

and *Alaurinæ* are to be regarded merely as families of the Rhabdocœla, a view which has already been expressed by Leuckart, at least with regard to the former. The peculiarities of the sexual organs and fission can no longer be accepted as ordinal characters, since we have become acquainted with the proliferous *Catenula* and the Rhabdocœla with the sexes separate.

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XII.—*On the Reproduction and Embryogeny of the Aphides.*

By M. BALBIANI\*.

OF the questions relating to the generation of animals, one of those which are still most open to discussion is that of the mode of propagation of the viviparous Aphides. According to the ideas which observers have formed of the nature of the reproductive organs of these insects, their multiplication has been referred sometimes to the phenomena of alternate generations, sometimes to those of parthenogenesis or virgin-generation. As to the opinion which consists in assuming an androgynous condition in these animals, which is still maintained by some authors, as well as by Leeuwenhoek, Cestoni, and Réaumur, it rests upon a mere hypothesis which has not yet received its material demonstration by the detection of the male element in the viviparous Aphides.

It is this last view that I propose to defend here by bringing forward the positive proof for which science has waited since the time of the illustrious observers who first pronounced in favour of the hermaphroditism of these creatures. I propose, in fact, to show that this state is the normal condition of the Aphides throughout the viviparous period of their existence, and I shall also show in what manner the separation of the sexes is effected in them, when, under the influence of certain determinate conditions, their mode of reproduction reverts to the law common to the generality of species of animals.

The evolution and physiological function of the generative organs commencing at a very slightly advanced period of the embryonic life of these insects, and their history being, so to speak, inseparable from that of the development of the ovum itself, I shall have to trace faithfully, though concisely, the principal phases of this development. It is by following this course in my observations that I have succeeded in coming to an understanding of this question which has been so long in debate. This investigation will also, as we shall see, reveal some remarkable facts which I regard as of high interest with respect to the origin of the male and female generative elements,

\* Translated from the 'Comptes Rendus,' June 4, 1866, pp. 1231-1234.

and their relations to the rest of the organism. But, in the first place, it is necessary to give an idea of the structure presented, according to my observations, by the organ in which the embryo originates—that is to say, the female sexual apparatus or ovary of the viviparous Aphides.

This apparatus consists, as in most other insects, of a variable number of tubes or sheaths, each of which is dilated at its anterior extremity into a terminal cell or chamber containing a group of small cells. One of these occupies the centre of the group and is entirely surrounded by the others. This central cell is the most important of all; for it represents the generative element or the mother cell of all the ovules in each sheath which are destined to become converted into embryos. These ovules originate in the form of true buds, which, separating successively from the central cell, appear at the bottom of the terminal chamber before passing into the upper part of the sheath. The peripheral cells, attached to the former by hollow pedicles, are its nutritive cells, its sole function being to emit incessantly new ovular buds.

At the moment when the ovule penetrates into the ovarian sheath, it clearly presents a germinal vesicle and spot. A delicate filament still attaches it for a time to the mother cell; but this union is soon broken, and the ovule remains completely isolated in its chamber. It is generally at this moment that the modifications which are to lead to the formation of the embryo commence in the ovum. The germinal spot first disappears, and is soon followed by the vesicle which contained it. During this period some nuclei, at first rare, have made their appearance on the surface of the vitellus, and condensed around them the transparent homogeneous substance of which it is composed. By this means are formed the first blastodermic cells. No membrane as yet surrounds them. The rather wide intervals separating them at first are quickly filled up by the appearance of new nuclei and cells. The ovule is thus finally clothed over the whole of its surface by a continuous layer of cells arranged in a single series and pressed against each other. At this period they all present a very recognizable proper envelope.

While the blastoderm has thus been completing its formation, the ovum has increased in size and passed from a spherical form to that of an elongated oval; at the same time it has descended a little in the interior of the ovarian sheath. The central vitelline mass enclosed in the cavity of the blastoderm has lost its homogeneous aspect and become penetrated by fine colourless granulations. Soon afterwards an orifice is formed at the posterior pole of the blastoderm\*, in consequence of the separation at

\* I give the name of posterior pole of the blastoderm or ovum to the

this point of the cells composing it; and the internal granular mass projects through this orifice. We then clearly perceive, either directly or by means of reagents, that the whole inner surface of the blastoderm is lined with a delicate membrane which extends like an envelope round the central vitelline mass.

