

SCIENCE

VOL. 92

FRIDAY, DECEMBER 13, 1940

No. 2398

<i>The Beginnings of Social Behavior in Unicellular Organisms</i> : PROFESSOR H. S. JENNINGS	539	<i>Societies and Meetings:</i>	
<i>Obituary:</i>		<i>The Autumn General Meeting of the American Philosophical Society</i> : PROFESSOR EDWIN G. CONKLIN	557
<i>Rodney Howard True</i> : DR. H. L. SHANTZ. <i>Howard J. Banker</i> : DR. ALBERT F. BLAKESLEE. <i>Recent Deaths</i>	546	<i>Special Articles:</i>	
<i>Scientific Events:</i>		<i>Suggestions on Plant Virus Nomenclature as Exemplified by Names for Citrus Viruses</i> : DR. HOWARD S. FAWCETT. <i>Solar Rays and Vitamin C</i> : DR. EDWARD F. KOHMAN and DONALD R. PORTER. <i>Inefficacy of Pantothenic Acid against the Graying of Fur</i> : DR. R. R. WILLIAMS	559
<i>Damage to Scientific Institutions in London; The Classification of Tool Steels; The New Hydraulic Laboratory of the National Research Council of Canada; The Proposed New Cancer Hospital in New York City; Symposium on Malaria; The Pacific Division of the American Association for the Advancement of Science; The Cold Spring Harbor Biological Laboratory; Medalists of the Royal Society</i>	548	<i>Science News</i>	8
<i>Scientific Notes and News</i>	551		
<i>Discussion:</i>			
<i>Collecting Pelagic Foraminifera</i> : DR. FRED B. PHLEGER, JR. <i>On the Specificity of Renin</i> : JUAN CARLOS FASCILO and OTHERS. <i>Exchange Periodicals from Foreign Countries</i> : PRISCILLA B. MONTGOMERY. <i>Antique Galenicals</i> : DR. HOBART A. REIMANN	553		
<i>Scientific Books:</i>			
<i>Mathematical Papers of Sir William Rowan Hamilton</i> : PROFESSOR F. D. MURNAGHAN. <i>Recent Developments in the Study of Rocks</i> : PROFESSOR ESPER S. LARSEN	555		

SCIENCE: A Weekly Journal devoted to the Advancement of Science, edited by J. MCKEEN CATTELL and published every Friday by

THE SCIENCE PRESS

Lancaster, Pa. Garrison, N. Y.

New York City: Grand Central Terminal

Annual Subscription, \$6.00 Single Copies, 15 Cts.

SCIENCE is the official organ of the American Association for the Advancement of Science. Information regarding membership in the Association may be secured from the office of the permanent secretary in the Smithsonian Institution Building, Washington, D. C.

THE BEGINNINGS OF SOCIAL BEHAVIOR IN UNICELLULAR ORGANISMS¹

By Professor H. S. JENNINGS

THE UNIVERSITY OF CALIFORNIA AT LOS ANGELES

By social behavior we mean the behavior and reactions of individuals with relation to other individuals as such; reactions to individuals as individuals, either singly or in combination, not merely reactions to physical forces or to masses present in the environment.

How far down in the biological scale does such social behavior extend? Are social urges and instincts and reactions part of the life of the very cells of which organisms are made? Or are they manifestations only of relations that have first come into existence in the great complexes of cells that constitute higher organisms?

I have of late been forced in the course of investi-

gations to become intimately familiar with the daily and most private life of certain organisms, each of which is a single microscopic cell. The phenomena that thus come under observation throw light on the most primitive manifestations of social behavior. I shall try to present the main features of these phenomena, with certain of the reflections and conclusions to which they give rise. They raise the question: What is the nature of the earliest manifestations of social behavior; and perhaps they help us to answer it. They bear also upon the problem of the unity of the manifestations of life in higher and lower organisms. And they lead to a reconsideration of certain other questions that are related to the problems of social behavior: particularly to a question that has been discussed as the problem of self-consciousness in animals.

¹ Leidy Lecture, delivered before the section on Natural Sciences of the University of Pennsylvania Bicentennial Conference, Philadelphia, September 18, 1940.

