XVIII. On the Ova and Pseudova of Insects.
By John Lubbock, Esq., F.R.S., F.L.S., F.G.S.

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If, in his celebrated work on "Alternations of Generations," Professor Steenstrup has not succeeded in explaining the phenomena of asexual reproduction, he has at least the great merit of having brought together many interesting observations, the relations of which had remained unrecognized up to his time. The value of his suggestions is well shown by the number of memoirs which in the last few years have appeared on this subject, and by their having produced a discussion in which almost every naturalist has taken some part. It is, however, perhaps not going too far to say that as yet no satisfactory explanation of the phenomena has been suggested, and that we are now just as far from knowing as we were twenty years ago, what are the different conditions under which some eggs remain undeveloped unless they are brought under the influence of the spermatozoa, while others contain within themselves the power of producing young without the necessity of any external stimulus. Still, though we have been unable to obtain any insight into the philosophy of the subject, we have in this period collected together a great mass of facts which will perhaps ere long lead us to some satisfactory conclusion.

In a paper "On the Double Method of Reproduction in Daphnia*," I lately endeavoured to show that eggs and buds are in fact identical, that they are the two extremes of a long series, and that therefore every intermediate gradation between them will probably exist or has existed in nature. I however suggested that it would probably "be convenient to apply some distinguishing name to those eggs which do not require impregnation as a necessary antecedent to development," and Professor Huxley has since proposed to call them Pseudova†.

This name seems to me very appropriate, and I intend therefore to adopt it, merely repeating that we cannot, in my opinion, draw any definite line between eggs on the one hand and pseudova on the other, and that in the Bee and many Lepidoptera the same body is capable of becoming either the one or the other.

In the above-mentioned memoir, I described at length the development of the agamic eggs, or pseudova, of Daphnia, in order to show that it is essentially the same as that of the ordinary eggs of a Crustacean. Professor Huxley, however, has since presented to the Linnean Society an excellent work on the ova and pseudova of Aphid, and shown that in this genus at least there are important differences between the ovarian development of the ova, and that of the so-called internal buds or pseudova; and he suggested to me that it

* Philosophical Transactions, 1857.
† Linnean Transactions, vol. xxi. p. 111.
would be desirable to examine the formation of the ova in *Coccus hesperidum*, an insect which, according to Dr. Leydig *, offers in this respect several very remarkable peculiarities.

This investigation was completed, the drawings were all made, and the results written out almost exactly in their present form, by the beginning of June last, but I delayed the publication of them, in order to present at the same time some observations on the pseudova of *Cynips* and on the ovarian ova of the Insecta generally.

In the mean time Professor Leuckart published a paper on the same subject in Möleschott's *Untersuchungen zur Naturlehre des Menschen und der Thiere* for 1858†, in which he anticipated the greater part of what I had to say about *Coccus*. It was, however, very satisfactory to me to find my observations confirmed by so eminent a naturalist, and the more so as in a great many points the descriptions and conclusions of Dr. Leydig seemed to me to be inaccurate. Although, therefore, most of the following description of the development of the pseudova of *Coccus* agrees with what has been published by Professor Leuckart, yet when two such eminent anatomists came to very different conclusions, it seemed to me that the results obtained by a third observer were worthy of publication.

It is well known that in *Aphis* the self-fertile individuals are viviparous, and the differences which have been pointed out by Professor Huxley, and more recently by Professor Leuckart (*l. c.*), between the development of the ovarian product in the oviparous and viviparous forms, depend perhaps more on the different nature of the body that is to be produced than on the presence or absence of impregnation. According to Professors Huxley and Leuckart, the vitelligenous cells are very distinct in the oviparous *Aphis*, while they are not developed or are inconspicuous in the viviparous form. The latter is, I believe, the true state of the case; it is admitted that there are in the upper chamber of the egg-tube in the viviparous form, certain round cells, originally identical with the one which has developed itself into the germinal vesicle, and I consider these to represent the vitelligenous cells.

In *Coccus* also we have one species, *C. persicae*, which is truly oviparous, and in which the eggs when laid do not contain an embryo, while in *Lecanium hesperidum* the pseudova are rapidly developed in the ovary, and when laid contain a fully-formed larva, which emerges from the egg-shell in a few hours. This latter species is therefore very nearly viviparous. Now it is remarkable, that whereas in the oviparous *C. persicae* the vitelligenous cells (Plate XVIII. figs. 11 & 12) are very conspicuous, in *C. hesperidum* they are often with difficulty perceptible. Acetic acid generally renders their walls visible; but if an ovary is examined in syrup, the majority of the egg-tubes show hardly a trace of the vitelligenous cells. In order, however, to compare the formation of the pseudova in *Coccus* and *Cynips* with that of the ova in insects generally, it is necessary to give an account of the latter, because up to the present time very little has been written on the subject, and that little is almost unknown in this country. Thanks, indeed, to the

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† Zur Kenntniss des Generationswechsels und der Parthenogenesis bei den Insekten.
indefatigable labours of M. Léon Dufour and others, we are tolerably well acquainted with the external form of insect-ovaries, but very few writers have paid any attention to the histology and internal structure of these organs. In this country, indeed, Dr. Allen Thomson* is almost the only one who has written on this matter, and he was so limited in time and space, that he was unable to enter at length into this portion of his subject.

I propose, therefore, first, to give an account of the process of egg-formation throughout the Insecta, and then to describe the pseudova of Coccus, Cynips, and Solenobia, in order to show that, as far as we are yet acquainted with these secrets of nature, the two processes are perfectly identical.

In all female insects there are two ovaries, each generally consisting of several egg-tubes opening into a common chamber, called the uterus. At its posterior end the uterus contracts into the oviduct. The two oviducts converge to the middle line of the body, where they unite to form the egg-canal, to which various appendages are usually attached. The upper or anterior end of each of the egg-tubes is kept in its place by a connecting filament, which is generally attached to the dorsal vessel, either separately or after having united with the other filaments belonging to the same ovary.

The egg originates and generally attains its full size in the egg-tubes, which differ very much in different groups of insects. In all the large orders, except perhaps the Lepidoptera and Heteroptera, we find some species in which they are very few, and others in which they are very numerous, as, for instance, among Coleoptera, in Lytta vesicatoria†; among Orthoptera, in Acheta domestica; among Neuroptera, in Libellula; among Diptera, in the Tipulidae and Culicidae; among Homoptera, in Coccus; and among Hymenoptera, in Apis mellifica, which has about 170‡.

On the other hand there are, among the Coleoptera, in Lixus§ and Anthonomus‖, only two, in Hypophleus§ and Lathridius porcatus‖‖ only three; among Orthoptera, in which, on the whole, they are most numerous, as, for instance, among Locusta had only six; among Neuroptera, Psocus has only five; among Diptera, Melophagus has only two¶; among Homoptera, Schizoneura corni** and Aphis padi** have respectively only two and three; and among Hymenoptera, in Chelonus only two; and even in Apis mellifica the workers have only from two to twelve, the general number being five or six††.

A very remarkable instance of this difference occurs in the Forficulidae, in which family F. auricularia possesses a large number of very short egg-tubes, whilst Labidura gigantea has only five, which however are much longer‡‡.

According to Burmeister§§, the ovaries in Ephemera and Stratiumys are simple bags.

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* Todd’s Encyclopædia, Article ‘Ovum.’
‡ Leuckart, l. c. p. 421. § Frey and Leuckart, Lehrbuch zur Zootomie.
‖ Stein, Der weiblichen Geschlechtsorganen der Kafer, p. 27.
§§ Manual of Entomology, translated by Shuckard, p. 184
in which the germs of the eggs are contained. This form of ovary, if it did really exist, would be a type entirely aberrant from that of the Insecta generally. Burmeister, however, adds, that "egg is linked to egg by an exceedingly fine filament;" and Léon Dufour* gives a very different description of the ovary in Ephemera. Each ovary, he says, consists of a prodigious number of small egg-tubes inserted into the superior wall of a common calyx or uterus, as is the case in Libellula. I have little doubt that this account is correct, and that in Stratiomys also the egg-tubes are in reality present, but have been overlooked.

The number of egg-tubes is most constant in the Lepidoptera, almost all of which possess four†. Pterophorus, however, is said to have only three‡.

The Heteroptera also vary but little in this respect. Hydrometra†, Aradus§, and Gerris have four; Nepa and Ranatra§ five; Notonecta† six or seven; Coreus§, Pentatoma§, Alydus§, Scutellera§, Pyrrhocoris§, Lygaeus§, Cimex§, Reduvius§, Pelagonus§, Corixa§, and Naucoris cimicoides§ seven; while Naucoris aptera has only five§.

In the Homoptera, on the contrary, the number varies greatly. Schizoneura corni has only two; Aphis padu‖ three or four; Aphrophora spumaria¶, eight; A. salicina§, fifteen; Ledra§ and Dorthesia§, ten to twelve; Psylla† and Cercopis§, about thirty; Cicada†, from fifty to sixty; and Coccus an unlimited number.

The egg-tubes are numerous in Locusta migratoria‡, Phasma gigas‡, Gryllotalpa vulgaris‡, Acheta domestica, the Mantodea‡, and in most Orthoptera; but in a small species of Locusta I found only six, and the Blattæ have eight**. Edipoda** biguttula has six or seven, and E. carulescens** fourteen; Tetríx** subulata has twenty; Ecanthus**, eight to ten; and Ephippigera vesPERTina** thirty to forty.

