HEREDITY, VARIATION AND EVOLUTION IN PROTOZOA

I THE FATE OF NEW STRUCTURAL CHARACTERS IN PARAME-CIUM, IN CONNECTION WITH THE PROBLEM OF THE INHERITANCE OF ACQUIRED CHARACTERS IN UNICELLULAR ORGANISMS

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WITH 22 FIGURES

INTRODUCTION

1 Object of the Work

The investigations of which the first instalment is here presented are designed as the beginning of a study of the problems

of evolution in unicellular organisms.   The question in the center
of interest is: How do new inherited characteristics arise ?   To
study this question a knowledge of the normal phenomena of vari-
ation and inheritance is required.   Our first contributions will
therefore deal with these normal phenomena, with incidental
attacks on the main problem as opportunity presents.   We shall
take up inheritance, variation, specific differences, correlation,
growth, regulation, selection, and related topics, dealing with
them by experimental, observational and statistical methods.   A
large part of such a study, in the common infusorian Paramecium,
is now complete.   The present instalment deals with the definite
and circumscribed problem of the fate of new structural characters.

2   General Plan of the Investigation and Principles Guiding It

In presenting the first instalment of an extensive series of inves-
tigations, it will be well to set forth in an introductory way the
general considerations which have guided the work, together with
its relations to previous investigations by the author.   Though
apparently a complete departure from the matters dealt with in
most of my work up to this time, it is in reality a logical continu-
ation of my previous work.   The latter has lain hitherto in the
field of the physiology of behavior and reactions.   In this field I
have endeavored to analyze and isolate, so far as possible, the
various factors at work, keeping in the foreground of interest the
problem of how the behavior happens to be so largely *adaptive*.
It is possible to show that certain of the features of behavior—
and precisely certain adaptive features—arise during the life-
time of the individual, by physiological processes which appear
quite intelligible from a thoroughly causal standpoint.   These
are the processes known variously as the formation of habits; as
learning; as modification by experience; as expressions of the
readier resolution of physiological states after repetition, etc.

But in this field, as in all other parts of biology, we find many
characteristics, and particularly many *adaptive* features, which
have not arisen during the lifetime of the individual.   Certain
structures, certain processes, certain reactions, often highly adap-

tive in character, are found to be constituent parts of the organism, yet they have not arisen in the way mentioned, but are "inherited" from past generations. Such characteristics, in the field of behavior, are spoken of as reflexes, tropisms, instincts, etc.; they are often of a highly complex character.

Our next task is then to investigate the processes by which these characteristics have arisen. The problem is parallel—perhaps rather identical—with that which the student of structure sets himself when he asks how it happens that the animal possesses certain complex adaptive structures that are inherited from its progenitors. We cannot hold that complex characteristics can arise without any processes leading to them, unless we are prepared to abandon the scientific method Where shall we look for the processes giving rise to characteristics that do not take origin in the lifetime of the present individual?

Clearly, there is but one possibility here. What we call the "individual life" is not the entire history of this mass of matter and energy that we call "an animal." It has existed for numberless ages in connection with other individuals, as "germ cell," or the like. Since the animal becomes modified and adapted in accordance with certain physiological laws, even in the brief span of its individual life, it is evident that the unmeasured ages of its previous existence could hardly pass without the occurrence of processes of modification. And it is only in this period that the processes could have occurred which have given it the complex inherited characteristics that it now has. We have then no alternative but to study the nature of these processes, if we wish to understand the origin of the characteristics under discussion.

Such a study of the processes by which organisms become modified in the life history of the race is of course as much a part of physiology as is the study of the processes of metabolism, and it must be pursued in the same spirit. Most of the existing science of physiology deals with the rapid processes taking place in the lifetime of the individual and in its "body." But of course the slower processes occurring in the germ material and resulting in modifications which become apparent in later generations are processes occurring in space and time, and open to objective experi-

mental investigation, exactly as are other physiological processes.
There is the same reason to suppose them detectible by chemico-
physical means as in the rest of physiology.   There is indeed no
reason for making any distinction in principle between these and
the processes of movement or metabolism.   The investigator in
this field simply works on a part of the domain of physiology which
has been mainly cultivated independently of the remainder of
that science.   In no way is the study of racial processes to be so
much advanced as by considering this field, what it really is, a
constituent part of physiology, and by attacking it from the same
standpoints that have proved their worth in the rest of this science.
Study of essentially this character is well under way in the work of
the modern students of heredity—Bateson, De Vries, Davenport,
Tower, Herbst, and others—though the point of departure has
been in most cases not primarily physiological.

The *special* methods used—the *technique*—in a physiological
investigation of racial processes will of course be extremely dif-
ferent from those of an investigation of metabolism or contrac-
tility; it is only in fundamentals that the method of attack must
be the same.   Every problem requires its own technique.   In
the study of racial processes we have to deal with certain problems
and phenomena which have as a rule not been looked at from a
physiological point of view.   They are nevertheless physiological
matters, and need restatement in physiological terms.   Let us
attempt this:

Evolution, from this standpoint, is a general name for the physio-
logical processes which result in change of characteristics from
generation to generation.   The physiological study of evolution
is the objective and experimental investigation of these processes.

Adaptiveness, purposiveness, teleology, etc., are concepts based
on the observed phenomena that the characteristics of organisms
are largely of such a nature as to maintain the processes which we
call life, and thus keep the organisms in existence.   From a purely
physiological point of view the teleological problem is essentially
this: How does it happen that combinations of such complexity

of structure and action can continue to exist?* Or to put the question in a way that leads directly toward investigation: What processes lead to the production of lasting combinations, of such complexity of structure and action as are found in organisms?

In considering this question, we are struck by the evident fact that certain combinations of the various factors making up the universe *are more lasting than others*. Two constituents (as gold and oxygen) come in contact; they do not unite, and the combination constituted by their juxtaposition is quickly dissolved by the incidence of other forces. Two other constituents (as iron and oxygen) come into contact; they unite, and the combination resulting from their juxtaposition is a relatively lasting one. Such varying permanence of different combinations is seen in every field, but it is particularly striking among such complex bodies as go to make up organisms. Here the persistence of certain combinations and the evanescence of others is commonly spoken of as *selection*. The combinations which persist are said to be *selected*. The term is undoubtedly, for certain reasons, an unfortunate one.

In the study of organisms, as we have seen, one great class of problems lies in the question, How can such complex combinations as organisms be *lasting?* Now, the study of what combinations are lasting is precisely the study of so-called selection, and so it happens that in the investigation of the processes by which organisms have acquired their characteristics, the study of selection necessarily plays a very large part.

Selection has often been looked at from an extremely narrow loophole, so that only a small part of it has been seen. In a common case, only the fact that certain *individual animals* are more lasting than others is taken into account; on this selection from among individuals attempts have been made to base an entire theory of organic evolution. It would seem incredible that anyone should suppose the principle of selection to be limited in its operation to this one class of combinations, did not history show that such views have been held. Selection is merely a name for certain aspects of the way the world process takes place. The

*This formulation of the problem we owe essentially to Jensen ('07), whose valuable paper cannot be too strongly recommended to those who wish to view such problems from a physiological standpoint.

greater permanence of certain combinations and activities is evident everywhere outside the limits of organisms, while within the system making up the individual organism there are conditions which require the prevalence of this principle of operation, on a large scale.   To selection, or the greater permanence of certain combinations, *within* the organism, we must look for an understanding of many of the most important problems of biology, and particularly of those having to do with adaptation.   The study of the internal adaptations of organisms might indeed be defined as the search for those combinations of structure and activity that are most lasting.   The study of the laws in accordance with which certain combinations are lasting, while others are fleeting, must become one of the main lines of investigation.   The pioneer work of Roux ('81) in this line was most promising, and has been followed up to a certain extent; but thorough experimental investigations along such lines are what is needed.   In the meantime, the relative permanence of those combinations which we call individuals must remain one of the chief objects of study.   As Kellogg ('07) has well noticed, we have few, if any, cases even of this, that are clearly and accurately observed and analyzed.

All together, it is clear that a study of the processes which result in the complex "adapted" organism must be largely a study of the relative permanence of different combinations—a study of selection.   This of course requires a study of the chemico-physical laws in accordance with which the processes are brought about, and in accordance with which some of their products are more lasting than others.   It is in many respects unfortunate for an understanding of this line of work that it has received the figurative and anthropomorphic name of *selection*.   When we speak merely of the relative permanence of different combinations (whether these combinations are individuals, processes, or chemical compounds), we call up no associations foreign to the matter in hand, and thus run no risk of arousing misconceptions and prejudice due to such associations.

In studying the racial processes, that have resulted in giving the organism its "hereditary" properties, we meet one great difficulty.   We cannot reproduce the long series of conditions which

have acted upon the organism when it lived in connection with individuals of past generations. We cannot hope, then, to study the precise processes which have given rise to the particular combination of characteristics which we find in Paramecium or the dog or in any particular existing organism. All we can hope to do is to study similar processes in progress, controlling and analyzing them experimentally, till we work out the laws and principles of their action. By application of what we thus gain to the results of processes past, we may hope to reach an understanding of how organisms have arisen.

3 Place of the Present Investigations in this Plan

In taking up a study of these racial processes, we must first learn as accurately as possible what occurs in the passage from one generation to another; what resemblances and differences are normally found between members of succeeding generations, and the like. In other words, we must have a knowledge of the normal phenomena of heredity and variation, such as is now being acquired on a large scale in higher animals. When this is obtained we may proceed to attempt to modify experimentally the processes and their results—thus approaching the central problem: How do inherited modifications arise ?

In such work, the relations found in the simplest organisms deserve investigation. Here we have reproduction taking place rapidly (a generation or more a day) and in the simplest forms. I have therefore undertaken a study of the physiology of racial processes in the Protozoa. Bearing more or less directly on this matter we have already a large amount of most valuable work, such as that by Maupas, Hertwig, Schaudinn, Calkins, Woodruff, Enriques, and others. I have approached the matter however from a different standpoint, setting the problems of inheritance and variation definitely in the center of interest. This results in somewhat different methods of attacking the subject.

ASSUMED DIFFERENCE IN HEREDITY BETWEEN UNICELLULAR AND
    MULTICELLULAR ANIMALS—THE "INHERITANCE OF ACQUIRED
    CHARACTERS"

It is often said, and it seems to be generally assumed, that uni-
cellular animals differ fundamentally from multicellular ones in
heredity.*   In the Protozoa there is no separation into cells which
normally die after a certain period ("somatic" or "body" cells),
and cells which continue to live and multiply ("germ" cells).   The
parent produces progeny by simply dividing, so that parents and
progeny are identical.

This seems to simplify extremely the problem of heredity, or
indeed to remove everything problematical from the subject.
Parents and progeny must be *alike*, it is said, because they are
the same.   In particular it is commonly held that this removes
from the Protozoa all difficulty as to the "inheritance of acquired
characters"—characters added during the lifetime of the indi-
vidual and due to environmental action, experience, use, accident,
or the like.   Such characters are in multicellular organisms often
called somatic, as distinguished from germinal, and such somatic
characters are commonly held not to be inherited.   Where there
is no such distinction between soma and germ, it would seem clear
that there can be no distinction between somatic and germinal
characteristics.

To this difference in heredity between Protozoa and Metazoa
much importance has been attached.   If the difference really
exists, the Protozoa are much more plastic in evolution than are
the Metazoa; through the inheritance of the effects of experience,
use and environment, the Protozoa must permit of the ready and
rapid production of varied and adapted types.   This point has
been emphasized by many writers.   For example, in attempting
to account for the great diversities of organization and action
found among animals Whitman ('99) writes as follows:

"In primitive organisms multiplying by simple fission, struc-
tural modifications acquired during the lifetime of the individual

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*I use the word "heredity" merely as a brief and convenient term for "the resemblance between
parents and progeny," without implying any underlying entity, and without prejudice as to the
grounds of this resemblance.

would be carried right on from generation to generation, and hence structural foundations for a whole animal world such as we now see could be laid in a relatively short period as compared with the time necessary to advance organization in forms limited to reproduction by germs. In fact the fundamentals could all be established within the realm of the unicellular Protozoa" (p. 307).

In my book on the Behavior of Lower Organisms, I expressed similar ideas, with particular reference to the inheritance of ways of behaving:

"In the unicellular organisms there seems to be nothing in the way of this inheritance by the offspring of the reaction-methods acquired by the parent. There is no distinction between the germ cells and body cells in these organisms: all acquirements pertain to the reproductive cells. Through reproduction by division the offspring *are* the parents, merely subdivided, and there is no evident reason why they should not retain the characteristics of the parents, however these characteristics were attained. If this is the real state of the case, then in unicellular organisms the life of the race is a direct continuation of the life of the individuals, and any acquirements made by the individuals are preserved to the race" (Jennings '06, p. 320).

Now, if this difference between unicellular and multicellular organisms actually exists, it is evidently of the highest interest and importance. Yet there have been no investigations of the matter to see if there really is such a difference. Our first task is then to examine the phenomena from this standpoint; attempting to determine whether characteristics acquired during the lifetime of the individual* are inherited by the progeny. At the same time, we shall keep in mind the broader aspects of our problem, endeavoring to work out in general the relation of reproduction in the Protozoa to heredity.