I must, then, first ask you to make the acquaintance of the single-cell creatures about which our discussion will center and to follow some of their manners and customs. These creatures are minute green particles, so small that the single individual is hardly visible to the naked eye: their acquaintance must be made under the microscope. They are animals, although they are green; the green color is due to extremely minute plant cells that are growing within their bodies. They are typical ciliate infusoria. This species has received the name *Paramecium bursaria*. They live in fresh water, among lily pads and other plants. They may be kept alive under the microscope, in a few drops of water, or in a single drop. Their generations may be followed for months or years in the laboratory.

Each of these animals is constructed as a single cell, having one large active nucleus and a very minute reserve nucleus. The individual, though a single cell, is complex in structure, having parts which serve as mouth, as organs of locomotion, as sensory and conducting structures, as secretory and digestive portions.

The manifestations of social life that appear most deep-seated—remaining among the most conspicuous even at the stage which we humans have reached—are those connected with mating and the family. In the infusorian, too, these are conspicuous; they will form the basis of our discussion. We shall try to gain an insight into what might be called the courtship, mating, family life and social system of the infusorian.

In the infusorian, as in man, it is not the custom for close relatives to mate. Families are very large. The single individual, as you know, divides into two; these two soon divide again into four, and this continues, so that in a few days the single individual has produced a large family. Such a family is a set of identical twins, containing not two, not five, but thousands, of individuals. Such a family is called a clone.

The members of such a family do not mate together. But if members of an unrelated family are introduced among them, mating occurs between the unrelated individuals. And the behavior of the organisms leading up to the matings is of an extraordinary character.

On the introduction of unrelated individuals, or on mixing two unrelated families in the same drop of water, there is a sudden and strong reaction. The individuals of the different families cling together. Several individuals of one family may cling to one individual of the second family. These are joined by other individuals of both families. In this way tight groups or clots are quickly formed, many individuals of the two families adhering together as if their bodies were covered with glue. They thus form masses of dozens or hundreds of adhering individuals. (See the photographs of this behavior in the papers of Jen-

nings,² 1939 and 1939a; these photographs were here shown on the screen.)

In these clotted masses the individuals adhere firmly together, as if covered by some adhesive material. The clinging together is not an active reaction, nor is it brought about by organs of attachment. It appears to be a physical adhesion; any part of the body of one individual thus adheres to any part of the individual of the other family. Often an individual visibly struggles as if trying to escape from the attachment to another individual, but in vain.

The great clotted masses remain thus with the component individuals stuck irregularly together for some hours. Then they begin to break up into smaller clots and often into chains of individuals attached end to end. This breaking up continues perhaps for two or three hours, the clots becoming smaller, until there remain only groups of two.

That is, in the course of this long and irregular adhesion the individuals constituting the two families have paired off, two by two, so that now almost all the individuals are in pairs (see the fourth photograph of those published by Jennings, 1939 and 1939a; this was here shown on the screen). In every case the two individuals of any pair are members of the two different families. This is readily demonstrated when the individuals of the two families differ in color or in other ways, as is often the case.

The two mates remain intimately united for 24 to 36 hours. While united they exchange halves of their nuclei, halves of their chromosomes (see the figures published by Chen,³ 1940: these were shown at this point on the screen). They then separate. Each individual is now a new combination of nucleus and cytoplasm, since each has lost half of its chromosomes and has received half of its mate's chromosomes.

These are the fundamental phenomena, sketched in their simplicity. But, as you will see, the phenomena are subject to many variations and conditions. When the manners and customs connected with mating are observed, one finds them surprisingly complex. There is, as it were, a complicated code of taboos, inhibitions and permissible practices connected with the mating behavior: a complex social system.

It was mentioned at the beginning that members of the same family or clone do not thus cling together and mate, while members of different families may do so. But it is by no means true that members of *any* two different families will mate. Some families quite refuse to unite; if mixed together they continue to swim about freely and indifferently. Members of other families unite readily in the way described.