Among the Neuroptera the egg-tubes are extremely numerous in Ephemeræ††, Perla††, Libellula striolata, Aeshna cyanea, and the Libellulida generally. There are also a good many in Stalis+++, Limnephilus and Phryganea+++; and in one of the Leptoceridae I found over forty. Termes has thirty†; in Panorpa communis I found ten, which is the number also in Myrmeleo†† and Hemerobius††; and the minute genus Psocus has only five.

We are indebted to Stein (l. c.) for an excellent work on the female generative organs of the Coleoptera. He found three egg-tubes only in one species, Lathridius porcatus; four is also an uncommon number, but exists in Hister sinuatus, Platysoma frontale, Dromius truncatellus, Scydmænus tarsatus, Triphyllus bifasciatus. In Engis humeralis and Trox sabulosus there are five; six in Clivina arenaria, Notiophilus aquaticus, Noterus crassicornis, in many Brachylytra, and in many Lamellicorns. Seven egg-tubes occur in

† Frey and Leuckart, l. c.
‡ Burmeister, l. c. p. 186.
†† Léon Dufour, Mém. de l’Institut, 1841.
Pterostichus vernalis, Aphodius finetarius, Cassida equestris, and Coccidula pectoralis; eight in Bembidium femoratum and Laphrophleus monilis; nine in Nitidula obsoleta and Diaperis boleti; ten to twelve in Cicindelinae, Carabus granulatus, hortensis (and violaceus); twelve in Clerus formicarius; fourteen to sixteen in Hyphodorus ovatus, Hydroporus palustris, Coccinella globosa and quinquepunctata; about twenty in many Chrysomelidae; twenty-five to thirty in Elater atrerrimus and Coccinella septempunctata; thirty to forty in Allecula morio, Lagria hirta, Colymbetes fuscus, Acilius sulcatus, and most of the large species of Dytiscus. The largest number observed by Stein was fifty-two, in Helops caraboides.

According to Frey and Leuckart (l. c), Lixus and Anthonomus have only two egg-tubes, Hypophleus only three, most Longicornis eight to ten, and most Buprestids twenty to thirty. Burmeister (l. c) ascribes seven tubes to Silpha atrata, seven to ten to Tenebrio, Leptura and Saperda, from ten to fifteen to Dytiscus, Staphylinus, Hydrophilus, Cerambyx, and Lamia tristis, and thirty to Blaps mortisaga.

According to Burmeister, Sarcophaga carnaria possesses only one egg-tube, and Melophagus ovinus* has only two; but in the majority of the Diptera they are short and very numerous.

In the Hymenoptera Chelonus has only two, and Odynerus only three egg-tubes. According to Frey and Leuckart, Anthidium, Crabro, Chrysis, and Xylocopa have also three; but Leon Dufour attributes four to the two latter genera. Anthophora, Crocista†, Melitta†, Vipio†, and Bombus† have four: Frey and Leuckart indeed attribute eight to Bombus, and Burmeister‡ from seven to ten; but I only found four in B. terrestris and B. muscorum.

Nomada† and Sapyga†, and according to Frey and Leuckart, all the Ichneumonidae, have five, but I find ten in Ophion luteum (Plate XVII. fig. 6). Leucospis†, Chalcis†, and Eulophus†, five or six; Formica rufa||, 100 to 120; F. nigra, thirty to forty; Vespa vulgaris, seven; Psithyrus†, eight; Pimpla†, Pontianus† and Diapria†, eight to ten; Athalia§ has twelve, but most of the Tenthredinidae† only ten; Myrmica and Xiphydria†, twenty; Banchus†, twenty-five; Cynips, a considerable number; and Apis mellifica|| as many as 170.

The number of egg-germs which are produced in each egg-tube offers also many variations, from Coccyx on the one hand, in which there is only one, to Pontia on the other, in which there are, according to Herold¶, more than a hundred.

The number is not, however, so easy to determine, as it might at first sight appear to be; for as the eggs are produced successively, there must in every case be a time when only one egg-germ is present, though this stage of development is generally past before the insect arrives at the perfect state. Moreover, before the last egg begins to grow the first one has generally already left the ovarian tube. These sources of error have

* Leuckart, l. c.
† Léon Dufour, Sur les Orthoptères, &c., Mém. de l'Institut, 1841.
‡ Burmeister, l. c. p. 187.
§ Frey and Leuckart, l. c.
∥ Leuckart, l. c.
¶ See Herold, Entwickelungsgeschichte Schmetterlinge, 1815, pl. 31.
already led to several misstatements in works on insect anatomy. There is, however, I believe, in every species, except perhaps when the egg-germs are very numerous, a certain normal number which are present in each egg-tube when the oldest, and therefore the posterior egg-germ has attained to maturity, and is ready to descend into the uterus. Still in most egg-tubes the egg-germs become so “small by degrees and gradually less,” that it is difficult if not impossible to say exactly how many are present. Where, therefore, the exact number is not mentioned, it must not be inferred that the number varies, but only that it was not more accurately determined. Probably, however, when the number is considerable, it admits of certain variations, even in the same species.

In the Lepidoptera the egg-germs are very numerous, varying from twelve to more than a hundred. In the Orthoptera they are rather fewer. Burmeister*, indeed, ascribes only three to Gryllus migratorius, and six to Blatta; but in B. orientalis I found rather more than twenty. He does not mention to what species he alludes, but there is seldom much variation in this respect in species of the same genus, so that probably he examined a young specimen in which only a few egg-germs had as yet been produced.

In the Hymenoptera the eggs are rather less numerous in each egg-tube. Chrysis and Xylocopa are said to have only three; Bombus terrestris† only six (but this again I doubt, as in B. muscorum I have found in July from twelve to fifteen); in Cynips lignicola there are thirteen; Apis mellifica‡ has seventeen, and in some Ichneumonidae they are still more numerous.

In Pulex irritans I found fourteen egg-germs occupying the whole width of the egg-tube, and a large number which had not yet arrived at that stage.

Among the Neuroptera the number of egg-germs in each egg-tube is nearly the same as in the Hymenoptera. In Aeschna there are about fifteen; in Libellula striolata about the same number; in Panorpa about twelve; in Chrysopa about ten; in Psecus only five.

The egg-development of the Coleoptera has been carefully described by Stein, from whose excellent work I have extracted many details concerning this order. He finds (l. c. p. 32) the greatest number of egg-chambers in the Curculionidae, where frequently as many as twenty are present. Thus, Brachyderes incanus has twenty-one, Hylobius abietis and Sitones lineatus eighteen.

In the Cyphonidae also the number is considerable; Cyphon pubescens has as many as fifteen. In Telephorus dispar he found seven or eight; in the Cicindelidae, Carabidae, and Hydrocantharidae also, each tube has several egg-germs. In Colymbetes fuscus there are twelve; the number in Notiophilus aquaticus, Carabus granulatus, and Cicindela campestris is seven.

The remaining families of this great order have less than five egg-germs in each tube.

The egg-development in the Diptera has been little studied, and from the small size of the ovaries, and indeed of the generative organs generally, it presents great diffi-

* Loc. cit. p. 187. † Ibid. ‡ Burmeister, l. c.
culties. Each egg-tube contains generally very few egg-germs, though in a small species belonging to the Syrphidae, and I believe to the genus Cheilosia, there were as many as nine. In Melophagus ovinus Leuckart has figured three, and I have found the same number in Musca and Eristalis tenax. In Tipula and Culex I found only one egg-germ besides the terminal chamber, which is present throughout this order as in the Coleoptera.

In the Hemiptera the egg-germs are few in number, and each egg-tube has a large terminal chamber.

In the Homoptera but few species have been examined. They appear, however, to agree with the Hemiptera in having few egg-germs, and a terminal chamber containing vitelligenous cells. In Coccus hesperidum and C. persicae I found only one egg-germ, in Aphrophora spumaria three; and Leydig and Huxley* have figured five in an Aphis†.

**Histology.**

The egg-tubes consist of two membranes. I did not, indeed, succeed in seeing the outer muscular one clearly in every species I examined, and in some insects all the egg-tubes are enveloped by one common covering; but in most instances the outer membrane was distinctly visible between each two egg-chambers, where, unlike the inner membrane, it is not contracted, but retains nearly the same diameter, only tapering gradually from the most mature egg-germ up to the youngest. It is figured in Plate XVI. figs. 3 and 9, and Plate XVII. fig. 7.

On the inner side of the internal membrane lie a number of cells. These form in most parts a continuous layer; but in those insects which have between each of the egg-germs a small group of the remarkable vitelligenous cells, presently to be described, the epithelial cells at these parts of the egg-tube are scattered more sparingly, and are less distinctly visible. These epithelial cells take probably an active part in the secretion of the yolk, and subsequently in that of the chorion.

Between each of the egg-germs in Lepidoptera, Hymenoptera, Geodephaga, Hydadephaga, and Neuroptera (except the Libellulina), is situated a group of cells, which increase in size from the anterior to the posterior end of the egg-tube.

These cells, which, adopting the convenient name proposed by Professor Huxley, I propose to call the vitelligenous cells, were first noticed by Herold‡, who however describes them as rings, and offers no opinion on their homologies or function. Stein, in his excellent work to which I have already had occasion to allude, gives a faithful description of these cells, and expresses a decided opinion that they secrete yolk-matter. Hermann Meyer§ also has described these bodies in the egg-tube of Saturnia Carpini; but he considers them abortive ova; an opinion, which, although adopted by Dr. Allen Thomson||, appears to me quite untenable.

