

new genus (*Beimarochloa*), nine new species, and to change the names (new combinations) in but nineteen cases.

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SPECIAL ARTICLES

SECONDARY CHROMOSOME-COUPPLINGS AND THE SEXUAL RELATIONS IN ABRAXAS

IN Professor Castle's interesting communication on sex-heredity, published in the issue of SCIENCE for March 5, a view is advanced that is akin to the "provisional formulation" that I recently offered,¹ but seems to me a decided improvement upon it. In the course of his discussion Professor Castle points out that the "XX and X" formula, which holds true for so many insects, apparently can not be applied to the conditions in *Abraxas*, as indicated by the experimental results of Doncaster and Raynor. These results only seem explicable under the view that the relation with which we have become familiar in other insects is here reversed, the female being heterozygous and the male homozygous in respect to sex (Bateson, Doncaster); and with this conclusion I concur. Definite cytological evidence has now been produced that the same is true of some other animals. The work of Baltzer, done in Boveri's laboratory² shows that in the sea-urchin all the sperm-nuclei are alike, while the egg-nuclei are of two classes, approximately equal in number. All of the gamete-nuclei contain 18 chromosomes. In all of the sperm-nuclei and in one class of egg 17 of these are rod-shaped in the metaphase and anaphases of cleavage, and have a terminal attachment to the spindle, while one is a long chromosome that has a subterminal attachment and therefore is hook-shaped. In the other class of egg one of the rods is replaced by a second somewhat shorter hook-shaped chromosome. The latter, therefore, forms a distinctive differential between the sexes; and cytologically considered the female is heterozygous, the male homozygous. A

¹ SCIENCE, January 8, 1909.

² Reported by Baltzer in *Verh. d. deutsch. Zool. Ges.*, 1908, and more recently by Boveri in *Sitzungsber. d. phys.-med. Ges., Würzburg*, 1909.

cytological parallel to the condition inferred from the experimental data in the case of *Abraxas* is thus demonstrated. Furthermore, if the differential chromosome in the sea-urchin is of the same general nature as the X-element of the insects, a confirmation is given of Castle's assumption that in one class of cases (*e. g.*, Hemiptera) XX means the female condition and X the male, while in another class of cases the presence of X means the female, its absence the male.

From the point of view thus given the importance of a cytological study of *Abraxas* is manifest. Thanks to the courtesy of Mr. Doncaster, I have for some time had this material under investigation; but unfortunately it presents great practical difficulties. So much may, however, be said, that while the spermatogonial divisions present a normal appearance, the spermatocyte divisions, in both the hybrid and the pure forms, show remarkably complicated and puzzling phenomena that are unlike anything hitherto described in other insects. A detailed analysis of the distribution of the chromosomes in maturation will, I fear, prove impracticable, and as far as this particular case is concerned we are for the present reduced to mere speculative guess-work. I think, however, that we should not hesitate to guess if indications for direct observation can thus be found.

Professor Castle's assumption is that the "repulsion" between the *grossulariata* factor ("G") and the female-producing factor ("X"), postulated by Bateson, "is doubtless due to the fact that the *grossulariata* character acts as the synaptic mate to the X-element." This is, perhaps, admissible; but from the standpoint of the chromosome-hypothesis it involves the following difficulty. In the heterozygous female (GLX in Castle's formula) G is assumed to couple in synapsis, not with its own homologue or allelomorph, L (as it must do in the male GL or GG), but with a different element, X. The L factor is thus left with no synaptic mate; and this result, when followed out, is found to involve still further difficulties. Even though L be regarded as merely the absence of G, this probably does not mean the absence of an entire

chromosome, but rather the absence from the G-chromosome of a particular pigment-producing factor. I would therefore regard it as a more plausible guess that a Y-element is present in both sexes, and that both have the same number of chromosomes, the female zygote formula being XY and the male YY, as the facts in the sea-urchin suggest. The female heterozygote thus becomes GLXY, the male GLYY, and the homozygous male GGY or LLY. All the facts are then consistently accounted for by the single assumption that G, while acting as the synaptic mate of L, always undergoes also a secondary coupling with Y.

