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SOME PROBLEMS IN THE GENETICS OF THE FUNGI[1]

By Dr. B. O. DODGE

THE NEW YORK BOTANICAL GARDEN

INTRODUCTION

NOT every one has had an opportunity, or the desire, to study the fungi critically. Most people, however, are more or less familiar with molds, mildews, mushrooms and yeasts. Those of you who were brought up in the country districts may remember how you enjoyed kicking over toadstools and puffing puffballs in each other's faces. The man who collects wild mushrooms in woodlands for food seldom thinks of them as plants. Botanists, on the theory that all living things must be either plants or animals, place the fungi in the plant kingdom. They say that if fungi ever had chlorophyll they have lost it through degeneration, and degenerates make little progress in evolution. It is a very common belief that the fungi are of little economic importance except as they cause decay and disease, and, since they show little evolution, their study would promise little as to throwing light on the great life processes. As a matter of fact, just to mention two examples, the fungi and bacteria are of incalculable value in building the soil and maintaining its fertility. Yeasts rival our boasted billion dollar corn crop, if we count the value of alcohol and other useful products of fermentation.

The old attitude is changing, as witness the interest in sex and genetics of fungi manifested during the past ten or fifteen years. This work will certainly be greatly facilitated in the next decade by the use of growth substances and sex hormones to bring into fertile cultures species of obligate parasites not now at all adapted for this type of genetic study. We may

[1] Presented at a general session of the Third International Congress for Microbiology, New York, September 6, 1939.

then hope to see a recognition of the fungi more in accord with their real importance in the great kingdoms of living things.

The farmer has known for sixty or seventy years that he should destroy the barberry because it is the alternate host of wheat rust. It is only very recently that a more important reason for destroying the barberry has been discovered, namely, it provides the opportunity, through mutation and hybridization, for the rust to develop new biologic races. Dr. M. B. Waite of the Department of Agriculture, who spent many years breeding pears for blight resistance, used to say that the real function of a plant pathologist was to turn plant breeder and develop new races of economic plants for disease resistance. It was suggested to him that while man was busy breeding up races of the host for resistance, mother nature was probably busy breeding up new races of the parasite for pathogenicity.[2] This brings us to the subject of this discussion—problems confronting those who are interested in resistance and immunity as well as those who would take up this rather new subject, mycogenetics.

Genes in Diploid and Haploid Structures

In genetic studies of higher plants and animals the effects of factors of inheritance are usually manifest in connection with diploid structures, where each nucleus carries two sets of genes, one set contributed by each parent. The haploid mycelium of a fungus shows many variations as to color, types of growth and in the production of propagating bodies of all sorts. The foundation structures of the fruit bodies themselves are haploid. One is, therefore, enabled to observe in the fungi the effects of a single set of genes without the complications which are bound to arise when two different sets are present, as in diploids.

Asexual and Sexual Stages of Fungi

At some time in the normal life cycle of a fungus there occur certain nuclear fusions. This phase is called the sexual stage, in contrast to the asexual stage which is a purely vegetative one where propagating bodies may or may not be developed. It was early found in all fungi where the story was complete, that the primordial reproductive structures both arose from a common stalk or branch of the mycelium. The classic text-book figures of *Aspergillus, Penicillium* and *Sporodinia* illustrate this type of development. This was accepted as proof that in the fungi each cell, or each nucleus, carried all of the inheritance of the species. Every individual was totipotent. Reproduction involving two different individuals was thought to be impossible. If a mycelium derived from a single spore did not produce zygospores, ascocarps or a mushroom, as the case might be, it was because the conditions were not suitable. This notion, held by our ultra-conservative leaders in botany, blocked mycological progress for years.