² H. S. Jennings, 1939, *Genetics*, 24: 202-233; 1939a, Introduction (pp. 385-389); *Paramecium bursaria* (pp. 414-431) *Am. Nat.*, 73: 385-456.

³ T. T. Chen, 1940, *Jour. Hered.*, 31: 185-196, 1940.

This selectiveness is not a temporary matter; families 1 and 2 never mate, no matter how often their members are brought together; and the same is true of families 1 and 3; they never mate. But members of families 1 and 4 clump together and mate whenever they are mixed.

In higher organisms, of course, there are two differing sets of individuals, such that members of one of the sets never unite together, but members of one set may mate with members of the other set. We call these two sets the two sexes.

Is this the situation also in the infusorian? Does family 1 belong to one sex, family 4 to the other sex—so that they will mate together? Do all families that will not mate together belong to the same sex?

There are no visible differences, no structural differences, between the two individuals or families that mate together. So far as one can see the two are exactly alike. But of course there might be chemical differences distinguishing the two sexes.

Whether there are thus two sexes, all families belonging to one or the other, is readily determined by successively mixing different families. Before showing what happens in such successive mixtures the result of the observations may be stated. Prolonged study shows that there are not two sexes. On the contrary, there are four different sets, or in one variety eight different sets, which mate together, or refuse to mate together according to sharply defined rules.

These things are discovered in the following way: Two families, which we may call A and B, mate when mixed together, so that if there are two sexes, A represents one sex, B the other. With family A we mix a third family. These two refuse to mate. This third family must therefore be of the same sex as A. We will call it A1. Next we mix another family, which we may call C, with family A. We find that A and C mate together, so that C would have to be considered, like family B, a member of the opposite sex from A: it should then be of the same sex as B. We try mixing families B and C together. But we find that they mate together. So it is clear that B and C do not belong to the same sex. C does not belong to the same sex as either A or B. It belongs to a third type. A and B mate together and C will mate with either of the two.

We are evidently not dealing simply with two sexes. We have thus far found three types, A, B and C. To each of these belong many families, so that we may distinguish A1, A2, A3, B1, B2, B3, C1, C2, C3, and so on. There are many families that act like A; they will not mate with any other family belonging to the A type, but will mate with any family belonging to the B type or to the C type.

And as we continue making mixtures, we presently

come upon a fourth set of families, which we may call D. Any family that belongs to the D set will mate with A or with B or with C, but no two families of the D set will mate together. These creatures are divided into castes, which mate or refuse to mate according to rigid rules. Members of any one set or caste will not mate with other members of that set, but will mate with members of any other set. In the variety with which we have thus far dealt there are just four of these castes.

If we call our four castes by the letters A-B-C-D, the mating relations between them are represented by Table 1 (on the screen).

TABLE 1

A - B - C - D

	A	B	C	D
A	-	+	+	+
B	+	-	+	+
C	+	+	-	+
D	+	+	+	-

A plus sign indicates that the two sets readily mate together; a minus sign that they do not.

Many different and unrelated families belong to type A, many to type B, many each to types C and D.

How do members of the different castes recognize each other? There must be some chemical or delicate physical differences among the four different types. When two individuals of different type come in contact they stick together just as if their surfaces were covered with a strong adhesive. But when members of the same type come in contact they do not stick together. The adhesion is a reciprocal relation between diverse types, not a general tendency to adhere to objects.

The mating relations between the individuals thus turn out to be somewhat complex, in a systematic way. But the half has not yet been told. As we continue to extend our acquaintance among different families of the green *Paramecium*, we come upon another set of families that will have nothing to do with the families that constitute the four castes that we have called A, B, C and D. Mix animals of the new set of families with any of those of the four types just mentioned. The individuals pass each other by undisturbed, unmoved—even though they may come into actual contact. There is no adhering together; no forming of clots or pairs.

But members of different families belonging to this second group quickly respond to each other. They cling together, form clots and pair off just as occurs in families of the first group. The families in this second group, like those in the first group, belong to different castes or types. Prolonged study shows that in this second group there are eight different types, in place of the four of the first group. Members of

families that belong to the same one of these eight types will not mate together. But they mate at once with members of any of the other seven types of this group, though they will not mate with any of the types of Group I.