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*I use for convenience the term "individual," as commonly employed, to signify in the Protozoa the separate free cells. I have no wish thereby to take any stand on Calkins' contention that the entire cycle of cells derived from a conjugating pair corresponds to the individual of the Metazoan (Calkins '06). The present paper deals with certain existing phenomena, which are not altered by the views one may hold on this point. The relation of conjugation to heredity is to be taken up in a later communication.

THE FATE OF NEW STRUCTURAL CHARACTERS ("ACQUIRED
CHARACTERS")

As we have just seen, it is commonly held that "acquired characters" are inherited in the Protozoa, though not in the Metazoa. Do experiment and observation show that this is true? Does the separation of germ and body cells make a fundamental difference in heredity?

1 Localized and Unlocalized Characteristics

In dealing with new or "acquired" characters, it is well to distinguish two classes. On the one hand are those characters (mainly structural), that are localized in a definite part of the body, as cilia, setæ, a mouth, etc. On the other hand there are characters that affect the organism as a whole; such are acclimatization or other general modifications due to heat, cold, chemical agents, etc.; size, method of growth, and the like. The inheritance of the latter class of characteristics, however acquired, presents much less apparent difficulty than does the inheritance of the former. The importance of this distinction between localized and unlocalized characteristics, in investigations of heredity, has often been emphasized. Weismann has repeatedly demanded as proof of the inheritance of somatogenic characters in Metazoa a demonstration of "the transmission of changes of single definite parts of the parents to the corresponding parts of the progeny;" of the inheritance of "definite parts or localized functions." It is clear that a somewhat different problem is involved in the two classes of cases. We shall take up first localized characters in the Protozoa.

2 Typical Examples of Inheritance and its Problems in Protozoa

To appreciate the problem of the inheritance of localized characters, we will look at one or two simple cases in the Protozoa; these will serve to bring the whole problem of inheritance in these animals to a point.

Paramecium (Fig. 1) has a blunt anterior end and a pointed posterior end. How does it happen that after fission similar

features are found in the progeny ? The animal has in the anterior half an oral groove; near its middle a mouth; near the aboral side two contractile vacuoles. How does it happen that the progeny have similar structures ? If one of these structures should become modified in the parent, would this modification appear in the progeny ?

For a more complex case, we have in Oxytricha (Fig. 2), a definite, typical distribution of the organs of locomotion. There are, for example, regularly five large setæ in a row near the pos-
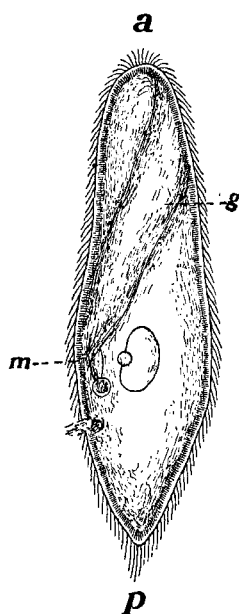

Fig. 1 Paramecium, to illustrate the problems of inheritance in Protozoa. By mere transverse fission the blunt, grooved anterior end *a* would be left with only one individual, the sharp posterior end (*p*) with another. *m*, mouth; *g*, oral groove.

terior end (*S*, Fig. 2). In other infusoria, related to this one, these setæ appear in different form, number or arrangement. How does it happen that after fission the progeny have setæ of the same size, structure, arrangement and position as did the parent ? If the parent loses one of these setæ, will the reduced number appear

in the progeny ?   Similar questions must be asked for each of
the organs of locomotion and other structures, seen in Fig. 2.

These questions regarding details show that we do not after
all gain much for understanding inheritance in Protozoa by such
statements as that "parent and progeny are the same and so must
be alike."   For in simple transverse fission of Paramecium there
is no reason that is at once apparent, why the anterior product
should have at its posterior end a point, as its parent had, nor why
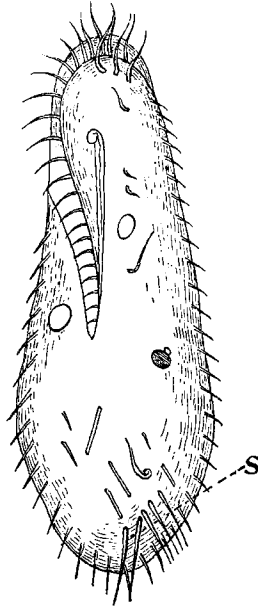the posterior product should have a blunt anterior end with a

Fig. 2   Oxytricha fallax.   Mere transverse fission would leave the five large setæ *s* with only one of
the resulting individuals.

groove along one side; these are not simply passed on, ready made,
to the progeny.   Again, the simple transverse fission of Oxytricha
does not account in the least for the fact that the anterior product
of division has the row of five setæ at its posterior end.   The five
setæ might be transmitted directly to the posterior daughter-infus-
orian, but the anterior individual would naturally be left quite
without such structures.   Indeed, by repeated mere divisions

(even if followed by increase in size), progeny would after a time be produced that would have little resemblance to the parent.

Thus it is evident that even in the Protozoa heredity is not a mere result of subdivision. The question returns with force: How does it happen that the localized structures of the progeny are the same as those of the parent ? And *are* they the same in all cases ? Are they the same when the characteristics of the parent have become changed during its lifetime as an individual ?

We shall take up first the simplest and most marked characteristics—new appendages, spines and the like; marked changes in the form of parts of the body; all sorts of things that might be characterized as mutations, abnormalities, monstrosities, etc. We shall deal at the same time with mutilations.

THE FATE OF NEW LOCALIZED STRUCTURES IN PARAMECIUM, WITH OBSERVATIONS ON GROWTH AND REGULATION OF FORM IN THIS INFUSORIAN

By examination of dense cultures of Paramecium* many individuals were found which differed in certain respects from the usual form or structure. Some had a short, truncate anterior end; others a blunt or truncate posterior end in place of the sharp tip; others were crooked or otherwise modified in form; others showed angles, teeth or spines on various parts of the body. Many of these were isolated and allowed to reproduce under observation, so as to follow the fate of the peculiarity in question.

The method of isolation and culture was essentially that described by Calkins ('02). The individuals were placed separately in the concavities of hollow-ground glass slides, in three or four drops of hay infusion, which was changed either every day or every two days. The animals were examined once or twice a day.

1   History of a Large New Appendage in Paramecium

I shall first describe in detail a typical case of a new structure; an individual that bore on its body a spine (Fig. 3). This case is particularly instructive because the origin of the peculiarity

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*The animals studied had the characteristics usually attributed to Paramecium caudatum. The question of distinguishing species will be taken up in later parts of this general investigation.

was observed, and its history followed for many generations. The observations on this structure likewise give certain important results as to the method of growth in Paramecium.

First generation. The ancestor of the race we are to study was a crooked individual (Fig. 3, *a*), found in a culture containing many specimens, where food was getting scarce. I have called this individual *a*; we shall use this designation for the race as a whole, appending certain exponents to indicate the various members of the different generations. The anterior individual resulting from fission will be designated by the exponent (^{1}), the posterior individual by the exponent (^{2}).

The original individual *a* was bent just in front of its middle at practically a right angle (Fig. 3, *a*). It was isolated at 2.50 p.m., May 2, 1907.

Second generation. The first division, during the night of May 2, showed that the crookedness was not to be inherited, though it had its effects on the progeny. The animal divided transversely, posterior to the bend in its body. The posterior product (a^2) was normal in all respects, so that it need not concern us further. The anterior product (a^1) was of about the form that would be expected from dividing *a* behind the bend in its body, save that the posterior end had become still more irregular. This end was broad and truncate; nearly triangular when seen from the rear; it extended backward at two of the angles as two pronounced points (Fig. 3, ^{2}).

Shortly after division the daughter individual a^1 changed shape greatly; the posterior end budded out a new structure of nearly the normal shape for the posterior half of the body (Fig. 3, ^{3}). But this new part formed an angle with the anterior half, so that the body of this individual was again crooked. At the same time the anterior end extended a little. The two teeth remained near the middle of the body, the larger one having been carried back a little, so that it was a little behind the smaller one.

Third generation. At the next division (forenoon, May 4) the constriction appeared between the two tooth-like projections, and the plane of division was oblique (Fig. 3, ^{3}). Thus the smaller one of the two projections was at the posterior end of the
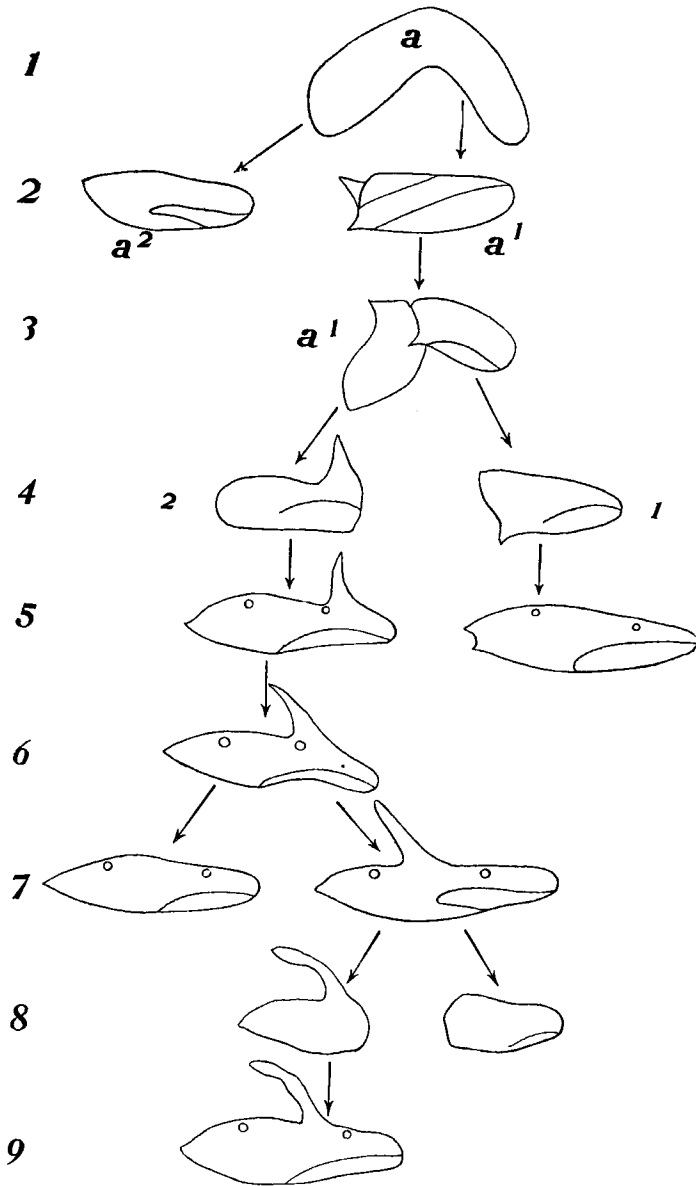
Fig. 3 Transformations in the race *a* during the first four generations. The anterior end is to the right. *a*, the original crooked individual (first generation). *a*¹, *a*², the anterior and posterior products of its fission. At *3* the individual *a*¹ has grown and is dividing, giving the individual *1* (anterior) and *2* (posterior). The arrows show the origin and transformations of each individual. For details, see text.

anterior product $a^{1\cdot1}$, while the larger projection was at the anterior end of the posterior individual $a^{1\cdot2}$.   In the period just before and after the separation of the two parts (which occurred at 10.55) this larger projection grew rapidly still larger, longer and sharper, as if it were being pushed out under pressure.   Immediately after division the posterior product $a^{1\cdot2}$ had the form shown in Fig. 3, [4], the projecting spine being as long as the body was thick, and situated on the aboral side, nearly at the anterior end.

Now this posterior individual $a^{1\cdot2}$ began to grow rapidly. Growth was most rapid at the anterior tip; this pushed out so as to leave the spine at some distance from the anterior end.   The spine itself became still longer and stouter.   At the same time the entire body increased in length, the growth seeming most rapid at the anterior end and decreasing toward the rear.   Twenty minutes after division the posterior individual $a^{1\cdot2}$ had the form shown in Fig. 3, [5].

The change of form now continued much more slowly, so that at the end of four hours the shape was that shown in Fig. 3, [6].

In the anterior individual ($a^{1\cdot1}$) a parallel process of growth occurred; the anterior part of the body pushed out rapidly, while the posterior part merely changed shape a certain amount.   The small projection was thus left near the posterior end, on the oral surface (Fig. 3, [5]).

Thus we have now on each of these individuals a definite new structure, the origin of which we know, while the animals are quite normal in other respects.   The new structures have arisen during the reproductive processes—at a period comparable, if there is any such in the life of the infusorian, to the germ cell period, just before development begins, in a Metazoan.   Tower ('06) found that in certain Metazoa changes wrought in the organism at this stage of its life give rise to permanent inherited modifications, though environmental effects at other stages are not inherited.   We have then perhaps as favorable a case for studying the transmission of a suddenly produced new structure as we could expect to find in the Protozoa.