Heterothallism and Homothallism

Blakeslee, in 1904, proved that in a number of species of the zygomycetes one can obtain zygospores only when two mycelia of opposite sex are mated. Gametangia are never produced on mycelia from single spores. Blakeslee suggested that such species be called *heterothallic.* Sexual reproduction requires mating what he called + and − races. Segregation of the sex factors is strictly bipolar and genetic. Species like *Sporodinia* are *homothallic,* because zygospores are produced on individual mycelia. Since that time heterothallism and homothallism have been found side by side in genera of all of the great groups of fungi, and this fact must be taken into account in all genetic studies involving the fungi, directly or indirectly.

Mendelism in the Neurospora (Monilia) Bakery Molds

The salmon-pink bakery molds are of world-wide distribution, and are found especially in the tropics on burned-over sugarcane fields and on forest trees scorched by fires. The aerial branches bearing the monilioid conidia are also brightly colored. It was long thought that these molds had lost their power to reproduce sexually because they had evolved such an efficient method of propagating themselves asexually. The ascocarps, small pear-shaped fruit bodies about ½ mm in diameter, are obtained in culture only when two races of opposite sex are grown together. In three species the asci have eight spores each. These species are obligately heterothallic, so that four spores in an ascus are of one sex and four of the opposite sex, in their reaction. Three other species have 4-spored asci. They are not homothallic, although a single spore contains all of the essentials for reproduction. Each spore is originally provided with two nuclei of opposite sex.

Mutations and Segregations

Medical mycologists in culturing skin disease fungi often find their old cultures "going pleomorphic" as they say. Sectors or spots of growth appear which are perhaps lighter in color, more fluffy and devoid of a certain kind of spores. This phenomenon probably does not differ from that to be observed in cultures of many other fungi. The question as to whether sectoring represents a true mutation or is a temporary phenotypic change due to cultural conditions is not

[2] We were just learning that we could cross races and species of the bakery molds just as easily as one could cross smooth and wrinkled peas, and with comparable results.

easily answered unless the sexual stage of a species is known. The application of growth substances and sex hormones here would be well worth trying out.

Mutations occur in these pink bakery molds as in other fungi and many different types of growth can be obtained in culture. We have one mutant albino non-conidial race which is stable. It may serve to demonstrate Mendelian segregation and how well these fungi are adapted for genetic study.

When we mate the albino race in culture with a normal salmon-pink race, hundreds of ascocarps mature within a few days. These are all exactly alike genetically, because every cell of a mycelium is potentially a gamete, and these must all be alike. The identical cross can be made over and over again through a term of years. We sometimes call these ascocarps developed from the mating, *hybrid* ascocarps, but it is only the individual young asci that are actually diploid and, therefore, hybrid, because their fusion nuclei do contain the inheritance contributed by both parents. Crushing out the ascus cluster from the fruit body, we find that the asci are all 8-spored and look alike. The ascus is a mother-cell in which the chromosomes undergo reduction, with segregations and new combinations of factors just as at maturation in animals and seed plants. When the eight spores are isolated one by one in order and are grown in tubes, we see a perfect demonstration of simple Mendelian segregation. Four races are albinos, the other four are orange-colored. By test it is proved that four races are of one sex and four of the other. We have now something new which has been obtained by hybridization, namely, a new albino race of the sex opposite to that of the one we started with. When there are four kinds of races it is possible to mate two albinos and find that all of their f_1 progeny are albinos, and so with the orange-colored races.

The mechanism by which the spores become so regularly distributed is very simple. The reduction division spindle and those of the second division are longitudinal, while those of the third division are transverse. When segregation for any pair of factors occurs in the second division the spores alternate two and two for these factors. If one pair of factors segregates in the first division and some other pair segregates in the second division, four kinds, and only four kinds, of spores can be found in one ascus. Lindegren was the first to suggest that second division segregation here is due to crossing-over. He has since proved, through the use of several linked genes, that second division segregation percentages are accurate measures of crossing-over percentages and he has constructed the first chromosome maps in the fungi on that basis. The eight spores from an ascus are comparable to the four eggs and four sperms in animals. Since, in *Neurospora,* gametes of both kinds are derived from a single mother cell the exact relationship of all eight is known. The closest possible inbreeding can be done without loss of three out of four gametes as is the case in animals and seed plants.

