4. Prof. Valentin Haecker's Critical Review on Bastardization and Formation of the Sex Cells.

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A very interesting review has recently appeared from the pen of Prof. Haecker entitled »Bastardierung und Geschlechtszellenbildung«, dealing with questions that are receiving much attention at the present time. There are a few points in this review which need some emendation, due mainly to a misinterpretation or misunderstanding on the part of Prof. Haecker of certain papers which he critizises.

In the first place Prof. Haecker states my conclusion correctly that the reduction in number of the chromosomes is effected previous to the first maturation mitosis by a temporary conjugation of every two chromosomes; my conclusion that this is a union in each case of a paternal with a maternal chromosome; and my conclusion that such chromosomes become separated from each other in the first maturation division. But he is wrong in interpreting my position to be that as a result of this division all the paternal chromosomes pass into one of the daughter cells, and all the maternal into another. In this respect his diagram III of Tafel 12 is erroneous. For in none of my papers have I hinted at such a view; my paper (1901) rendered it very probable that this could not be the case, and this is clear from the context, though not stated in so many words, in my last contribution (1904) to the subject. Indeed, my position is exactly that of Sutton (1902) who argued that it would be purely a matter of chance as to which daughter cell a particular chromosome would enter. The only differences between the results of Sutton and myself is as to the generation of the reduction division, Sutton finding it to be second mitosis, and I to be the first. Accordingly the diagrammatic series III and IV of Tafel 12 of Prof. Haecker's review show a difference between the conclusions of Sutton and myself which neither of us has maintained.

Again: in foot-note 2 of page 199 of Prof. Häcker's review we read: »Wenn nun nach Montgomery in der Synapsis durch Contraction der verbindenden Lininfasern eine Vereinigung je zweier univalenter Elemente erfolgt, so ist nach meiner Ansicht dieser Modus der Vierergruppenbildung nicht principiell verschieden von dem von Vom Rath, mir und Rückert beschriebenen.« But there is nevertheless a cardinal difference. Rückert (1894a), and Haecker and others after him, concluded that there is a continuous chromatin spirem preceding the first maturation mitosis, and that the apparent reduction in number of the chromosomes is effected by this chromatin spirem segmenting into only half the normal number of chromosomes. I showed for *Peripatus* (1900), on the contrary, that a continuous linin spirem is present at this stage but not a continuous chromatin spirem, and that the bivalent chromosomes are produced by a later conjugation without the formation of a continuous chromatin loop. According to Rückert it is a case of chromosomes already closely connected remaining so; according to me, of chromosomes not in contact at first becoming so secondarily. Hence I spoke of this act as the "conjugation" of the chromosomes, and argued that this is the important criterion of the synapsis stage.

Then Prof. Haecker writes (p. 190): »Dagegen wird die von Montgomery vertretene Anschauung, daß die schließliche Paarung der Chromosomen die Verjüngung (rejuvenation) derselben zum Zwecke habe (1901. S. 223), sich heut zu Tage kaum mehr ungetheilter Zustimmung erfreuen, nachdem die Grundlagen der Verjüngungstheorie von verschiedenen Seiten mit so triftigen Gründen angefochten worden sind.« I argued in line with the conclusions of Maupas (1889) and R. Hertwig (1889) that a very essential result of the act of fertilization is rejuvenation of the gametes, occasioned by the new intermixture of living substances; and that the conjugation of the chromosomes in the synapsis stage of the spermatocytes is the last part of the fertilization process. An objection can be brought to this view from the work of Calkins (1902) on *Paramoecium*. Calkins shows that without conjugation of two individuals a new cycle of reproduction may be initiated by the stimulus of foods, and argues accordingly that periods of reproductive activity may be inaugurated by other factors than conjugation. No one will dispute this point. But it by no means disproves that fertilization, conjugation of individuals, arose and was perpetuated because by the the interchange of substances each conjoint became thereby refreshed. Similarly with the cases of artifically fertilized eggs, where the eggs are stimulated to cleavage by various chemical solutions, experiments made first by R. Hertwig; such experiments do not at all prove that the spermatozoon is unessential in fertilization, nor yet that the essential part process in fertilization is simply an induced change in the chemical nature of the egg. The fact remains that all Metazoa, and all the Protozoa for which the life-history is known, have, at least periodically, a process of fertilization by the conjugation of two individuals (the mature germ cells being necessarily individuals). It is from such experiments on inducing eggs to cleave by means of unnatural agencies, that there has grown up, but very unreasonably, a doubt as to the value of the factor of rejuvenation in fertilization. I pointed out that immediately after the act of conjugation of the chromosomes the germ cells enter upon a period of tremendous metabolic activity, in the case of the ovocyte at least the most intense and prolonged in the whole germinal cycle, namely the growth period preceding the first maturation mitosis. A good teleological explanation of the pairing of the chromosomes has been given by Sutton (1903); but I dealt with the question of the origin of this process, and the idea of rejuvenation explains the facts as well as any view yet offered.