We shall here follow only the history of the large anterior spine, in $a^{1\cdot2}$ (Fig. 3, [6]), taking up later the fate of the short tooth in $a^{1\cdot1}$.

Fourth generation. We left the individual with the long anterior spine in the condition shown in Fig. 3, [6]. At the next fission (night of May 4) the spine remained with the anterior product $a^{1\cdot 2\cdot 1}$, while the posterior product $a^{1\cdot 2\cdot 2}$ was a typical individual without a spine. In this fourth generation, since the division had taken place at the middle and there was subsequent outgrowth of the anterior tip, the spine was left behind the middle of the new individual (Fig. 3, [7]). The spine itself had become still longer and more slender. In structure it was a tube of ectosarc enclosing a narrow canal filled with endosarc. It was flexible, bending readily when it came in contact with obstacles, but it did not show active movements.

Fifth generation. At the next division (noon, May 6) the plane of division lay just in front of the base of the spine, so that the latter went to the posterior individual ($a^{1\cdot 2\cdot 1\cdot 2}$), and was situated at its anterior end (Fig. 3, [8]). The other (anterior) individual ($a^{1\cdot 2\cdot 1\cdot 1}$) was normal, as usual. In the process of growth, consisting largely in the pushing out of the anterior end, the spine came to lie farther back than at first, so that in the adult infusorian it was a little in front of the middle (Fig. 3, [9]). The spine had become slightly enlarged at its tip, and bent to the right at about its middle.

Sixth generation. The plane of the next division (night of May 6) passed just behind the spine, so that the latter was now left on the *anterior* specimen, $a^{1\cdot 2\cdot 1\cdot 2\cdot 1}$, while the posterior specimen was normal. The spine was now bent near the base, so as to extend backward parallel with the body axis (Fig. 4, [6]).

Seventh generation. At the next division (night of May 7), the spine of course went to the posterior individual, $a^{1\cdot 2\cdot 1\cdot 2\cdot 1\cdot 2}$ (Fig. 4, [7]). It was situated a trifle in front of the middle of the body. The spine was now long and curved downward and backward over the right side of the animal. Its base was much broader than before, and a shorter spine had pushed out forward from the angle between the base of the spine and its main body.

Eighth generation. At the next division (night of May 8), the spine went to the anterior individual ($a^{1\cdot 2\cdot 1\cdot 2\cdot 1\cdot 2\cdot 1}$) and was situated very nearly at its posterior end, though a little displaced toward
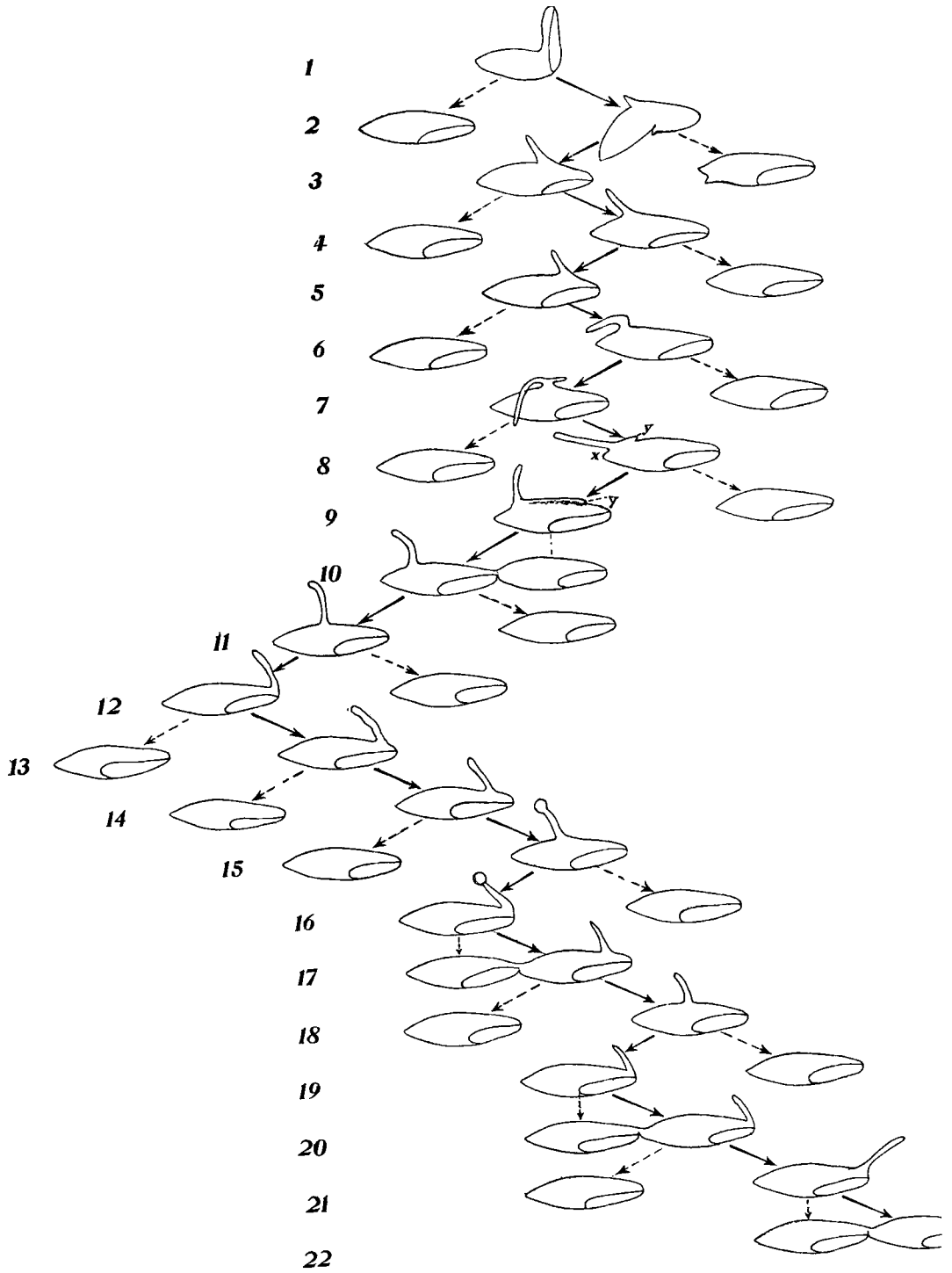
Fig. 4 Diagram of the history of the race *a*, bearing the spine, for the entire twenty-two generations. The anterior end and anterior individual are throughout to the right. The numbers at the left indicate the generations, counting the original crooked specimen as the first. The arrows show the lines of descent. Only the fission of the individual bearing the spine is followed out in each generation. For details, see text.

the aboral side. Its base had become broad and low, extending between x and y, Fig. 4, [8]. There is reason to think that it actually extended back of x, to the posterior end. It would naturally be carried back in the backward growth of the posterior tip, but owing to the abrupt point naturally found here, there is nothing to mark the end of the base, as there is at y. The anterior point (at y) had dwindled to a mere knob, while the main spine trailed behind, half the length of the body.

Ninth generation. At the next division (night of May 9), the spine passed, as was to be expected, to the posterior individual $a^{1\cdot 2\cdot 1\cdot 2\cdot 1\cdot 2\cdot 1\cdot 2}$. Certain interesting changes have taken place in the position and structure of the spine, which throw light on the processes of growth, and which have important consequences for succeeding generations. The free part of the spine is still very near the posterior end, and stands again at right angles to the body (Fig. 4, [9]). The broad base of the appendage (x-y, Fig. 4, [8]) has been still farther drawn out in the processes of growth, so that it extends forward almost to the anterior end (to the point y, Fig. 4, [9]). Posteriorly its end is not evident, but it doubtless reaches to the posterior tip. Thus the base of the spine now extends nearly the entire length of the body, so that it must be cut by the next fission plane.

It will be observed that up to this time the spine has regularly alternated between the anterior and posterior individuals in the successive generations. This is indicated in the designation employed ($a^{1\cdot 2\cdot 1\cdot 2\cdot 1\cdot 2\cdot 1\cdot 2}$), the exponent ([1]) indicating in each case the anterior product of fission, the exponent ([2]), the posterior product. When situated on the anterior individual the spine lies back of the middle of the body (see Fig. 4, [4,6,8,10], etc.) When on the posterior individual it has always lain in front of the middle of the body (see Fig. 4, [3,5,7]), till in the present generation (Fig. 4, [9]). These changes in position are due to the growth occurring after fission; they give us a means of analyzing this growth—a matter to be taken up later.

Tenth generation. At the next fission (May 10, day) the free portion of the spine went again to the posterior individual, thus breaking the regular alternation which has prevailed up to this

time. The individual bearing the spine is therefore $a^{1\cdot2\cdot1\cdot2\cdot1\cdot2\cdot1\cdot2\cdot2}$.
The effect of the ridge forming originally the base of the spine
(x-y, Fig. 4, [8]) is shown in the fact that the two individuals did
not separate, as usually happens; they remained connected by a
sort of bridge passing along the aboral surface (Fig. 4, [10]). Evi-
dently the substance formed by the extended base of the spine is
not so easily cut by the processes of fission as are the other parts
of the body; it therefore forms the bridge. The two individuals
thus connected did not move in unison; there was much pulling,
bending and twisting of the slender connecting bridge, so that the
latter appeared likely to break. In the course of time this hap-
pened; the two individuals separated some time during the next
night, before the next fission occurred.

As will appear in the sequel, this tendency to remain connected
even after the adult condition is reached persisted in the progeny
of these individuals for many generations. We have therefore
something resembling the inheritance of a new characteristic.
This matter will be taken up in a separate section.

The spine still remained near the posterior end of the individual,
though not so near it as in the previous generation. The posterior
tip has pushed backward from the spine, in the growth that takes
place after division. It carries with it some portion of the base
of the spine, just as happens in front.

Eleventh generation. Again the spine went to the posterior
individual (night of May 10). As would be expected, the spine
is now further forward; it is again nearly straight and at right
angles to the body (Fig. 4, [11]).

Twelfth and thirteenth generations. During the night of May
11 there were two fissions, giving three specimens of the normal
form, and one with the spine. It appears clear that at the first
of these two divisions the plane of fission was just in front of the
spine, so that the latter was left almost squarely on the anterior
tip of the posterior individual; here it remained till the next divi-
sion. This time of course the spine went to the anterior indi-
vidual, still remaining almost exactly at the anterior end. In its
outgrowth the anterior tip has carried the spine with it, owing to
the fact that the latter was almost at the very end. The individual

bearing the spine in the thirteenth generation is therefore to be designated $a^{1\cdot2\cdot1\cdot2\cdot1\cdot2\cdot1\cdot2\cdot2\cdot2\cdot1}$.

Fourteenth and fifteenth generations. During the night of May 12 there were again two divisions, giving three normal individuals and one with the spine. The spine is now situated at about the middle of the body (Fig. 4, [15]). The only way this result can have been reached is as follows: The spine went to the anterior individual in both of these divisions, and in the growth processes after each division it moved backward about one-fourth the length of the body (or rather, the anterior tip grew forward that amount). The individual of the fifteenth generation is therefore $a^{1\cdot2\cdot1\cdot2\cdot1\cdot2\cdot1\cdot2\cdot2\cdot2\cdot2\cdot1\cdot1}$.

The spine now bears a ball at its tip (Fig. 4, [15]). This is due to the fact that at the time of fission some of the endosarc is squeezed out through the tube of ectosarc, thus forming the ball. This indicates that at the time of fission, or in the period of rapid growth just following it, the internal contents must be under much pressure.

Sixteenth generation. The plane of fission (night of May 13) passed just in front of the base of the spine, leaving the latter at the anterior tip of the posterior individual (Fig. 4, [16]). Again it failed to be displaced backward in the growth following fission. The ball at the end of the appendage was gradually constricted off from the tip, becoming completely separated at 10.15, May 14.

Seventeenth and eighteenth generations. During the night of May 14 the animal again divided twice. The method of division is shown clearly by the fact that the three individuals without the spine remained connected in a chain, only the animal bearing the spine being free. The spine went to the anterior individual in both fissions, being displaced backward about one-fourth the body length in each growth period.

Nineteenth generation. In the next division (night of May 15), the spine went to the posterior individual, being borne again at the anterior tip (Fig. 4, [19]).

Twentieth and twenty-first generations. During the night of May 16 there were two generations, the spine going to the anterior individual in each case. This is demonstrated by the fact that the three individuals without the spine have remained united in a chain

while the spined animal is free. *The spine is still at the anterior tip*; it has not moved backward for two generations.