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* Huxley, i. e. pl. 40. fig. 1. † Zeitschrift für Wissenschaftliche Zoologie, 1849, pl. 5.
‡ De Generatione Insectorum in Ovo. § Zeitschrift für Wissenschaftliche Zoologie, 1849.
|| Article 'Ovum,' p. 113, Todd's Cyclopædia.
Dr. Leydig*, in his paper on the Agamic Reproduction of *Aphis*, and Professor Huxley (l. c. pl. 36) have figured in the terminal chamber certain round, nucleated cells, any one of which may develop itself into a germinal vesicle, and so pass down the tube and form around itself the future egg. These so-called cells are probably homologous with the nuclei of the vitelligenous cells.

Dr. Leydig also, in his paper on *Coccus hesperidum*, figures certain large nucleated cells in the upper chamber of the short egg-tubes, but having overlooked the true germinal vesicle, he seems to have (if I understand him right) considered these bodies as the equivalents of the germinal vesicle, whereas in fact they are true vitelligenous cells, differing neither in position nor appearance from the type present in the other Homoptera.

Professor Leuckart also (l. c.) has described these cells in *Aphis*, *Coccus*, and *Solenobia lichenella*, and adopts in reference to them the same opinion as Professors Stein and Huxley.

In adopting the term “vitelligenous” as applicable to these bodies, I have expressed my opinion of their function; an opinion, I may add, which was adopted independently by Professor Stein, Professor Huxley, and myself. In proof of this view I would refer to the egg-tubes of any Lepidopterus or Hymenopterus insect, or to Herold’s figs. 15, 16, 14, 13 and 12 (l. c. pl. 1). It will there be seen that although the vitelligenous cells increase individually in size, as does the yolk-mass, yet that the latter constantly grows at the expense of the former, which become fewer in number, and finally disappear altogether.

Professor Stein has observed that in *Acilius sulcatus*, in which the yolks are brightly coloured, the vitelligenous cells are of the same hue; and in all insects the contents of these cells closely resemble the mass of yolks substance.

Professor Huxley has observed in *Aphis*, and I have noticed in certain Hemiptera (see Plate XVII. figs. 7 and 9), that a tube, or channel, leads down from the terminal chamber into the second and third egg-chambers, which seems evidently intended to convey the yolks-matter to the developing eggs.

Finally, if, as Professor Stein also remarks, we press the vitelligenous cells out of one of the egg-chambers, we shall generally find some of them in which the cell-wall is almost entirely absorbed, so that on the application of but slight pressure the contents spread in all directions.

The two theories respecting the nature of these cells are not quite so opposite as would at first sight appear to be the case. In their earliest stage the egg-cell and the vitelligenous cells cannot be distinguished from one another; and no one, I think, who has carefully examined the upper part of the egg-tube in any Hemipterus or Dipterous insect, can fail to be of the same opinion. The egg-tube contains indeed at this end cells which are neither vitelligenous nor egg-cells, but which are capable of becoming under certain circumstances either the one or the other.

* Zeitschrift für Wissenschaftliche Zoologie, 1849, pl. 5.
Professor Stein, indeed, appears to consider that the vitelligenous cell is homologous with the germinal vesicle, and that the yolk is deposited round it without being enclosed at first in any distinct membrane.

In the Diptera (Plate XVII. fig. 8, and Plate XVI. fig. 9) and the Hemiptera (Plate XVII. fig. 7) it is, I think, evident that the germinal vesicle corresponds to the nucleus of the vitelligenous cell, and that the yolk-mass is in the early stages of egg-formation enclosed in a membranous envelope or cell, homologous with the cell-wall of the vitelligenous cell, and like it destined soon to be absorbed, but which in the mean time I propose to call the egg-cell; and even in the Lepidoptera, Hymenoptera, Geodephaga, and Neuroptera, though the matter is not quite so clear, any one who examines carefully the upper end of the egg-tubes will, I think, come to the same conclusion.

Our knowledge of the modes of egg-formation in the Insecta is perhaps hardly yet sufficient to enable us to generalize with much confidence; the following Table exhibits, however, the present state of our information on the subject; and though many of the aberrant forms, as for instance Thrips and the Strepsiptera, are not included, and it is therefore very incomplete, yet it will probably be found correct as far as it goes. The only two cases in which any families differ greatly, as regards the vitelligenous cells, from the remainder of the order to which they belong, are the Geodephaga and Hydradephaga from the remainder of the Coleoptera, and the Libellulina from the Neuroptera.

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In thus dividing the Insecta into two sections, according to whether or no each egg-germ carries with it a group of vitelligenous cells, we get a classification which is far from natural, inasmuch as it separates the Libellulina from the rest of the Neuroptera, Pulex from the Diptera, and the two first sections of the Coleoptera from the remainder of that order.

It is rather difficult to decide in which group the genus Forficula (Earwig) ought to be placed, since each egg appears to consist of an egg-cell and one vitelligenous cell only.

The second section, containing the insects which possess groups of vitelligenous cells forming a part of each egg-germ, combines most of the insects in which the power of flight is largely developed; but the Libellulina, which are pre-eminent in this respect, belong to the other series.

The development of the prothorax appears to have some curious connexion with the presence of alternate groups of vitelligenous cells. Lacordaire* says, "Si le prothorax

* Introduction à Entomologie, p. 326.
a acquis un développement extraordinaire, et s'est en quelque sorte séparé du mésothorax et du métathorax, on aura le thorax d'un Coléoptère, d'un Dermaptère, d'un Orthoptère et d'un Hémiptère. Si au contraire le prothorax est réduit à des dimensions très-exiguës, et que le mésothorax intimement uni au métathorax ait pris un accroissement énorme, on aura celui d'un Hyménoptère, d'un Lépidoptère et d'un Diptère.” And again, in page 332, after having described the prothorax of the Coleoptera, Dermoptera, Orthoptera and Hemiptera, he says, “Avant de considérer le prothorax des mêmes ordres sous un point de vue plus en rapport avec ses usages dans la nomenclature, il est essentiel de connaitre les modifications qu'il subit chez les Hyménoptères, les Lépidoptères, les Diptères et quelques Neuroptères.”

The Diptera, Hymenoptera, and Lepidoptera, thus nearly allied to one another by the structure of the thorax, also agree very nearly in the type of egg-development.

In the Libellulina also (Dragon-flies), the prothorax is rather large and distinct from the rest of the thorax.

The Geodephaga and Hydradephaga, however, are subversive of this curious coincidence, which would otherwise have been as complete as that of the coexistence of rumination and cloven feet; or the inward bending of the condyle of the lower jaw, with the other characters of the Marsupialia.

In the Orthoptera we find, on the whole, perhaps the simplest type of egg-formation which occurs in insects, the large vitelligenous cells being entirely absent, and their functions probably monopolized, instead of being only shared, by the small cells which line the membrane of the egg-tube.

The number of egg-chambers in each egg-tube is generally numerous; in Blatta orientalis (Plate XVI. fig. 1) amounting to as many as twenty-three. In each of the egg-chambers the germinal vesicle is easily visible, lying nearly in the centre, and possessing a distinct macula. The germinal vesicle in Blatta orientalis (Cockroach) is rounded in the upper chambers, but in the lower ones is somewhat elongated transversely. The macula germinativa is small, round and simple, as is the case in Acheta. In a species of Locusta (Grasshopper) I found the germinal vesicle in the lower chambers, lying near the posterior end of the egg; in other words, near the end which is turned towards the vulva. In Acheta domestica (Cricket), as in Blatta, the macula is a small round vesicle \( \frac{1}{1000} \) in diameter in the lowest egg-chamber in which it is visible, and gradually diminishing to \( \frac{1}{500} \). In the lower chambers a minute nucleolus can be seen in it, which is about \( \frac{1}{1000} \) in diameter. I never found in Acheta any other vesicular structures in the germinal vesicle, but there is in the anterior or smallest germinal vesicles, a conspicuous, dark, granular mass, which both Wagner and Stein* seem to have taken for the true macula. This dark granular mass is single in about the first four egg-chambers, and often conceals the true macula; it then gradually breaks up, and in the three or four most mature egg-germs is reduced to a cloudy mass of very fine granules.

The type of egg-formation which is represented in Plate XVI. fig. 1, is found in Blatta,

* Loc. cit. p. 49.
Gryllus, Locusta, and Acheta, and probably prevails also through the Phasmidae* and Mantideæ, which two latter families, however, I have as yet had no opportunity of examining. It is, however, quite possible, if not probable, that we may find in them some approach to the peculiar type exhibited by the remarkable genus Forficula (Earwig).

In the Libellulina the egg development is remarkably similar to that of the Orthoptera, with which it agrees in the absence of the large vitelligenous cells, and of any terminal germ-chamber. The egg-tubes are excessively numerous, and I have generally found from twelve to twenty eggs in each.

The macula of Eschna (Dragon-fly) consisted apparently of several small vesicles, which gradually increased in size in unequal ratios, until at length one large one became pre-eminent. The end of each egg-tube terminates in a chord-like tube.

In Pulex (Flea) also the type appears to be the same. There is here the same absence of the vitelligenous cells and of the terminal germ-chamber. If, however, a young specimen be examined, fewer egg-chambers will be found; and at the end of the egg-tube there will be a false, or rather perhaps a temporary germ-chamber, destined eventually to be entirely occupied by egg-germs, and to lose gradually its special character. In the most advanced tube I found fourteen egg-germs occupying the whole width of the bore, besides a great many others in less forward stages.

