John Bonner who gave the 1993 Gandhi Memorial Lecture (published below) has created for himself a niche in his field of research. He is considered the world's greatest authority on Slime Moulds. He was the Visiting Raman Professor of the Indian Academy of Sciences (IASc).

For over 50 years in his researches he has always picked the right question, designed incisive experiments and has presented his findings in articles which are models of scientific writing. IASc has brought out a volume of his selected papers, which has received rave reviews. Slime mould amoebae are living micro-organisms that periodically gather together to form macroscopic fruiting bodies. John Bonner sees the universe in this micro-organism. It is in this philosophical and social vein that he gives the Gandhi Memorial Lecture.

Editor

Dividing the labour in cells and societies

J. T. Bonner

In all collections of living entities, from cells within an organism to individual organisms within a society, the greater the size of the group, the greater the division of labour. Yet there are important differences in how the labour comes to be divided in cells and in societies.

I felt enormously honoured when asked to give this Gandhi Memorial Lecture, but at the same time I was struck with awe when I considered what I might say. How can I connect my modest lifetime interest in biology with the ideas and thoughts of a giant who did so much not only to change India, but to change the whole world. The answer is that I can only fail and this lecture will be testimony to that failure. However, I shall try very hard to make it an interesting failure!

My intention is to discuss a grand and important generalization that applies to all living things. To state it simply in one sentence, it is that at all levels of life, from cells in a multicellular organism to individual organisms in an animal society, there is a division of labour, and the extent of that division of labour depends directly upon the size of the community. This is an aspect of the organization of nature which has interested me for many years, and here I would like to share some of those thoughts with you.

My plan is to begin with examples from the living world that show both a division of labour, and a correlation of the extent of this division of labour with size. I shall begin with lowly slime moulds and end with a discussion of human societies.

The important question is why does one have such a relationship: that is the real purpose of this lecture—to explore the 'why'. I will argue that this relation of division of labour to size is not some mysterious law of nature that so far has defied identification and is in need of revelation. Rather I will urge on my listeners the straightforward idea that it can be explained in the simplest way, using well-known principles. There will be differences in the details of the relation at different levels; what happens among cells is not identical to what happens in societies. Yet despite those differences there are certain things that are the same at all levels, and this will be the main object of our quest.

Finally, there is always the hope that any insights into something as fundamental as the relationship between size and division of labour may help us to understand our present day human condition. It would, however, be misleading to imply that such searchings will provide solutions for our troubled world, but perhaps they can give some insight, some understanding, and understanding is the first step in all human progress.

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My initial interest in the size-division of labour question came when I started as an experimental biologist. I was interested in embryology, in how animals develop, but I was dismayed that animal embryos, especially amphibian embryos, which were the main object of study of embryologists at that time, were so complex. In my search for something simpler, I was very lucky to find little known organisms called cellular slime moulds, and I began my work on these many years ago as an undergraduate.

These minute organisms live in the soil[1,2]. They feed as separate amoebae and in many respects, both as to size and appearance, they resemble our white blood cells. They feed on bacteria and after they have cleaned an area of food they do a remarkable thing; they stream together by aggregation to form multicellular masses of cells, usually of about ten to a hundred thousand cells (Figure 1). The multicellular structure has a front and hind end, it is covered with a slime sheath and in all ways behaves as an individual multicellular organism. For instance, this 'slug' will go towards light and orient in heat gradients. It is very small—a large one will be a millimeter long and something in the order of a tenth of a millimeter in diameter.

After a period of wandering, this slug will right itself and send a small fruiting body up into the air. It does this by having the anterior cells form a stalk by a sort

