and difficult. The general results are satisfactory in the highest degree. It may be convenient to condense them into the shape of a few recapitulatory statements.

1. In the Lumbricina (including the Naides) only a few of the segmental organs are concerned in the office of reproduction. The others are diverted to a subsidiary purpose, viz. to eliminate the chylaqueous fluid. This may *possibly* be the case in *Clepsina* and *Nephelis*.

2. In the Hirudinei the great majority are dedicated to the development of the feminine or ovario-utricular system, and only two, or four (according to the species), to the male apparatus. It is not yet clearly proved whether in this family the collateral function of discharging the cavitary fluid is or is not accomplished by this organ. The Hirudinei, the Lumbricina, and Planaridæ amongst the Annelids are hermaphrodite. No other Annelid falls under this designation.

3. In the Terebellidæ and Arenicolidæ, the segmental organs are definite in number, but bearing no reference in their number, although in position, either to the segments of the body or to the branchiæ. They communicate with the cavity of the body, which stands to the ova in the relation of a vitellarium. This is the *only group* in the entire class of Annelids in which the perigastric chamber is made a place of sojourn for the reproductive elements.

4. At the Sabellidæ and Serpulidæ commences the Nereid type. The segmental organ becomes now a simple looped vascular tube, *both ends* of which open externally, and through the interior of which is driven, by ciliary force, a current of the *external element* (water), and to which is affixed a gland-like appendage, in which in the female the ova, in the male the sperm-cells, are retained after these products escape from the true testes and ovaria.

5. This description applies in every sense to the segmental and reproductive system of the entire Nereid group. In this and the former division every segmental organ in the body, both in the male and female, is engaged in the reproductive function. There are no non-generative organs as in the Lumbricinæ. The distinctive characteristic of this and the former group is that the generative products, although *formed* in the segmental organs, are not retained in them, nor are ushered into the perigastric cavity. They sojourn in appended pouches as already defined.

6. This definition applies also to the Chloræmea.

7. The segmental organs of the Nemertidæ or Cestoid Annelids conform in structure with the type of the lateral ovarian pouches of the Hirudinei, differing from the latter in having the sexes on separate individuals.

8. In the Planariea the type of the organ changes. There are only four original

segmental organs, which are now fused into two. The external orifice is single, and the organ is branched and unciliated.

9. In the Aphroditadæ the segmental organ forms a bilateral series, each organ having a single orifice and branched, the sexes being separate.

Homology of the Segmental and Reproductive Organs of the Annelida.

The history of this system of organs has now been traced uninterruptedly throughout every important division of the class of Annelids. Its continuity as an organic system within these limits has, the author trusts, been fully and completely demonstrated. But the homological relations of this system do not terminate at the limits which define the Annelids proper into an independent class; they are traceable with clearness and certainty into other and apparently very differently organized classes of animals. They will serve to connect together large groups of inferior forms between which, as hitherto believed, no zoological affinity existed. In this sense the inquiry into the morphological relations of the segmental organs of the Annelids assumes a character of unusual importance. A few detached conjectures upon this subject some years ago were thrown out by LEYDIG:—"Das 'arabeskenförmige Organ' der Nephelis und das 'rosettenförmige Wimperorgan' der Clepsine, worauf auch bereits Gegenbauer angespielt hat, nichts weiteres sind, als die Endstücke der Respirationskanäle dieser Hirudineen. Von gleicher Bedeutung halte ich die eigenthümlichen 'pantoffel- und füllhornförmigen Organe' der Synapta digitata, welche JOH. MÜLLER (Archiv für Anat. u. Physiol. 1852), aufgefunden und deren feine Cilien ebenfalls nach einwärts schlagen*."

In a very recent paper "über Hydatina Senta†," LEYDIG speaks of the ciliated tubes as "Respirationsorgane."

From these passages it is evident that this comparison between the ciliated organs of *Clepsina* and *Nephelis* and those of *Synapta digitata*, was suggested to the mind of LEYDIG simply by the fact, that in each instance the organ terminated internally by an expanded ciliated umbrella-like extremity. His comparison ends where this arbitrary and unimportant point of resemblance ceases. He originates no morphological principle. The resemblance which he suggests is a mere accidental observation.