The germinal vesicle is dark, large, circular, and very distinct. I could not see in it any macula; but in two or three cases, shortly before its disappearance, it looked as if it was breaking up into a number of small ovate bodies.

It is very remarkable, that in spite of the numerous affinities existing between Pulex and the Diptera (Gnats and Flies), the mode of egg-formation in these two groups is entirely different.

In the Hemiptera (Plate XVII. fig. 7), the egg-tube terminates in a large terminal chamber full of round cells, each of which can apparently become an egg-cell or a vitelligenous cell. In this type, therefore, the vitelligenous cells, instead of being divided into small groups, one at the posterior end of each of the egg-cells, are all collected into a common germ-chamber at the end of the egg-tube.

I was for some time in doubt whether the cells in this common germ-chamber did really contribute to the formation of the yolk. In Aphis, however, in which the same type of ovary exists, Professor Huxley† discovered, as before remarked, a duct or passage leading from the germ-chamber through the anterior, to the more developed egg-chambers. A similar structure exists in Nepa (Water Scorpion) (Plate XVII. fig. 7), and some other Hemiptera; and as there can, I think, be no doubt that it is really a duct through which the yolk-substance descends to the growing egg, it follows that some at least of the cells in the terminal germ-chamber do really fulfil the office of vitelligenous cells.

In the common Nepa cinerea I once found as many as five of these vitelliferous ducts (Plate XVI. fig. 10) in an egg-tube containing seven egg-germs, so that it seems probable

† Loc. cit.
that each egg-germ has its own peculiar vitelliferous duct, and that the duct is obliterated when the egg has received a sufficient amount of yolk.

I could not see in the common germ-chamber more than one sort of cell, except that near the posterior end some few are evidently changing (Plate XVII. fig. 7) into egg-cells; and I conclude, therefore, that each of the cells in the germ-chamber is capable of becoming either vitelligenous or egg-cells. Those which develop themselves into egg-cells gradually swell, and their nucleus also increases in size and becomes the germinal vesicle; after awhile a small cell-like macula makes its appearance in this latter.

The common germ-chamber is at its posterior end somewhat contracted, and at this place one or two narrow egg-germs generally lie transversely across, occupying the whole width of the tube. The next egg-germ is somewhat square-shaped, as are the three following; the seventh is somewhat barrel-shaped; and the eighth shows on one side the projection which is so conspicuous in the mature egg, and on which the micropyle is situated. I found also at this period (end of September) some few egg-tubes in which the projection was also commencing in the penultimate chamber. In the four anterior egg-germs the germinal vesicle occupied a central position, but in the more mature egg-chambers it laid alternately, first on one side and then on the other, close to the layer of epithelial cells. It is worthy of remark, that in all my specimens the lateral projection was situated on the same side as the germinal vesicle.

In the oldest egg-germs the yolk contained numerous granules and small oil-globules. In each ovary there are five egg-tubes.

In the Coleoptera, excepting the Geodephaga and Hydradephaga, we find the same type of ovarian tube as in the Hemiptera, but the terminal germ-chamber is generally smaller in proportion. The cells contained in the germ-chamber are apparently of the same nature as in the Hemiptera, and probably therefore secrete part of the yolk-substance. I have not yet, however, met with the yolk-duct. Since, however, I became familiar with this structure in Nepa, &c., I have been able to examine but few Coleoptera.

In Telephorus (Plate XVI. fig. 4) the epithelial cells are small and indistinct, but in a Galeruca I found them very large.

I have examined only few species of Coleoptera, since Stein has devoted so much attention to them, that, as far as the female generative organs are concerned, there is no order with which we are better acquainted.

In the Homoptera I have examined Aphrophora spumaria, Coccus hesperidum, and C. persica; Professor Huxley (l. c.) has described a species of Aphis, and Professor Leuckart three or four allied forms. All these present the same type of ovary as the Hemiptera; but the terminal germ-chamber is generally smaller, and the cells contained in it much less numerous, being in fact, in C. hesperidum, only three in number. Indeed in this genus, as there is only one egg in each tube, there is in fact a group of vitelligenous cells to each egg-chamber; and this form of ovary forms an intermediate link between the types found in the Hemiptera and the Hymenoptera.
The latter part of this paper will contain a full account of the formation of the egg in *C. hesperidum*, to which therefore I need not here allude in greater detail.

In *Forficula auricularia* the egg-tubes are short and very numerous; each contains a large egg more or less mature, and two or three small rudimentary ones. The large egg is pear-shaped, and the other two germs, together with the membrane containing them, may not unfitly be compared to the stalk.

The large egg-germs consist of two parts. The posterior part consists of the yelk, and encloses the germinal vesicle; the yelk-mass contains dark granules and small oil-globules. The anterior part is lighter, browner, more homogeneous, and appears to consist of a single large vitelligenous cell. In this anterior portion several vermiform masses may be perceived, but I am unwilling at present to offer any suggestion as to their origin and functions. At first the anterior portion occupies the larger portion of the egg-chamber, but the posterior portion grows both absolutely and relatively larger, until at length it fills almost, or altogether, the whole of the egg-chamber. I believe that I am correct in considering the anterior portion as a yelk-cell, but I was never able to see the nucleus.

The terminal, smaller part of the egg-tube is not represented in Wiedemann's 'Archiv für Zoologie et Zootomie,' Bd. xi. tab. 111; it has, however, been described by Stein*. It consists of two or three egg-germs, each situated in a chamber which is separated from the next by a rather slight constriction, and each consisting of two parts, the posterior or egg-cell, and the anterior or vitelligenous cell. Sometimes, however, there were two vitelligenous cells to each egg-cell. In some of the more advanced of these egg-germs an indistinctly bordered granular nucleus was visible. This small terminal portion of the egg-tube is bent down on to the large egg, so that it might easily be overlooked. At an earlier period in the summer, as for instance in July, the difference of size between the last and penultimate egg-germs is not nearly so decided as it becomes towards the end of August.

M. Léon Dufour also, in his paper on the *Forficulidae†*, has overlooked the small terminal chambers of the egg-tube, which consequently he considers as consisting of only one egg-chamber. In the same paper he describes and figures the ovary of *Labidura gigantea*, which differs in the most remarkable manner from that of *Forficula auricularia*, and consists of five long egg-tubes enclosing twenty, or a lesser number of egg-germs. It is impossible to determine, either from the description or the figure, upon what type the egg-germ is formed, but there is no reason to suppose that the process is different from that which occurs in the small species.

It is very interesting to meet with such an important difference in the ovaries of two species which are in other respects so nearly allied, and to find thus in *Forficula* a type of ovary entirely different either from the Coleoptera on the one hand, or the Orthoptera on the other. If the terminal chamber is really absent, *Labidura gigantea* resembles the latter order rather than the former.

The Neuroptera (with the exception of the Dragon-flies) offer the next step towards the type which prevails in the Lepidoptera, &c. Each egg-chamber is generally divided by a constriction, the posterior portion containing the yolk, germinal vesicle, and germinal cells; and the anterior part enclosing in *Panorpa communis* generally two vitelligenous cells, in *Psocus* three, in one of the *Leptoceridae* four, and in *Chrysopa perla* five or six. Besides being few in number, the vitelligenous cells in the Neuroptera are somewhat indistinct, especially in *Panorpa*, and do not present a well-defined nucleus.

In *Panorpa* also, and in one of the *Leptoceridae*, it seemed to me evident that the whole egg-cell, and not only the germinal vesicle, was equivalent to the vitelligenous cell.

In the Diptera* I have only examined *Cheilosis, Eristalis, Musca*, and the *Tipulidae* and *Culicidae*; nor am I aware of any other observations on the ovary of this order except those of Loew, which I have not been able to obtain, of Leuckart on *Melophagus*, and SOWERDAM on *Stratiomya*, which latter refer rather to the external form than to the histological structure. Probably, however, we shall find in the remainder of the order, as in the forms already examined, that the ovarian tubes are very short and extremely numerous. In a small species of *Cheilosis*, indeed (Plate XVI. fig. 9), there were as many as eight egg-chambers, but in *Musca* and *Eristalis* there are only two or three, and in *Culex* and *Tipula* only one or two.

In all cases, besides the egg-chambers, there is a terminal germ-chamber. The layer of epithelial cells is early and strongly developed, and the constriction between each two egg-chambers is very deep. In many cases, indeed, there is a considerable interval between each two egg-chambers, which gives to the egg-tubes a remarkable and peculiar appearance. There is no constriction between the germ- and yolk-portions of the egg-chamber, but the two together form a round mass, which gradually becomes oval, and finally more or less elongated, according to the shape of the mature egg. The vitelligenous cells are large, polygonal from mutual pressure, and in some cases provided with a distinct nucleus.

It is worthy of observation, that this type of egg-formation is very different from that of *Pulex*, or indeed of any other insects. The external membrane of the egg-tube may generally be seen forming a series of bridges, projecting from one egg-chamber to another. The vitellogenous cell which lies at the posterior end of the egg does not at first differ from the others. Gradually, however, it grows darker, and its nucleus becomes the germinal vesicle. It is, however, only in the two lowest egg-chambers that this, which evidently corresponds to what I have called the egg-cell, becomes much larger than the true vitelligenous cells. At this stage it appears to lose its true cell-wall and to become a mere yolk-mass, which, as the vitelligenous cells gradually disappear, absorbs the yolk-matter supplied by them, and finally occupies the whole egg-chamber.