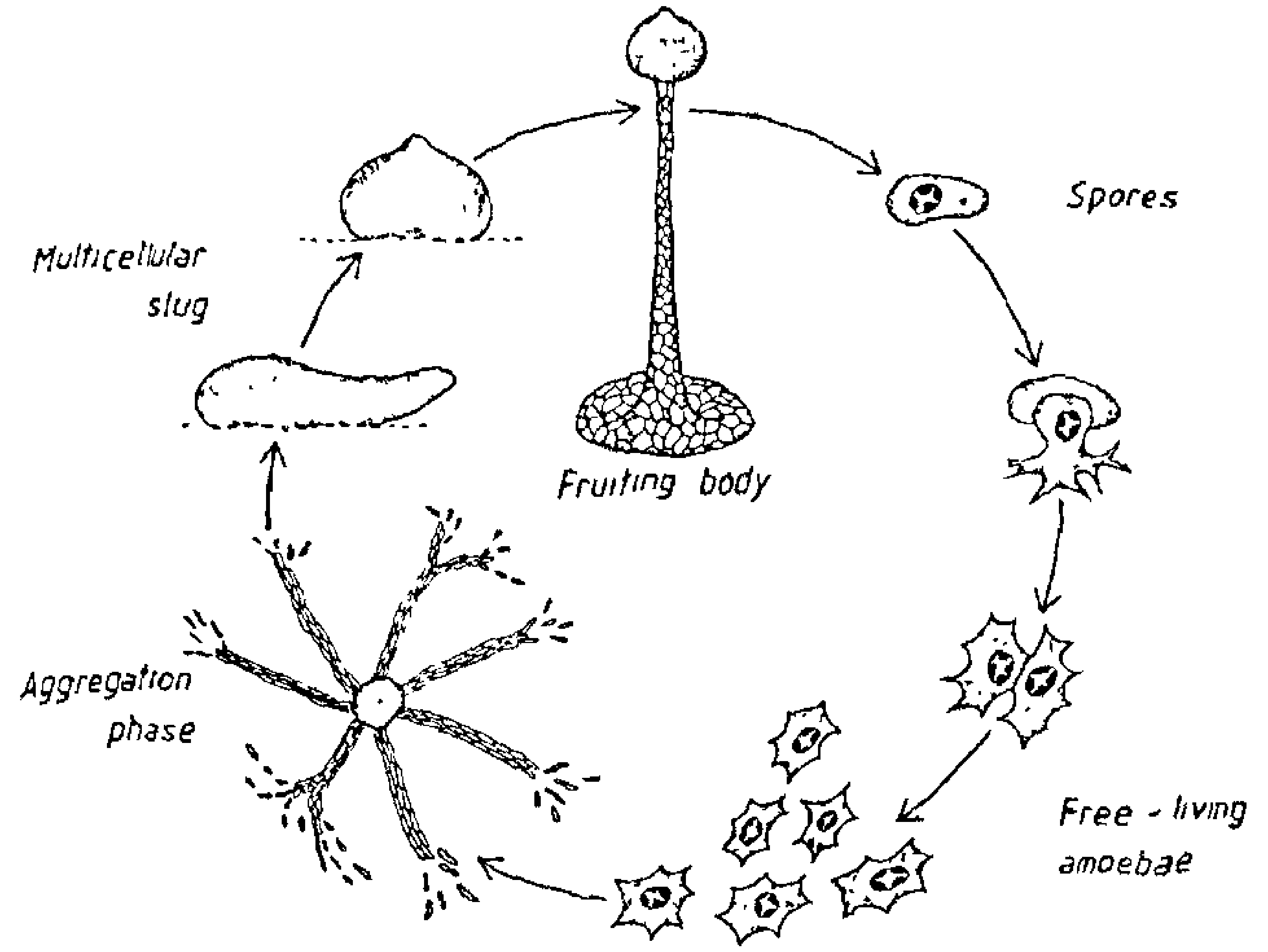

Figure 1. A highly schematic diagram of the life cycle of the slime mould *Dictyostelium discoideum*. (Drawing by Harry Williams, after Olive, 1970).

of reverse fountain movement in which the cells climb to the tip and then go into a central stalk cylinder of cellulose that they have secreted. Once inside this cylinder they become large and vacuoleate and in the process deposit more cellulose in the form of cross struts which appear to give the stalk greater strength. (During this process the cells die, but this is not material to the point I wish to make here.) As the anterior cells pour onto the tip, the stalk becomes progressively elongate and as this occurs the posterior cells, each one of which is to become an encapsulated spore, are lifted into the air at the tip of the stalk. The end result is a ball of mature spores raised one or two or a few more millimeters into the air on a thin, delicate, tapering stalk. It is presumed, and this is a reasonable assumption, that this social phase is advantageous because it provides a means of effectively dispersing the spores so that they can land on fresh deposits of bacteria some distances away in the soil.

One of my reasons for dwelling in such detail on these slime moulds is a personal prejudice: I have spent so much of my life working on them in the laboratory. Besides my inordinate fondness for them, they provide an excellent example of a primitive division of labour. Some of the cells make up the supporting stalk, and the rest become spores, capable of starting the next generation. The separation of these two functions—support and propagation—could not be more sharply defined.

If now one were to compare these 'social amoebae' with their solitary ancestors, one would see that by coming social two changes have occurred. They are collectively larger than single, solitary amoebae and they have differentiated into two cell types. Solitary soil amoebae will form single-cell spores or cysts, but they obviously do not have supporting cells. So in this primitive evolution from solitary to social amoebae I have already illustrated how from the very origin of multicellularity there is a correlation between overall size and division of labour.

For contrast, let me now go to the other extreme and consider a type of multicellular organism that has the greatest division of labour, and by that I again mean the greatest number of different cell types, each with a different function. Vertebrates are supreme in this kind of complexity and our own species provides an excellent example. We have muscle cells for movement, nerve cells to transmit rapid messages from one part of the body to another, cartilage and bone cells to deposit the supporting structures of our skeleton, gland cells of many kinds to secrete hormones and digestive enzymes of different sorts. We have lens cells in our eyes that are specialized by becoming transparent, pigment cells in the retina in the back of our eye that are stimulated by light; and even these divide the labour, for some are responsive only to red light, some to green, and some to blue, as they contain different photoreceptive pigments. We have cells that specialize in carrying oxygen (our red blood cells) to the tissues, and a variety of cells in our kidneys responsible for the elimination of wastes in the blood. I could go on and on for the degree of division of labour is formidable, but let me end with just one more example. Nerve cells have in common the ability to transmit impulses, but not all nerve cells are the same; there is a considerable amount of division of labour within our very complex nervous system. Some of these differences are morphological, but the majority of them are chemical. They have specific receptors that can only respond to specific stimuli, chemical or physical, or they can secrete specific chemical messages.

It is perhaps of no great avail to say how many cell types there are in our bodies, but it is obvious that they are very numerous. And certainly, if one compares them to slime moulds with their stalk cells and spores, the division of labour within the cells of a mammal is vast! Let me add, parenthetically, that this also makes clear why, as a young student, I was eager to find a simple organism in order to study the mechanism of development.

Between these two extremes—slime moulds and mammals—there are great numbers of other organisms, invertebrates and plants of all descriptions, that have an intermediate number of cell types. Take, for example, higher plants. They have specialized cell types of various sorts in the leaves, such as the outside layer of cells which contain the pores that allow oxygen and carbon dioxide to pass through during photosynthesis and respiration. They have a variety of cell types in the vascular tissue—some for the support of the plant, and some for the transport of water and others for the transport of food from the leaves to the rest of the plant. When all these (and more that I have not mentioned) are added together, they make but a small fraction of the number of different cell types found in our bodies, but they certainly greatly exceed what is found in slime moulds.