The author will now proceed to develope the views, with the importance of which he is deeply impressed, which he has been inductively led to adopt from a clear and convincing recognition of an *essential unity of design* in the structure and uses of the segmental system of organs throughout the classes to which his observations relate. The subject may be conveniently distributed under the following arrangement of heads:—

* Zeitsch. f. W. Zool. 1854.

† MÜLLER, Archiv f. Anat. u. Phys., 1857.

The segmental organs of the	Are immediately homologous with those of the
Lumbricina, Naidea	Hydrozoa, Actinozoa, Rotifera. (Cœlenterata.)
Hirudinei, Clepsina, Nephelis	Synaptiadæ. Holothuriadæ.
Terebellidæ, Arenicolidæ	Sipunculidæ. Echiuridæ.
Nereidæ, Chloræmea	
Planariea	Trematoda.
Aphroditadæ	Echinadæ. Asteriadæ.

The author has drawn up the above table of homologies from an extensive and careful series of dissections and practical comparisons. He is deeply imbued with the conviction, that the parallelism which it purports to sketch will acquire greater and greater importance as special anatomical investigations extend.

If the generative system of *Lucernaria* be compared with that of *Actinia*, a close and striking resemblance in structure and disposition will be at once perceived, notwithstanding that in *Lucernaria* the organ is branched and multiplied by lateral cæcal tubuli, hitherto undescribed. In both there is a coiled ciliated tube; in both there is an appended mass of ova or sperm-cells, according to the sex. So intimate is the similarity of form between the complex tubuli which are attached to the mesenteric septa in *Actinia*, and the ciliated or segmental organs of the Lumbricina, that the idea of their typical identity at once arises in the mind. If it be conceded that these two forms are the homologues of each other, it follows that the ciliated tubes of *Lumbricus* and *Nais* are in truth the homologues of the radiated reproductive system of *Lucernaria*, and, through this zoophyte, of that of the entire group of the Hydrozoa*. And this conclusion (startling as it may now appear), as minute anatomy proceeds in her course of discovery, will certainly come to be universally admitted.

The mode in which the ovarian and sperm-masses are connected with the convoluted chords in the generative organs of *Actinia*, affords a strong proof in favour of the view

* The segmental organ in the hydroid polypes sinks into a condition of rudimentary abeyance. But that they do exist along the lines which indicate the positions of the vertical septa of the higher grades of polypes, I am persuaded. The time will come when it will be necessary to review the entire doctrine of generation in connexion with the system of the segmental organs. My observations have strongly suggested to my mind the belief that the gemmæ in the hydroid polypes only arise along those vertical lines of the body of the parent, beneath which there lie *rudimentary* segmental organs, and that the *gemma* most probably proceeds from an *ovum*, and not from any indifferent portion of the parent-structure.

which the author has given as to the relation in which the great ovarian and testicular masses in *Nais* and *Lumbricus* stand to the ciliated tubes.

If the author's interpretation with reference to the reproductive system in these two genera be founded in truth, then it must follow, of absolute necessity, that the reproductive masses in the Rotifera bear to the "trumpet-ending ciliated tubes" an exactly similar relation.

This inference however, thus forcibly pressed upon the morphologist, is directly contradicted by one of the most recent writers on natural history, who declares most emphatically that the ciliated tubes of the Rotifera, which, like those of *Lumbricus*, *Nais* and the Hirudinei, open by trumpet-shaped extremities into the perigastric chamber, "have nothing whatever to do with the generative organs*!" LEYDIG has already suggested a form-likeness between the "arabeskenförmige Organ der Nephelis" and the "rosettenförmige Wimperorgan der Clepsine," and the "Respirationsorgan" (as called by him) of the Rotifera. With the most unfeigned respect for this sincere and straightforward naturalist, the author is compelled to observe that he has only understood one-half of this great homological question. The form-likeness does not end with the ciliated tubes. It extends to the *function*, to the associated germinal masses: though in both the tubes are excretion organs, they are something more and deeper.