It is this membrane, with a portion of its contents, that projects, as just stated, through the orifice at the posterior extremity of the blastoderm. This hernial portion attaches itself to the corresponding epithelial cells of the ovarian chamber, which are hypertrophied, and becomes as it were engrafted upon them. When this connexion is established, the vitelline vesicle becomes constricted in the interior of the cavity of the blastoderm like a cell in process of division, and then separates into two juxtaposed secondary cells,—the posterior adherent to the epithelium of the chamber, the other, or anterior, being completely free in the above-mentioned cavity. I have sometimes succeeded in detecting a very pale granular nucleus in the posterior vesicle, and less distinctly in the anterior one; they, therefore, present all the characters of true cells. These vesicles or cells are to be the origin of the male and female generative elements of the future animal—that is to say, of the ova on the one hand, and the spermatic cells on the other. In fact, by a phenomenon of germination which I cannot describe here in detail, each of them becomes covered at its surface by a generation of small cells, which, when once produced, increase in size and continue to multiply on their own account. From this results the formation of two very distinct cellular groups placed side by side in the cavity of the blastoderm. The group produced by the herniated vesicle engrafted upon the exterior epithelium represents the male element, and will give origin to the fecundating corpuscles; that which originates from the free vesicle in the interior of the ovum is, on the contrary, formed by the totality of the female elements—that is to say, the generative cells of the future ovules, surrounded by their nutritive cells. This latter group soon subdivides into a certain number of secondary groups, corresponding with that of the ovarian sheaths which are subsequently to be formed. The cells which compose it remain always transparent and colourless, and are also smaller than those of the first group, the cells of which, on the other hand, are soon permeated by numerous small green or yellow granulations, which enable them to be recognized with the greatest facility\*. The generative vesicles of the two sexual masses be-

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extremity which is directed towards the external sexual orifice, and that of anterior pole to that which looks towards the terminal chamber of the ovarian sheath.

\* This yellow or green mass, which is met with in most Aphides at all

have in a very different manner in the sequel of the development: that which has given origin to the female elements disappears immediately afterwards, whilst the vesicle which has generated the male or spermatic elements, far from disappearing, continues its development, often becomes very large, and after forming connexions with the female generative apparatus, constitutes a reservoir for the fecundative corpuscles—becoming, in fact, a true seminal vesicle for this hermaphrodite apparatus.

When the curious phenomena just described summarily have terminated, the embryonic development, properly so-called, has not yet commenced. We may, indeed, observe that the cells of the blastoderm have multiplied at the anterior pole so as to produce a very considerable thickening there; but this modification is not followed by the formation of any new part. This thicker layer, in fact, soon gradually diminishes, and is at last entirely effaced\*.

### XIII.—On the Reproduction and Embryogeny of the Aphides.

By M. BALBIANI. (Second Note.)†

IN the viviparous *Aphides* the blastoderm assists to a certain extent in the formation of the embryo, but its part is exclusively limited to the production of the laminae which complete the cephalic extremity in front. All the rest, on the contrary, results from an entirely new part superadded to the blastoderm.

The first phenomenon which denotes the commencement of embryonic development is a budding forth of cells upon one of the halves of the circumference of the aperture (of which I have already indicated the purpose and mode of formation) at the posterior pole of the blastoderm. The result of this budding is the production of a cellular lamina, which gradually rises from the margin of the preceding aperture into the interior of the ovum, folding back against the inner wall of the blastoderm, which it appears in some degree to double for a certain extent. When arrived within a short distance of the anterior pole, it folds inwards, inversely to its former direction, as if to descend again towards the aperture which was its point of departure, but without passing, at least at this time, the middle of the ascending

periods of embryonic development and even after birth, has been described sometimes as serving for the nutrition of the embryo (*pseudo-vitellus* of Huxley), sometimes as a plastic mass destined for the formation of the vegetative organs (Leydig).

\* This transitory production of the blastoderm of the Aphides is probably the analogue of the "primitive cumulus" described by Claparède as preceding the formation of the embryonal rudiment in the ova of the Spiders.

† Translated from the 'Comptes Rendus,' June 11th, 1866, pp. 1285-1289.



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