As to the "types" of reduction distinguished by Prof. Haecker, I thoroughly agree with him that there is no well proven case where both mitoses are equational; and I believe that we may have a very reasonable doubt as to whether in any Metazoan both maturation divisions are equational. For those cases where there is a reduction division (a separation of entire univalent chromosomes from each other), I have suggested that for the particular division in which this is effected the term "heterotypic" mitosis may be employed. Flemming (1887) introduced this word for those cases (spermatogenesis of Amphibia) where the chromosomes differ in form from all other generations (in the particular case, ring shaped). Now though Flemming believed that the split or space in each such chromosome represents an equational split, and that therefore their mode of division is equational and not reductional (a view which I, 1903, 1904, have endeavoured to prove is erroneous), we may nevertheless apply the term heterotypic to each reduction mitosis, because these are the particular mitoses where the form of the chromosomes differs from those in any other divison of the germinal cycle. This is sufficient answer to Prof. Haecker's foot-note on p. 211. A heterotypic mitosis is one where the chromosomes are formed and behave differently from any other mitosis, just because they are formed differently; and it is of no importance at all whether they have ring form or not, for in the same cell some of the bivalent chromosomes may be in the form of dumb-bells, others of V's H's, of two parallel rods, or of rings (e. g. some Hemiptera, *Peripatus*).

On p. 229 of the review under discussion we read as the describer of the egg of *Crepidula* the name of Calkins; this is of course a mistake for Conklin.

Finally a word as to Prof. Haecker's own interpretations of the ovogenesis of *Cyclops*. Rückert (1894a) concluded from the study of several species of Copepoda that the number of chromosomes is reduced one half before the first maturation mitosis; that the first maturation is an equation division and the second reductional. And in his review (1894b) on reduction Rückert states, p. 576: »Alle genaueren

Untersuchungen der letzten Jahre stimmen darin überein, daß schon vor der ersten Reifungsteilung Chromatinportionen auftreten, deren Zahl die Hälfte beträgt von der Normalzahl der Chromosomen der betreffenden Species«. Prof. Haecker's former views coincided with these; and to-day, ten years after Rückert's Referat, we can say that pretty general uniformity has been reached in this matter. But Prof. Haecker (1902) has recently completely changed his opinion again. According to his present view there is no reduction in number of chromosomes preceding the first maturation division, but after this division there takes place a reduction in number by a pairing of the chromosomes in the second ovocyte. Thus there would be 12 chromosomes, in the first ovocyte, 6 bivalent ones in the second, and 6 bivalent ones in the ovotid. The 12 chromosomes of the first polar spindle are said to be arranged in two groups of 6 each, each group corresponding to a gonomere of the germinal vesicle; each of the 12 is segmented both longitudinally and transversely, and is therefore bivalent. In the first division each is halved equationally, so that each second ovocyte receives 12 bivalent chromosomes, each of which has a transverse but no longitudinal split. Before the arrangement into the equator of the second polar spindle these 12 bivalent chromosomes conjugate to form 6 (the before quadrivalent) chromosomes. As he states (1904. p. 192): »Es entstehen H- oder X-förmige Figuren, welche demnach je aus einem Chromosom zusammengesetzt sind... Bei der zweiten Theilung treten diese neugeformten bivalenten Elemente aus einander... Demnach erhält schließlich der Eikern 6 bivalente Elemente, welche je aus einer väterlichen und einer mütterlichen, oder, da die reife Eizelle bereits eine neue Generation repräsentiert, aus einer großväterlichen und großmütterlichen Hälfte besteht.«

It is with a feeling of much reserve that I would critizise observations on an object which I have not personally studied. I would not for an instant doubt Prof. Haecker's statement of facts, but this is a question of interpretation, and in matters of interpretation all observers may sometimes go wrong. These results are so much at variance with the conclusions on Vertebrates, Insects, Peripatus and Polyclades, that it would seem there must be either some error of interpretation, ore else that the particular ova studied showed pathological conditions. Now in the first place in his »Praxis und Theorie« (1899) Prof. Haecker states (p. 172) that the normal number of chromosomes in *Cyclops brevicornis* is 24, that there are 12 in the earlier generations of the germ cells and 6 in the ovotid. But Rückert found for other related Copepoda, as has been found indeed for most objects, that the normal number is the same for somatic cells and the earlier generations of the germ cells. The ovocytes and spermatocytes of the first order have on the contrary half this normal number, and so does the mature ovotid or spermatid. How then does it come about that Prof. Haecker finds in the mature egg on-quarter the normal number of chromosomes? For that must be the case if the somatic cells contain each 24 and the ovotid 6. Again, why should Rückert, and Prof. Haecker himself in his earlier contributions, have entirely overlooked the double nature of the chromosomes of the ovotid, if they are double (bivalent) as Prof. Haecker now concludes? If there is any particular conclusion of which cytologists can feel reasonable certain, it is that the chromosomes of the mature germ cell are univalent and in half the normal number.