This individual did not divide for more than twenty-four hours, and during its lifetime the spine became a little shorter. The animal now *used the spine* almost continually. It placed the tip of the spine against the bottom of the vessel or against any other surface, then ran along the surface, keeping the tip of the spine in contact, while currents of water passed down the oral groove (Fig. 5). This use of the spine is of course incidental to the common habit of these animals, of placing one side of the body against a surface and running along it. But this is the first generation in
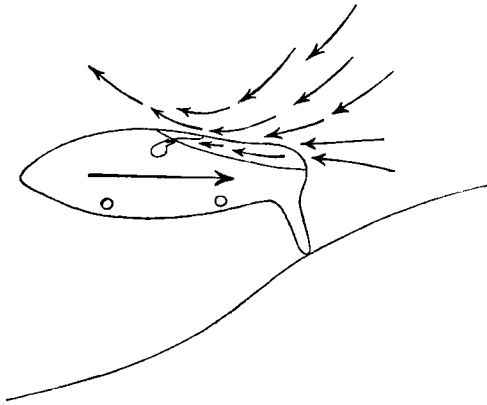

Fig. 5 Use of the spine by the individual of the twenty-first generation. The tip of the spine is pressed against a surface and the animal runs along it, in the direction indicated by the large internal arrow, while the currents of water down the oral groove to the mouth are indicated by the small arrows.

which such a use of the appendage occurred. This, taken with the fact that the appendage seemed to be gaining a permanent position at the anterior tip suggested possible interesting developments in the future.

Twenty-second generation. The spine again remained at the anterior tip. The division (afternoon of May 18) was at first not complete (Fig. 4, [22]), the animals remaining connected for more than twenty-four hours.

On the morning of May 20, the two had separated, but had not divided farther. Both were swollen and opaque; they were evi-

dently in an unhealthy condition. Investigation showed that the wrong sort of bacteria had multiplied in the culture fluid last made, making it opaque and sirupy. All the specimens (for various other experiments) that had been placed in this fluid were unhealthy or dying. This multiplication of injurious bacteria in culture fluid made in the usual way, is a not uncommon and most disastrous occurrence. To it we shall return in another connection.

The two sister individuals (one with the spine, the other without) were transferred to clean water, and later to new culture fluid. They were still living May 21, three days after the last preceding fission. But on the morning of May 22 I found, to my great regret, that the individual with the spine had died. Its sister recovered and propagated the race for many generations, of which we shall have to speak in our account of the hereditary tendency to remain connected after fission.

The last individual bearing the spine was designated $a^{1.2.1.2.1.2.1.2.2.2.1.1.1.2.1.1.2.1.1.1}$. These exponents show to which individual the spine passed at each division—(^{1}) indicating the anterior individual, (^{2}) the posterior one. The spine was traced through twenty-one generations (the first generation not having the spine). Fig. 4 gives a diagram of the entire history of this structure.

In this history of a localized new structure for twenty-one generations, certain general relations appear, which we will here set forth, though a full discussion of their significance will be reserved till other cases have been considered.

2 General Relations and Processes Shown in the History of the New Structure

1 The new structure was transmitted in each generation *to but one individual*. Thus, in the sixth generation there were thirty-two individuals, with but one bearing the spine (see Fig. 6); in the eleventh generation, out of 1024 individuals, but one had the spine; in the twenty-second generation the spine was found on but one individual out of 2,097,152.

Furthermore, the spine occupied a definite place in the series of individuals produced. As we have seen, and shall see farther,

sometimes Paramecia do not completely separate after division, but remain united in chains. If we conceive of all the individuals of each generation as thus forming a chain, each being in the position that the method of transverse fission gives it, then on such
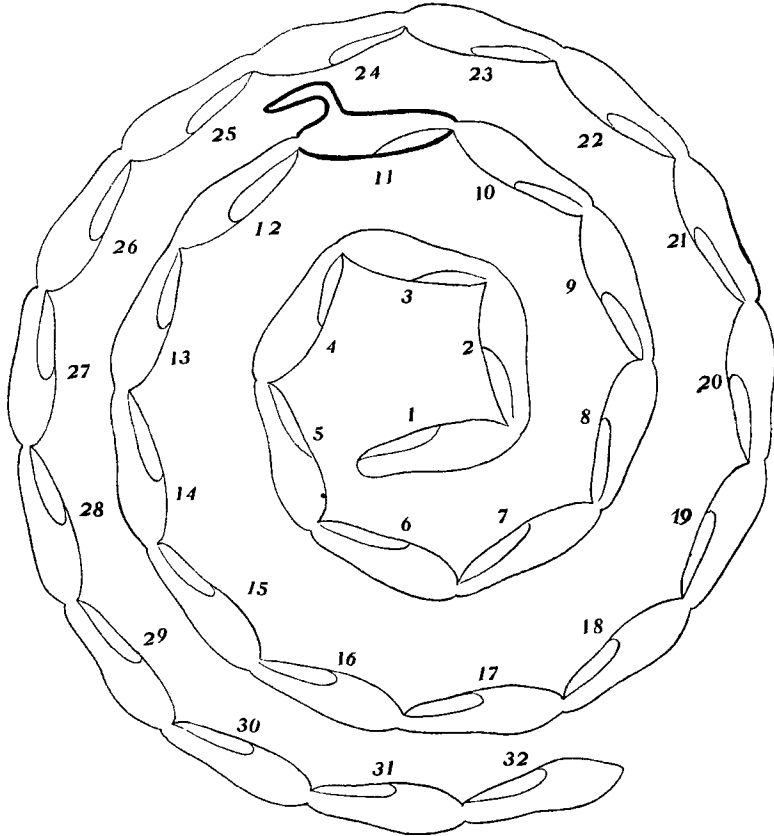

Fig. 6 Diagram showing the position and relations of the spine of *a* in the sixth generation, when thirty-two individuals are present. The individuals are conceived to have remained united, in the positions given them by the successive fissions. The spine would be found on the eleventh individual from the anterior end of the chain (drawn with a heavy outline).

a chain we would find but one spine, having a certain definite position. Thus, in the sixth generation, where thirty-two individuals were present, the spine would have been situated as shown in Fig. 6, on the eleventh individual from the anterior end of the

series. In the ninth generation, after eight regular alternations from the anterior individual to the posterior one and back, in the fissions, we should have a chain of 256 individuals, with the spine on the 171st individual counting from the posterior end of the chain. In the twenty-second (final) generation, the chain would be 2,097,152 individuals long, and would bear but a single spine situated on the individual numbered 1,393,592 from the posterior end.* Such a chain would be about 419 meters long, with the spine about 278 meters from the posterior end.†

Thus though the new structure is transmitted it is not multiplied, and there is no tendency to produce a race with this characteristic. There is evidently a fundamental difference between on the one hand this simple handing on of a localized structure to one of the new individuals, and on the other hand, the reappearance of the localized structure in all or many of the individuals resulting from fission. The difference is in some respects similar to that between "somatic" and "germinal" characters in Metazoa. This point we shall take up later.

2   The position of such a structure on the body of the individual is not permanent and the same in succeeding generations. The same structure is found in one generation at the anterior end, in another at the posterior end; now at the middle; now in some intermediate position. At first the structure alternated regularly between a position nearer the posterior end, and one nearer the anterior end; later its wanderings were wider.

These fluctuations of position are due mainly to the processes of growth following fission. These processes will be analyzed quantitatively in later communications; here we see merely the main facts in a general way. After fission the entire body lengthens, both ends pushing out rapidly. The anterior tip pushes out somewhat more than the posterior one. In consequence, a structure located, just after fission, near the anterior end (Fig. 3, [8]) is

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*The rule for finding which individual of a given generation would bear the appendage is as follows: If in a certain generation the number of individuals posterior to the one bearing the spine is x, then in the next generation, if the spine goes to the posterior product the number posterior to the spined individual will be $2x$; if the spine goes to the anterior product, the number will be $2x + 1$.

†The length of a single individual being taken as 200μ.

left behind in the growth of the tip of the body, so that in the adult
infusorian it lies halfway back to the middle of the animal (Fig. 3, [9]).
At the next fission it of course goes to the anterior product, lying
at or behind its middle. By the greater growth of the anterior
end it is further displaced backward, so as to lie clearly behind the
middle. At the next fission it must then go to the posterior prod-
uct, and be near its anterior end. Now it is again displaced
slowly backward, the same processes being repeated. Thus the
process is normally one of steady movement backward, interrupted
by fissions which at intervals leave the spine near the anterior
end of the posterior individual. A diagram showing this normal
course of events is given in Fig. 7.

Sometimes through irregularities in growth, or other cause, the
structure comes to be situated very near to or at one end (as in
Fig. 4, [8,12,19-22]). Then the course of events becomes slightly
different. If the structure is near the posterior end (Fig. 4, [8]) the
posterior tip grows back from it only a little, so that it still remains
behind the middle of the body. At the next fission it therefore goes
to the posterior individual (as it would in the "normal" course).
Now the posterior end again grows back but a little, while the
anterior tip grows much, so that the spine is still behind the middle.
It therefore goes again to the posterior individual. It may thus re-
quire as many as three fissions to bring the structure to the middle,
so that it passes again to the anterior individual, reëstablishing
the alternations (Fig. 4, [8 to 12]).

Is situated at or very near the anterior tip, the structure is car-
ried forward in the growth processes; it may therefore remain for
several generations in this region (Fig. 4, [19 to 22]), before it is dis-
placed backward sufficiently to lie behind the middle. Possibly
a structure might in the course of time attain a permanent posi-
tion at the anterior tip. This seems indicated by the last three
generations of *a*.

Thus on the whole the general tendency of the growth processes
is to shift any surface structure from the ends toward the middle
of the body, while the fissions again transfer it toward one end;
with the further result of an alternation of position from the
anterior to the posterior product of fission and back again .

In general then it must be realized that the parts of the body of the infusorian do not have a permanent definite relation to the form or structure. A portion of substance that is anterior in one generation is posterior or median in another. Thus definite
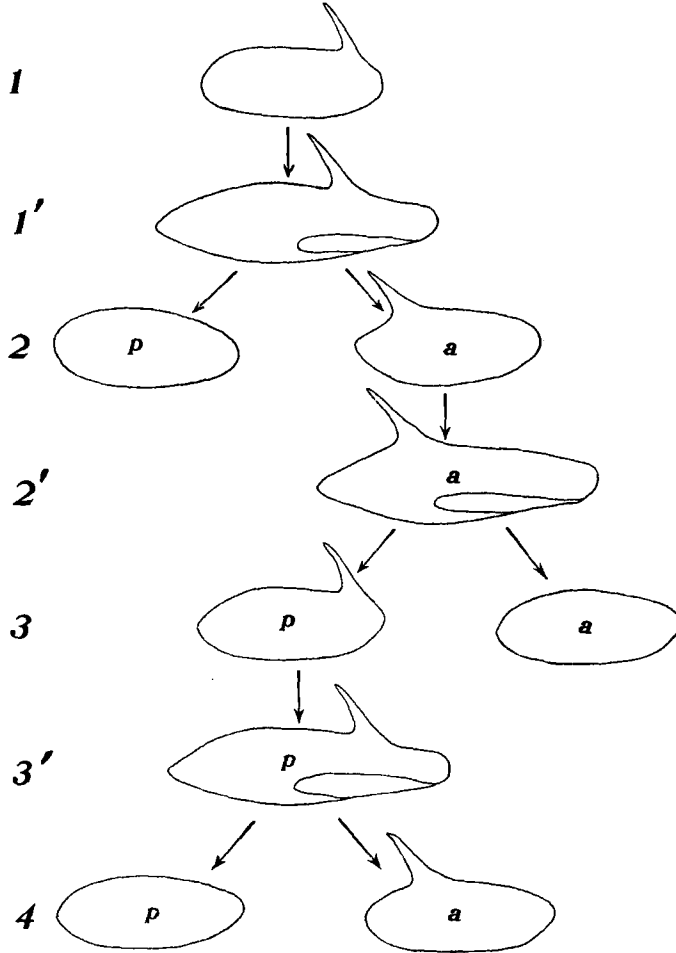

Fig. 7 Diagram showing the usual regular changes in form and alternations in position of the spine through four generations. The numbers at the left indicate the generations, a younger and an older stage being shown in each generation (save the fourth). *a* is the anterior product of fission, *p* the posterior one. In generations 1 and 3 the spine is on the anterior half of the posterior daughter cell; in generations 2 and 4 it is on the posterior half of the anterior daughter cell.

pieces of substance are not necessarily permanently differentiated to play certain parts. The organism is plastic, and is made over at fission. The normal reproduction involves the same working over and re-differentiation—"morphallaxis"—that occurs in regeneration.

3 Yet this making over is not complete. Oral and aboral surfaces retained their relative position throughout these twenty-two generations, the spine remaining always on the aboral surface. Furthermore, the entire history shows that a given structure may be bodily transmitted for many generations without becoming greatly changed. It may even, finally, acquire a more or less permanent position, remaining for at least several generations.

In the normal reproduction we find structures which behave in both of these ways—some being directly transmitted, others re-made. The two contractile vacuoles of Paramecium pass bodily, one to each of the progeny—though each individual forms likewise one new one. The mouth and pharynx are said to pass to the anterior product of fission, the posterior product forming new ones. The oral groove, the blunt anterior and the pointed posterior end, these are examples of structures that disappear in reproduction and are made anew. The cilia and setæ of the Hypotricha are not transmitted, but produced anew in the new individuals. Fission is on the whole mainly a process of reorganization and new production, rather than of transmission.