Mendelism in Yeast Fungi

Because of the great economic importance of breadmaking and the commercial value of alcoholic fermentation the yeasts have been the object of intensive research. Sexual reproduction with nuclear fusion at ascus formation has long been known for certain genera of yeasts. The common bakers' yeasts, wine yeasts and brewers' yeasts, however, were presumed to develop parthenogenetically, spores being formed without reduction of chromosome numbers. Hybridization of these most useful yeasts was deemed impossible on this account. Winge has shown how false this notion was, as he has made fourteen hybrids to date. He says that after spore germination a short period of budding occurs, then two of these small roundish buds fuse to form a larger ellipsoid cell which becomes diploid by nuclear fusion. This is a departure from what is known for other fungi where normally the vegetative phase is strictly haploid. Christiansen and Chilton have reported solo-pathogenic individual cases of corn smut where the mycelium is diploid, but at reduction normal haploid sporidia are formed, showing that this is merely a temporary aberration.

Winge and Laustsen have shown in a very simple way Mendelian segregation in the slime flux yeast *Saccharomycodes Ludwigii,* where the two spores at either end of the long ascus must be of opposite sex. Normally they germinate within the ascus and immediately fuse. Budding out of elongated diploid cells then occurs. By isolating the four spores from an ascus before they have germinated and fused in pairs, it is found that they will germinate in culture. One spore of each pair will give rise to a haploid yeast either with short buds or with long buds depending on its genotype. These haploid yeasts can be grown indefinitely in culture. The other two spores from the ascus, if they germinate, soon die.

It was assumed that two pairs of factors are operating to account for this behavior; N/n control spore germination, and L/l determine whether the growth shall be by long buds or short buds. Any spore containing the factor n may germinate but it will always die. The authors are not clear as to the sex factors operating here. From their report one could assume that there is a very close linkage between the $+/-$ sex factors, and the L/l, growth type factors. They later found that in one ascus, both spores of one pair germinated and produced haploid yeasts, one with short buds and the other with long buds. They allowed the other pair of spores to germinate in the ascus and they then proved by further analysis that the factor

n had mutated to N. The diploid growth, when allowed to form new asci, showed that these asci were homozygous for the factor N, because all four of their spores germinated to produce haploid yeasts.

It looks as though n were a lethal factor that prevents germination and that it was originally itself a mutant which later *reverted* to the normal N or wild type. That is, in passing from n to N it represents a reversion to and not a mutation from the wild type.

Should we expect a wild yeast to be heterozygous for two such distinct specific types of growth? Mutations are apt to occur in fungi kept long in cultures. This point could be settled by analysis of other cultures of this species collected from the wild or from other sources. If, on the other hand, *S. Ludwigii* is heterozygous through previous hybridization, it could mean that fusions do occur between haploid cells outside of the ascus. Possibly the application of growth substances or sex hormones would bring on cell fusions and hybridization outside the ascus as in other yeasts where Winge has already obtained fourteen hybrids, as noted above.

As the result of a mutation or some other irregularity, a bisexual race of *Neurospora tetrasperma* appeared in culture in which the nuclei of one sex carried a lethal factor. This lethal operates to prevent an ascospore with a single nucleus from germinating to form a functional mycelium. If this lethal nucleus is carried in the same spore with a normal nucleus, that spore germinates normally to produce, under suitable cultural conditions, a functional mycelium which will mature ascocarps with asci. Then the situation is exactly comparable to that described by Winge.

Sex-linked Characters

Haemophilia and color blindness are familiar examples of what are called sex-linked characters in humans, characters which are inherited by a man from his maternal grandmother. In genetic language this means that certain lethal factors are carried on the sex chromosome, X. In our heterothallic ascomycetes we have chromosomes which carry factors determining sex reactions. Any genes in these chromosomes would, in a sense, be sex-linked, although we do not have maleness and femaleness here as in animals.