In the early part of September the ovary of *Eristalis tenax* is a white body, shaped

* Leuckart and Willrich have described a partial segmentation as occurring in the eggs of Diptera; but this is probably a mistake, into which they may have been led by the vitelligenous cells.
like a cucumber. It consists of a large number of egg-tubes, each formed of two chambers, one more or less spherical, and the other a miniature representation of the ovary itself, as far as shape is concerned.

The external membrane is in this species very distinct, and the internal structure of the egg-tube cannot distinctly be seen until it has been removed. It is, however, easily torn off, and the egg-tube will then be generally found attached by the upper part, and with the end next to the spherical chamber floating loose. The part of the egg-tube also below the spherical chamber is very thin, and tapers rapidly to a very delicate filament, while the upper part retains to the end a much more considerable diameter. These facts puzzled me a little at first, and made me doubt for awhile which was the ovarian end of the egg-duct. I soon found, however, that the germinal vesicle was always at the side of the egg-germ which was turned away from the cylindrical chamber; and a specimen occurred in which the lower part of the cylindrical chamber was beginning to separate itself from the remainder, and to form a new egg-germ (Plate XVII. fig. 8). Towards the middle of October, all, or nearly all the egg-tubes were in this stage. The vitelligenous cells contained no distinct nucleus, and varied much in size, some being larger, and others smaller than the egg-cell.

In the Geodephaga and Hydradephaga, Stein has already observed that we find a type of egg-formation differing entirely from that of the other Coleoptera, and closely resembling that of the Hymenoptera, from which indeed it only differs (so far as our knowledge at present extends) in possessing a terminal germ-chamber.

This terminal germ-chamber is, however, less largely developed in the present group than in most other Coleoptera, and in old specimens, indeed, is very much reduced in size.

Plate XVII. fig. 1 represents one of the egg-tubes of Carabus violaceus, magnified thirty times. At the lower or posterior end was a glandular part containing a yellow mass, which Stein, apparently with justice, considers as analogous with the “corpus luteum.” The lowest egg-chamber was very opaque, so that no structure could be perceived in it. In the second or penultimate egg-chamber, and the two following, the constriction separating the germ-chamber from the yolk-chamber is well marked; the three following have a constriction separating them from one another, but the chambers themselves have an entire margin; and still nearer to the end are several egg-germs, which are not sufficiently large to occupy the whole diameter of the egg-tube.

Plate XVIII. fig. 18 represents a germinal vesicle of Pterostichus melanarius. In this specimen the macula germinativa contains five large equal-sized vesicles. I have found other specimens presenting very nearly the same appearance, but it is by no means usual, and was not present in two other germinal vesicles belonging to the same egg-tube. In the smallest of these (Plate XVIII. fig. 18), the germinal vesicle contained two small equal-sized vesicles. In the second (Plate XVIII. fig. 18), the germinal vesicle contained three vesicles, one rather large and the other two smaller.

The vitelligenous cells present nearly the same appearance as in the egg-tube of a
Hymenopterous insect. At first small and round, they become larger in each successive egg-chamber, and are gradually forced to take a polygonal form, by the pressure which they mutually exert upon one another. The nucleus continues round, and is somewhat darker than the surrounding cell. The vitelligenous cells in each chamber are not, however, all of the same size; on the contrary, they vary a good deal in this respect, and those which lie nearest to the egg-germ are larger than those at the anterior extremity.

The yolks themselves are clear, transparent, and contained, in the lower egg-germs of the specimen figured, a cloud of reddish-brown granules just behind the germinal vesicle. In most specimens, however, I found these granules collected all round the germinal vesicle, so as to obscure it very much. The epithelial cells are not much developed in Carabus, perhaps owing to their function being in part fulfilled by the vitelligenous cells.

The macula germinativa, as is I believe the case in all insects, has the form of a round vesicle. In the second chamber of the figure the germinal vesicle was about $\frac{3}{50}$ in diameter, and the macula about $\frac{1}{50}$. In the other egg-germs they became gradually smaller. The macula germinativa seemed to be composed of a number of small oval masses, enclosed apparently by a very delicate membrane. In one case it appeared to me as if the macula was broken up, and these little bodies were floating about loose in the germinal vesicle. Besides the true macula, each germinal vesicle contained a number of smaller vesicles, which seemed to become more numerous in the larger egg-germs. They were none of them, however, nearly so large as the true macula.

In Steropus madidus, also, the germinal vesicle contains some of these small vesicles, which however are not so numerous as in Carabus violaceus. In young egg-germs of Steropus, two or three of the vesicles are at first sometimes of equal, or very nearly equal size. Gradually, however, one of them surpasses the rest, and becomes the macula germinativa. Probably, therefore, these small vesicles are of no great functional importance.

The development of the eggs in the Lepidoptera has attracted the attention of naturalists more than has been the case in any other order. Heroldt, Meyer, Stein, and Leuckart have all given more or less accurate figures and descriptions of these organs. The type is essentially the same as in the Geodephagous beetles, and differs merely in the smaller number of egg-tubes, with a greater number of egg-chambers in each, and in the absence of any terminal chamber.

As in the Geodephaga, the vitelligenous cells are large and polygonal, and each presents a distinct nucleus. The constrictions are deep, but the egg-chambers follow one another immediately, without ever presenting any long narrow portion, as in some Diptera; and the yolks-cell grows much more rapidly than in that order.

In the pseudovaria of Solenobia lichenella the egg-tubes are, according to Leuckart, very short, but otherwise the type of formation is precisely the same as in any of the more normal orders of the group. The mode of egg-formation exemplified in Plate XVIII. fig. 17, except as far as regards the shortness of the tube, is precisely the same as that of any other Lepidopterous insect.

Moreover many instances have been established of unfecundated eggs proving to be
fertile; and as no doubt can exist that these eggs also were capable of fertilization, it seems to follow that they must have been produced in the ordinary manner.

An opinion is prevalent among entomologists in this country, that caterpillars hatched from such eggs as these are weak, and can seldom be reared,—as if the vital force was indeed sufficient to carry the egg up to the point of hatching, but was by that exertion almost exhausted*.

In the Hymenoptera the process of egg-development very much resembles that of the Lepidoptera, but the ovaries differ generally in possessing more numerous egg-tubes, each with a fewer number of egg-germs. They differ from the Diptera, and agree with the Lepidoptera, Geodephaga, Hydradephaga, and most of the Neuroptera, in having each egg-chamber divided transversely into two parts. The vitelligenous cells are generally round, as in most of the Neuroptera; but sometimes they are polygonal, as in the Diptera and other orders possessing alternate groups of these cells. The nucleus of the vitelligenous cells is very indistinct, and can seldom be perceived plainly. In each chamber the vitelligenous cells differ considerably in size, being larger and darker towards the lowest end. The yolk is generally opake, and not nearly so pale and transparent as in some other groups. These circumstances are not favourable to observations on the germinal vesicle, which, however, appears to be in most instances (Plate XVII. figs. 2, 4, 5) a round vesicle, of rather small size in proportion to the size of the egg.

Plate XVII. figs. 2 and 3, represents two egg-tubes of Cynips lignicola, which I shall describe more fully; and I therefore content myself with mentioning here, that the process in this group offers no essential difference, and that there are no peculiarities in the formation of these pseudova, except those which arise from their very peculiar form. It is, however, of course possible, that when we shall have obtained a deeper insight into the mysterious processes of embryonic development, some differences will be detected between these pseudova and ordinary eggs.

The egg-formation in Chelonus oculator is remarkable, but its peculiarities have been much exaggerated by M. Léon Dufour. According to this eminent anatomist, Chelonus possesses neither ovary nor eggs, but instead of them, four matrices containing a great number of living embryos, or perhaps nymphs?. I was naturally very anxious to examine such an extraordinary insect, and by the kindness of Mr. Frederick Smith was enabled to do so.

M. Léon Dufour has correctly described the external form of the generative organs. There are four similar matrices, two on each side, and divided by a transverse constriction into two chambers, the lower chamber being the smaller of the two. The lower ends of the four matrices unite into a very short oviduct. The upper ends are gradually contracted into a narrow egg-tube. There are therefore four egg-tubes altogether; they are of very considerable length, and each pair is closely united together. At the free end they swell into an oblong terminal chamber. M. Léon Dufour has given also an excellent figure of these organs. He denies, however, to these long tubes the name of

* This idea is confirmed by Leuckart, Zur Kenntniss, &c. p. 376, and Herold.
egg-tube, because it is not divided into egg-chambers; but in this they only resemble the egg-tubes of other Hymenoptera, which are quite cylindrical as long as they retain their outer membrane. It is the inner membrane only which is constricted.

Secondly, M. Léon DuFour found in them no eggs; but if he had examined fresh specimens with a powerful glass, he would have found in them a succession of eggs as usual, but more numerous than in most of the Hymenoptera. Each egg is formed on the normal type, and consists of a double chamber, the lower half containing the true yolk, and the upper being full of the vitelligenous cells. It appeared to me that the vitelline membrane was in these eggs developed earlier than usual; for on cutting the lower part of the egg-tubes the eggs came out, and both the germ-chamber and the yolk-chamber appeared to be enclosed in a common membrane (Plate XVIII. figs. 13 to 17). By the time, however, that the eggs had reached the matrix the constriction had disappeared, and they were now cylindrical bodies, slightly larger at one end than the other.