Did such secondary coupling not take place the female GLXY would give rise to the bivalents G/L and Y/X, producing the four classes of gametes GX, GY, LX and LY. If, however, in addition to the primary synaptic coupling of X and Y, G also couples secondarily with Y, the result should be a quadrivalent element, which might have either the tetrad grouping



or the linear grouping



giving in either case the two classes of gametes GY and LX. In the males, GLYY or GGY, the gametes will of course be GY, LY or GY, GY respectively. This gives a series of formulas identical with those of Bateson and Doncaster, as recast by Castle, if Y be everywhere inserted in its proper place, as follows:

Parents	Constitution	Gametes	Offspring
(1) <i>Lact.</i> ♀	LLXY	LX, LY	GLXY = <i>gross.</i> ♀
<i>Gross.</i> ♂	GGYY	GY, GY	GLYY = <i>gross.</i> ♂
(2) <i>Het.</i> ♀	GLXY	GY, LX	GGYY = <i>gross.</i> ♂
<i>Het.</i> ♂	GLYY	GY, LY	GLXY = <i>gross.</i> ♀
(3) <i>Lact.</i> ♀	LLXY	LX, LY	GLXY = <i>gross.</i> ♀
<i>Het.</i> ♂	GLYY	GY, LY	GLYY = <i>gross.</i> ♂
			LLXY = <i>lact.</i> ♀
			LLYY = <i>lact.</i> ♂
(4) <i>Het.</i> ♀	GLXY	GY, LX	GLYY = <i>gross.</i> ♂
<i>Lact.</i> ♂	LLYY	LY, LY	LLXY = <i>lact.</i> ♀

This adds nothing in principle to Castle's suggestions, but seems more in accordance with cytological expectation.

Such a mode of coupling may seem very improbable; but I wish to point out that there are at least some approximate analogies to it in cytological facts known in other animals. Several different types of multiple elements, formed by definite chromosome-couplings, are now known. An example is given by *Metapodius* (which I have recently described in detail). In individuals having "supernumerary" chromosomes these regularly couple with the idiochromosome-bivalent in the second division to form triad, tetrad, pentad and even hexad complexes; and the components are often arranged in linear series. I have recently obtained an individual of *M. femoratus* which differs from all other individuals of the species thus far examined in possessing a single odd or accessory chromosome, while the missing small idiochromosome is replaced by a third "m-chromosome." The latter does not, as might have been expected, play the part of a synaptic mate to the odd chromosome, but shows throughout the spermatogenesis the characteristic behavior of its own kind. In the first division it is always coupled with the two other m-chromosomes to form a triad element, the three components almost always forming a linear series. Again, in *Thyanta* there are three sex-chromosomes (the Y-element and two components of the X-element) which divide separately in the first division but are always coupled in the second to form a linear triad series. In the reduvioids, as Payne has recently shown, the sex-chromosomes form in the second division dyad, triad or tetrad groups; in *Gelastocoris* they form a pentad complex; and in each case the components show a definite arrangement and mode of distribution.

A closer approximation to the secondary coupling suggested in *Abraxas* is given by the observation of Sinéty on *Leptynia* (one of the Phasmidæ), and especially by the discoveries of McClung in *Hesperotettix* and some other Acrididæ, that the X-element (accessory chromosome) is in these cases regularly coupled in the maturation-divisions with one of the

bivalents. I have found a somewhat similar condition in the coreid *Pachylis*, though the coupling is here less constant. The most significant fact, emphasized by McClung, is that in *Hesperotettix* the odd chromosome always couples with a particular bivalent that can be distinguished from the others by its size. Such a phenomenon is evidently to a certain extent of the same type as the secondary coupling surmised above as the possible explanation of the facts in *Abraxas*; and it would be most interesting to attempt crossing experiments with these grasshoppers from the point of view that is thus suggested.