Saccharomycodes Ludwigii is normally a diploid yeast, according to Winge, and always heterozygous for the sex factors which segregate at the formation of ascospores. If the growth-type factors, L/l, are so strongly linked with the sex factors that crossing-over is difficult or impossible, the yeast could very naturally exist in nature in a heterozygous condition for these factors and be a "balanced heterozygote." Here is a sex-linked differentiation which some will insist is a real sex difference. Of course, the larger and longer bud types are female, the smaller buds are male! That is, we have here male and female yeasts! Further work will no doubt disprove such a statement.

We have in *Neurospora tetrasperma* a similar example where certain factors are strongly linked with the sex factors. Races of one sex produce golden orange conidia; races of the other sex produce conidial masses more pinkish in color. We have never proved a cross-over. A culture of this species from Texas also showed a similar linkage. One can readily tell by their appearance which progeny races will mate and which will not. This situation is comparable to that found by Blakeslee and which led him to designate as "+," races that produced more sporangia than the others which he called "–." This is another good example of "sex-linkage" in fungi.

"Hybrid" Mushrooms

The discovery of heterothallism and the secret of clamp formation in mushrooms by Bensaude and Kneip independently during the last World War, proved a great stimulus to genetic work in this type of fungi. Students have stated that they have obtained hybrids by uniting differently colored haploid races, say, pink and white of opposite sex, through anastomoses, to form a dicaryophytic growth of binucleate cells. Three questions arise here. (1) Are the cells of the dicaryophyte diploid? (2) Is the dicaryophyte heterozygous? (3) Is pink dominant over white? To all of these questions the answer is no. A diploid cell as defined by Strasburger is one in which its nucleus contains the double number of chromosomes. Such a diploid cell is to be clearly distinguished from a cell containing two haploid nuclei even though they are of opposite sex. Since only diploid nuclei can be heterozygous, pink could not be dominant over white. We can not think of a sperm as being heterozygous. The fertilized egg could be heterozygous. The basidia of the mushroom are diploid and normally they are the only cells in connection with which dominance could be expressed.

Dicaryophytes or mixochimeras are among the most interesting and important phenomena in the whole biology of the fungi. They occur in several groups of fungi. They are more interesting for what they *are* than for what they *are not*. If the two nuclei fused as they came into a cell to give us a true hybrid mycelium so that a true hybrid mushroom would result in the end, that would cease to be interesting because that is exactly what ought to happen, judging from the way embryos are developed in animals and seed plants. It is easy to understand what is meant by a diploid phase, but we have not yet opened our eyes to the beauty and significance of these dicaryophytic haploid partnerships. Dicaryophytes in general constitute one of the most important problems in the genetics of fungi.

It is difficult to see how one could obtain a true hybrid mycelium under normal conditions. The larger part of fruit bodies of mushrooms and ascomycetes are haploid; therefore we should not use the term hybrid to describe a mere intermingling of hyphae or nuclei of two different races to form the framework of such structures. If commercially valuable as mushrooms they could be propagated as spawn and given a trade name. They are a sort of chimera or graft hybrid, and any apparent dominance is a false one. After the fusion of two nuclei to form a hybrid basidium or an ascus, the spores that are produced after reduction may give rise to various sorts of mycelia because of new combinations of factors; but, as these new f_1 mycelia are haploid, they are not heterozygous and not hybrids.

DOMINANCE IN FUNGI

Real dominance in fungi is well demonstrated when one crosses an 8-spored species of *Neurospora* with a 4-spored species. All F_1 asci are 8-spored, although there is much spore abortion in these interspecific hybrid asci. Eight-sporedness is dominant over 4-sporedness. Real dominance is also shown when a race of smut with smooth spores is crossed with a race having rough spores and the F_1 spores are rough.