3 Fate of Other New Structures in Reproduction

The fate of many other new structural peculiarities was followed in various individual lines; after the detailed account we have given above, these can be set forth briefly.

a Spines, Points or Appendages

In many cases studied the history of points or appendages on the body differed from what we have described above for the line a.

1 This is the case with the small point on $a^{1\cdot1}$, already mentioned. (Fig. 4, [3]). As will be recalled, there resulted from the division of a^1 two individuals bearing spines or points; we have followed

the history of the large spine of $a^{1.2}$ and its descendants. We will now follow briefly that of the short posterior spine of $a^{1.1}$ (Fig.8, ^{1}).

The next division (night of May 7) was of course at about the middle of the body, so that the anterior product $a^{1.1.1}$ was a normal individual without a spine. The posterior product $a^{1.1.2}$ had the spine in about the same position as in the previous generation, though it shifted during growth a little farther forward (Fig. 8, ^{2}).

At the next (fourth) division the point passed to the posterior product $(a^{1.1.2.2})$ and remained in nearly the same position as before (Fig. 8, ^{3}). It had become smaller, so that it was now a mere lump, hardly noticeable.
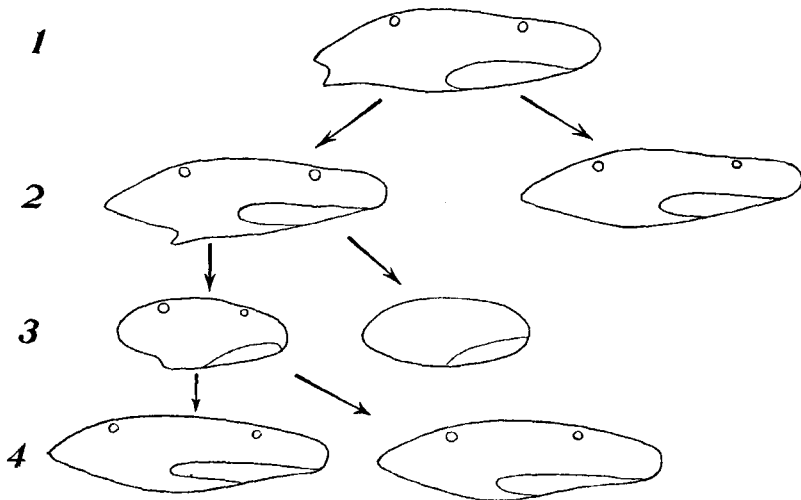

Fig. 8   Diagram of the history of the small tooth in the race *a*.   See text.

At the next fission (fifth) the point or lump quite disappeared, being in some way reduced during the growth processes accompanying division. Both individuals resulting from fission were of the normal form (Fig. 8, ^{4}).

Thus this small posterior point persisted through but three generations, and in each generation it was found in but one individual. A process of regulation of form took place slowly, accompanying the changes involved in fission, till finally the new structure had disappeared.

2   In a line or race which I called *am*, the course of events was
as follows: The ancestor *am* was a short individual, seeming to
lack almost completely the posterior half of the body.   In the
first two fissions the anterior product was in each case a normal
individual, while the posterior product was more or less abnor-
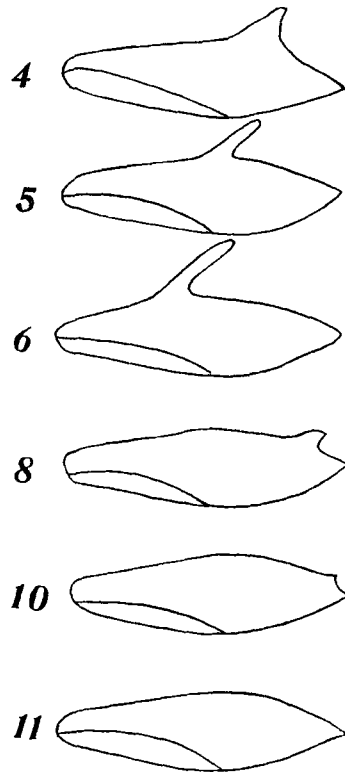mal, with a blunt irregular posterior end.   In the fourth genera-

Fig. 9   A number of generations in the history of the race *am*, showing the shifting, transformations,
and gradual disappearance of the spine.   The numbers at the left indicate the generations figured.   The
spine first appeared in generation 4 and disappeared in generation 11.

tion there were two abnormal individuals, one of which bore a
short spine projecting from its aboral surface, at about the middle
of the posterior half of the body (Fig. 9, ⁴).

In the fifth generation the anterior individual was normal, while
the posterior one bore the spine a little farther forward than in

the previous generation. The spine itself was a little longer (Fig. 9, [5]).

In the sixth generation it still further increased in length at the time of division, and went again to the posterior individual (Fig. 9, [6]).

In the next two divisions the tooth went in each case to the posterior product, and continued to grow smaller. It remained near the posterior end, and in the tenth generation $(am^{2.2.1.2.2.1.2.2.2})$ it was hardly noticeable (Fig. 9, [10]). During the next division it
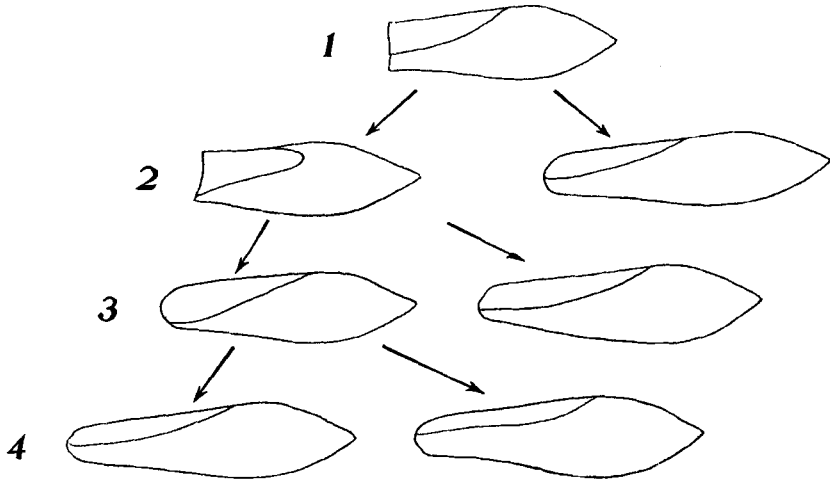

Fig. 10   History of a race derived from an individual with a truncate anterior end. The numbers indicate the generations figured. The truncate end is barely visible in generation 3, but had quite disappeared in generation 4.

disappeared completely, both products being typical individuals (Fig. 9, [11]).

Thus this spine persisted through seven generations, first increasing in size, then decreasing, till it disappeared.

b   Anterior End Truncate

In three cases I followed the history of the progeny of individuals having the anterior end short and sharply truncate, as if cut off by a knife (Fig. 10).

In each case the truncation of the anterior end persisted for a few generations (two to five), being transmitted of course to but one individual in each generation. At each fission, as a rule, the peculiarity of the anterior end of this individual became less marked, till it became invisible. There is thus a marked tendency at the time of division to regulate the body form, bringing it back to the normal condition.

c Posterior Part of the Body Truncate or Lacking

Many individuals were found in which the posterior half of the body seemed almost lacking. The body ended bluntly just
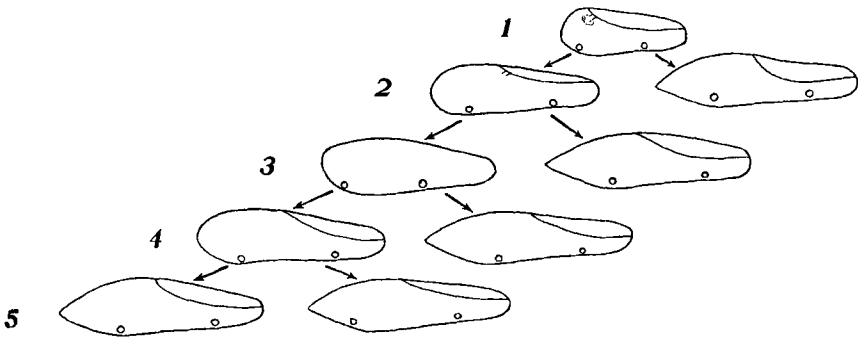

Fig. 11 History of a race derived from an individual in which the posterior part of the body was extremely short and rounded. The posterior end is to the left. The peculiarity was transmitted to one, individual in each generation, becoming less and less marked, till in generation 5 it has disappeared.

behind the mouth. The animals were about half the normal size, and presented much the appearance that would result if they had been cut in two transversely just behind the mouth (Fig. 11).

I followed the history of ten cases of this sort. In all cases the bluntness of the posterior end is transmitted, usually in weakened form, to the posterior individual resulting from division, while the anterior individual is quite normal in form. This continues as a rule for three or four generations, the posterior end approaching after each division more nearly the normal form, till finally regulation is complete, and all the progeny have the usual shape. A typical case is shown in Fig. 11.

In one case the sharply truncate form of the posterior end was transmitted almost unchanged to the posterior progeny of the first divisions, though the posterior half of the progeny was much longer than in the parent. But in three more generations the posterior individual, like all the others, had reached the normal form.

d   Anterior End with a Projecting Angle

In a certain culture there occurred a number of individuals in which the angle at the right of the anterior end was in a marked degree longer than others. These Paramecia ran over the bottom with the oblique surface of the anterior tip against the solid, suggesting that the projecting angle was due to this action. The angle disappeared in the changes connected with fission and did not reappear in the progeny.

e   Crookedness or General Irregularity of Form

A considerable number of cases were studied in which the body of the progenitor was crooked, or was otherwise irregular in varied ways.

Such irregularities do not pass as such to the progeny. They usually cause modifications in some or all of the progeny for several generations, but these modifications are not repetitions of the parent forms. They result from abnormalities in fission due to the irregular form of the parent. Four categories of cases may be distinguished: (1) Those in which the irregularity of the ancestor induces in certain of the progeny various peculiarities that continue indefinitely; (2) those in which complete regulation finally occurs, all the individuals returning, after a number of generations to the normal form; (3) cases in which the result is to cause, in some or all of the progeny, still greater irregularities, resulting finally in monstrosities which cannot perform the vital functions properly, and therefore die; (4) cases in which the irregular individuals do not reproduce at all; they persist for a time, and finally die. Typical cases of each of these categories may be described.

1   The individual *a*, whose history has already been followed (pp. 589–604), is an example of the first category. Here the crooked-

ness of the parent (Fig. 4, [1]) caused a spine to appear on one of the progeny; this persisted on a single member of each generation, as long as it was followed (22 generations). The other progeny were normal.

2   The individual *al* was bent a little in front of the middle so as to form nearly a right angle (Fig. 12, [1]). At the first division the posterior product was of the normal form, while the anterior product was somewhat irregular (Fig. 12, [2]) but less so than the parent. When this divided, the two individuals resulting were both of the normal form. Regulation occurs during the process of fission.
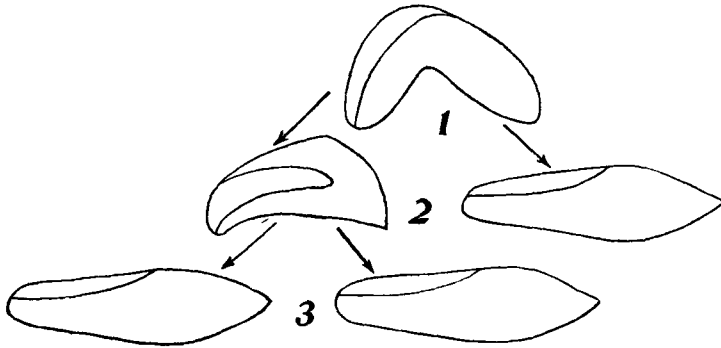

Fig. 12   History of a race derived from a crooked specimen. The crookedness had disappeared in the third generation.

The individual *ab* had the posterior end crooked (Fig. 13). When this animal was placed in the culture fluid, it became plumper, and the abnormality of form was less marked ([1']). When it divided the anterior product was of the normal form, while the posterior product had the posterior point slightly displaced toward the aboral side, but was otherwise normal (Fig. 13,[2]). When it again divided, its progeny were both normal in form.

The case of *aj* belongs partly in the second category, partly in the third. The body of the parent *aj* was small and irregular, with a broad anterior end, which bore on one angle a projecting point (Fig. 14, [1]).

When this was placed in the culture fluid it did not divide for three days. The body increased in size and especially in thick-

ness, and the projecting angle became more marked (Fig. 14, ¹'). On the third day it divided; the posterior product was normal in shape, though smaller than usual, while the anterior product was extremely irregular, having the form shown in Fig. 14, ².

In the next twenty-four hours this irregular structure underwent a partial division, increasing its size and irregularity of form (Fig. 14, ³). The structure thus produced was double, since it had two mouths (*m*), both of which took food; and there were two independent protoplasmic circuits for the digestion of food.