The "füllhornförmige Wimperorgane am Gekröse hängend" (MÜLLER) of *Synapta digitata*, have already been compared by LEYDIG to the "arabeskenförmige Organ" of *Nephelis*, and to the "rosettenförmige Wimperorgan" of *Clepsina*. But this comparison involves only one-half of the truth. If there be any probability in the view maintained in this memoir, the ciliated organs of *Synapta* are themselves only modifications of the cæca or tubules, upon which the office of reproduction devolves, being *ovaria* in the female and testes in the male.

Both are equally homologous with the typical organ.

At present it would merit the censure of being speculative, if an attempt were made to interpret the "respiratory tree" of *Holothuria* and *its* generative system. It is not improbable that, when *correctly described*, they will legitimately fall within the definition of the segmental system as propounded in this memoir. This Echinoderm is so rare however in the British seas, that conjecture as to the nature and character of its segmental system must for the present be postponed.

The form which the segmental organ exhibits in the Terebellidæ and Arenicolidæ, meets with an exact counterpart in that of the Sipunculidæ and Echinidæ. In the Sipunculan Echinoderms there is no *ciliated* organ. Those which are present are engaged in the generative function. They are simple cæcal pouches. They fail in their resemblance to their homologues in the Arenicolidæ in this respect, that at their attached extremities they are not divided into two limbs or tubular processes as in the

* This is all that I am willing to say in this place; but I trust, in my forthcoming Report on the Annelids, in the Transactions of the British Association, to enter at much greater length into the important and interesting history of the "segmental organ."

latter. As far as it is possible at present to determine, however, they have only a single external opening. But it is certain there exists between their tubular interior and the perigastric cavity some *open communication*, since the ova and sperm-cells find a path from the former place into the latter.

The segmental organ of the Nereid group must be looked upon as only a variation from the type of that of the Terebellidæ and Arenicolidæ.

So obvious is the unity of type between the segmental system of the Planariea and that of the Trematoda, that no controversy can for a moment be thought of.

The segmental system of organs in the Aphroditadæ is now first demonstrated. Neither its nature nor its homologue has ever before been brought within the reach of demonstration.

But so unquestionable is the morphological resemblance between it and the reproductive organs of the Echinidæ and Asteriadæ, that it is impossible to doubt their morphological affinity. They agree in two points of structure: both have a *single* external orifice or attachment; both are cæcally branched. And it may be added, that in all, the germinal products are retained within the proper membranous limits of these organs in all these families; at no time do they escape into the general cavity of the body.

Thus, through the morphological relations of the "segmental organ," not only are the orders and genera of the Annelids themselves linked into one consistent chain of reciprocal relationships, but a new point of comparison, a new bond of teleological affinity has been discovered between great divisions of annuloid and radiated animals which hitherto have been held as irreconcilably separated.

Swansea, October 1857.

Explanation of the Plates.

PLATE VI.

Fig. 1. A, B, a pair of the "ordinary" segmental organs of *Nais serpentina*; A *a*, the attached extremity opening externally, the arrow shows the direction of the ciliary current; *b*, the trumpet-shaped ciliated internal extremity, which floats freely in the fluid of the general cavity of the body. The current excited by the cilia (see arrows) sets strongly *into* the mouth of the tube. *c* is a thick-walled enlargement of the tube, which aids the current either by its sucking or propelling power. At *d* the tube is attached to the roof of the cavity, or side of the septum, by means of a bridle of threads. From *a* to *f* the tube is single, and the contained current is single; from *f* to *e* it is complexly folded upon itself, as shown at *i*, *h* and *j*. B represents the corresponding tube in the other moiety of the segment, in outline.

Fig. 2. A view of two generative (a and a^2) and three pairs (f, g, h) of non-generative or ordinary segmental organs from *Nais filiformis*; $a\ k$ is the male organ; $a^2\ b$ is the female. The masses i, j are testes; b, c are the ovaria; k, e denote the umbrella-shaped internal extremities of the generative ciliated tubes, $a\ k$ and $a^2\ b$. The dilated portions, $a\ l$, $a^2\ c$, act as organs of expulsion to the generative products. On comparison it will be at once seen that every part of the generative segmental organ has an exact counterpart in the ordinary or non-generative organs, f, g, $g\ h$. The one therefore is only a modification of the other.