In *N. tetrasperma,* when both parents in a mating carry a certain recessive factor for ascus abortion, all of the F_1 asci from a mating, being homozygous, abort without spore formation. However, if one parent is normal and the other carries the lethal, all the F_1 asci are heterozygous and form spores normally. The wild type factor is dominant over the recessive lethal. In another race of this same species, asci that are heterozygous for a certain other lethal usually abort and become indurated. Here the lethal is dominant over the corresponding factor carried by the normal wild type race.

HYBRID VIGOR

Hugh Dixon, working with *Neurospora crassa,* has recently reported a race which he says shows hybrid vigor because the mycelium grows so much faster than does that of either parent. Since the mycelium must be haploid it could not show hybrid vigor. It is a new race which happens to have a different combination of factors that affect growth. These were contributed to it at the development of the spores in the F_1 ascus which was a real hybrid.

Winge and his associates have reported, as noted previously, that a number of our common yeasts of the industries are actually diploid. They point out, further, that some of their new races show a certain amount of hybrid vigor, or the effects of heterosis. This is clearly possible and no doubt true if their yeasts are actually diploid. This is the first time that an improvement of yeast strains has been undertaken by geneticists.

PROTOPLASMIC STREAMING

Protoplasmic streaming in coenocytic fungi as well as in fungi with septate mycelia is often so vigorous in young growth as to carry vacuoles and other inclusions rapidly in the stream. The question arises: are the nuclei ever carried in the stream like other inclusions, or are the nuclear migrations in *Neurospora* and *Gelasinospora* due to sex attractions? Two races of opposite sex grown together in culture become heterocaryotic; but would intermingling of genetically different races of the same sex also give rise to a heterocaryotic mycelium because of nuclear migrations due to streaming?

PHENOTYPIC AND GENOTYPIC SEX DIFFERENCES

No antheridia or archegonia are produced in one-spore cultures of *Ascobolus magnificus,* which is strictly heterothallic. When + and – races are grown opposite each other, antheridia and archegonia are produced in the zone where hyphae of both races intermingle. These organs always arise from different branches. Due to the maze of branching and anastomosing, it is impossible to trace their origin back very far one way or the other. This species ought to respond to the application of sex hormones to determine whether only antheridia are produced by one race and archegonia by the race of opposite sex reaction, proving that +/– relations are strongly linked with factors representing morphologically differentiated organs.

Blakeslee long ago made tests of +/– races of *Phycomyces* against hermaphroditic species of *Zygorhynchus* and *Absidia.* His results would indicate that mere size differentiations are not a reliable test for sexuality. If sex-linked genes are concerned, we must expect crossing-over, provided cell size factors and sex reaction factors are neither identical nor alleles.

Raper has added support for the theory that sex stuffs or sex hormones play an important part in sexual differentiations and sex reactions. This is not saying that I accept the statements by Moreau and his associates to the effect that a unisexual race of *Neurospora* derived from a single spore from an 8-spored ascus can be induced to mature ascocarps with asci and spores simply by the stimulus furnished by hormones produced by a mycelium of the opposite sex reaction. I have repeated their experiments many times without finding any evidence in support of their claims. I have faith, however, that growth substances and hormones will prove very useful in inducing a fungus race to develop to the full extent of its potentialities as represented by its factors of inheritance.