A few years ago I examined a large number of organisms with respect to the number of cell types they contained and drew on a graph the approximate number of cell types plotted against the size of the organism (Figure 2). Admittedly the correlation was very rough because for any one level of division of labour, there was a great range in sizes. In the case of flowering plants one could have at one end of the scale a minute duckweed, while at the other a giant sequoia. Among vertebrates one had small fish, or humming birds, or shrews at one end and a huge whale at the other. Yet despite this great variation in size of any one level of cell types, or division of labour, there is clearly a trend: the larger organisms have more cell types. Particularly relevant is the fact that in cases where there has been an extreme reduction in cell type of a particular species compared to the norm of its group, then there has been a loss of cell types. This can be seen in duckweed, that has a few less cell types than larger plants, and in rotifers where again the smallest species have lost some cell types.

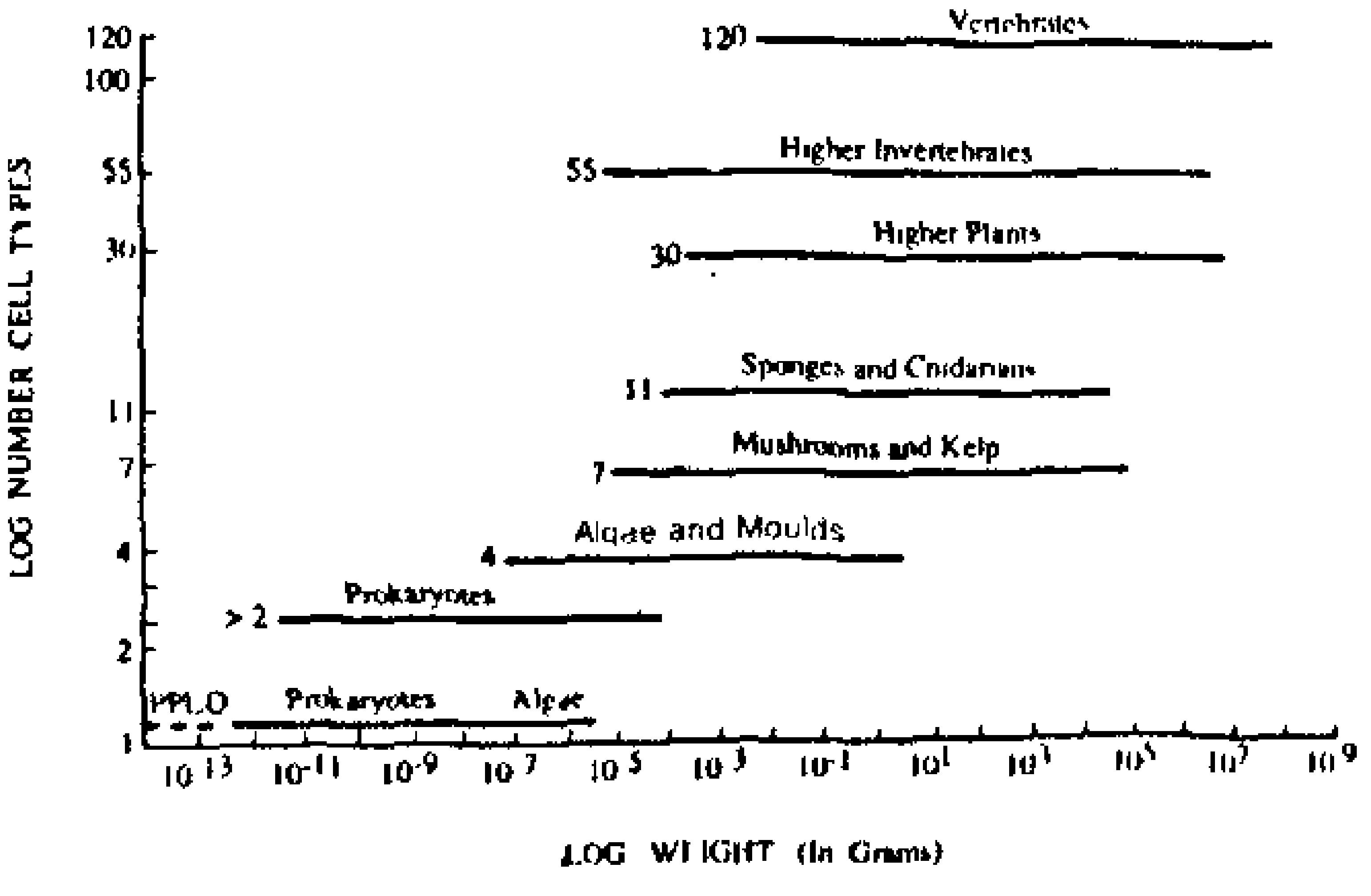

Figure 2. A graph (log–log) showing the size ranges (by weight) of groups of organisms containing different numbers of cell types (From Bonner, 1988).

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Before discussing societies, I would like to pause and ask why, in multicellular organisms, there is this size-division of labour relationship. The explanation has two parts, both of which are essential.

The first is that there are certain physical constraints that would make it impossible for large organisms to exist were there no division of labour. How could something as large as a human being exist if it had only one cell type, like a collection of amoebae? It could not support itself lacking a skeleton; it could not get enough oxygen or food into its inner cells because there is no circulatory system and gut to bring the food inside, nor any way to eliminate the waste products of the metabolism of the internal cells. The insides of this giant mass of amoebae would die from lack of food and oxygen, and from the accumulation of toxic wastes.