If we call the eight types of this second group by the eight letters of the alphabet from E to M, then the mating relations of the eight types to each other are shown in Table 2 (on the screen).

TABLE 2								
E - F - G - H - J - K - L - M								
E	-	+	+	+	+	+	+	+
F	+	-	+	+	+	+	+	+
G	+	+	-	+	+	+	+	+
H	+	+	+	-	+	+	+	+
J	+	+	+	+	-	+	+	+
K	+	+	+	+	+	-	+	+
L	+	+	+	+	+	+	-	+
M	+	+	+	+	+	+	+	-

In Table 2 a plus sign indicates that two families of the types indicated readily mate together; while a minus sign signifies that they never mate together.

It is remarkable that in all this complex and rather violent mating behavior, the animals observe rigidly certain hours. The adhesion and mating is limited to certain times of the day. It does not occur in the early morning, nor in the evening after five o'clock, nor in the night. It begins at about 8 or 9 in the morning, but the tendency to unite is then very weak; the animals cling together only faintly, in small groups. As the day wears on the tendency to cling together becomes stronger; large groups are formed, in the way that was shown in the photographs. At about four in the afternoon the tendency to cling together may be seen to weaken. The large groups earlier formed break up, and by 5 or 6 o'clock the individuals have completely separated and are swimming about singly again—except the ones that have already become firmly united in pairs. If in the morning or evening we mix together families belonging to different types, they swim about undisturbed, not adhering together nor forming pairs; though the same families if mixed in the middle of the day at once adhere in clots and masses and form pairs.

The conditions thus far described are not the end of the social complications in our infusorian, *Paramecium bursaria*. The social system is indeed enormously complex. There is still another group of families that will not react or pair with any of the families that belong to Group I, nor with any of those that belong to Group II. But the families of this third group mate together in ways and according to rules that are like those already described for Groups I and II. There is one curious difference, however. In this Group III mating is not limited to certain

hours, but will occur at any time of the day or night. In this third group there are, it turns out, just four castes or mating types, as there are in Group I. If we call the four mating types of this group by the letters N-O-P-Q, their mating relations are those shown in Table 3 (on the screen).

TABLE 3

N - O - P - Q				
N	-	+	+	+
O	+	-	+	+
P	+	+	-	+
Q	+	+	+	-

Families belonging to any one type will not mate together. But families of any one of the types will mate with families of any of the other three types.

Thus our microscopic green cells are organized socially into sixteen different mating types, which are divided into three large groups, in the way shown in Table 4 (on the screen).

TABLE 4

A B C D	-----	E F G H J K L M	-----	N O P Q
I		II		III

Members of any one group will not react or mate with members of either of the other two groups. Within any group there are several mating types—four in groups I and III, eight in group II. These mating types within the groups mate with each other in accordance with the rules already set forth. The entire complex system of mating is indicated in Table 5 (on the screen).

TABLE 5

	I				II								III			
	A	B	C	D	E	F	G	H	J	K	L	M	N	O	P	Q
I	A	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-
	B	+	-	+	+	-	-	-	-	-	-	-	-	-	-	-
	C	+	+	-	+	-	-	-	-	-	-	-	-	-	-	-
	D	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-
II	E	-	-	-	-	+	+	+	+	+	+	+	-	-	-	-
	F	-	-	-	-	+	-	+	+	+	+	+	-	-	-	-
	G	-	-	-	-	+	+	-	+	+	+	+	-	-	-	-
	H	-	-	-	-	+	+	+	-	+	+	+	-	-	-	-
	J	-	-	-	-	+	+	+	+	-	+	+	-	-	-	-
	K	-	-	-	-	+	+	+	+	+	-	+	-	-	-	-
	L	-	-	-	-	+	+	+	+	+	+	-	-	-	-	-
	M	-	-	-	-	+	+	+	+	+	+	+	-	-	-	-
III	N	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+
	O	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+
	P	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-
	Q	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-

