

in 10 days, a difference in vigor amounting to more than 17 divisions in ten days. In other words, if the two individuals, one of which formed the J series, had not conjugated, they would have had only enough metabolic vigor to divide at the rate of one division in 40 days, but, having conjugated, their metabolic vigor was such that they actually divided at the rate of 71.6 divisions in 40 days. This is an extreme case; if conjugation occurs before vitality runs so low, the difference between parent and offspring is less. Thus, the C, D and H series came directly from this same A series, C from individuals in the 78th generation, D from the 137th and H from the 237th generation, of the parent series. For the first 60 days of each filial series the mean division rates for ten days of offspring and parent were: C 17.26, A 15.73; D 17.16, A 14.13; and H 17.33, A 12.53, the differences being 1.53, 3.03 and 4.80.

Exactly similar results were obtained with the F₂, F₃ and F₄ generations of the original A series, some of which are dividing today with the optimum vigor of 17 + divisions in ten days.

Directing attention again to the fact that all series are treated in the same identical way as regards food and environmental conditions, and that conjugations were invariably between two individuals of the same age, the conclusion is incontestable that one fundamental effect of conjugation is the renewal of vitality, or rejuvenescence, of the protoplasm.

37 (1412)

Endomixis and size variations in pure lines of *Paramecium aurelia*.

By RHODA ERDMANN.

[*From the Osborn Zoölogical Laboratory, Yale University, New Haven, Conn.*]

Jennings¹ considers the mean size of a pure line as strictly hereditary throughout the pure line; it belongs to one of the fundamental characteristics of this individual pure line. Eight years

¹ Jennings, H. S., *Proc. Amer. Philos. Soc.*, 47, 393-546.

later the same author¹ reverses his opinion and based on extensive studies, claims that a single stock, *i. e.*, a pure line derived by fission from a single progenitor gradually differentiates into such hereditarily diverse stocks; so that by selection marked results are produced. His former conception of the genotype was gained by experiments with the highly specialized infusorian species *Paramecium caudatum* and *aurelia*, his later ideas by his results with *Diffugia corona*, an amœbina of simpler cytological structure.

Diffugia has definite structural characters that can be counted and measured, which are unchanged by growth and environmental conditions, but still are "hereditary, yet variable." This coincidence of favorable conditions—besides theoretical considerations—gives a priori more support to views that do not maintain the absolute constancy of the genotype, though they contradict the current conception of the "so-called" pure line. *Paramecium* is changed in size by its daily divisions and by the influences of the environment, thus complicating genetic studies; Jennings's results have been challenged by Walton² and Castle,³ as statistically considered far from conclusive. The mean length, a constant after his opinion, varies between 114.033, 123.606, 130.120 and 144.880 microns for mass cultures, derived from the same animal. A new complication arose after the discovery of endomixis,⁴ a dynamic, periodic reorganization process, involving the disintegration and absorption of the old macronuclear and micronuclear material without the introduction of foreign nuclear material. It was evident that the discrepancies in Jennings's measurements might be explained, if there are periodically appearing fluctuations during the intermitic periods. Further, before the influence of conjugation in *Paramecium* can be studied, it is necessary to know first the isolated influences of division, clearly shown by Jennings and reinvestigated for the lines I worked with, to eliminate the changes produced by environmental conditions and the most difficult process, to find, if endomixis has influences on the variability of the quantities of the line. These are the preparatory

¹ Jennings, H. S., *Genetics*, 1, 407-534.

² Walton, L. B., *American Naturalist*, 49, 642-652.

³ Castle, W. E., *American Naturalist*, 50, 179-183.

⁴ Woodruff, L. L., and Erdmann, Rh., *Jour. Exp. Zool.*, 17, 425-516; Erdmann, Rh., and Woodruff, L. L., *Jour. Exp. Zool.*, 20, 59-96.

steps to be taken, before attempting to decide, if conjugation has an effect and which particular effect in *Paramecia*. All authors till now have studied the combined influences of unrecorded occurrences of endomixis and influences of recorded occurrence of conjugation. The intermictic period of 28 days duration alternates with the endomictic phase indefinitely. The climax, when the most important steps of the reorganization process take place, lasts one or two days, while the ascending and descending phases of the endomictic period overlap either with the first days or last days of the intermictic period. The number of daily divisions amounts to one or two, hence approximately 50 in one intermictic period, which we have divided for convenience into three subperiods. Changes effected by the constantly occurring divisions and by the approaching of the next endomixis go parallel and can not be considered separately.

By our culture methods we can create a constant environment, by previous observations we can recognize how a culture changes in mean length and mean breadth, standard deviation and correlation between length and breadth before, in and after division. We eliminate further by our methods all animals while dividing or in constriction and then we are able to recognize periodical regular combinations of the four quantities in question in each intermictic subperiod. In the second subperiod the animals reach their mean length, have a medium to high standard deviation and correlation; in the third subperiod they do not reach their mean length, but have a very high standard deviation and correlation. In glancing over the changes in the quantities shortly after or in division, we know that the four quantities in question change too in value, *i. e.*, the standard deviation is low immediately after division, and high shortly before division. Therefore in each intermictic period the values of the four quantities are in the whole measurements either balanced, augmented or diminished. We find that a culture shortly before the onset of the next endomixis is distinguished by a low division rate, a low mean length, a high mean breadth, a high standard deviation and high coefficient of correlation. In Line I the standard deviation passes through the following values during the intermictic period, Line I 5530₁₀ with $2.424 \pm .105$, Line I 5530₁₄ with

3.593 + .156, and Line I 5530₂₄ with 4.259 + .185 units for the different mean lengths in each different subperiod. These changes appear in each investigated line, Line I, Line IE and Line O, in each intermictic period, thus affording opportunity to select the best period for deriving comparable values in our subsequent measurements. When, after 14 days the animal of known number of generations is transferred from the isolated slide culture into the medium and is allowed to multiply, the mass culture is best for our purposes: it is on the height of the second subperiod of the intermictic period, when the culture as a whole attains its highest mean length.