All of these problems, which are solved by a division of labour, are the consequence of a very simple physical principle. The volume, the weight of an organism, increases with an increase in size, by the cube of the linear dimensions (l^3) while two key properties of all physical structures go up by the square of the linear dimensions (l^2). One of those is strength: the strength of a muscle or a bone is related to its cross section area (l^2), and this means the heavier an animal or plant becomes, the supporting structures must become disproportionately thick to compensate for the increase in weight. Weight rises by l^3 and strength by l^2, and therefore the latter must increase more rapidly to give the strength necessary for the size increase. This is why gazelles have slender legs and elephants have huge stumps; an elephant with gazelle's legs would collapse under its own weight.

The other key property which rises by l^2 is the surface. Metabolism rises with the volume (l^3) with increase in size, but the ability to get oxygen and food depends on those substances going through the surface of an organism, and to achieve this in large organisms there must be a disproportionate increase in cell surface. This is the reason for our lungs with many pockets to increase its internal surface; this is the reason for our long, convoluted gut with its innumerable projections (villi) that increase its surface of absorption of food. We have gone much further to solve these problems by adding a circulatory system where blood is pumped from the lungs to the tissues, and from the gut to the tissues so that all the cells get their food and oxygen. In this case we have a far more compelling reason for a division of labour than in the case of strength. All the devices in our body that cope with gas and food exchange involve a very large number of different cell types when one thinks of all the complex systems involved, but for strength it mainly, but not entirely, involves an increase in the efficiency and thickness of the supporting structures.

The second reason for a division of labour has to do with Darwinian natural selection. Here the change, the evolution of organisms are determined by reproductive success. Those individuals which are successful in producing offspring will be the ones that perpetuate their genes. Success in reproduction also means success in survival, and only those organisms that are constructed efficiently are the ones that will pass on their genes to the next generation. In other words there is a continual selection pressure for efficiency, which is the same thing as saying that those organisms that best solve the physical problems imposed by strength-surface-volume considerations, will be the ones that are successful in passing their genes on to subsequent generations.

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I would now like to shift from cells to societies. First I will consider insect societies, and then go on to two different aspects of human societies. One is a direct examination of the division of labour in different size communities, and the other is a similar examination of human institutions, such as business corporations and universities.

Insect societies are quite remarkable for their size and their diversity[3]. Some ant colonies will have one queen with millions of sterile workers attending to all the activities or functions within the nest. These consist primarily of feeding and caring for the young, foraging for food, and the protection of the colonies. Some species of termites will have equally large colonies, but they differ from ants, bees and wasps in a few important respects, although those differences are not directly germane to my argument here. At the other end of the size spectrum there are certain primitive social wasps and bees that will have very small colonies consisting sometimes of less than a dozen individuals.

The difficulty in making my case here is that while the various functions of the workers are obvious enough, it is less clear that there are specific individuals assigned to carry out specific functions, or that there is a rigid division of labour.

In the more primitive social wasps there are no morphological differences among the females that come together to form a small colony. There is, however, a dominance hierarchy, that is, there are behavioural differences. One female will remain queen by lording it over the others, and she alone will lay eggs for the next generation; she will forcibly prevent other fertile females from doing so. In a careful study of these behavioural characteristics Gadagkar and Joshi[4] showed that the females did not all share the activities of the colony equally, but some spent more time foraging, some, fighting, and some just loafing. In other words, these *primitive social wasps do divide the labour, but only by* using subtle, behavioural means of doing so.

By contrast, in large colonies of ants and termites there are morphological differences between the workers. They may not only differ in size, but in shape as well, and those differences are associated with specific tasks within the colony. The smallest workers may be primarily occupied with the care of the young, the middle size workers are busy foraging for food, while the largest workers, the soldiers, will guard and protect the nest. To see if one could measure the extent of this morphological division of labour in relation to the size of the colony, I took a table from Hölldobler's and Wilson's recent great tome on ants[5], which gave the colony size for a large number of species of ants. I broke this up into groups based on colony size and Wilson was kind enough to indicate how many morphological castes there were for each of these species. He pointed out to me that for some it was easy, for the castes are discrete in their shape; but for others there is a continuum, and therefore assigning a number for the different castes is difficult and subjective. I was fortunate to be able to rely on his great experience in observing ants, and was able to plot colony size versus caste numbers and show that, as expected, there is a clear and significant increase in the number of castes with an increase in the size of the colony, despite a considerable scatter of the points (Figure 3).

In this case the explanation of why there should be such a relation is undoubtedly again natural selection. Insect colonies, with their one fertile and mated queen, pass all their genetic information from one generation to the next through her eggs and in particular those eggs that produce offspring that are not sterile and will start the next generation. If the queen carries genes which produce a large colony, clearly those colonies in which the labour is efficiently divided will survive. As the famous entomologist Wheeler[6] pointed out many years ago, a specialized worker in an insect society is