But the account of social behavior in these single cells is not yet complete. Description has been given

of the behavior which culminates at once in the mating of the individuals: behavior that is regulated in accordance with manifold and systematic preferences and inhibitions. In its operation this behavior appears a bit brutal. The individual (I had almost said the victim) is as it were seized and dragged struggling to the pairing. One is reminded a bit of the shotgun marriages of melodrama. This violent character of the behavior is striking as one observes particular individuals. Two individuals of different mating type (but belonging to the same group) are swimming about in the graceful way characteristic of these minute animals. Accidentally they come in contact. Thereupon they stick firmly together by any parts of the body that happen to touch. Both are brought to a halt with a jerk. Each tries to continue in the direction it was going. The stronger one drags the other away against his efforts—drags him backward or sideways. Such an adhesion may finally after a struggle result in a complete mating. Or other individuals get stuck to one or the other of the two, so that several or many individuals become stuck together in irregular ways; they flounder about helplessly. Sketches of such adhering individuals, irregularly united in groups of two or three or four, are given by Jennings 1939 (footnote 2), Fig. 3 (reproduced on the screen). The individuals seemingly fall helpless victims to the mating reactions.

But as in higher organisms, there is other behavior that tends in the same direction, yet is not violent and brutal; behavior that appears merely a preparation for the definitive mating reactions: behavior that may or may not lead to the selection of a mate. This behavior is of a type that tempts one to characterize it as the objective aspect of courting, or perhaps in some cases flirting.

This behavior shows itself, not in great mass reactions such as were earlier shown in photographs, but in the activities of individuals—or rather of pairs of individuals. Two individuals touch each other gently. They do not stick together, but swim off in coordinated motion side by side, continuing in contact. They proceed in a graceful path—a spiral—through the water. They may keep this up for but a few seconds, then separate, or it may continue for a much longer time, leading finally to a mating of the two. Most often, however, this caressing behavior lasts but a few moments, then the two individuals separate—possibly coming together again in a similar way a few seconds later. Sketches of characteristic postures and motions in such behavior are given by Jennings, 1939 (footnote 2), Fig. 2 (reproduced on the screen).

There is great variety in these reactions, the one common feature being that the individuals swim together in a coordinated way, in such a manner as to

keep their bodies in contact. The bodies may shift, changing the regions of contact; then the two continue in coordinated motion as before. The two after swimming a considerable distance together may separate for a short distance, then come together again. As the animals swim in a graceful spiral, they make a pretty sight, reminding one of couples in a dance.

Such behavior often occurs in two individuals that belong to different mating types. In these cases the gentle caressing behavior is often after a time replaced by the strong physical adhesion before described, and the two individuals finally unite in conjugation.

But such behavior is also seen in pairs of individuals that belong to the same mating type, so that they never finally mate. Such pairs swim about in the varied coordinated way that I have described, but finally separate. It appears that the function of this type of behavior is that of a trial: it gives opportunity for the violent adhesive type to supervene if the two individuals are appropriate mates.

It is a curious fact that although the spectacular clumping in great masses which you have seen in photographs was only recently discovered in these animals, this gentle behavior—courtship or flirting as it might be called—was seen long ago in some of the infusoria. The older microscopists of fifty years ago were a good deal excited about it and its possible psychological implications. One may read a summary of the older observations in the great papers of Maupas⁴ published in 1889. Some of the authors described such behavior and its possible, psychological bearing with enthusiasm and exuberance. But zoologists have of late been disposed to frown upon it, to hush it up, pass over it unmentioned. For it is not the sort of behavior that lends itself most readily to formulation in the simple terms that are dear to the hearts of mechanistic biologists—particularly in relation to single cells. Yet this is behavior that does occur in unicellular animals, that is widespread among them, and in relation to the unity of life phenomena among organisms appears of great significance. Certainly any adequate account of the biology of unicellular organisms must deal with these phenomena, as it must also with the entire system of social relations above described.

To complete the sketch of social organization in the infusoria, one other matter is required. Since this organization is based on mating relations, the conditions of youthfulness, adolescence and adulthood play a role. Two mates that unite become the parents of a new generation. After mating is completed, with its formation of new nuclear combinations, the two parents separate, and each multiplies by fission; in this way the two produce a biparental family.