During the next twenty-four hours this structure divided into two very unequal parts. One product was a short, somewhat
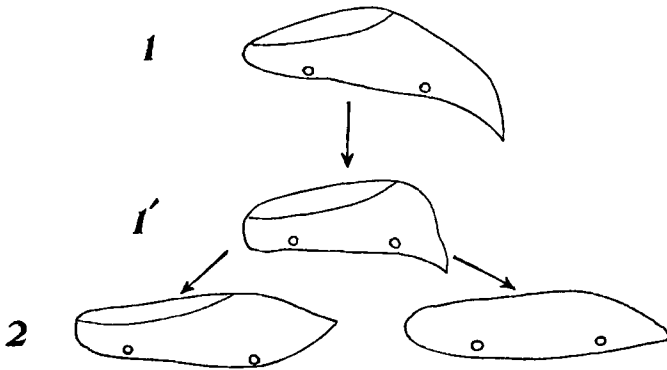

Fig. 13   History of a race derived from an individual with a crooked posterior tip.   The irregularity had nearly disappeared in the second generation; in the third (not shown) it was quite gone.

irregular individual.   The larger product was still very irregular; it represents three united individuals (Fig. 14, ⁴).

The smaller product divided again, producing progeny that were normal in form, though small in size.

The larger product, composed of three incompletely separated individuals, did not divide again; after two days it disintegrated.

3   The individual *aq* represents mainly the third category, in which the irregularity of form is increased in reproduction, till death occurs.   This specimen was curved as shown in Fig. 15, *a*. At its first division the products did not completely separate, but formed the structure shown in Fig. 15, *b*.   At the next division the right half divided in such a way as to produce one nearly nor-

mal free individual, while the other product remained attached
to the left half.   The latter underwent a partial, irregular division.
Thus the result is to produce an irregular structure consisting of
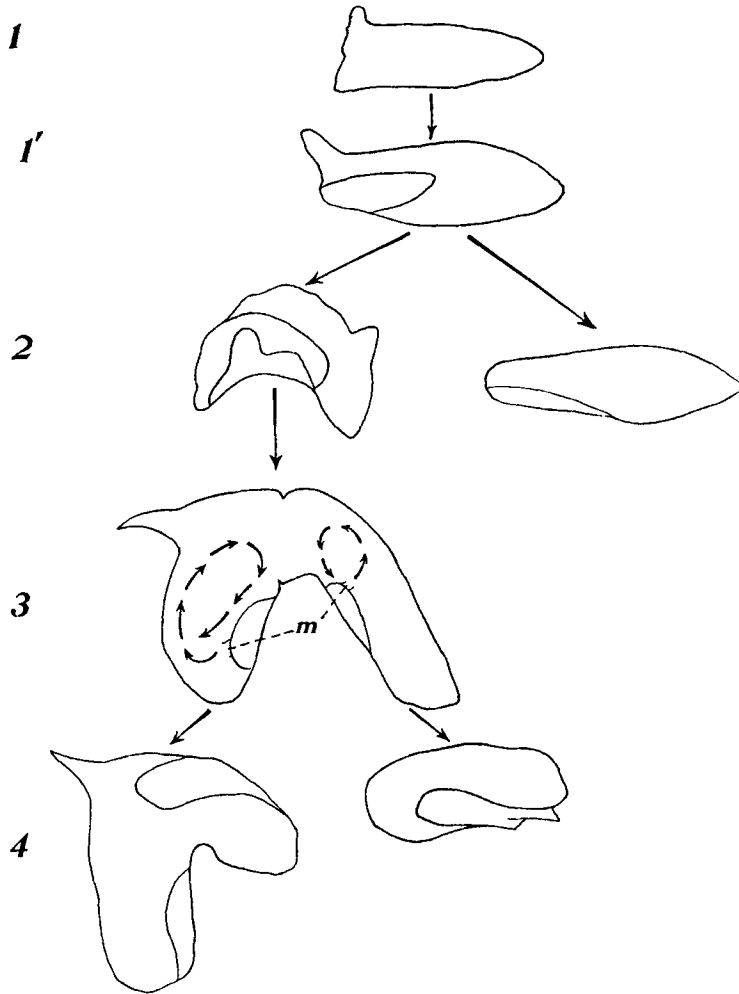three fused individuals (Fig. 15, c).

Fig. 14   Diagram of the history of the race derived from the irregular individual *aj*.   In the third and
fourth generations double and triple monsters appeared, with several mouths (*m*) and multiple proto-
plasmic circuits.   Two such circuits are shown by arrows at *3*.

This structure underwent other partial fissions, giving the irregular monster shown in Fig. 15, *d*. This lived for about four days, then disintegrated.

4 Instances of the fourth category, in which no divisions occurred, are given by aq^1 (Fig. 16, *a*) and $am^{2.2.2}$ (Fig. 16, *b*).
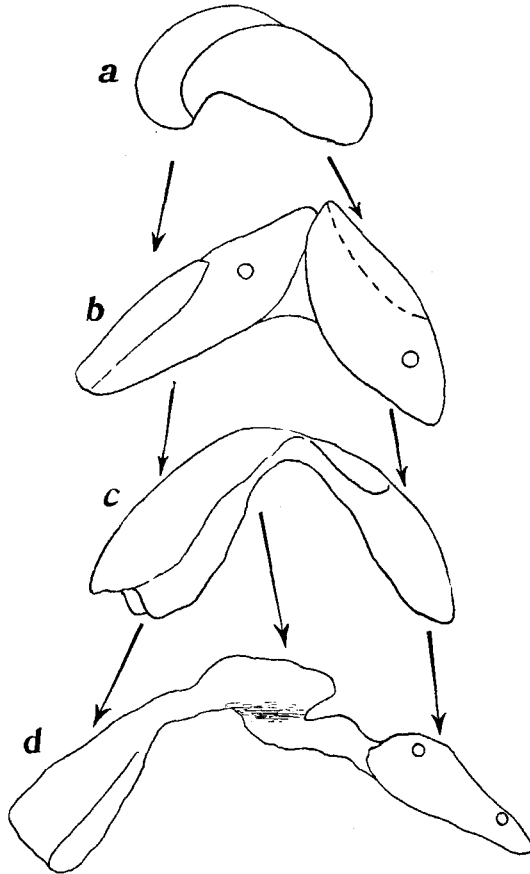

Fig. 15 History of the race derived from the irregular individual *aq*. See text.

These both lived for five days without dividing or taking food; both then disintegrated.

The mass *ar* was the result of partial fission, so that it included several partial individuals. As successive partial fissions occurred

it took various forms, of which the three given in Fig. 16, *c, d, e* are types. This structure took food by five or six mouths, and had a number of partly independent systems of circulation. It reached a length of 450μ, with a breadth of 150u. The normal Paramecia in the same culture in which it occurred showed dimensions of about 150μ x 60μ. This structure had therefore the bulk of about twenty normal individuals.

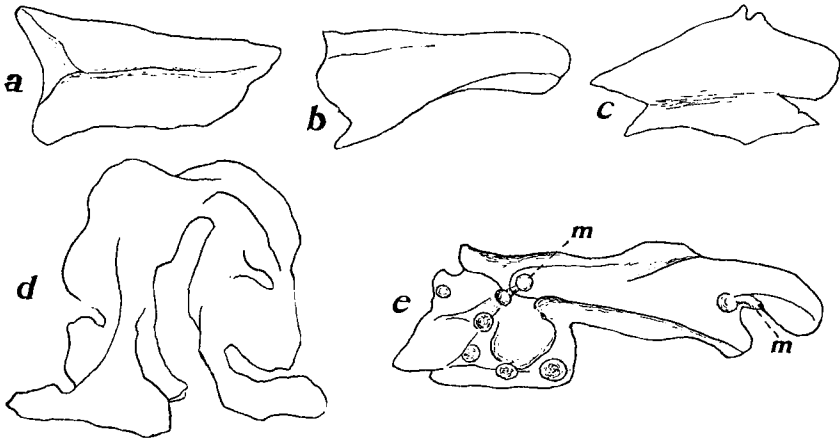This was kept for ten days, but finally it disintegrated.

Fig. 16   Irregular individuals which do not divide farther.   *a* and *b* are separate individuals that finally died.   *c, d* and *e* are stages taken at intervals of several days in the complex mass *ar*.   *m*, mouths.

f Behavior of Mutilations in Reproduction

Paramecium differs from many of the infusoria in the fact that it does not stand mutilation well. The internal contents seem very fluid, so that they flow out as soon as the ectosarc is cut; the animal at once disintegrates. It is therefore difficult to study the regulation of injuries in this animal, either during the active life, or at reproduction.

However, from a large number of experiments, certain results were reached that show how mutilations behave, both in ordinary regulation and in reproduction.

1   *Mutilations in adults.*   Whenever the ectosarc is punctured, the internal contents flow out and the animal dies.   But in a few cases mutilations were produced without puncturing the ectosarc.

Thus, a fine glass rod was drawn across an individual near its middle; leaving a deep constriction, while the two halves of the body were swollen (Fig. 17, *a*).   This constriction persisted for some hours, becoming gradually less marked.   The next day the animal was perfectly normal.

In another similar experiment, blister-like swellings were produced, and the anterior portion of the body became totally irregular (Fig. 17, *b*).   But within 24 hours the normal form was completely restored.

Thus it is clear that the adult Paramecium has the same power of regulating form that is so well known in Stentor and other infu-
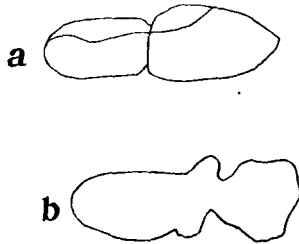

Fig. 17   Mutilations produced by drawing the tip of a glass rod across the adult animal.   See text.

soria.   But this can come into play only when the injury has not been of a nature to puncture the ectosarc and so to cause disintegration.

Many attempts were made to remove only a part of the internal fluid (endosarc), without causing death.   The ectosarc was pierced with the tip of an excessively fine capillary glass rod.*   But in all cases where any of the endosarc flowed out, the remainder followed, and the animal died.

2   *Mutilations in   dividing specimens.*   It was thought possible that specimens undergoing fission might show a different physical state of the protoplasm, such as to permit mutilations without immediate disintegration.   To a limited extent this was

*These can easily be made so fine that the tip is apparently not larger than a cilium of Paramecium.

found by experiment to be true. When a specimen undergoing fission is pierced with the tip of the glass rod or otherwise mutilated, it does not go to pieces so rapidly as the adult, though in most cases it finally disintegrates. But in a few instances specimens thus treated survived.

Thus, while the Paramecium *ma* was undergoing fission, its anterior half *ma*[1] was pierced with the rod, allowing a part of the internal contents to escape. This half became distorted (Fig. 18, *a*) while the other half became swollen. The latter resumed later its normal form, and fission continued. The injured half *a* retained its distorted form (Fig. 18, *b*). During growth the form became somewhat nearer normal (Fig. 18, *c*), but complete regulation did not take place in this generation.
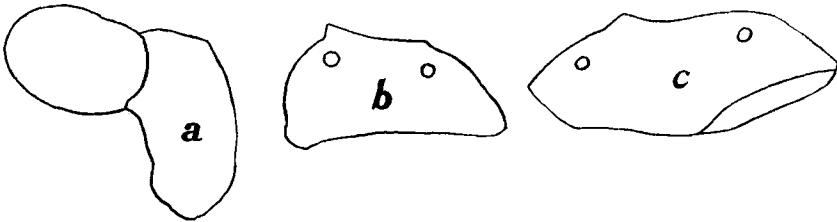

Fig. 18   History of the specimen *ma*, mutilated during fission. See text.

During the night the irregular individual divided. The anterior product was quite normal in shape; the posterior one still showed a slight irregularity of form at the posterior end. At the next fission this disappeared and both products were normal.

Thus the effects of the mutilation persisted in some of the individuals for three generations, then disappeared.

In a number of other cases young or dividing specimens were marked with deep furrows by pressing them with the rod. These marks lasted some hours, but disappeared before the next fission occurred.

In the dividing specimen *mb* the posterior part *mb*[2] was pierced with the glass rod, so that a part of its contents escaped, while by contraction most of the remainder of its contents were forced into the anterior half *mb*[1] (see Fig. 19, *b*). Thus the

pierced part became very small; later it increased in size and became irregular (Fig. 19, *c*). The fission was never completed, this irregular part remaining attached to the posterior end of the normal individual *mb*^{1}.

The normal part *mb*^{1} divided twice, budding off, as it were, two normal individuals at its anterior end; its posterior part remained with the irregular mass attached, as in Fig. 19, *d*.