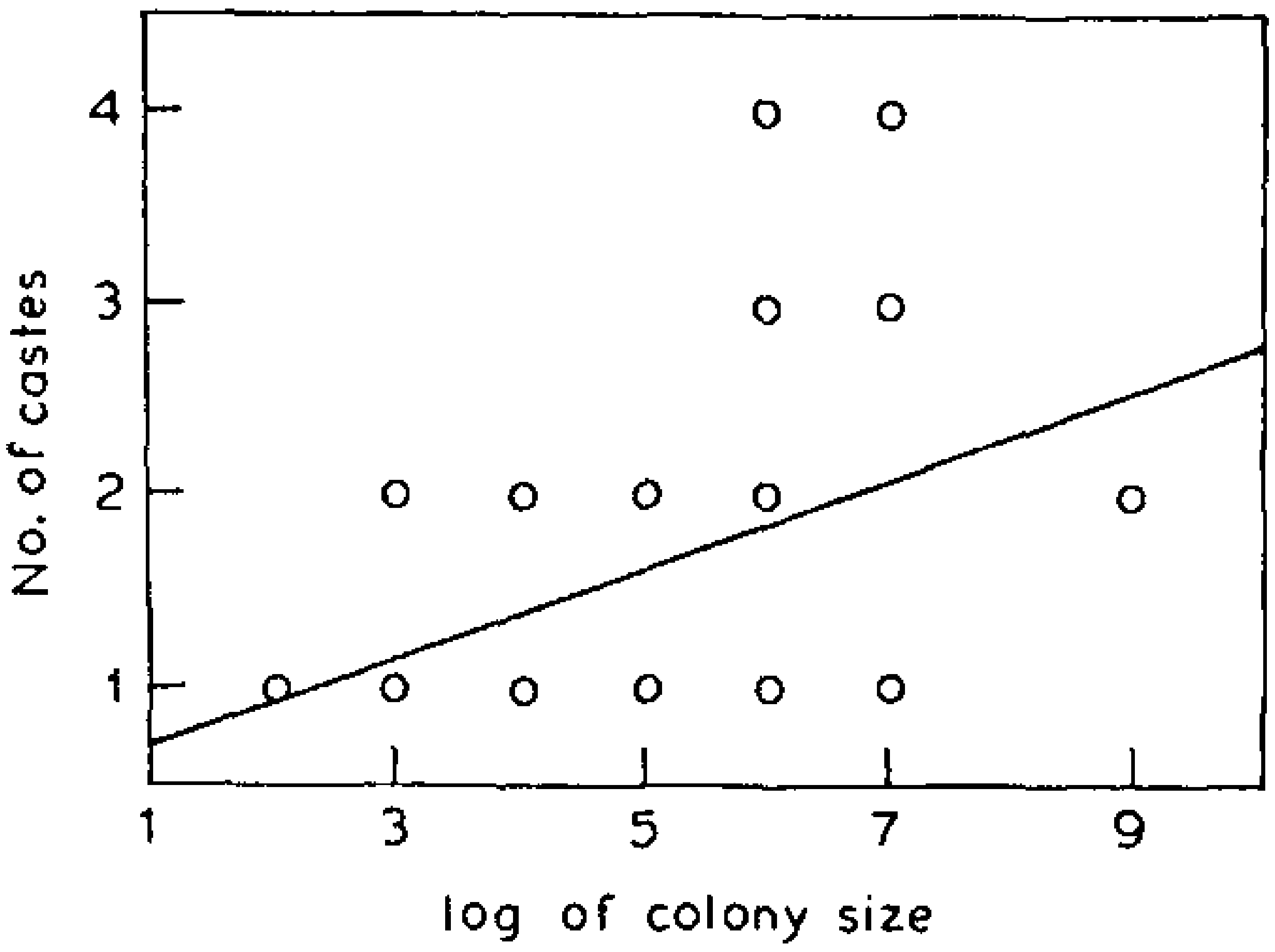

Figure 3. The estimated number of castes of 140 different species of ants plotted against the logarithm of their colony size. The line is a simple regression: there is a significant correlation between the number of ants and the number of different castes in a colony.

the equivalent of a specialized cell in a multicellular organism. Only the reproductive cells of our bodies carry our genes on to the next generation, and all our other cells die at the end of our life cycle. The cells which divide our labour are in all senses the equivalent of sterile workers of different castes of an ant colony. For both ant societies and multicellular organisms it is efficiency that leads to reproductive success, and that efficiency means an appropriate division of labour. The important point is that a complex insect society can easily be understood in the same way we explained the division of labour of cells within a multicellular organism: it has arisen by the natural selection of genetic variants, that is, it has a totally Darwinian explanation.

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The perception that there is a division of labour in human societies goes back at least to Adam Smith, the eighteenth century economist, and has been pursued by many others since then. Herbert Spencer, the nineteenth century sociologist-philosopher saw this in his enthusiasm for generalizing, as an important principle of biology and sociology. There is in his work the implication that the division of labour is related to size, but there was no effort until recently to measure the increase in the division of labour with an increase in size of the society. It was simply pointed out that in very small communities individuals were expected to carry on more than one craft, but as a village increased in population, there could be a clear separation so that one individual made shoes, a tailor made clothes, a butcher sold meat, a greengrocer sold fruit and vegetables, and so forth. These special trades or crafts could only be separated into the activities of single individuals when the community became big enough, for example, to give the cobbler a full time job. In a very small village he would have to do other things besides shoemaking to earn his bread.

These generalizations were put on a firmer footing by Carneiro[7], an anthropologist who, building on some earlier work of others, examined a number of societies of different sizes from different parts of the world. For each he measured the number of what he called 'organizational traits', which was an attempt to identify specific crafts and occupations in a society as well as the social structure. The smallest social groups were formed among the now extinct Tasmanians, which consisted of around 15 individuals and were differentiated into two organizational traits. The two largest groups in his study consisted of approximately 1500 individuals, and possessed a total of 32 and 52 organizational traits. In all he measured 46 single community societies and when he plotted these on a log–log graph he was able to show a linear relation between the size of a community and its division of labour (Figure 4).