When these descendants of the two parents are

⁴ E. Maupas, *Arch. Zool. Exp. et Gén.*, (2) 7: 149-517.

tested, they are found to be immature; they do not mate. They are youthful. They grow and multiply; hundreds of successive cell generations are produced, with millions of individuals. All these individuals are in appearance like the two individuals that have mated to produce them. But all are immature; they have nothing to do with mating. If during this period different families are mixed, there is no adhesion, no clotting together, no pairing.

Months later, among the many individuals of these young families signs of approaching maturity show themselves. In mixtures of different families, a few individuals show a weak tendency to adhere when they touch. In time two or three or half a dozen pairs are formed. This period of adolescence lasts for weeks or months; it lasts for many generations. The tendency to mate becomes slowly stronger, till in time the new individuals show the strong spectacular mating behavior that was first described. The new families are now mature.

When this period is reached it is possible to discover the mating type to which these new families belong. And this enables us to discover the effects of heredity in determining the mating type to which any individual belongs. The two parents of course always belong to different mating types, just as two human parents belong to different sexes. Let us suppose that one was of the type A, the other of type D (as in the case shown on the screen). If these two parents had not mated, but had continued to reproduce without mating, all descendants of A would continue to be of type A, all descendants of D would be of type D. But mating has changed this. After mating the two parents produce descendants that are alike, that are all of the same type. From one pair of parents that are A and D are produced descendants that are all of the A type. From another pair of parents A and D are produced descendants that are all of the D type. In these cases the descendants are all like one or the other of the two parents. Most of the pairs produce families of these types. But a few families whose parents are A and D produce descendants that are all of one of the other two types. Some produce descendants that are all of type B, others descendants that are all of type C (as shown on the screen).

If the parents belong to other types, as A and B or A and C, or B and C or C and D, inheritance occurs according to similar rules. Most of the biparental families produced are like one or the other of the two parents, while a few of them belong to the other mating types, to which the parents do not belong. But in all cases the two families descended from two individuals that have conjugated together belong to the same mating type; so that they do not conjugate to-

gether. The two constitute in effect one large family, all of the same mating type.

So at any given time a population of the infusorian, like a population of higher organisms, contains a lot of young, immature individuals, not concerned with mating, a lot of adolescents showing as it were an awakening interest in mating, and a great number of mature individuals, which mate in accordance with the complex social system that has been above described.

The question naturally arises: Does it also contain aged individuals that no longer mate and produce descendants—as does a population of higher animals?

This question has not been fully investigated in Protozoa in which different mating types are known. But the population usually does contain some individuals that are less vigorous than others, as if they had grown old. But these continue to reproduce by division as do both the mature and the immature individuals. Seemingly also they continue to mate. But according to the earlier accounts of Maupas (1889) and of Calkins⁵ (1919), in some species at least these less vigorous individuals when they mate do not produce offspring. They do not continue to multiply after conjugation, but soon die. It appears possible that these less vigorous individuals are merely those that have lived under poor conditions and grown sickly. All this is a question that is much disputed among observers of these animals. There is beyond doubt some indication that aged, decrepit individuals are finally produced. By aid of the discovery of the diverse mating types, it is to be hoped that this question may soon be fully settled.

In the population as we find it in nature therefore there occur young immature individuals, adolescents in various grades of development, possibly aged, senile individuals, and mature individuals. Among these mature individuals may be representatives of any or all of the 16 diverse mating types and the three different groups that have before been described.

How far is the situation just described in *Paramecium bursaria* typical for unicellular organisms? Investigation of such matters in the different Protozoa has hardly more than begun. Yet it has gone far enough to show that some such social organization as has just been described is of widespread occurrence among certain classes of Protozoa, particularly in the ciliate infusoria. But the details of organization differ greatly in different species. In *Paramecium aurelia* the extensive researches of Sonneborn⁶ (1937-1939) show that there are, as in *Paramecium bursaria*, three groups such that members of different groups will not conjugate together. But any single group is composed

⁵ G. N. Calkins, 1919, *Jour. Exp. Zool.*, 29: 121-156.