If, however, some of the eggs are removed from the matrix and put in water, one end of the greater number of them will gradually swell until many resemble Plate XVIII. fig. 17. This alteration in shape, however, appears to be due to endosmosis, and I never saw the eggs take any other form. I had forgotten, during my examination of them, that M. Léon DuFour attributed to them "une contractilité spontanée de tissu," and my attention was not specially directed to this point, but I did not notice anything of the sort.

The swollen end of the eggs often showed minute circular marks. I never was able to see the deposition of the eggs, and cannot say therefore that the species is not ovoviviparous. The eggs, however, never showed any distinct traces of an embryo; and having explained away the appearances on which that opinion was founded, I think myself justified in concluding that Chelonus is oviparous like the other Hymenoptera, although the process of egg-formation certainly does offer various peculiarities.

DEVELOPMENT OF PSEUDOVA.

Coccus hesperidum.—The generative organs of Coccus consist of a short egg-canal, which has more or less largely developed colleterial glands, and at its upper end separates into two tubes, each about \(\frac{1}{10}\) th of an inch in length, and constituting the ovaries. The whole surface of these two tubes is covered with egg-tubes in all stages of development, from a mere bud to an almost mature embryo. The ovary passes gradually into the oviduct, or rather the latter can hardly be said to exist as a distinct part of the system.

The spermatheca is a pyriform gland lying between the two ovaries, and connected with them by a duct which is attached to the egg-canal between the two ovaries.

It is correctly described and figured by Dr. Leydig, as it appears under the action of acetic acid, but in water or syrup it is coloured yellow by its contents. These are very minute, strongly refracting, yellow granules or globules, which offer no resemblance whatever to spermatozoa.

This organ is certainly homologous with the spermatheca of other allied species.
No one has yet seen a male of *C. hesperidum*, but this presence of the spermatheca indicates that this sex does occasionally occur. Whether the spermatheca fulfills any other function, as for instance that of a secreting gland, I am unable to assert.

The colleterial glands are very small in *C. hesperidum*, but in *C. persicae* they are very conspicuous. This difference is probably owing to the fact that the egg-shell is much more developed in the latter species than in the former.

The two tubes of which the ovary consists, and which in old specimens occasionally throw off short branches, are by no means homologous with the egg-tubes of other insects, but rather with the uterus, or ovarian cavity into which they fall, and the short egg-chamber is the true homologue of the egg-tube.

In its earliest stage the egg-follicle is a simple projection of the ovarian wall, which becomes gradually pear-shaped, and may then be seen to consist of a structureless outer membrane, a layer of epithelial cells, and three masses bounded by very delicate walls, and each containing a large nucleus (Plate XVIII. figs. 1, 2). These three masses evidently represent the vitelligenous cells of other insects, as LEUCKART* has correctly suggested; but they are often very indistinct, and in some cases were altogether undistinguishable, though acetic acid will generally make them visible. They are very seldom more than three in number; indeed I only found four in one or two specimens, and five once, out of many hundreds which I examined. Sometimes, indeed, only two or even one could be seen; but it is probable that in these instances the cells were not really absent, but were only rendered invisible by their refractive power being nearly the same as that of the surrounding medium. After the egg-tube has attained to a certain size the boundaries of these cells disappear, as seems to be sometimes the case in Hymenoptera and other insects, and the nuclei only remain visible. Each nucleus often contains a solid-looking, irregular, greenish body or nucleolus.

I am inclined to believe that these cells are originally the same as those constituting the epithelial layer, but on this point it is difficult to form a decided opinion. Their nucleolus is certainly very different, and under the action of water they become cloudy, whilst the epithelial cells remain perfectly clear.

The epithelial cells line the structureless membrane forming the outer covering of the egg-follicle. As in other insects, they are columnar in the lower egg-chamber, and very much flattened in the upper. They contain a distinct circular nucleus, whose tissue differs but little from that of the cell itself, so that they cannot be seen unless they are exactly in focus. Plate XVIII. fig. 1 represents the earliest follicle in which I have seen them; I did not not notice in this case the nuclei, but have no reason to doubt their presence. They differ very much in size in different specimens, though tolerably equal in each, except that they are generally larger in the upper chamber than in the lower. Water causes not only the epithelial cells, but also the whole upper chamber to swell considerably. They are originally round, or rather somewhat polygonal from mutual pressure, but as the follicle grows they are laterally distended so as to become

fusiform. At this period also they contain numerous very small greenish granules (Plate XVIII. fig. 6), which have probably been secreted by the inner surface of their walls; and as these granules cannot be distinguished from the smallest oil-globules, I presume that these also are secreted by the epithelial cells.

The columnar epithelial cells of the lower chamber are almost always visible, but the flatter ones lining the upper chamber can seldom be seen unless the specimen is put in water.

The germinal vesicle very soon makes its appearance, but it is very curious that though it is (when seen at all) very distinct indeed, yet in many instances in which I should have expected to see it, it could not be discerned. Compare for instance Plate XVIII. figs. 3 and 4; in the latter the germinal vesicle and its nucleus are quite plain, while in the former, which was taken from the same animal, was in the field of view at the same time, and is in other respects rather more developed, not a trace of germinal vesicle could be seen.

We are therefore compelled to believe, either that the germinal vesicle is in some instances absent, which is extremely improbable, or that the time of its appearance varies considerably. Of course I do not rest this conclusion upon the examination of this one specimen only, but from the comparison of a great many. In the youngest specimen in which I ever found the germinal vesicle, the egg-follicle was pyriform, .0032 in its greatest diameter, and about .0058 in length. The germinal vesicle was .0008 in diameter. It varies very little in different specimens either in appearance or size, the largest being .0009 and the smallest .0006; neither do these differences appear to have any reference to the state of maturity of the egg-follicle.

In the former part of my paper it has been mentioned that the vitelligenous cells and the egg-cell appear in insects generally to be modifications of the epithelial cells. The same is probably the case in Coccus; but in spite of my anxiety to throw light on this part of my subject, I was unable to do so. In one specimen, however, a few of the cells in the lower part of the upper chamber were larger than usual, and had a more distinct nucleus. The uppermost of these cells had very much the appearance of the germinal vesicle. If, however, this change takes place rapidly, there are evidently so many chances against our detecting the transitional forms, that it seemed desirable to record anything which may possibly be a link in the chain of evidence.

I did not find in Coccus any distinct membranous envelope surrounding the germinal vesicle, and it is therefore probably very soon absorbed, as in the Orthoptera and many other insects.

The later history of the germinal vesicle is equally obscure, for it soon disappears from view. At first I thought it was hidden by the oil-globules; but this can hardly be the case, because I never once succeeded in making the germinal vesicle visible by pressure when I could not see it otherwise. The largest specimen of the germinal vesicle I ever saw was very faint as it was disappearing, and I never saw two cells which could have resulted from the division of the germinal vesicle. Professor Leydig pro-
bably failed to perceive the germinal vesicle, because he generally examined his specimens in a weak solution of acetic acid, which causes it to swell and then disappear in a few moments.

At about the same time as the germinal vesicle, the oil-globules make their appearance, and soon become the most conspicuous part of the egg. They are at first very minute, but in a mature egg the larger ones are as much as 0.0016 in diameter, from which to a mere granule every intermediate stage may be found. These globules are of a yellowish colour, and refract light, like the oil-globules in milk. They are also affected in a similar manner by acetic acid and sulphuric ether, being dissolved and running into one another if subjected to the latter; while in the former they split at the edges, as in Plate XVI. fig. 7, and finally become marked by irregular fine lines, some of which also seem to project from the side. Neither oxalic nor tartaric acid have much effect on the oil-globules.

The epithelial cells contain almost always several yellowish-green minute globules, which appear to me to agree in every respect, except in size, with the oil-globules; and it seems to me probable therefore that these are partly secreted by that side of the epithelial cells which is turned towards the inside of the egg-follicle.

It is evidently very difficult to obtain any decisive proof upon this point, and it might rather perhaps be concluded, from the descriptions and figures of M. de Quatrefages*, that the oil-globules are secreted by the germinal vesicle. I have, however, never found that they are particularly collected round the germinal vesicle, which, moreover, is sometimes apparently absent after the formation of oil-globules has commenced (Plate XVIII. fig. 3). The oil-globules may often be seen lying somewhat compressed together (so as to have one or more straight sides), without running together, which indicates, I think, that the outer surface is covered by a somewhat harder pellicle or skin, though the effect of sulphuric ether shows, if any proof was wanting, that they are not covered by any distinct membrane.

Very soon after the appearance of the first oil-globules, the basal part of the egg-follicle begins to swell up, and to be separated from the upper part by a gradually deepening constriction, so that the egg-follicle comes, as described by MM. Leydig and Leuckart, to consist of two chambers, the upper one of which is spherical, and the lower fusiform. The upper chamber, though short, is at first much broader than the lower, and contains the three vitelligenous cells (e); the lower chamber contains the oil-globules, and the germinal vesicle is situated at the apical end of the lower chamber.

Besides the oil-globules, the lower chamber contains also some few small yolk-cells and immense numbers of very small greenish granules, resembling in many respects very minute oil-globules; and I am not, as already stated, inclined to believe that these latter are produced by the coalescence of the minute green globules.

The egg-follicle continues to grow, and the germinal vesicle remains visible for some time, the largest specimen in which I have seen it being Plate XVIII. fig. 5.