At the next division the two components remained connected, with the irregular mass attached to the posterior end (Fig. 19, *e*).
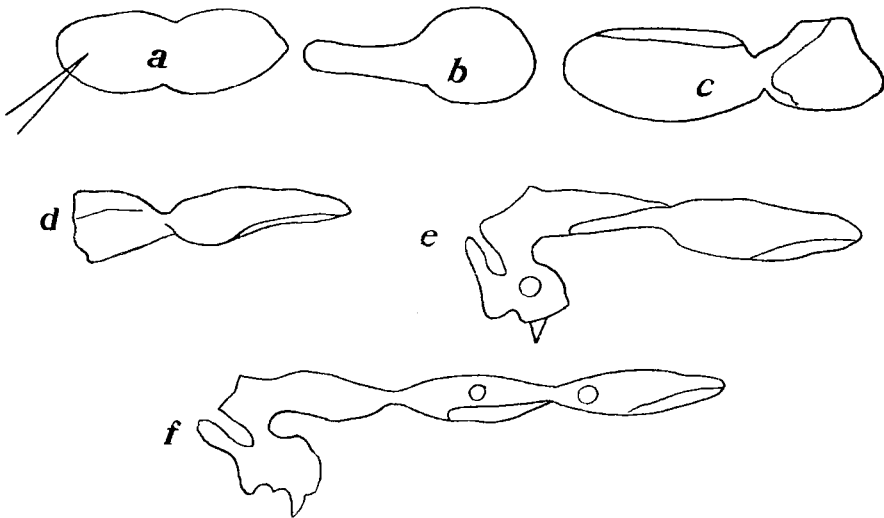
Fig. 19 Effect of mutilation during fission in the specimen *mb*. See text.

The irregular mass had itself made some attempts at fission, with the result that it became still more irregular.

There was no further change for three days; then another partial fission produced the results shown in Fig. 19, *f*.

During the next day the entire structure disintegrated. In this case the effects of the mutilation lasted for several generations, finally causing death.

All together, it is clear that while mutilations may be passed on bodily to certain of the products of division for a number of generations, there is no tendency for them to be inherited by all the

progeny; no tendency for the mutilation to be duplicated in new individuals. There is no tendency to produce a race of mutilated individuals, any more than there is in Metazoa. Regulation takes place at the time of fission, so that after several fissions the normal condition is restored.

4 *Acquired Characters That Tend to be Inherited*

g Acquirement and Inheritance of a Tendency for the Adults to Remain United in Chains

The acquired characteristics thus far described have shown no tendency to be inherited in such a way as to produce a race bearing the new character in question. We now come to a case in which such a tendency actually showed itself. The difference between this case and the others is instructive, suggesting what must be the essential nature of an acquired character that may be inherited.

The characteristic in question is a tendency for the adult individuals to remain united in chains. This tendency appeared in the line *a,* which we have already described in connection with the transmission of a long spine (pp. 589–604); the beginnings of the characteristic now under consideration have been set forth in that description. In the process of growth the broad base of the long spine (Fig. 4, [7]) became drawn out, till in the individual $a^{1.2.1.2.1.2.1.2}$ it formed a ridge running along the aboral surface nearly the entire length of the body (Fig. 4, [9]). At the next fission it was found that the fission plane did not pass so readily through this ridge as through the remainder of the body, so that the two resulting individuals did not separate, but remained connected by a bridge passing from the aboral surface of one to that of the other (Fig. 4, [10]).

The continued union of the two individuals after fission reappeared in succeeding generations, both in the individuals formed from the region anterior to the spine (as in Fig. 4, [10]), and in those formed from the region posterior to the spine (Fig. 4, [17, 19]). In the eighteenth and twenty-first generations three individuals formed a chain (Fig. 20, *a*). In succeeding generations many such connected individuals and chains were formed. In the fif-

teenth generation I began to save all the progeny of *a*; up to this time only the specimen bearing the spine had been kept alive. In the large number of progeny thus obtained many variants were to be observed in the matter of interconnection. Many individuals were free and separate. Pairs of united individuals were very common. Chains of three to eight or more (Fig. 20) were not uncommon. These longer chains were likely to break apart in the course of time, as a result of their bending and twisting movements.
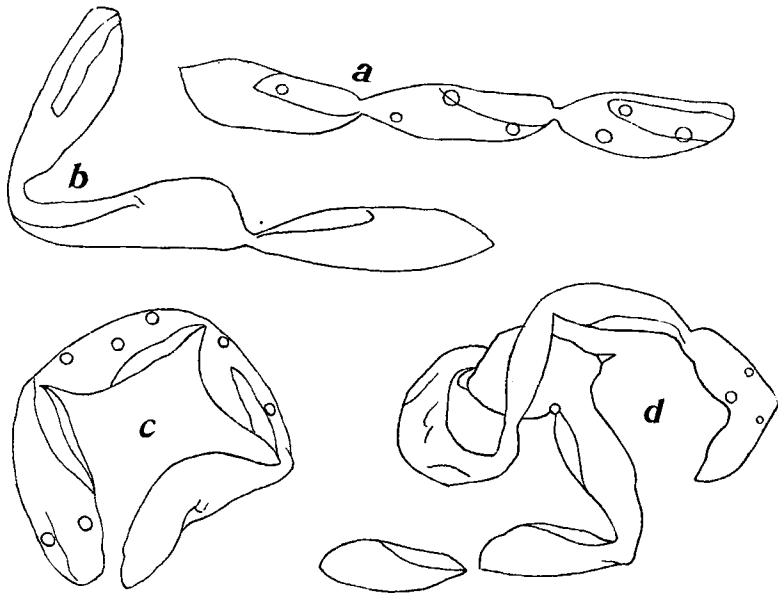
Fig. 20   Chains of individuals formed in the history of the race *a*, as a result of incomplete fission.

There was much variation in the extent and strength of the union. Sometimes there resulted from the division of united individuals specimens that were quite free. The division of free specimens often produced united pairs. In some cases the connecting band was very thick and strong, so as to hold the two specimens inflexibly in various positions (Fig. 20, *b*). In other cases the fission was so incomplete that mere partly double specimens resulted (parts of *d*, Fig. 20). Finally, the irregularities

of fission at times went so far as to produce mere monstrosities
(parts of *d*, Fig. 20). Such monstrosities were rare, while indi-
viduals neatly united in pairs or in chains were very common.

The first occurrence of such unions (Fig. 4, [10]) was on May 10.
Cultures were kept in watch glasses from that time till July 1
(probably about fifty generations); at that date the unions were
still abundant. In fifty generations the original individual which
underwent the modification causing the union would have pro-
duced progeny to a number running far up into the billions.

Effects of Artificial Selection

On June 22 I began experiments to determine the effect of selec-
tion on this peculiarity. Would it be possible by selection to pro-
duce on the one hand a series showing little or no tendency to
remain united, on the other hand a series in which most or all
the individuals remain in united pairs?

Two selected cultures were started in watch glasses. The first
contained twenty individuals united two by two in ten pairs.
The second contained twenty free individuals (descended from
the same ancestors as the united pairs).

Forty-eight hours later (June 24), both sets had multiplied to
about 100 specimens. In the first set (ancestors united) there were
ten united pairs. In the second set (free ancestors) there were
two united pairs.

From the first set I removed all the free individuals, leaving only
the ten united pairs. From the second set the two united pairs
were removed, leaving all free.

The further history was as follows:

Culture from free ancestors. On June 25 this had multiplied
to 200–400; among these were three or four united pairs. I re-
moved the latter and retained only 100 of the free individuals.

On June 26 these had multiplied two to four times but contained
no united specimens. This culture was kept for a week or so
longer, but developed no more united pairs. Thus, selection had
quite removed from this set the tendency to remain united.

Culture from united ancestors. After the second isolation of ten
united pairs (June 24), the number multiplied to about 50 in 24

hours; among these there were eight groups of united individuals—some of two, some of several, specimens united in chains. The eight groups were again isolated (June 25).

Effects of Natural Selection

These eight groups showed many imperfect individuals, and the groups were at a great disadvantage as compared with the free individuals. This was because they are not able to swim about actively, but must lie at the bottom and move about only irregularly. As a result they get comparatively little food, and are not able to avoid regions where the conditions are harmful. The bacteria multiplied much more rapidly than in the free culture, containing many individuals—the latter keeping down the number of bacteria by feeding on them.

In consequence of these bad conditions, the united groups began to die. Some multiplied farther, all the individuals remaining united. But forty-eight hours after the isolation of the second lot of eight groups, all were dead.

Thus it is easy to produce by selection a culture containing only free individuals and multiplying in the usual way. Artificial selection will likewise produce a culture of united specimens, multiplying mainly by incomplete fission. But at the same time natural selection acts; these groups die, owing to their inefficiency in getting food, keeping down the bacteria, avoiding harm, and in the performance of the general bodily functions.

This extinction by natural selection of the series multiplying by incomplete fission was shown in another way. A considerable number of the progeny of *a*, with both separated individuals and united groups, was allowed to accumulate in a shallow watch glass. Here the united groups flourished fairly well, because the vessel was so shallow that they received plenty of oxygen and of food while lying on the bottom, while the undue multiplication of the bacteria was prevented by the numerous free individuals. Now the culture was transferred to a large vessel, three inches deep. Here the culture multiplied enormously, but all the groups of united specimens quickly disappeared. They sank to the bottom

of the vessel, where the conditions were not such as to keep them alive, while the free individuals remained at the top and multiplied. Thus by continued natural selection all specimens multiplying by incomplete fission were removed, and in a few days the deep culture contained only normal, free individuals. In shallow cultures, on the other hand, the united groups persisted for about two months, as we have seen.

In this case then we have a new characteristic, of known origin, that is inherited by many individuals for many generations, and is finally extinguished only by the action of natural selection. The many other new characteristics that we have described were not inherited (save as they were handed on directly to a single specimen). In the one case the new feature becomes a race characteristic; in all the others it fails to do so.

WHAT MUST BE THE NATURE OF A NEW CHARACTER, THAT IT MAY BE INHERITED?

What is the peculiarity of the characteristic that was thus multiplied and inherited, and what light does it throw on the question as to what must be the nature of an acquired characteristic in order that it may be inherited?

The characteristic thus inherited was *a modification of the protoplasm of the cell, of such a character as to cause it to behave differently in reproduction.* The other characteristics, not inherited, were not such modifications of the protoplasm as to cause it to behave differently in reproduction.

Consideration of the facts of normal reproduction in the Protozoa, and of heredity in general, indicates that this difference is an essential one. *In order that it may be inherited* (by more than one of the progeny), *a characteristic must be the result of such a modification of the mother cell as will cause it to behave in a certain way at reproduction.* It makes no difference whether the mother cell in question is a germ cell, in a Metazoan, or a differentiated Protozoan.

Thus we know that in the inheritance of the setæ of the Hypotricha, for example (Fig. 21), these are not simply handed over in

finished form, like the spine of *a* (Fig. 4), but are *produced anew* on each product of fission. The old setæ and cilia degenerate and disappear as fission sets in. In the daughter individuals the new setæ appear in a small group with a totally different arrangement from that seen in the adult parent (Fig. 21, *x*) and the final arrangement is reached by complicated processes of differentiation and distribution. Thus the presence of setæ in the posterity could have been brought about in the beginning only by such modifications of the protoplasm of the mother cell as would cause it at fission *to produce setæ*. Any change in the structure, number, or
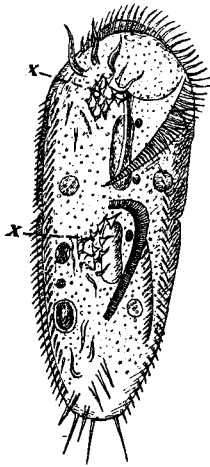
Fig. 21 Dividing Stylonychia, from Bütschli, showing at *x* the appearance of the new setæ in a close group.

arrangement of the setæ could result only from such a modification of the mother cell as would alter in a definite way the processes occurring at reproduction. The thing transmitted from the parent cell to the young progeny is, not the setæ themselves, but the change in the protoplasm causing the production of setæ in a definite way.

To return to a specific problem—How then could such a localized appendage as the spine of *a* (Fig. 4) become an inherited characteristic? *Only through such a modification of the protoplasm*

*of the parent cell as would cause at fission the production of such
an appendage on each of the progeny.*

At first thought it appears difficult to conceive how this could
occur. This will be made easier, perhaps, by a consideration
of the origin of certain characteristics in the race *a* (Fig. 4, etc.).

Examples of Modifications from which New Inherited Characters Might Result

Let us take first the origin of the spine whose history is traced
in Fig. 4. The original ancestor of the race *a* was without spines.
But it was so deformed and modified that at the time of fission
two short teeth were produced during the processes of division
(Fig. 3, [2]). At the next fission one of these short teeth formed as
it were a region of weakness, where a long spine was pushed out,
as an accompaniment of the processes of fission (Fig. 3, [4, 5]).
Such a region of weakness might well exist without a visible tooth
to show its position; then at fission a spine would be produced in
this spot. It is evident that active physical and chemical processes
are in progress at the time of fission; these may easily result, under
the influence of a local modification of the parent cell, in the push-
ing out of a spine or other structure of characteristic form.

