

Embryology. — *On lens-induction*. By M. W. WOERDEMAN.

(Communicated at the meeting of March 25, 1939.)

On a previous occasion I communicated the results of an investigation into the inducing capacity of the eye vesicle in *Axolotl* embryos (see Proc. Kon. Ned. Akad. v. Wetensch., Vol. XLI, 4, 336, 1938).

Eye vesicles of different ages were grafted into the abdominal wall and covered with ectoderm, likewise of varying age. The eye vesicles proved to be able to induce not only lenses but also nasal pits and ear vesicles.

By this time I can communicate that experiments on embryos of *Triton taeniatus* yielded similar results.

A number of supplementary observations, however, made it necessary to pay special attention to the induction of lenses.

As a rule this is conceived as follows: During embryonic development the eye vesicle (presumptive retina) comes into contact with the ectoderm of the head and there induces a cell proliferation which is transformed into a vesicle (lens vesicle) and then separates from the ectoderm. The wall of the vesicle, in touch with the presumptive retina (I will call it "inner wall"), displays a differentiation of the cells into lens fibres, the wall turned towards the ectoderm ("outer wall") producing the lens epithelium. The formation of lens fibres is likewise based upon an inducing activity of the retina.

In my experimental embryos now I found not only lenses normally situated in the pupil of the grafted eye cup but also some which without contact with the eye lay rather far away from the graft or were in touch with the pigment layer of the retina (tapetum). Moreover, I observed embryos containing a large number of lenses in the neighbourhood of the grafted eye vesicle, some of which were more highly differentiated, others less so.

Frequently I found the grafted eyes in an abnormal position, e.g. with the pupil turned inside, while they had all been grafted with the pupil on the outside.

Further I often found a lens in the pupil, situated far from the ectoderm, which gave the impression that the eye vesicle had induced a lens out of other material than the epidermis of the head. As a matter of course, such abnormal positions occur frequently on grafting the eye vesicle into the blastocoele, which operation I performed a number of times as well (see the above-mentioned report in the Proceedings).

In the literature similar observations have been published, while conclusions were drawn which I consider not entirely proved.

In order to be able to judge these conclusions, I have considered how the lens rudiment will react when sooner or later in its development the contact with the eye vesicle is broken.

For various reasons the experiments were first made on embryos of *Rana esculenta*.

As starting-point were taken the stages with beginning tail bud formation. They were chosen in such a way that the lens anlage of the experimental embryo had not yet been formed into a vesicle. I might now have extirpated the eye rudiment and left the lens proliferation where it was, as some workers did, but in order to eliminate the influence of neighbouring head organs, which a priori may not be excluded (OKADA and MIKAMI, DRAGOMIROV 1929, FILATOW 1925, IKEDA, HOLTFRETER), I chose another technique. The lens proliferation was extirpated and grafted under the ectoderm of the abdomen. Lens proliferations were also cultivated *in vitro*, but this method yielded less satisfactory results.

Five or six days after the operation the experimental embryos were killed and examined microscopically.

It became evident that very young lens proliferations had not developed further than to the vesicular stage and showed no or hardly any lens fibre formation. Slightly older lens proliferations had developed into lens vesicles with fibres, but the fibre formation was neither regular nor extensive. In some cases fibres developed from the original inner wall of the lens vesicle, in spite of the fact that against the outer wall a fragment of retinal tissue was situated which had been grafted at the same time.

Consequently I obtained the impression that the formation of a vesicle and of fibres during the development of the lens may take place without contact with the presumptive retina, i.e. that these processes are induced already in an early stage of development and that only a short contact of eye vesicle and ectoderm is needed.

For a satisfactory development of the fibres, however, apparently a longer contact or a constant influence of the retina is necessary (see also PERRI, 1934).

This is in contradiction with the opinion of SPEMANN that in *Rana esculenta* a so-called "independent" lens formation occurs. During numerous previous experiments on lens development in this animal I never observed an independent lens formation. Other workers likewise state that they cannot confirm SPEMANN's opinion, although in the literature also observations are recorded involving a confirmation. It is not impossible that here differences between *esculenta* races are responsible for the varying results.

The opinion, that for induction of a lens only a short contact between epidermis and eye vesicle is required, is also supported by DRAGOMIROV (1930) and by FILATOW (1934). Concerning the exact time, at which the lens components are determined, opinions still differ.