According to Dr. Leydig, the constriction separating the two chambers begins after a while to become less marked, and finally disappears, the egg itself being formed in and filling both chambers, so that the contents of the upper chamber occupy the apical end of the egg, and form the commencement of the blastoderm. In this I have no doubt he is mistaken, and that M. Leuckart's account is correct, although I too have seen some instances which might account for his mistake. These, however, are quite exceptional; and as a general rule, after the constriction is formed, the upper chamber ceases to grow larger; and as, on the contrary, the lower one continues to expand, it forms gradually a larger and larger fraction of the whole. After remaining of the same size for some time, during which the lower part has considerably increased, the upper chamber begins to diminish, and finally becomes atrophied.

According to Dr. Leydig, if I understand him right, the three vitelligenous cells, which he considers as germinal vesicles, divide and subdivide, carrying with them each time a portion of periplast, so that when the reunion of the two chambers takes place, the apical portion contains a number of nucleated cells, which together constitute the blastoderm.

This description is entirely erroneous, as M. Leuckart also has mentioned. Plate XVIII. fig. 7 shows a nearly full-grown egg, in the upper chamber of which the three vitelligenous cells (e), larger indeed than at first, but otherwise unaltered, are plainly visible. This is no solitary instance, but is, on the contrary, the usual process. Moreover, if several large egg-follicles are placed in water, it will probably happen that the upper chamber of one, at least, will burst, and one or more of the vitelligenous cells will be pressed out. They then present a cloudy appearance, but no orifice could ever be seen in them.

After having fulfilled their functions, and when the upper chamber is becoming atrophied, the vitelligenous cells sometimes break up into small irregular balls, which become smaller and smaller, and finally disappear.

The general cavity of the body of the female Coccus contains an immense number of oval green cells, which are apparently of vegetable nature. They are about $\frac{1}{5000}$ in breadth and $\frac{3}{8000}$ in length. Some specimens, however, are considerably longer, and present a constriction in the middle; these are evidently undergoing transverse division. I have also found similar cells in the larvae at various ages, as at the beginning of June and July.

Almost always at the period when the vitelligenous cells have disappeared, and sometimes earlier, a mass of these oval green cells may be found at the lower part of the upper chamber. As the upper chamber becomes atrophied, they find their way down to the front of the egg. Thus we may say, almost without a metaphor, that the germs of future disease can be detected even in the unlayed egg*. I have scarcely ever found

* Entozoa have been found in foetus, but not, so far as I know, in an egg which would have hatched properly. See Allen Thomson's article 'Ovum,' in Todd's Cyclopaedia, p. 12. It is true that M. Nordmann has described certain parasites as being produced from the yolk of Terebripes, without arresting the development of the embryo. M. Voor, however, considers, with reason, that the supposed parasites are only detached cells, and not independent animals.
these oval green cells in a specimen which still contained the three vitelligenous cells unaltered, but believe that I have done so in a few instances.

These parasitic cells are present in such great numbers in the full-grown female, that there is no difficulty in accounting for the entry of some of them into the egg; but it is difficult to understand why they do not appear in other parts of the egg-follicle, and why they increase so rapidly at a particular period in the development of the egg.

Weak solutions of oxalic acid, of tartaric acid, and of sulphuric ether produced no effect upon these cells.

The mature egg, besides the oil-globules and the surrounding fluid, contains also numerous vitelline spherules, which have every appearance of being true cells, but that they contain no nucleus.

I have sometimes found a few of these spherules (or others very nearly resembling them) in egg-tubes which had not yet lost their pyriform shape; but as a general rule, even in specimens as far advanced as Plate XVIII. fig. 6, few, if any, could be perceived. Soon, however, after the germinal vesicle ceases to be visible they make their appearance, and rapidly increase in numbers, apparently at the expense of the oil-globules and surrounding fluid.

At an early period they are small, not exceeding \( \frac{3}{8000} \) in diameter, but in more mature ova they vary from \( \frac{9}{8000} \) to \( \frac{7}{8000} \).

Weak solutions of acetic or tartaric acid dissolved the yolk-cells, or at least rendered them invisible, and left instead a flocculent mass.

In the greenish eggs of Phryganea, as described by Zaddach, the colour is owing to the yolkglobules themselves. In Coccus this is not the case. The yolkglobules are slightly yellow, and the green hue of the eggs is at first owing to the green granules, which I have already mentioned as being perhaps only very minute oil-globules. When, however, the egg is full-grown, and the upper chamber has been absorbed, these green granules will be found to be replaced by dark-green globules, regular in size, and about \( \frac{5}{8000} \) in diameter, and which appear, therefore, to be in no way represented in the yolk of Phryganea eggs.

The vitelline membrane is formed so gradually that it is difficult to ascertain the exact time of its formation; when, however, the egg is full-grown, it may clearly be seen to be enclosed by this membrane, which is firm in texture, quite colourless, and shows no structure.

I could see no trace of micropyle, which under the circumstances is quite natural.

The mature egg is a light green, oval mass, \( \frac{28}{2000} \) in length and \( \frac{18}{2000} \) in breadth. It is enclosed in an outer structureless membrane, probably the vitelline membrane, but, like Stein*, I never could find a trace of a second, though the eggs of most insects are generally said to have double covering.

Since these eggs are hatched almost immediately after leaving the body of the mother, it is evident that they do not require so thick a shell as those which are deposited in

* Loc. cit. p. 66.
water or in the open air, and this may perhaps account for the small size of the colleterial glands.

At this period the egg-contents consist of yellowish oil-globules, colourless yelk-cells, a small quantity of fluid, the green globules which give the egg its colour, and the parasitic, oval green cells, which are congregated near the cephalic end.

Dr. Leydig describes the first trace of the embryo as arising at the free end of the egg, and then extending with a waved course as a clear streak across the egg. It seems to me, however, that the first trace of embryo is at the basal end of the egg, and I think that he has been led into error by supposing that this embryonic structure arises immediately from the division of the vitelligenous cells (e), which we have already seen is not the case. Professor Leuckart also asserts that the thickening of the blastoderm commences at the hinder pole*.

The remainder of the egg consists, as before, of oil-globules, yelk-globules, and green globules, which latter, however, are more numerous round the embryo than elsewhere.

Gradually, however, the yelk-cells become smaller, tolerably equal in size; and as the embryo continues to enlarge, they diminish greatly, being no doubt changed in some manner into the nucleated cellular tissue of which it consists. At the time when the antennae make their appearance the yelk-cells have almost entirely disappeared.

At this period the tissue of the embryo consists of minute cells about $\frac{1}{400}$ in diameter, and each containing a bright central spot. When pressed out into water they often lose their distinctness, and sometimes they seem to change into green bodies, apparently somewhat cubic in shape, and separated a little from one another by a colourless, structureless substance. What conditions are necessary to this change I was unable to determine.

The small cells constituting the embryo at a very early period, when subjected to a weak solution of either tartaric or oxalic acid, took a variety of forms, more or less oval, and pointed at the narrow end. Their contents became granular. Acetic acid made the cell-wall less distinct and the contents opake, as if coagulated.

Thus we see that the different bodies, which are either contained in the egg, or have contributed to its formation, are by no means few in number. We have, first, the structureless external membrane of the egg-follicle; secondly, the cells forming the epithelium; thirdly, their nuclei; fourthly, the vitelligenous cells; then the germinal vesicle with its nucleus, the oil-globules, the periplast, in which the three last substances are contained, the yelk-cells, the parasitic vegetable cells, the green globules, the blastodermic cells and their nuclei, and, finally, the vitelline membrane.

Up to this period, and indeed until the different appendages of the embryo have become quite distinct, the egg has not altered its position, but still remains in the follicle in which it was formed; and its head, as usual in insects, is always furthest from the vulva, or rather is at the free end of the follicle.

* Fortpflanzung und Entwicklung der Pupiparen. Halle, 1858, p. 69.
Coccus Persicae.—On the 22nd of May I found in our garden some specimens of C. persicae, which I was much surprised to find is oviparous and not nearly ovoviviparous, like C. hesperidum. The females were, at the period in question, rapidly approaching the term of their existence, and most of them had already laid many eggs. These latter are developed almost in a similar manner to those of the preceding species, with however some interesting differences.

The form of the ovaries and arrangement of the egg-tubes is very nearly the same in both species. The spermatheca of C. persicae, however, is less firm, and is pale in colour. The colleterial glands, which, probably in consequence of that species being ovoviviparous, have become small and inconspicuous, are in the Peach-coccus large and pedunculated.

They are six in number, four large and two small, these latter being apparently attached by a short stalk to the peduncle of the large one, which is furthest from the vulva. They lie three on each side, and their ducts open into the egg-canal close together, and about half-way between the vulva, and the division of the egg-canal into two oviducts.

The internal structure is very distinct and interesting. It consists of many cells lying loose in the internal cavity, and resembling very much in form, size, and appearance the vitelligenous cells of the egg-follicle. Indeed, if one of these bodies was lying free from its attachments, I believe it would be quite impossible to decide whether it belonged to these colleterial glands or had come from an egg-follicle. I counted about six in the smaller glands, and from twenty-five to thirty in each of the large ones; they were nearly the same size in all the glands.

As might be expected, several specimens did not show this structure, but in others it was very distinct. In one specimen the glandular bodies were more numerous and smaller. In this case, however, they varied considerably in size.

The egg-follicle is tougher, and the epithelian layer is more distinct than in the preceding species. The number of vitelligenous cells is greater, varying between five and eight in each chamber, and they are also more distinct and rounder.

As might be expected, their number does not depend upon the age of the follicle. I have seen a very young one with seven cells, and have often found old ones with only five. The size sometimes varies considerably in the same follicle, and did not appear to depend upon the stage of growth.