The theory of relative sexuality is being lifted above the realm of mysticism by Moewus and his associates and presented in a form that can be more generally accepted. They are studying the simple one-celled algae genetically. *Chlamydomonas Braunii* is a species having gametes of two different sizes, male and female, as they are called. It is strictly heterothallic genetically. Evidently the factors for heterothallism or +/− sex reaction characters, are very closely linked with the factors that determine cell size. *C. eugametos* occurs in several forms, one is isogametic and heterothallic. These sex factors segregate according to the Mendelian ration 50 : 50. By mating races of this species against ♀ and ♂ races of *C. Braunii,* Moewus proves that the "+" race of *C. eugametos* is female and the "−" race is male, and from this point on he discards the +/− symbols. This is interesting, coming from one of the foremost exponents of the theory of relative sexuality. He says in effect that two gametes morphologically exactly alike can be genotypically *male* and *female* because of the way they *function.* Other varieties of this species are hermaphroditic in the sense that sex differentiation is phenotypic so that each cell of the sporeling develops gametes, the progeny of which may fuse. Moewus explains this apparent anomaly by assuming that the realizators F and M are located on homologous chromosomes, but they are not alleles. Time does not permit further analysis of this work, but it should certainly prove illuminating and helpful to those who are working with similar problems in the fungi, such as species of *Glomerella* and other homothallic fungi.

Every mycelium of *Neurospora sitophila* develops: (1) incipient ascocarps with receptive organs; (2) small microconidia or spermatia and (3) large monilioid conidia. In earlier days I would have insisted that the receptive structures are female, the microconidia are male, and the monilioid conidia are asexual spores. To-day I am not so sure. If the spermatia are male because they can function in fertilization, then the monilioid conidia are super-males because they can do everything the spermatia can do and do it better. Suppose you take a little brush and wipe up some of the orange-colored powder from an infected loaf of bread, and then paint this on a culture of a mycelium of the opposite sex. Observe what follows after 24 hours and then sit down and write me definitions of sex, male and female, that will apply equally well to animals, higher plants and the fungi.

Double Fertilization in Ascomycetes

The older mycologists assumed a nuclear fusion in the primordia of ascocarps to be the essential stimulus for further development. Such an assumption would seem logical if we again consider embryo and seed formation in animals and plants. The discovery, half a century ago, that two nuclei fuse at the origin of the ascus and the basidium, stimulated cytological research to find nuclear fusions in the ascocarp primordia. As a result of these studies double fertilization or two sets of nuclear fusions in the life cycle of a number of species of ascomycetes have been reported, the fusion in the primordia being the true fecundation, that in the ascus merely a compensating fusion. This has been supported by cytological evidence that a double reduction of the number of chromosomes occurs in the nuclear divisions in the ascus. Gwynne-Vaughan and her associates have reported double fertilization and double reduction in *Ascobolus magnificus* and *A. stercorarius.* From what we now know of the genetics of *Neurospora* and the phenomenon of crossing-over it would not be difficult to settle this old controversy once and for all by a genetic study of the two species of *Ascobolus* just mentioned. In crosses involving three pairs of genetic factors such as factors for sex, for spore color and for type of mycelial growth, we should find that the spores would alternate either *four* and *four* or *two* and *two* for any pair of factors, if there has been only one nuclear fusion. Regardless of how many pairs of factors should be represented in the mating no ascus should ever show over four kinds of spores.

Those who uphold the theory of a double fertilization and double reduction could prove their point absolutely by finding either that the eight spores alternate *one* and *one* for a certain pair of factors, or that sometimes eight genotypically different kinds of spores occur in an ascus. *Ascobolus carbonarius, A. geophilus* and *A. immersus* are also heterothallic. Analysis of spores from individual asci have been made by Betts for the first two species and by Rizet for the last one. They found no *"one and one"* alternation. Until this is done we must assume that in all ascomycetes, as in all other plants and animals, only one nuclear fusion occurs in a life cycle.

No genetic evidence has been obtained in *Neurospora* for such a double fertilization. All are agreed that no nuclear fusion occurs in *Neurospora* at the origin of the ascocarp.

Conclusion

In closing I may point out that we should discuss topics arising in genetic studies of the fungi with the view to aid rather than to interfere with progress. Clearness of understanding of what one aims to accomplish in the end is certainly desirable and helpful.