The »Gedankengang« which has apparently led Prof. Haecker to his present standpoint in regard to the maintenance of the separate grouping of the paternal and maternal chromosomes in the germ cells, a condition first pointed out by Rückert (1895) and since corroborated by a number of observers. Long before this it had been shown by van Beneden (1883) for the early cleavages of *Ascaris*. This is most marked in the early cleavages, both the gonomerity of the nuclei and the vesicular separateness of the chromosomes. The fertilized egg has an equal number of chromosomes of its own (maternal chromosomes) and of chromosomes (paternal) indroduced by the spermatozoon, as van Beneden first showed (1883). These keep in two groups during the earlier cleavages. According to my results (1901), in opposition to Prof. Haecker, just after the last spermatogonic division each paternal chromosome pairs with a maternal one; and from the time of this conjugation up to the stage of another fertilization there can be no maintenance of two distinct groups of chromosomes. For this pairing means the closest union of the two sets of chromosomes. As I pointed out in my last paper (1904) in the last generations of spermatogonia of Urodelea there is certainly no separateness of the maternal and paternal elements, for it is very probable that in the chromatin spirem of the prophase of the last generation of spermatogonia each paternal chromosome is contiguous to the maternal chromosome with which it will conjugate in the daughter cell. Therefore it would be probable that the two gonomeres are most distinct in the earliest stages, while in later generations of the germ cells this division of the nucleus of a germ cell into a maternal and a paternal half gradually becomes obliterated. At one end are the two completely separate pronuclei before the first cleavage; at the other the close union of maternal with paternal chromosomes in the synapsis stage.

From these observations of my own, now being corroborated by others, and in entire concordance with our knowledge of the general behavior of the chromosomes in the germinal cycle, it is clear that the nucleus of a germ cell cannot consist of a paternal and a maternal gonomere after the synapsis stage. The synapsis stage effects the pairing of each paternal chromosome with a maternal chromosome in those cases where there is an even number of chromosomes; in those cases where there is an uneven number the odd chromosome does not unite with any other, as I first showed for four species of Hemiptera, and as Rosenberg has recently confirmed by the study of the chromosomes of a Drosera hybrid. Each bivalent chromosome then consists of a paternal and a maternal element. The reduction division separates these two components of each bivalent chromosome. Therefore nucleus of an ovocyte or spermatocyte of the first order cannot be divided into two gonomeres; and therefore, also, the mature ovotid or spermatid can have only univalent chromosomes.

It clearly follows from this, then, that if *Cyclops brevicornis* has in the ovotid bivalent chromosomes, each a conjoint of a paternal and a maternal, this Crustacean would present unique chromosomal phenomena. And because entirely different results have come from much patient and careful observation on the part of others, it would seem probable that the recent observations of Prof. Haecker on *Cyclops* may be in error. And the three vertical diagrams which he gives on Tafel 12 of his last paper to represent three different types of chromosomal behavior, may well be reduced to one.

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5. Die Bildung der Eihüllen und ihrer Anhänge bei den Chitonen.

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(Mit 13 Figuren.)

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Das fertige Ei der Chitonen ist von einer Schale umgeben, die ein eigentümlicher Besatz bei den einzelnen Arten sehr verschieden geformter Anhänge ziert. Außerdem läßt sich in vielen Fällen noch eine zweite, innere Eihülle nachweisen, eine Dotterhaut. Die Angaben der Forscher über die Bildung und Natur dieser Hüllen gehen weit auseinander. Dem ausführlichen Berichte meiner Untersuchungen über die Bildung der Eihüllen nebst Anhängen bei den Chitonen geht eine Charakteristik über den Stand unsrer Kenntnisse dieser Vorgänge voraus. Diese Untersuchungen werden in den Zoologischen Jahrbüchern Supplementbd. VI, Heft 2, 1904 veröffentlicht werden. Hier will ich nur folgendes erwähnen:

Von Ihering (1878) betrachtet die Eihülle nebst Anhängen von *Chiton squamosus* Poli als ein Ausscheidungsprodukt der Follikelzellen. Dasselbe behauptet dieser Forscher in bezug auf die anhangslose Eihülle von *Chiton fascicularis* L. Bei Sabatier (1885) findet sich zuerst die bestimmte Angabe, daß die Follikelzellen bei *Chiton polii* sich direkt in die Eihüllenanhänge umwandeln. Diese Ansicht von der direkten Umwandlung der Follikelzellen in die Eihülle nebst Anhängen wird am entschiedensten von Garnault (1888) für *Chiton cinereus* vertreten. Schließlich stellt Pelseneer (1899) einen sowohl der v. Iheringschen, wie der Garnaultschen Darstellung der Bildung der Eihüllen nebst Anhängen widersprechenden Bildungsmodus auf, indem er für eine Reihe von Formen (u. a. auch für *Boreochiton marginatus* = *Chiton cinereus*) die Existenz eines Follikelepithels bestreitet und so sich zur Behauptung gezwungen sieht, die Eihülle nebst Anhängen sei bei diesen Arten ein Ausscheidungsprodukt des Eies selbst,