Fig. 3. A view of the generative and non-generative segmental organs of *Lumbricus Jordanii* (mihi); a, a^2, attached ends; g, c, dilated portion; f, testes; b, b, ovaria; d, coiled highly ciliated tube terminating in a pyriform open extremity, e and i; k, bridle.

$j\ m$, $j\ m$, a pair of ordinary segmental organs; B, one of the generative tubes from a young worm.

Fig. 4. The segmental organs of another species of *Lumbricus* in a very young state, *Lumbricus Kauii*, mihi; a, a, a, ordinary organ; B, enlarged view of the same; C, a generative segmental organ having attached to one side the reproductive masses c; a, mouth; b, outlet.

Fig. 5. One of the ordinary or non-generative segmental organs of the common Earth-worm, *Lumbricus terrestris*; a^2, outlet; b, enlarged portion filled with minute entozoa, k; at j the enlarged non-ciliated portion ends, and the smooth-walled ciliated portion, $j\ i$, begins; from i to d extends a curiously camerated and highly vascular division of the tube, lined with slowly acting minute cilia. From d to e, the tube is again smooth-walled, dotted with the nuclei of cells along its walls; f, the ciliated fan-shaped termination suspended in the general cavity, having a very wide opening, as indicated by the arrows; n, g, g, main vascular trunk of the organ; h, h, botryoidal appendages.

Fig. 6. An outline view of the reproductive masses and ciliated tubes of the common Earth-worm *in situ*:—i, i, posterior testicular masses; h, its corresponding segmental organ; f, ovarian; i^b, its own segmental organ; l, calciferous glands; e, second ovarian mass with its own segmental organ; d, the third ovarian mass and organ; c, j, anterior testicular masses with their own segmental organs, b, b; a, a, ordinary segmental organs; k, median structure.

Fig. 7. Diagram showing the mode in which the duct of the testes (a) opens into the ciliated tube (b) to form a common duct (c) opening outwards at d.

Fig. 8. Shows the mode in which the ovarian masses (a) surround the ciliated tube, $e\ b$.

Plate VII.

Fig. 9. A full and complete representation, in the mature condition, of the ovarian segmental organ of the common Leech (*Hirudo officinalis*); a, a^2, the ends of the

two limbs (*g*, *c*) of the loop *b*. In *a* the ova, *j*, are large and mature; in the limb a^2, which is the true ovary and ingoing limb, they are small, pellucid (*k*) and destitute of vitellus. The arrows indicate the ova pursuing their path outwards; *d h* is the duct by which the so-called "respiratory sac" of DUGÈS, *l m*, communicates with the ingoing limb of the segmental organ; *i* is the orifice by which the sac of DUGÈS communicates with the general cavity of the body; *e f*, the vascular system of the ovarian limb.

Fig. 10. The ovarian segmental organ of *Albione muricata*, differing very triflingly from the former:—*d*, ovarian limb; *f*, immature ova; *h*, loop; *c*, duct leading from the sac, *a*; *b*, internal opening; *e*, oviduct or outgoing limb; *g*, mature ova contained in it.

Fig. 11. Segmental organ of *Arenicola piscatorum*, with its vascular appendage:—A^b, external orifice or commencement of ingoing limb, A *d*, which opens into the fundus, *c m*, of the organ; *b*, B, B^b, the outgoing limb, from which, at *n*, diverges a process by which the ova and sperm-cells are conducted into the general cavity of the body; *l* represents a large glandular organ, into which, about the middle of its course, the limb developes itself; *i h* and g^1 g^2, great vascular trunks of the organ; *e*, *e*, the great lateral blood-pouches, loop-shaped; *k*, capillary plexus, by which the body of the organ is supplied with blood.

Fig. 12. Two segmental organs (from the same side) of *Terebella nebulosa*. B, full-drawn; A, in outline, to show the course of the internal ciliary currents. Each organ is divided into two well-marked halves. B *m m*, dark glandular and ingoing half; *n n*, light-coloured, membranous, outgoing half; *f*, true seat of ovogenesis with its complex vascular apparatus, *h*; at *e* diverges the tube along which the ova and spermatozoa find their way into the general cavity.