The nucleus of the cells could almost always be distinguished. It consists of an irregularly-shaped body of a greenish colour, and presents often projections which appear to be undergoing a process of separation. Sometimes this appears to have taken place, and we find then two to four smaller and more regular nuclei.

They never contained granulations, like those described by Huxley, in the corresponding cells of Aphis.

They appear finally to break up and to be absorbed, exactly as has been already described; but it is difficult to prove this satisfactorily, as in large follicles their cell-wall becomes very indistinct.
In the early stages of egg-development there appear to be fewer oil-globules than in C. hesperidum, but more numerous granules. These latter are about $\frac{1}{16,000}$ in diameter, and are congregated principally round the germinal vesicle. They disappear if subjected to the action of tartaric acid.

The germinal vesicle is small, but it is so much covered by the granules that I never could obtain a satisfactory view of it, and still less of the nucleus. It is, however, smaller than the vitelligenous cells.

The production of the parasitic green cells occurs in the same manner and position as in C. hesperidum. Instead of being oval, however, they are shaped like a sausage. They are $\frac{3}{6000}$ in length by about $\frac{1}{7000}$ in breadth. They are, however, multiplied by division, and consequently vary in size as much as the corresponding parasite of C. hesperidum; and in one specimen I found them much longer than usual.

In an egg almost full-grown the contents were of two sorts; first, oil-globules from $\frac{3}{6000}$ to $\frac{1}{6000}$ in diameter, and of a whitish colour; and, secondly, small globules $\frac{1}{8000}$ to $\frac{1}{16,000}$ in diameter. These latter are rendered invisible by tartaric acid. The eggs when laid are of a brilliant white colour, $\frac{13}{1000}$ in length, and $\frac{7}{1000}$ in breadth. They generally showed the commencement of the blastodermic layer, and in some this had even extended quite across the egg.

The oil-globules are by far the most conspicuous part of the egg-contents; the remainder appears to consist of a periplastic substance.

The small granules, which at an earlier period were very numerous, have almost disappeared; and the yolk-globules, which are so conspicuous in C. hesperidum, were in the present species very few and of a small size.

The outer surface of the egg-shell is covered by minute rings, of which the ends somewhat overlap. These rings are from $\frac{3}{6000}$ to $\frac{1}{4000}$ in diameter, and are no doubt identical with the white substance which exudes from pores on the underside of the body. Immersion in spirits of wine for thirty-six hours had no apparent effect on them. I also placed them in dilute sulphuric acid for two hours and a half with the same result.

In June the females covered a number of eggs, besides those which were not yet deposited. I examined a good many of the former, and found that each contained an embryo consisting of a waved line of small nucleated cells, extending from one end of the egg to the other*.

Cynips lignicola.—Although the gall insects are so common and so numerous, the female sex only has yet been found, so that the males are probably only produced at distant intervals. Except, however, in so far as the peculiar shape of the egg is concerned, the mode of egg-formation does not differ from that which occurs in other Hymenoptera.

The ovary consists of a great number of tubes, which form a verticillated bunch, and fall into a common oviduct. Each tube contains about thirteen eggs (figs. 2 and 3); in the earliest stages there is absolutely nothing to distinguish the egg-formation in this

* Leydig, loc. cit. pl. 1. fig. 4 i.
species from the type common in insects. A glance at the figures is sufficient to show this, so that it is unnecessary to enter into any detailed description.

Each of the pseudova, even after it has attained its full length, is surrounded by a distinct layer of nucleated cells. The walls of the tube appear to be constituted by a delicate, structureless membrane, so that I suppose it is the epithelial layer (consisting of nucleated cells) which has in some places detached itself from the outer membrane in order to form a close covering for the eggs. After the egg has arrived at maturity, this cellular layer gradually disappears.

At the lower end, in Plate XVII. fig. 2, one of the eggs is elongating and pushing its narrow end up the tube. This process appears to be somewhat rapid, at least there is always at this stage a considerable difference between the form of the lowest egg and that of the one immediately preceding it.

The egg gradually becomes longer and longer, the narrow end at the same time forcing itself up the tube; and the other eggs successively undergo the same changes, until at length the ovarian tube offers the appearance represented in fig. 3, Plate XVII. The narrow ends now all lie at the upper end of the tube, and the swollen ends at the lower.

The germinal vesicle is present, as usual in insects, but it remains visible longer than I have found to be the case in most other species, and indeed may be seen after the pseudovum has attained its mature form.

The development of the pseudova of *Solenobia lichenella* appears also to offer no great peculiarities. Plate XVIII. fig. 17, copied from Leuckart, represents one of the egg-tubes taken from a caterpillar of *S. lichenella*, and it resembles, in all important particulars, a similar organ of any other Lepidopterous insect. The epithelial cells, the large vitiligious cells with their nuclei, and the egg-cell itself, with its germinal vesicle, are all of the usual structure, and arranged in the ordinary manner.

Many other Lepidoptera have presented us with individual instances of parthenogenesis, in which the eggs, though fertile without impregnation, were no doubt identical with the true ova, and would have been impregnated under ordinary circumstances*.

In the Hive-bee, also, the ovarian development of the ova and pseudova must apparently be identical, since it would appear that in normal instances, it is not decided until after the ovarian product has entered the oviduct, whether it is to be an ovum or a pseudovum, in other words, whether it is to be impregnated or not.

At the same time the sex of the future animal is determined, since, according to MM. Leuckart and Siebold, eggs always in this species produce females, and pseudova give birth to males.

We are then, I think, justified in asserting that in the present state of our knowledge no difference can be pointed out between the ovarian development of the pseudovum in insects and that of the true ovum.

DESCRIPTION OF THE PLATES.

PLATE XVI.

Fig. 1. Egg-tube of *Blatta orientalis*. ×30.
Fig. 2. Egg-tube of *Æschna cyanea*. ×60.
Fig. 3. Egg-tube of *Pulex irritans*. ×60.
Fig. 4. Egg-tube of *Telephorus*. ×60.
Fig. 5. Egg-tube of *Forficula auricularia*. ×60.
Fig. 6. Terminal portion of *Forficula auricularia*. ×250.
Fig. 7. Egg-tube of *Psocus*. ×250.
Fig. 8. Egg-tube of *Panorpa communis*. ×60.
Fig. 9. Egg-tube of *Cheiloscia*. ×60.
Fig. 10. Part of egg-tube of *Nepa*, to show the yolk-ducts. ×80.

PLATE XVII.

Fig. 1. Egg-tube of *Carabus violaceus*. ×30.
Fig. 2. Egg-tube of *Cynips lignicola*. ×60.
Fig. 3. Egg-tube of *Cynips lignicola*. ×60, in a more advanced state.
Fig. 4. Egg of *Cynips lignicola*. ×60.
Fig. 5. Egg-tube of *Odynerus*. ×60.
Fig. 6. Egg-tubes of *Ophion luteum*. ×30.
Fig. 7. Egg-tubes of *Nepa cinerea*. ×60.
Fig. 8. Egg-tubes of *Eristalis tenax*. ×250.
Fig. 9. End of egg of *Cynips lignicola*. ×120.

PLATE XVIII.

Fig. 1. Very young egg-tube of *Coccus hesperidum*, showing epithelial cells. ×250.
Fig. 2. Very young egg-tube of *Coccus hesperidum*, showing vitelligenous cells. ×250.
Fig. 3. Egg-tube of *Coccus hesperidum*. ×250.
Fig. 4. Egg-tube of *Coccus hesperidum*. ×250.
Fig. 5. Egg-tube of *Coccus hesperidum*. ×250. More advanced.
Fig. 6. Egg-tube of *Coccus hesperidum*. ×250. More advanced.
Fig. 7. Egg-tube of *Coccus hesperidum*. ×250. More advanced.
Fig. 8. Egg-tube of *Coccus hesperidum*. ×250. More advanced.
Fig. 9. Egg-tube of *Coccus hesperidum*. ×250. More advanced.
Fig. 10. Egg-tube of *Coccus hesperidum*. ×250. More advanced.
Fig. 11. Egg-tube of *C. persicae*. ×250.
Fig. 12. Very young tube of *C. persicae*. 
Fig. 13. Egg of *Chelonus oculator*, from the lower part of the egg-tube. ×60.
Fig. 14. Egg of *Chelonus oculator*, from the matrix of the egg-tube. ×60.
Fig. 15. Egg of *Chelonus oculator*, from the matrix under the action of water. ×60.
Fig. 16. Egg of *Chelonus oculator*, from the matrix under the action of water. ×60.
Fig. 17. Egg-tube of *Solenobia lichenella*. After Leuckart.
Fig. 18. Three germinal vesicles of *Pterostichus melanarius*, from three successive egg-cells. ×250.

The letters refer to the same parts in all the Plates.

*m*. Muscular or outer membrane.
*i*. Inner membrane.
*a*. Epithelial cells.
*b*. Nucleus of epithelial cells.
*e*. Egg-chamber, often divided into
*y*. Yolk-chamber.
*z*. Germ-chamber.
*t*. Terminal chamber of egg-tube.
*f*. Terminal filament of egg-tube.

*v*. Vitelligenous cell.
*u*. Nucleus of vitelligenous cell.
*s*. Egg-cell.
*g*. Germinal vesicle.
*h*. Macula germinativa.
*o*. Oil-globules.
*p*. Parasitic cells.
*d*. Yolk-duct.