Reverting now to the observations which gave rise to the above-mentioned

investigation, I am inclined to think that an eye vesicle under ectoderm can induce numerous lenses, if by the growth of neighbouring organs it is placed in different positions and, now in this place, then in another, comes into contact with the ectoderm. My previous investigation, namely, revealed that the eye vesicle during a long time possesses the capacity to induce lenses. The lenses, induced in this way, will develop differently, according as the eye sooner or later loses contact with the lens anlage.

If during that process the eye vesicle is turned, it may take the induced lens along with it. The latter, if replaced as well, may later give the incorrect impression that it has been induced out of other material than ectoderm. Thus the results of POPOFF (1937) might be explained. He thought, namely, that he had found lens formation out of different tissues if an abnormally orientated eye vesicle came into contact with them. Only his recent researches (grafting of different tissues into the cavity of the eye cup) can produce evidence in favour of his opinion.

Besides, the fact that a lens is found against the tapetum of the eye (POLITZER) may not lead to the conclusion that this layer also can induce a lens.

Finally I will mention that in *Triton taeniatus* I repeatedly noticed lens formation out of the margin of the iris and even directly out of the retina of the grafted eye vesicles. Nevertheless, these eyes had also induced lenses out of ectoderm. The presence of a regenerated lens consequently does not deprive the eye of its capacity to induce lenses.

The phenomenon that an eye vesicle, grafted at a very young stage without a lens rudiment, regenerates a lens out of its retina or iris may also account for some cases described in the literature of so-called lens induction out of other tissues than ectoderm. The observed lenses might have been regenerated lenses. In *Axolotl* and *Rana esculenta* I observed these regenerated lenses only rarely, but there is no doubt that this type of lens formation occurs. In *Triton taeniatus* the phenomenon may be frequently observed.

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**Physics.** — *Some considerations on the fields of stress connected with dislocations in a regular crystal lattice. I.* By J. M. BURGERS. (Mededeeling N<sup>o</sup>. 34 uit het Laboratorium voor Aero- en Hydrodynamica der Technische Hoogeschool te Delft.)

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1. In order to explain the mechanism of plastic deformation of a crystal in its most simple form, as it is presented by the shearing process due to slipping along planes of a definite crystallographic orientation, several authors have assumed that the basic phenomenon leading to slip is the migration through the lattice of a well defined type of deviation from the ideal structure, a so-called *dislocation*<sup>1)</sup>.

It has been in particular TAYLOR who has investigated the characteristic properties of an elementary, two-dimensional type of dislocation, the possibilities for its displacement through the lattice, and the influence of the fields of stress connected with a system of such dislocations upon this displacement<sup>2)</sup>. An account of some of the results of this work, together with suggestions for certain modifications which made it possible to construct a connection with views developed by BECKER and by OROWAN, has been given by W. G. BURGERS and the present author in the "First Report on Viscosity and Plasticity", pp. 199 and seq. The problem, however, presented itself whether the two-dimensional type of dislocation, which must extend in a straight line through the lattice from one boundary surface of the crystal to the opposite boundary, really leads to an appropriate description of what is to be found in an actual crystal; it would appear that dislocations characterized by disturbances of a more general, three-dimensional type, which for instance may be confined to a region of finite extent, might lead to a more adequate picture<sup>3)</sup>. It is the object of the following pages to make a few contributions towards the development

<sup>1)</sup> Compare: "First Report on Viscosity and Plasticity" (Verhand. Kon. Nederl. Akad. v. Wetenschappen te Amsterdam, 1e sectie, XV, No. 3, 1935), p. 198 and the literature mentioned there; "Second Report on Viscosity and Plasticity" (ibidem, XVI, No. 4, 1938), p. 200.

See also papers by A. KOCHENDÖRFER, Zeitschr. f. Physik **108**, p. 244, 1938 and Zeitschr. f. Metallkunde **30**, p. 299, 1938.

<sup>2)</sup> G. I. TAYLOR, Proc. Roy. Soc. (London) **A 145**, p. 362, 1934.

<sup>3)</sup> "Second Report on Viscosity and Plasticity", p. 201. — KOCHENDÖRFER in his second paper (see footnote 1, above) alludes to the same problem; however, the few lines devoted by him to this matter (*l.c.* p. 300, second column) apparently are not based upon a sufficiently developed investigation of the geometric features of dislocations of three-dimensional type.