Fig. 13. Segmental organ of *Sabella alveola*, viewed as a transparent object, differing in several respects from that of *Terebella*:—*a*, ingoing limb; *f g e*, vascular appendage; *d*, fundus of the loop; *d b*, outgoing limb; *c*, point at which the ova enter the reproductive appendage; *h*, ova; *i*, spermatozoa.

Fig. 14. Two segments of the body (near the tail) of a very young *Nereis margaritacea*, showing the relative position of the segmental organs, *d*, *d*, *d*, *d*, viewed as a transparent object, under strong pressure:—*c*, *c*, sacculi of the intestine; *d*, *d*, ingoing limbs of the segmental organs; *a*, fundus; *e e*, vascular appendage; *b*, long tubular outgoing limb.

Fig. 15. Vertical section of one half (left) of a ring or segment of the body of a full-sized female *Nereis margaritacea*, and looked at from the side, showing the relative places of the appended ovarian mass, *g i e*, and the segmental organ; *a b d*, intestine.

Fig. 16. The cirrus A of the former figure enlarged, representing the intimate blending of the ovarian mass, *d e c*, and the vessels, *b*.

Fig. 17. Vertical section through the entire body of *Aricia Cuvieri*, giving a correct view of the relative position of the viscera. Dark centre, intestine; above it, section of dorsal artery; *i*, *i*, ingoing limbs of segmental organs; *j*, *j*, outgoing limbs of the same; *a h c*, the great ovarian mass filling the cavity of the body and the hollow bases of the feet; *e e*, branchiæ; *f*, *g*, setiferous feet.

Fig. 18. Two rings, viewed as transparent objects under pressure, from the posterior third of the body of *Nerine* vel *Spio vulgaris*, exemplifying the exact position of the segmental organs in the segmental chambers:—*a*, *a*, mouths of ingoing limbs; *b*, *b*, vascular appendage; *c*, *c*, outgoing tubular limb.

Plate VIII.

Fig. 19. One (a male) of the segmental organs of *Spio vulgaris*, figured separately, in order to illustrate the mode in which the appended testicular mass, *c c c*, clings to and arises from the ciliated tubes, *a b*; *d*, the trunk of the associated vascular apparatus.

Fig. 20. Segmental organ of *Eunice gigantea*:—*b*, the ingoing limb; *e*, fundus; *a*, outgoing limb; *c*, the vascular tuft which supplies the ovarian limb with blood; *d*, branchial heart.

Fig. 21. Segmental organ and appended germinal mass of *Psamathe fusca*:—*a*, ingoing limb; *b*, outgoing limb; *c*, fundus; *d*, vascular appendage; *e e*, gland-like testicular body appended thereto.

Fig. 22. Segmental organ of *Cirrhatulus Lamarckii*:—*a*, ingoing limb; *b*, outgoing limb; *c*, fundus; *d*, vascular appendage.

Fig. 23. Male and female segmental and reproductive systems of *Chloræma Dujardinii*. First is to be noticed the long horizontal loop *a a*, *a b*, having its turn or fundus at *a*; then the two secondary or lateral loops, *j*, *j*; to each of these loops is appended a separate germinal mass, *e*, *e*, *e*; the ingoing limb of the long horizontal loop, *b c*, is filled with pellucid, transparent ova, and is of thrice the diameter of the other, *a a*, which is of a dark colour: the appended masses are filled with ova in the female, A, and sperm-cells in the male, B; *c*, enlarged view of the tube *a*; *c* B, sperm-tube.