I have been fortunate for many reasons to return to India and one of the benefits has been to discover that M. Gadgil and N. V. Joshi have been working with K. S. Singh and his colleagues in the People of India project carried out by the Anthropological Survey of India, who are making a wonderfully rich collection of measurements of communities from all over India[8]. Joshi very kindly retrieved from this pool of data the population size of different Indian states and the number of occupations found in each. Again on a log–log plot there is a clear relation: the larger the population, the greater the number of occupations, or division of labour (Figure 5). The smallest state has a population of 40,000 with a total of 13 occupations, while the largest state has a population of slightly over 110,000,000 and 142 occupations.

Before asking the question of why this is so, I would like to consider another kind of human activity where one finds the same principle. This is in organizations that are connected with human activities, such as businesses, universities, government bureaucracies and other similar institutions. There too, as they increase in size they increasingly divide the labour. Consider, for instance, a country store in a small village. It sells everything from food to clothing to tools to stationery. They will not have a large stock of any of these items, but the variety will be sufficient to meet the major needs of the villagers. In a larger town, each one of these items will be sold in a separate store, at least that used to be the case a few years ago. The larger village had a baker, a hairdresser, a butcher, a greengrocer, and so on. It will even have a division of labour among the professions, so that there will be a doctor, a lawyer, and a banker to take care of one's more sophisticated needs.

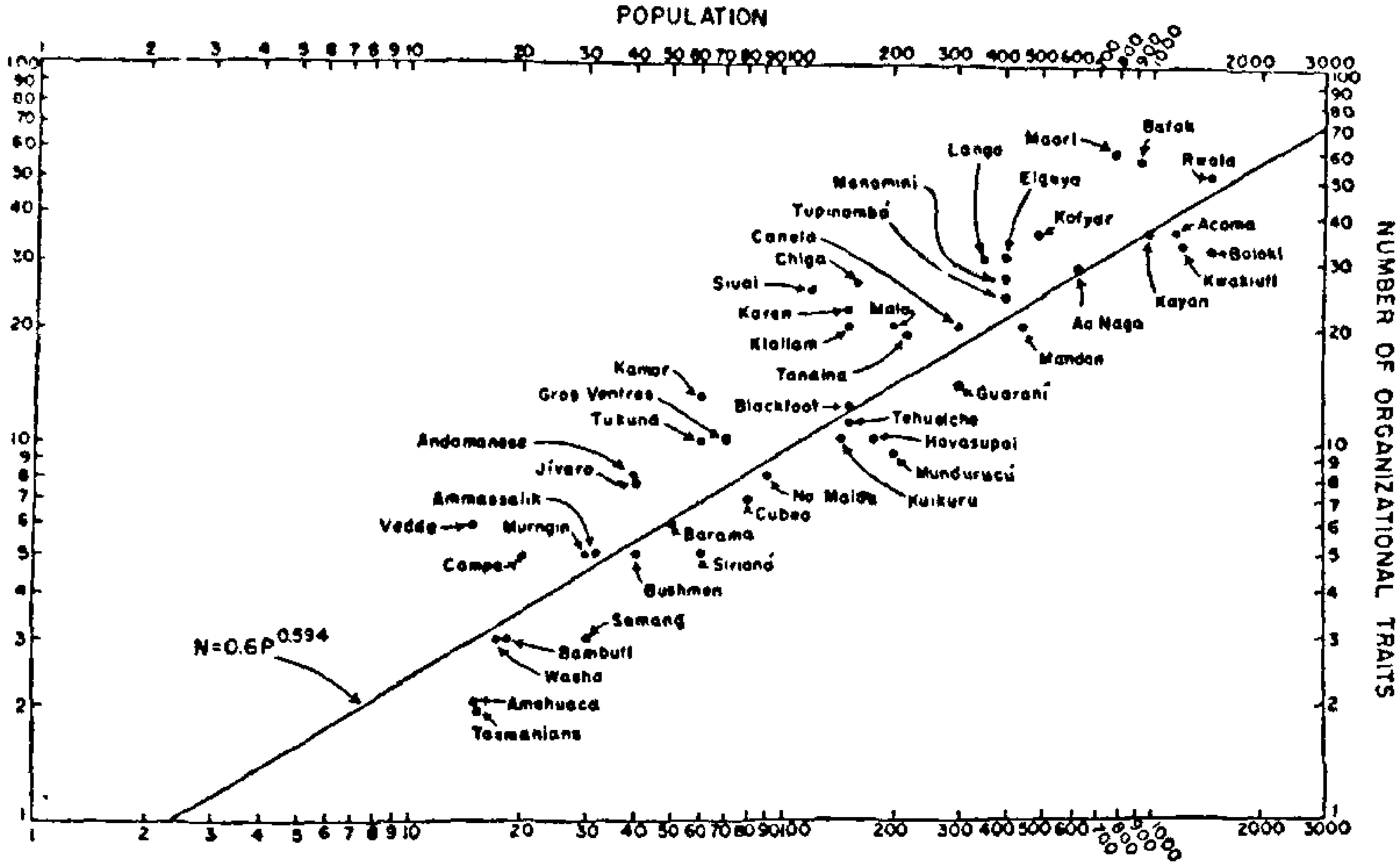

Figure 4. The number of organizational traits plotted (log–log) against population size for 46 single-community societies. (From Carneiro[7]).