Knowledge of the principles of inheritance in the fungi accumulated to date, should serve to warn those charged with breeding economic plants for resistance that they must first be informed regarding the stability or limits of variability of the parasites they seek to circumvent. We know now that new races of fungi are arising through natural hybridization. Hybrid structures have been obtained showing dominance and Mendelian segregations with crossing-over at reduction which is such an important feature in furthering evolution. We also find in the fungi: mutants, lethal factors, deficient chromosomes, sex-chromosomes, sex-linked characters and other genetic features. To repeat what I have said elsewhere: "The fungi in their reproduction and inheritance follow exactly the same laws that govern these activities in higher plants and animals."

I have tried to show that the fungi are not degenerate organisms which are on their way out in a scheme of evolution and so of little economic importance and scientific interest. The fungi, on the contrary, are progressive, ever changing and evolving rapidly in their own way, so that they are capable of becoming readily adapted to every condition of life. We may rest assured that as green plants and animals disappear one by one from the face of the globe, some of the fungi will always be present to dispose of the last remains.

CHEWING AS A TECHNIQUE OF RELAXATION

By Professor H. L. HOLLINGWORTH

BARNARD COLLEGE, COLUMBIA UNIVERSITY

MOTOR automatisms in great variety have often been explained as "tension outlets." Tics and other accessory movements have been said to be the expression of "inner tensions" or perhaps to be the "symbolic release" of such tensions. Fidgeting, wriggling, pipe smoking, gum chewing, automobiling and various active sports have received a like extenuation. There has been, however, little precise definition of the character of these alleged "tensions," and experimental evidence of their relief by the collateral activities cited is not abundant. We present here a brief summary of a protracted series of experiments on this topic, conducted during the period of a year and involving the measurement of a considerable number of processes in 20 subjects during 20 experimental days.[1]

The experimental approach requires first of all specific measures of various forms of "tension," since this word has many meanings. It requires also a technique of producing collateral motor automatisms and maintaining them, under controlled conditions. Perhaps the most popular of the automatisms referred to is chewing. Our subjects have been studied under three conditions: (*a*) Normal—not chewing and having nothing in the mouth; (*b*) Chewing—the masticatory being ordinary confectioned chicle, sweetened and flavored; (*c*) Control—allowing a flavored candy wafer to melt in the mouth, as a control over such things as suggestion, sensory stimulation and like influences. The studies of the Carnegie Nutrition Laboratory have shown that the metabolism costs of chewing are the same, whether a gum or a rubber stopper be used.

The experimental schedules were so arranged as to equalize such factors as practise, fatigue and individual differences. In all cases a preliminary base was secured, and the experimental variations gave measures which could always be expressed in terms of the base for the particular working period. The subjects were throughout engaged in various types of standardized work, proficiency in which was always measured. Concurrently the various measures of tension were secured.

Tension as Nervous Restlessness. Without the knowledge of the subjects, special observers watched them throughout the working day and periodically rated each on a scale of motor restlessness. A restless movement was described as any motor activity irrelevant to the work being done at the moment. The units of comparison are steps on the rating scale, and since these may not be quantitatively equal the measures are relative only; but their direction is clear and consistent.

In one experiment (6 subjects, 6 full days of work and observation) a decrease of 9 per cent. in restless movement was found in the chewing periods. In another experiment (4 subjects, 4 days) a decrease of 10 per cent. was found. On the whole, therefore, there is a decrease of some 10 per cent. in restlessness while the masticatory is in use.

Tension as Feeling of Strain. After each round of work (about 45 minutes) the subjects rated on a linear rating scale their subjective feelings during the period. The linear scale was marked off into 20 equal steps, ranging from extreme strain at one end to extreme relaxation at the other. The rating was made by crossing this line with a pencil at some point between these two extremes. The units of comparison are again steps on the rating scale.

The workers unanimously report themselves as feeling more relaxed while chewing than during either of the other two conditions (normal and control). In

[1] The data are reported in full in the writer's recent monograph, "Psycho-Dynamics of Chewing," *Archives of Psychology*, No. 239, July, 1939, pp. 90.