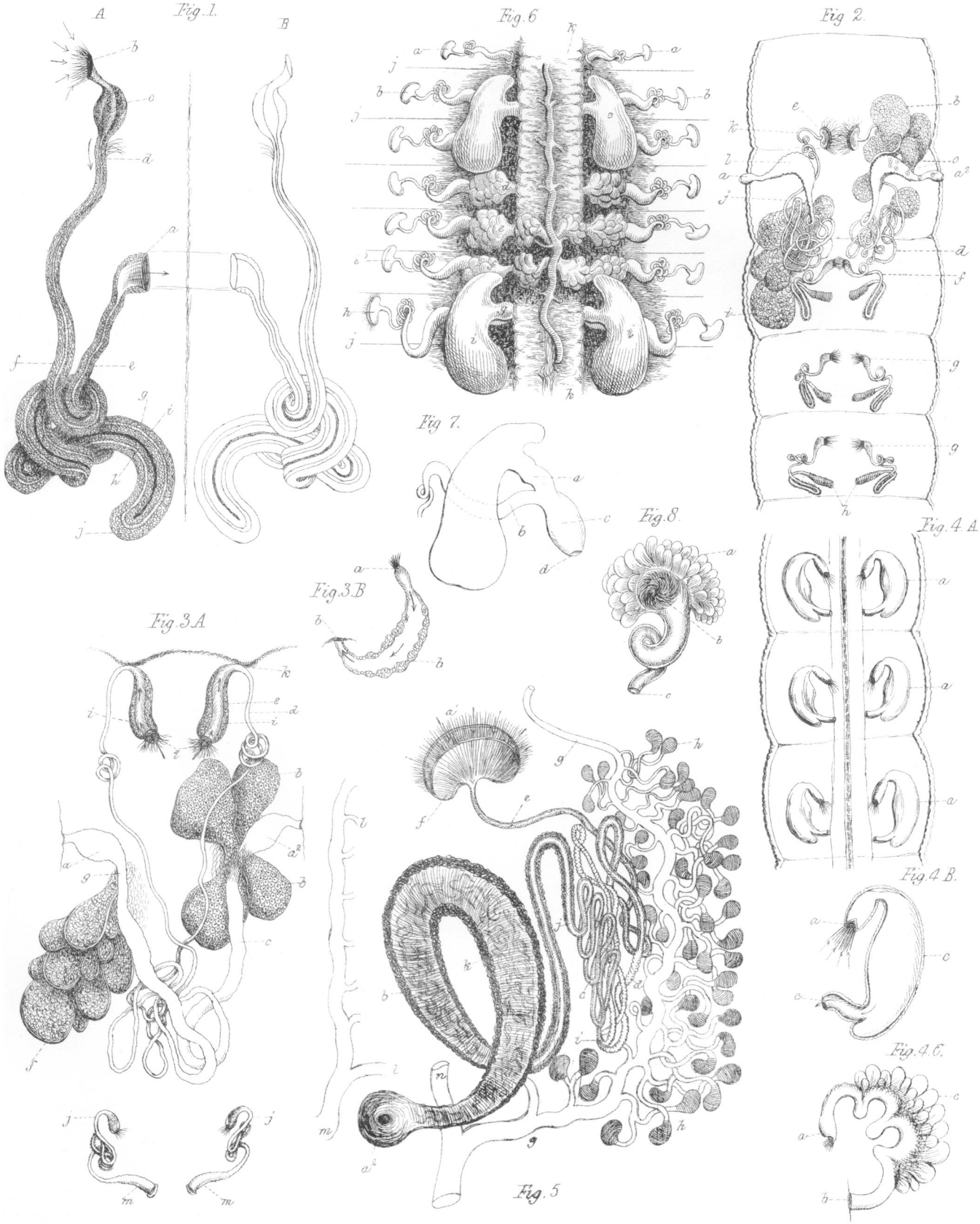
Fig. 24. A, two ovarian or female segmental organs of *Polia quadrioculata*:—*a*, *a*, *a*, alimentary or stomachal cæca; *b*, *b*, segmental organs filled with ova; B, enlarged view of the same.

Fig. 25. A complete diagram of the segmental and reproductive system of *Planarea lactea*:—*a*, œsophagus; *b*, central sac in which meet the two segmental testicular organs, *e*, *e*; *c*, central sac in which meet the two branched ovarian segmental organs, *d d*, *f f*; B, a small portion of an ovarian tube enlarged.

Fig. 26. A complete view of the alimentary and segmental systems of *Aphrodita aculeata*:—*e*, termination of œsophagus; *a*, *a*, digestive cæca; *d d d*, *b b*, *c c*, branchings of segmental organs; *e*, *e*, *e*, *e*, *e*, ciliated attached ends of same.