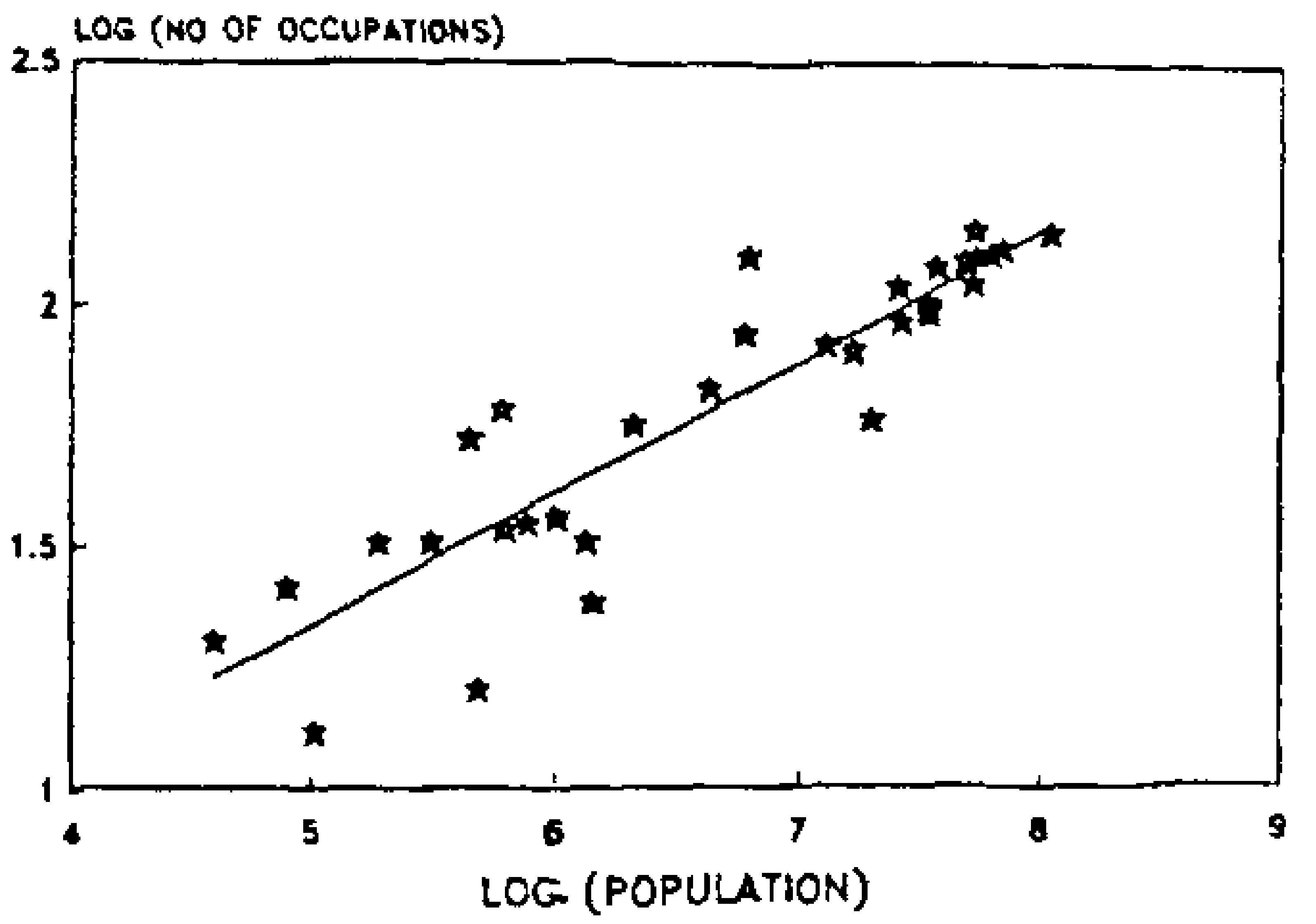

Figure 5. The number of occupations found in each of the states in India plotted (log–log) against the population size of each state (Graph by N. V. Joshi).

It is easy to see that one finds the very same trends if one goes from small businesses to larger ones or small universities to larger ones, or even departments within a university. With increase in size these institutions generate a need for an internal structure that not only divides the labour, but does it so that there is good communication between the more numerous members and that the job of each does not overlap, but dovetails with all the others. This is obviously necessary for a business to be competitive and effective. If that is not achieved, the company will fail, and therefore at each size level there is an increasing, but optimal division of labour, so the business, no matter what its size, can succeed.

In recent years, businesses have also undergone what one might call the 'supermarket' phenomena. Instead of remaining discrete, and, for instance, manufacturing one product, there has been a strong tendency for companies to diversify so that, like supermarkets, they are concerned with many commodities. This has even led to the merger of great companies into megacorporations. However, the principle that the division of labour increases with size holds equally well for these amalgamations; because their economic success depends upon the smooth inner working of all their parts, which must be effectively coordinated in their activities. The only place where efficiency is in danger is in the great government bureaucracies where the dividing line between success and failure is not so sharp.

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If we now ask why human societies seem to follow the same size-division of labour principle of cells, the answer is somewhat different from that for cells. There are no obvious physical constraints as we saw for cells; but even more important, there is a totally new element, namely behaviour. Individual organisms can only pass on information through their genes, but in the evolution of animals there arose an entirely new method of passing information, and that is by behavioural signals between one individual and another. In order to contrast this behavioural transmission of information with genetic transmission, Dawkins[9] has called the former 'memes'. A meme is any bit of information that can be passed from one individual to another by behavioural means.

The difference between memes and genes is very large, and the consequences of those differences are important. Genes can only be passed on, through egg and sperm, from one generation to the next, and therefore many generations over a long period of time are required for a particular gene to spread through a population. Memes, on the other hand, can pass from one individual to another in an instant of time, and as a result can spread very rapidly through a population.

There is, of course, much more to behaviour than the passing of information between individuals; we can solve problems. Animals also have the power to solve problems, but of all animals we are undoubtedly the most skilled in doing so. It is this problem-solving ability that is the key to how the labour is divided in societies.