In the mean lengths of subsequent measurements for the same Line IE from 1914 till 1917, covering 2,200 generations in the life history of this line, the maxima cluster all around the same number 105 microns or 30 of our units of measurement.

Line I, from which was derived at the 4,020 generation the above mentioned line IE, has a mean length of 112 microns or 32 units, another line O that was only recently in laboratory culture, and in which endomixis was observed from its occurrence in 179 till the 901 generation had a mean length of 41 units or 143.5 microns.

The periodical change in all dimensions proceeds while the culture passes the intermictic period, then endomixis occurs, effaces the high standard deviation and coefficient of correlation and a culture with low quantities appears in the first subperiod of the intermictic period, reaching later in the second subperiod the theoretical mean length and showing "constancy" of this dimension for years under the same environmental conditions. Endomixis therefore acts as a *stabilizer* and effaces the fluctuations around the mean, that Jennings had seen in his cultures.

But endomixis also acts as an *originator* of new lines with a mean length of their own. If the division products of the two divisions after endomixis are seeded out and the progeny of these eight lines measured, these lines show different mean lengths, though bred in the same conditions and closely related. Only five animals produced mass cultures, the measurements are given on the following table.

If these lines are carefully carried through the next endomictic

LINE OHR AFTER OCCURRENCE OF ENDOMIXIS IN THE 896TH GENERATION IN ITS
BREAKING UP PROCESS; ONLY MEAN LENGTHS IN THREE SUBSEQUENT
ENDOMICTIC PERIODS ARE GIVEN IN UNITS.

(One unit = 3.5 microns.

Ohr 808				
$41.983 \pm .293$				
⋮				
Ohr 846				
$41.700 \pm .477$				
Ohr 896 _{va}	Ohr 896 _{vb}	Ohr 896 _{vc}	Ohr 896 _{vd}	Ohr 896 _{ve}
$39.625 \pm .152$	$39.941 \pm .277$	$37.708 \pm .180$	$37.598 \pm .380$	$42.695 \pm .176$
⋮	⋮	⋮	⋮	⋮
Ohr 932 _v	not further selected	died	died	Ohr 935 _{ve}
$39.755 \pm .234$				$42.450 \pm .12$
⋮				⋮
Ohr 978 _{va}				Ohr 981 _{ve} 9
$39.866 \pm .255$				$42.560 \pm .130$

period and the selection for a certain mean length repeated, it is possible to isolate lines with different characters. The table shows the measurements for two cultures, carried through three subsequent endomictic periods, derived both at the 896th generation, these lines Ohr 896_{va} and Ohr 896_{ve} remain "constant." The same phenomenon was unintentionally attained when during our joint studies, Dr. Woodruff and I kept for a long sequence of generations Line IE isolated from Line I, the famous Line already under laboratory observation since 1907. The breaking up in "hereditarily diverse stocks" in this line could not be attributed to the supposed effects of the culture methods that varied only for about 800 in the total 2,200 observed generations, for both lines. I cultivated Line O, either in hay infusion or bouillon, either in room temperature or in constant temperature. The dimensions in the beginning show a more or less marked decrease, but later come nearly to the old standard. Such a considerable difference as Lines I and IE or Lines Ohr 978_{va} and Ohr 981_{ve} show and maintain, can not be affected by environmental changes.

The production of new lines is caused by endomixis, the reorganization process in paramecium, so closely related to the sexual phenomenon of conjugation and still so essentially different from this process by being effected in one cell and not affording the introduction of foreign chromatin into the cell. We have to conclude that even in so called "asexually" propagated lines heritable variations can be produced by directed selection. But why do these new lines not oftener appear in nature or in the laboratory? First different observers have given different measurements for strains of *Paramecium*, isolated from populations; Jollos reports the breaking up of a line, and Jennings the appearance of lines with new heritable characters after conjugation. Owing to the difficult culture conditions he could, at that time, not prove definitely that the breaking up in different new lines is effected by conjugation. Now it is possible to do so. But the rôle of the organization process in question is twofold: Endomixis gives rise to new combinations that can be selected, but also stabilizes the line at each occurrence. If variations in mean length appear between 37 and 45 units, those lines will thrive best either in mass cultures or isolated lines, which can adapt themselves the quickest to the given environment. I have observed that all descendants of the O lines with 37, 43 and 45 units die in the constant environment I choose for all these experiments. The 41 mean length and 11 mean breadth had the best chances to survive in the same environment. The uniformity, a word that should be better used than constancy in the appearances of the genotype, is a product of the influences of the chosen environment and of the adaptability of the different recombinations appearing after endomixis. These recombinations will become "heritable," if the environment remains nearly constant, else other recombinations appear after endomixis that are better adapted to the new conditions.

What specific effects conjugation, the other reorganization process, has in the life of *Paramecium* is still unknown.

* Jollos, V., *Biol. Centralbl.*, 33, 222-236.