⁶ T. M. Sonneborn, 1937, *Proc. Nat. Acad. Sci.*, 23: 378-385; 1939, *Am. Nat.*, 73: 390-413.

of but two mating types—a situation like that in man and higher animals—in place of the four or eight types found in *Paramecium bursaria*. In *Paramecium caudatum*, Gilman⁷ (1939) finds a situation in many respects like that in *Paramecium aurelia*. In the infusorian *Euplotes* there occur, according to Kimball⁸ (1939), many different groups and many mating types in a group.

Turn now to certain general considerations; to interpretations, reflections and conclusions. As to conclusions, the facts speak for themselves so loudly that it is hardly necessary to state them in a general form. Social behavior is found in organisms that are single cells; it is even found in what must be called in certain respects a highly complex system.

As to interpretations, you will perhaps agree that in describing these social relations one is tempted to fall into the use of terms that are based on our own human experience, of terms that have a subjective background, terms that relate to conscious experiences. The whole picture tends to emphasize the unity of the biological world in such social relations as those of which I have spoken.

Of course there is no doubt at all that all the manifold social discriminations, attractions and repulsions have in the infusoria chemical or physical correlates; as they have indeed in man also. For many purposes it will be most useful to describe the behavior in terms of these physico-chemical relationships, when they become known; and this is what is usually striven for in scientific accounts. But for other purposes, such as for examining into the question of unity versus heterogeneity in biological phenomena, comparison with conditions in other organisms is required. And when one makes such comparisons, it becomes evident that some of the behavior of these simpler organisms much resembles that which in ourselves has subjective accompaniments, has even conscious awareness of relations. Whether there are faint glimmerings of consciousness in the infusorian we can of course never know.

But one thing we can know. The infusorian has no awareness of the complex social system into which its behavior fits, for the good reason that there is no way in which it could acquire the data requisite for being aware of it—even if it has or had the capability of conscious awareness. For to become acquainted with the system, one must subject himself to the experience of all its components and relations, and this the infusorian has no opportunity to do; it can not know the social system because it has never become acquainted with it.

This situation illustrates an important biological

principle: a principle that is indicated and perhaps we may say demonstrated and emphasized by many relations in the biology of behavior. This principle is as follows: In evolution, process and action are primary, consciousness, particularly conscious awareness, secondary. Conscious awareness, as of purpose, function or relations arises (if at all) *after* action: after the course of action has become established. The organism first acts, only later—in later generations—does it discover why it acts as it does, what function is performed by its action. Many things that are consciously done by higher organisms are likewise done by lower organisms, but certainly without that awareness of relations which appears to guide them in the higher animals. The performance of an action, even in accordance with a complex system of relations, comes in evolution before there is awareness of the action—or certainly of its relations. The action is not derived from conscious awareness or purpose, but the reverse is true. The action first comes to be performed, later in evolution the organism comes to be aware of it and of its functional relations. So our *Paramecium* operates on an elaborate system of social relations, of which it can not possibly be aware. Man-kind operates on a social system not too diverse from that of *Paramecium*, but he is aware of it, and sometimes has consciously planned certain aspects of it.

Social behavior—meaning distinctive and specialized reactions to individuals of one's own kind, such as we have seen in the infusorian—implies and is correlated with another aspect of behavior—an aspect which has always been stated in terms of consciousness. It is known as the problem of "self-consciousness." The individual in his social relations reacts as one individual among others, having attributes similar to those of other individuals. Stated in the subjective terms commonly employed, in self-consciousness the individual recognizes himself as a unit in the social group of individuals of his own kind. It has long been the custom to assert that while animals doubtless are conscious, only man has self-consciousness. The possession of self-consciousness has been asserted as a great distinctive feature of man. This is a traditional and hallowed doctrine, one that keeps for man his unique place in nature.

But certainly the objective correlate of self-consciousness is seen in organisms that react socially; organisms that find their place in a social system such as we observed in the infusorian. Such organisms react as members of a particular group; they react to individuals of that group (and of that only) as to fellow creatures of their own kind. In the mating behavior they declare themselves, as it were, to be individuals of the same kind as their mates. In these lowest organisms this is presumably done without con-

⁷ L. C. Gilman, 1939, *Am. Nat.*, 73: 446-450.