First let us again look briefly at ant societies. I made the point that their division of labour is primarily genetically based and therefore subject to natural selection. This is certainly true, but insects have behaviour as well, and perhaps even a modest ability to solve problems. Those who work with social insects can give you many examples, but here I shall just give one that is relevant. If, in an ant colony which has different castes performing different labours, one removes one of the castes, then some of the workers from other castes will take over and perform tasks which they never performed previously. In other words they show a behavioural flexibility, and, in a way, this could be considered an example of minor problem solving. By being flexible they see to it that all the functions, all the labours required for the welfare of the whole colony are carried out, despite the loss of one of the castes. From this one might conclude that in social insects there can be a mixture of behaviour in a background of a strong genetic basis for the division of labour.

For human beings the genetic component takes the back seat. No doubt the structure and abilities of our brain have primarily a genetic basis, but what we do with our brains in terms of thoughts, including problem solving, is way beyond our genes. Our skills may have a genetic basis, but what we do with those skills opens up a new world.

With this background let us now examine the size-division of labour structure of human societies. If we look at the relation between occupations and the size of the communities it is clear that for the economic survival of the individuals within the community they must follow a course which is dictated by the size of the community. If they fail to do so, those individuals may starve and ultimately the whole community will be jeopardized. But human beings are supreme problem solvers, and if there are not enough people in the community to keep a shoe or sandal maker occupied full time, he will take on other work as well and in one person combine more than one occupation.

If we compare this to natural selection, it is clear there is also a selection in human societies. The principal and immediate selection pressure, however, does not come from reproductive success, but rather from economic survival or economic stability. In the world of non-human animals and plants survival is also crucial. If an animal starves it will not reproduce, so in this sense there is no difference between the selection of human beings and other organisms. But in another sense there is a great difference, for human beings rely heavily on behavioural or cultural means of information transmission. So the success of any one human being depends upon his or her awareness of the immediate situation, the immediate environment and his or her ability to manage economically and make a way in the world. In other words the process of survival in human societies has become somewhat removed from reproductive success. The human mind not only can solve problems, but it can even make arbitrary decisions which may or may not foster reproductive success. In fact, often such decisions reduce reproductive success, such as electing celibacy for religious reasons. Our brains have allowed us a great variety of different kinds of behaviour that affect our social structures. They may primarily involve problem solving, but they also might be because of traditions, or superstitions, or purely thoughtless action. The significant point is that where there is human behaviour, reproductive success has taken a secondary role because it is overshadowed by all the remarkable mental activities that are within our command. We cannot escape natural selection, for we have genes and we do reproduce, and there is ample evidence that natural selection can and does affect the genetic constitution of our populations. It is simply that concern for genetic continuity seems to have taken a back seat in the minds of *Homo sapiens* and problem solving and other mental activities have become the all consuming occupations.

An important component of our search for stability, and even success, is to maintain, through the powers of our brain, a great effort for maximum efficiency. And one very important component of efficiency is a division of labour within the community in which one lives. Moreover, as the community changes in size, the requirements for efficiency change, and shifts in the extent of the division of labour become important. In other words I am arguing that for human societies and human institutions the most efficient division of labour needs to be optimized by our problem solving minds. It may even be that we achieve a reasonable ratio of division of labour to size by trial and error, but that simply is one of the ways we solve problems, as every experimental scientist knows. By contrast non-human animals, and especially cells within a multicellular organism, have a different kind of trial and error. It involves the production by random mutation of variants that effect the division of labour, and those that are most efficient will be passed on to the succeeding generations and ultimately fixed in the population. Again, we have distanced ourselves from our genetic selection, by our extraordinary ability to use our mental powers and to solve problems by behavioural means.

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Finally I would like to take my considerations here and apply them to the human condition. I do this with considerable trepidation for I am a mere biologist: not a sociologist, or a prophet, or a politician. I want to make one point that may be right or it may be wrong. My hope is that I can convince my audience that at the least it is worth thinking about.

There are two great problems for the people of the earth today. One is the galloping increase in our numbers and the other is the ever increasing instability of governments and institutions. Obviously the two problems go together. To put it in the terms of my lecture here, an increase in the population size has put great stress on our problem solving ability to keep up the division of labour within our society in order to produce the needed stability. It is true that when the world was small, there were wars and all other kinds of strife. So the need to solve new problems is not just a recent phenomenon. The only difference today is that all those problems seem to have become greatly magnified.

The prime cause for that magnification is undoubtedly the frightening increase in world population. It is ironic that the ultimate goal of Darwinian natural selection is reproductive success, and now we have been so successful that we are becoming too many. It is natural selection with its reproductive success that has led to overpopulation, and that success is so overwhelming that our problem solving abilities, wonderful though they be, seem unable to cope. It is as though, through the evolution of our brains, we have finally come to a battle between the forces of natural selection with its reproductive success and our survival and stability which can only be ensured by using our problem solving brains.

I wish I felt confident that this is a battle we can win. When I look at our governments, and even our academic institutions with which I am familiar, I fear for our future. There is at least the appearance that our communities today are more diverse, more pluralistic than were those of our ancestors. We collect and put together individuals of diametrically opposed views: some conservative, some liberal; some of one religion, others of another; some capitalist and some socialist, and so forth. In fact this is the basic underpinning of our democratic principles which we cherish. It may be that ultimately this heterogeneity produces the best solutions to our problems for we look at all sides before taking a course of action. I believe in this strongly myself, yet I am still uneasy because, however sure, this is a slow way to achieve stability and the rate of the rise in population is not waiting. How comforting it would be to think we could intervene before those Malthusian forces that are lurking in the wings—wars, pestilence and famine—take over.

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