How such a new structure might appear in each of the progeny
of each generation is illustrated in a simple way by certain other
phenomena seen in the race *a*. As we have already set forth, the
progeny of *a* showed after a certain period a tendency to remain
united in chains. At the same time there appeared among the
free progeny of *a* a considerable number of individuals which bore
at one or both ends a spike-like point (Fig. 22). This character
did not become general, but so many cases appeared that one
might say that there was an inherited tendency toward this. Ob-
servation of the process of fission showed that these points arose
by the pulling out of the protoplasm while in the plastic condition
at the time of fission; the two young animals were connected, at a
certain stage, by a bridge of this plastic protoplasm. By their
movements they drew this out to a long strand, which finally broke
at the middle, leaving a point at the ends of the two animals.

When this happened at successive fissions, the animal bore such a point at each end.

It is evident that these points are due to the same cause that produced the inherited tendency to remain united in chains (as in Fig. 20). They result from the ridge of new material along the aboral side of the animal, shown in Fig. 4, [9]. Now, it is easily conceivable that this new material might be of such texture and thickness that it would always be drawn out at fission in such a way as to produce points of a definite form and size. These would then appear regularly after fission; a race of Paramecia with this as
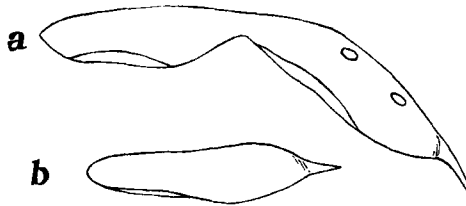

Fig. 22 Examples from the race *a*, of individuals having a point at the posterior end, due to the drawing out of the connecting band at the time of fission.

a new characteristic would have been produced. The spine would be hereditary, because produced anew in each generation, just as are the setæ of the Hypotricha, or the organs of the Metazoa.*

SUMMARY AND GENERAL DISCUSSION

The following general statements of the laws and principles bearing on heredity† that result from our investigation are made with direct reference to the Protozoa, and will best be grasped by keeping in mind concrete cases, such for example as those shown in Fig. 4, Fig. 20 and Fig. 22.

*It is of course possible that the origin of new permanently inherited characters is not normally through mere modifications of the external parts of the cell, such as we see in our illustrative cases. Possibly there must be originally some modification of more recondite parts—nucleus, chromosomes, or the like—and that these then secondarily act upon and change the outer parts. This would add farther complication, but would not change the essential point, which is, that in order that a characteristic may be inherited, it must be due to some modification that causes a change in the processes of reproduction.

†For a summary of results on other matters than heredity (on the changes during fission and growth, etc.), see pp. 599-604.

1   The "inheritance of acquired characters" meets the same
difficulty in the Protozoa as in Metazoa.   In both Protozoa and
Metazoa most characteristics acquired during the lifetime of the
individual are not inherited, and such inheritance does not occur
more readily in the one group than in the other.

2   The difficulty with the "inheritance of acquired characters"
lies, not in the separation of soma and germ, but in the process
of cell division.   If a cell bears a structure at one end, there is no
simple and direct reason why, when it divides, *both* the cells pro-
duced should bear the structure, and observation shows that *they
do not*, in the case of new structures.   There is no evident way in
which a structure of this sort can overleap the barrier of cell divi-
sion and appear on the other side.*

If we insist on making a comparison between the condition in
the Protozoa and the separation of soma and germ in the Metazoa,
the following is the state of the case.   If any Protozoan cell (as
in Fig. 7) is to be divided at the next fission into two parts a and p,
then, so far as inheritance of new structures is concerned, a stands
to p as soma to germ, and reciprocally, p stands to a as soma to
germ.   In other words, there is no evident transmission, and no
evident mechanism for transmission, of a new structure from a
to p or the reverse, just as there is no evident mechanism for trans-
mitting a structure from soma to germ.

3   In order that a character may be inherited (by more than
one of the progeny, so as to produce a race), it must be *produced
anew* in each generation.   This is what happens in the normal
reproduction of both Protozoa and Metazoa.

4   In order that a new (or "acquired") character may be
inherited, it must be the result of such a modification of the parent
cell as will cause a change in the processes of reproduction; and
specifically, precisely such a change in these processes as will pro-
duce the character in question.   This is equally true of Protozoa
and Metazoa.

5   Most characteristics acquired during the life-time of the

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* This will be most readily grasped by looking at the figure of a typical case, such as Fig. 4, [3]. Why,
when this animal divides transversely, should there be a spine upon the posterior (left) half, as well as
upon the anterior (right)? As a matter of fact, there is *not*.

individual are not the result of such modifications of the parent cell as will cause a change in the process of reproduction such as to produce anew these characteristics; hence they ar not inherited. This is true in both Protozoa and Metazoa.

6　Thus the problem of how new inherited characters arise is the same in Protozoa as in Metazoa. We may therefore work on the general problem ِas readily in the one group as in the other, and there is no reason why the principles reached in one group should not apply equally to the other. Thus a new line of attack on the problem is opened; in view of the rapid multiplication of the Protozoa and the ready accessibility of their reproductive cells both to environmental influences and to observation, this gives some marked advantages.

7　The search for the origin of new inherited characters (in both Protozoa and Metazoa) resolves itself experimentally into a search for agencies and processes which will permanently modify the cell in such a way as to cause it to act differently in reproduction.

8　When a given structural characteristic arises during the reproductive processes so as to appear in a given generation, that is not because the same structure was present in a preceding generation. Often indeed it was not present before; its origin is due to some change in the constitution (chemical or structural?) of the preceding reproductive cell. Thus, the production of a spine such as we see in Fig. 4 is evidently due to a spot of weakness at a certain point in the cell body, causing a protrusion during fission. Such a structure might result from the localized presence somewhere in the cell body of a certain chemical compound, which would react at a certain stage with some other substance, thus producing a spot of weakness, where a spine would be protruded. So, the appearance of the new anterior setæ in the posterior product of division in the Hypotricha (Fig. 21) is evidently due in some way to the constitution of the cell.

9　Thus, then, the cause of the appearance of a certain structure in a certain generation is *some other peculiarity* of the cell producing it; some chemical peculiarity, for example. We may generalize this by saying that the appearance in the progeny of a certain structure *b* is due to the existence in the mother cell of a quite different condition *a*.

10   It follows from what has been set forth in the paragraphs preceding, that in the production of a new inherited character the original modification will be something quite different from the visible structural characteristic which later appears in consequence of it.   The original modification will be some chemical or structural change in the reproductive cell or cells that are later to produce the structure in question.   (By producing in Paramecium a localized change in the character of the protoplasm, a spine is later produced at that spot, etc.)   The first appearance of the visible structure is *one generation after* the production of the modification to which it is due.

11   Not all modifications of the germ cells that result in the production of a new character in the *next* generation, will result in the repeated production of this character in succeeding generations.   In most cases, the new structure appears *but once*, and is not inherited.   In order that the new structure shall be inherited, the original modification to which it is due must be *transmitted* to the succeeding generation of germ cells.   This is by no means a matter of course; in fact, it is something *not to be expected*, as a rule.   The cell usually, by regulative processes, throws off after a time any modification which the environment has impressed upon it.   Many examples of this are seen in the foregoing pages.   Certain unusual conditions of the cell result in the production, at the next fission, of a spine.   But during fission regulation occurs; the unusual condition disappears, and the spine is not again produced.

This is doubtless the fate of most modifications of the cell.   We saw, however, one modification which persisted, producing its effect in succeeding generations (pp. 618–622).   Of such a nature must be all modifications which produce new inherited characteristics.   It is easy to so modify the cell that new characteristics shall appear in *one* succeeding generation; to so modify it that the new characteristic shall appear regularly in succeeding generations is a totally different matter.

We often hear it pointed out that *heredity is not transmission*, but new production; and this has been emphasized in the preceding pages.   But it needs to be realized that while it is true that

the inherited structure visibly appearing is not transmitted, *something is transmitted*, namely, the condition of the protoplasm which causes the production of the visible inherited structure. If this determining condition were not transmitted, the visible structure could not be produced in each generation. It is this "something" transmitted that lies at the basis of the figurative expression "bearer of heredity," or the like.

12 What sort of modifications will remain permanently and be transmitted to the progeny? Evidently, only such modifications as are not removed by the regulatory processes of the cell. The modifications that are removed by regulation are precisely those which interfere in one way or another with the physiological processes of the organism, while modifications which arise in harmony with, or as a result of, the normal functioning of the cell are not removed by regulation. Thus only characteristics of the latter class—namely, *adaptive* characteristics—will be retained and transmitted. Furthermore, it appears clear that the successive modifications in the reproductive processes induced by these adaptive characteristics must likewise be in harmony with the normal functioning of the cell, else they would be removed by the known regulatory activities of the cell. Thus all stages in the modification, including the final one, must be in harmonious adjustment to the normal activities of the organism. It would appear therefore that only the new characteristics that are *adaptive* will be inherited. Anything not in harmony with the normal functioning of the cell will be removed by regulation.

13 Let us now examine the problem of the "inheritance of acquired characters." What processes would be required for the inheritance by the progeny of the same characteristic that has already been produced *directly* in the parent, by environmental action?

Keeping the Protozoa in mind, we have evidently two cases here:

a If the "acquired character" is some *general* chemical or structural change in the parent cell—something that affects the cell as a whole—then there appears to be no special difficulty in the way of a direct transmission of this to the progeny, provided

it is not thrown off by regulation.   If new inherited characters of
any sort are ever produced by environmental action, such direct
transmission of an acquired internal modification must occur, as
we have already seen (paragraph 11).   In the Metazoa, it would
evidently be only general changes in the *germ cells* that would be
thus directly transmitted.

b   The case of a new *localized* modification or of a definite new
structure, such as a spine, which is directly produced by environ-
mental action, is wholly different.   As we have already seen (para-
graphs 9, 10, 11), in order that a new localized structure *b* shall
appear in each generation, a certain other condition *a* must be
produced in the mother cells; this condition *a* must be transmitted
from generation to generation, and must so modify the reproductive
processes as to cause, at each fission, the production of the new
structure *b*.

Now, if the new structure *b* was first produced *directly* in the
parent by environmental action, and is then to be inherited, the
processes required are the following.   The existence of the struc-
ture *b* (a spine, for example), in the parent cell, must cause the
production in that parent cell of precisely the "other" condition
a, that is of such a nature as to so change the processes of repro-
duction that they will again produce identically the character *b*
(the spine) which had first been produced by the environment.
Or, what amounts to practically the same thing, the environment
must coincidentally produce two heterogeneous effects: (1) it
must directly produce the structure *b*; (2) it must produce some
permanent change *a* in the constitution of the cell, such as will so
modify the processes of reproduction that they in their turn will
produce the same structure *b*.

Such coincidental production of a complex structure *b* in two
quite heterogeneous ways would be most extraordinary, and we
have as yet no glimmering of a mechanism by which the coinci-
dence could be produced.   Moreover, as we have seen, in most
cases (in *all* precisely observed cases) it is *not* produced; we have
little if any direct evidence that it ever occurs.

Yet if it *ever* occurred it would be of such importance that we
must of course continue to be on the watch, in all experimental

work, for any evidence of it. The question, put as simply as possible, is as follows:

Is there ever any mechanism or property in virtue of which, when a structural modification occurs in one part of the body, this will modify another part of the body (not in the same way, but) in such a way that this other part will, at reproduction, start up processes tending to produce a similar structural modification?

14 The propositions thus far set forth have had direct reference to the Protozoa; but in the main they apply *a fortiori* to the Metazoa also. The difference between the two groups as to heredity is not one of principle, but of complexity. The extreme difference in complexity may be put as follows:

In the Protozoa, when a new inherited character is to appear in the adult, this requires a modification of the adult of the previous generation, of such a character as to change in a definite way only the next fission and processes immediately connected with it. This requirement is sufficiently complex when we come to ask how the numerous locomotor organs of the Hypotricha, in their varied typical patterns, have arisen and become hereditary. But it is not to be compared in complexity with what we have to set forth next.

In the Metazoa the requirement for the appearance of a hereditary new structure in the adult is that the preceding germ cell shall be so modified that at the next fission the reproductive processes shall be changed, but the change shall not yet be of a character to produce the ultimate structures. In the next and the next, and in hundreds of succeeding fissions the processes must all be modified so as to keep in each cell the conditions for the final production of the ultimate new structure. These conditions will necessarily be different in the different cell generations, as differentiation occurs, and of course each of the intermediate conditions is something quite diverse from the final structure. At the end the new structure is produced, not by a modification in the reproductive processes of one cell, as in the Protozoa, nor by the *same* modifications in many cells, but by the diverse modifications of thousands and thousands of cells, all so modified as to coöperate in the production of the final structure. The mind refuses the useless attempt to conceive of such complexity of change.

As Conklin ('08) has so well set forth in a recent address, "the mechanism of heredity is merely the mechanism of differentiation." The questions with which we have to deal are those as to the nature of the determining conditions and of the processes, by which the constitution of the cell changes. Perhaps the most direct study of heredity possible in the Metazoa is such a study as Conklin is making of the internal determining conditions in the differentiating cells of the developing organism. When one comes to the study of heredity in the Protozoa, this simply coincides with a study of the determining causes of differentiation.

Johns Hopkins University
Baltimore, Md.
March 10, 1908

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