Fig. 27. Two organs from the *Polynoe semisquamosa*:—A, female; B, male: they are simple branched cæca, commencing at a single (double?) orifice, *a*, *a*; *c*, enlarged view of ovarian tube; *d*, enlarged view of sperm-tube.

Fig. 28. Male and female segmental organs of *Aphrodita aculeata*:—A, female; B, male; *a* A, and *a* B, ciliated dilated attached ends; *b*, *b*, branches; *d*, one of the branches of the ovarian organ enlarged; *e*, bridle at one end; *d* B, a portion of the sperm-tube enlarged.



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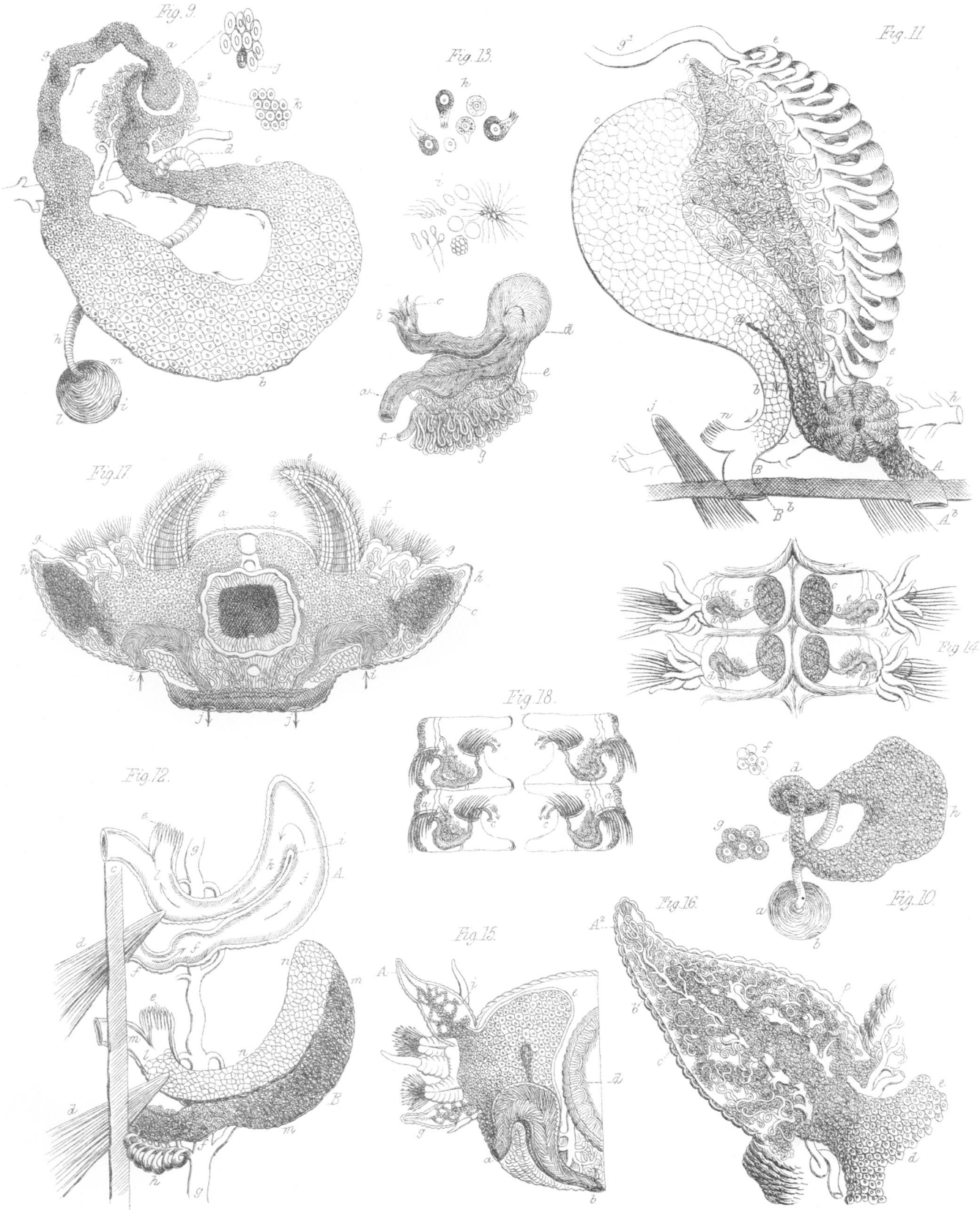