Professor Castle's tempting suggestion that the Y-element in the ordinary forms of insects may be the vehicle for the transmission of secondary male characters that are not represented in the female interests me because I had considered an identical view but withheld it for two reasons. One was that in forms like *Pachylis*, *Archimerus*, etc., where the Y-element is wanting, the male secondary characters are as well developed and characteristic as in forms where the Y-element is present. The other is given by the facts in *Metapodius* (since published in the fifth of my "Studies on Chromosomes"). In this case the evidence is nearly if not quite conclusive that the "supernumerary" chromosomes are duplicates of the Y-element; and they are found indifferently in either sex. The closest scrutiny of the original specimens (now in my cabinet) fails to show any trace of the male secondary characters in those females that possess supernumeraries. Since these characters are very conspicuous in *Metapodius* a decisive negative seems to be given to Castle's suggestion, as far at least as three species of this genus are concerned. The Y-element still remains a puzzle; and until it has been satisfactorily accounted for our cytological view of the problem will remain defective.

EDMUND B. WILSON

THE NATIONAL ACADEMY OF SCIENCES

THE National Academy of Sciences held its annual meeting at Washington on April 20, 21 and 22. The members in attendance were:

Henry L. Abbot, Alexander Agassiz, J. A. Allen,

George F. Becker, John S. Billings, Franz Boas, William H. Brewer, George J. Brush, J. McK. Cattell, Charles F. Chandler, Russell H. Chittenden, W. B. Clark, George C. Comstock, E. G. Conklin, James M. Crafts, Whitman Cross, William H. Dall, W. M. Davis, W. L. Elkin, S. F. Emmons, W. G. Farlow, Edwin B. Frost, Theo. Gill, Arnold Hague, William F. Hillebrand, William H. Holmes, Joseph P. Iddings, C. Hart Merriam, S. Weir Mitchell, Edward W. Morley, Edward S. Morse, Edward L. Nichols, H. F. Osborn, Michael I. Pupin, Ira Remsen, W. B. Scott, Charles D. Walcott, Arthur G. Webster, William H. Welch, Charles A. White, Edmund B. Wilson, Robert S. Woodward.

The program of scientific papers was as follows: "The Nature and Possible Origin of the Milky Way," G. C. Comstock.

"Determinations of Stellar Parallax from Photographs made by Arthur R. Hincks and the writer," H. N. Russel (introduced by G. C. Comstock).

"Strange Ceremonial Costumes of California Indians" (with lantern slides), C. Hart Merriam.

"Archeological Problems of the Titicacan Plateau" (with lantern slides), W. H. Holmes.

"Discovery of a Complete Skeleton of *Tyrannosaurus* in the Upper Cretaceous" (with lantern slides), H. F. Osborn.

"An Iguanodont Dinosaur (*Trachodon*) with the Epidermis Preserved" (with lantern slides), H. F. Osborn.

"Stratigraphic Relations and Paleontology of the Lower Member of the Fort Union Formation," F. H. Knowlton (introduced by Whitman Cross).

"The Deep-sea Bottom of the Eastern Tropical Pacific, from Observations on the *Albatross* Expedition," Sir John Murray (communicated by A. Agassiz).

"The Medusæ of the Eastern Tropical Pacific, from Observations on the *Albatross* Expedition," H. B. Bigelow (communicated by A. Agassiz).

"Mythology of the Mewan Indians of California," C. Hart Merriam.

"The Radiation from Gases heated by Sudden Compression," E. F. Nichols and G. P. Pegram.

"Biographical Memoir of Elliott Coues," J. A. Allen.

"Biographical Memoir of Ogden N. Rood," E. L. Nichols.

"The Electrolytic Separation of the Chlorides of Barium and Radium," Edgar F. Smith.

"The Orders of Teleostomous Fishes (Pisces)," Theo. Gill.