⁸ R. F. Kimball, 1939, *Am. Nat.*, 73: 451-456.

scious awareness of the relations involved. If so it is again an example of the fact that types of action come first, awareness of the relations involved coming later in evolution.

In animals that are more complex this type of action has developed in such a way as to indicate that there has arisen conscious awareness of the self as an individual among other like individuals. This is shown in many ways beside the mating behavior; one of the most striking of these is the exhibition of jealousy. When a dog is caressed in the presence of another dog the second dog is disturbed; he seeks to substitute himself for the one caressed. It is difficult to see how a creature that is unable to speak could indicate more clearly that he realizes himself to be an individual like the other dog, that he and the other dog are rivals. Such jealousy, with the same implications, is shown by many of the higher animals.

Related to this, and with a similar significance, are the demands of many of the higher organisms that dominance and subordination be observed; that the rights of precedence be not infringed. Any one who in his youth was accustomed to drive home the cows knows with what indignation it was received when one of the subordinates attempted to go first through the gate. It was quickly put in its place by well-directed shoves from the horns of the cow that had in earlier contests made good her claim to precedence.

This matter of dominance, of group precedence, in animals has of late been studied systematically, so that knowledge of it is by no means now in the anecdotal stage. Bird society has recognized orders of dominance, established originally by contests among indi-

viduals. This order of dominance is commonly known as the "pecking order." A certain individual established his right to peck, or to threaten to peck, any of the other members of the flock. The others recognize their subordinate relation and receive the pecking without resistance or resentment. Another individual is No. 2 in the pecking order, and so on down the line, there being a complete hierarchy.

Such demands for precedence, such recognition of one's self as a subordinate, or as occupying a clearly defined place in the social hierarchy, seem clearly to involve a consciousness of the self as an individual among others; or at least they involve the objective correlate of self-consciousness. Unless we arbitrarily deny all consciousness to other organisms than man, we can not consistently deny to them self-consciousness: that is, awareness of the self as an individual among like individuals. The attempts to reserve self-consciousness as a distinctive attribute of man therefore appear to be outmoded; they appear out of touch with scientific knowledge.

Among the many features of social behavior in animals that carry similar implications, doubtless the most primitive is the behavior in seeking mates. It is found generally in unicellular organisms. Indeed it is doubtful whether any organisms exist in which it does not occur. The seeking of mates appears to be the fountain head of both social behavior and self-consciousness. It involves the recognition of mates as of one's own kind; and correlatively the recognition of the self as of the same kind as mates. Here social consciousness and self-consciousness have their roots.

OBITUARY

RODNEY HOWARD TRUE

RODNEY HOWARD TRUE during his active and productive life lived through many stages in the development of botanical science here in America. His contributions, of which there are about seventy listed in the Department of Agriculture catalogue, cover many different phases of botanical work. Always interested in men and in human welfare, he was associated in the various papers with many other prominent botanists of his time. His breadth of interest is shown in his activities, the associations he founded and fostered, the various and diverse character of his publications and, above all, by his sincere and wholehearted appreciation of his associates. It would be impossible adequately to express this humanistic side without diverting too far from the scope of a notice such as this. He helped others often at great personal sacrifice and resigned from the Bureau of Plant Industry to meet a budget cut rather than reduce his staff in salary or number.

This was done with no position in sight, for he preferred a personal sacrifice to administrative injustice to the members of his staff. Many people looked to him for scientific advice which he was always ready to give, for help with personal matters and for pecuniary help in times of great need. This trait led him to take an active part in the welfare of federal employes, to work for a better organization of scientific and technical men and to serve on the Committee of 100 of the American Association for the Advancement of Science on scientific research. He was a leader in organizing the Agricultural History Society, founded in 1919 and incorporated in 1924, and was the first president of the society. He also served on the executive committee and was a life member of that organization. He was also a member of the general committee to revise the U. S. Pharmacopœia in the ninth edition.

He was a member and held important offices in many organizations such as the American Association of