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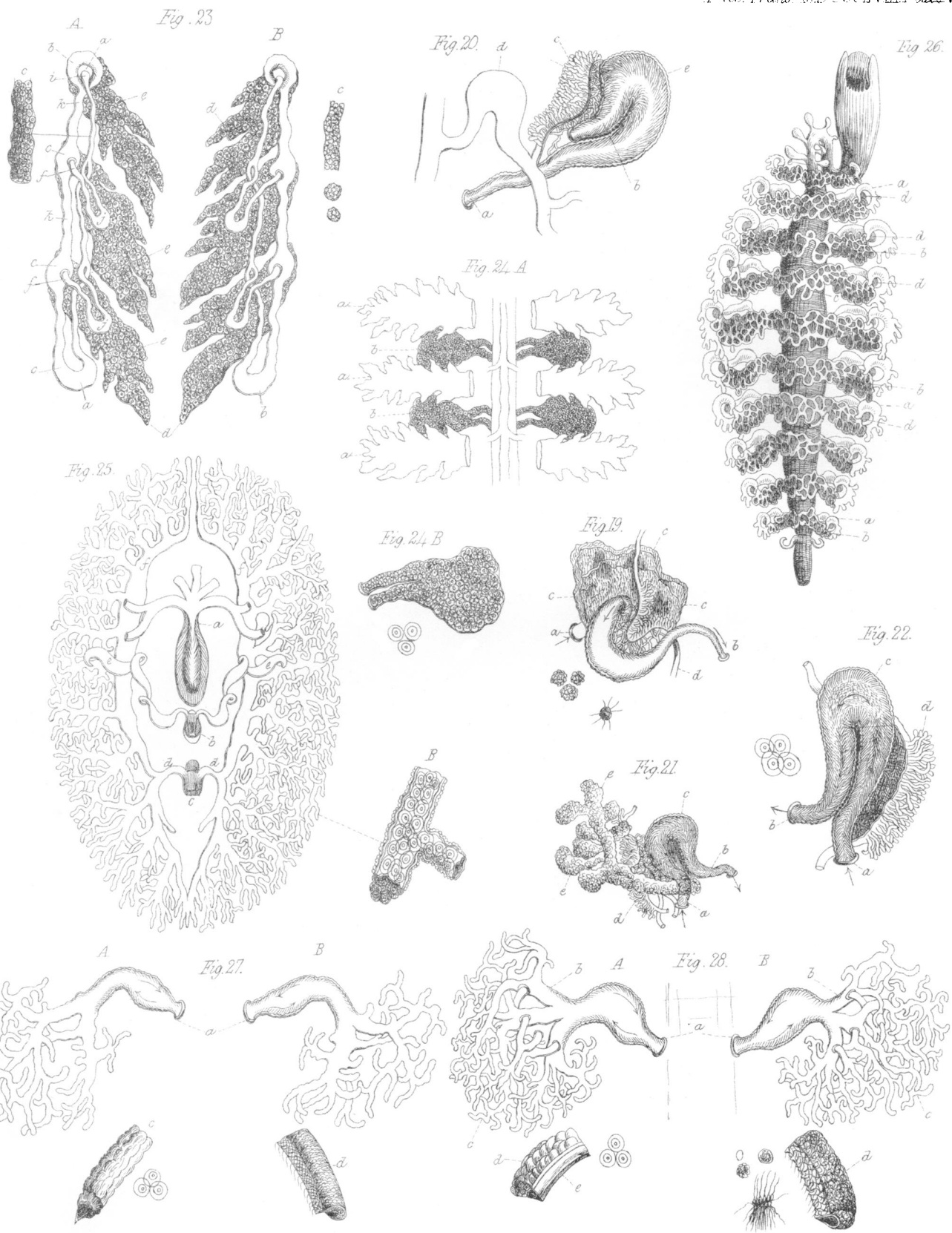

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