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DROSOPHILA AND SPECIATION[1]

By Dr. J. T. PATTERSON

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One of the duties of the office of vice-president, if not the only one, is that of giving the address on the occasion of the annual Zoologists' dinner. Examination of a number of the papers which have been read by my predecessors in office shows that the speaker has entire freedom in the selection of his subject and the method of its presentation. The several addresses which were examined deal with various topics, with some enlivened by much subtle humor and others revealing evidence of serious efforts to plumb the depths of the philosophy of biology. For me it seems safer to pursue a middle course.

I have selected for discussion a subject which, although venerable, is still capable of holding the attention of biologists. It is now more than eighty years since Charles Darwin posed the question of the origin of species, but until recently we did not have experimental proof of the exact method by which a given animal species might have arisen among wild populations. Following the appearance of Darwin's classical work, and prior to the development of the modern theory of Mendelian inheritance, most investigators were concerned with the problem of establishing the fact of evolution. They used largely the descriptive methods of comparative anatomy, embryology, paleontology and taxonomy coupled with geography. All this work was fundamental and im-

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[1] Address of the retiring vice-president and chairman of the Section for the Zoological Sciences of the American Association for the Advancement of Science, Dallas, Texas, December 30, 1941.

portant, but it left the main question raised by Darwin's conclusions still unanswered as it did not elucidate the *modus operandi* of species origin and differentiation.

This was the situation at the turn of the century with reference to the origin of species. Then, with the rediscovery of Mendelism, there followed a very rapid development in the fields of cytology and genetics, with the early deduction that chromosomes and hereditary factors could be definitely correlated. The final triumph of this deduction was brought about through the investigations of Morgan and his co-workers on the most common of the fruit-flies, *Drosophila melanogaster.* These studies resulted in the erection of a complicated system of genetic research which centers on the gene as the determiner of hereditary characters. As the system became more and more complicated, the fear or the hope, depending on the outlook of the commentator, was expressed that the whole structure was in danger of falling of its own weight; but, like the Leaning Tower of Pisa, it still stands.

The technical methods developed in connection with this work on *Drosophila* are indispensable for an analysis of the problem of the origin of species. In recent years two additional technical advances have been made which are of great importance. The first of these was Muller's demonstration that x-rays could be used as a means of inducing mutations and chromosomal rearrangements, and at a rate far exceeding that which occurs in untreated organisms. This method has made it possible to study in great detail various kinds of rearrangements, such as translocations, inversions, duplications and deficiencies, and has resulted in enriching our knowledge of the effects of such changes on genotype and phenotype.

The second advance was made by Painter's development of the salivary-gland chromosome technique and his demonstration that the bands of these giant elements precisely follow the sequence of loci of known mutant genes as revealed on the "genetic maps" of *Drosophila.* This technique is a very rapid and convenient method for detecting changes in chromosome structure, whether they have been produced by artificial means or have occurred spontaneously in wild populations.

Coincident with this development of technical methods, there has occurred a rapid advancement in the application of mathematics to the problem of evolution. In this connection the work of Professor Sewall Wright, in showing some of the evolutionary consequences of Mendelian inheritance, is especially noteworthy.

In the meantime, some very interesting investigations have been made on the relation of environment to evolution, especially on plants, which are more suitable for such studies than are most animal forms. Time will not allow for more than a brief reference to a recent publication by Clausen, Keck and Hiesey.[2] They experimented with a large number of the higher plants, selected from among many unlike species and families and taken from a wide range of habitats.

Their main experiment consisted in dividing the clone and planting the clone members in three different habitats or experimental gardens, located respectively at elevations of 100, 4,600 and 9,000 feet, in a transect across the central part of California. Here the plants were allowed to grow for several years and the changes arising in them under the different environmental conditions were noted and recorded. The first of their several general conclusions is as follows:

> The individual plant is subject to the interplay between heredity and environment. When grown under different environments it may be quantitatively changed in various degrees. The changes induced by a new environment give no evidence of permanence, but have been shown to be reversible modifications. Some of these changes in vegetative characters are quite spectacular, yet they never obscure the individuality of the plant, which is retained irrespective of the conditions of altitude, light and moisture in which the plant is grown.

This work shows that while environmental factors can induce modifications in phenotype, yet they do not change the genotype. It is clear that attempts to solve the problem of the origin of species must be attacked by genetic and cytological methods in a sexually reproducing diploid organism like *Drosophila.*

MATERIAL REQUIRED FOR THE PROBLEM

The series of technical methods outlined above are chiefly genetic and cytological in character and constitute a set of tools with which to attack the problem of speciation. But after all, they are tools and other requirements must be met if the problem of the origin of species is to be satisfactorily solved. One of the most important of these is the choice of material. The group of organisms selected for study should, among other requirements, meet the following conditions:

First, they should belong to a genus with many species living under a variety of environmental conditions and capable of being cultured in the laboratory. They should also be amenable to detailed genetic analysis, so that quantitative data on their genic differences can be obtained. Short life cycle and high fecundity are other desirable traits.

Second, the group selected should possess a relatively low number of chromosomes, and these should be large enough to permit accurate study and analysis. The dense metaphase chromosomes, usually de-

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[2] Carnegie Inst. of Wash. Pub. No. 520, 1940.

void of any distinguishable morphological features, are not satisfactory.

Third, the several species should not only occupy different ecological niches, but they should also exhibit a wide range of conditions of size, density and distribution of their populations. Otherwise, it would not be possible to test the relation between population type and genic variation.

Fourth, some of the forms within the group should be capable of producing hybrids, and at least some of these hybrids must be fertile, in order that the genetic mechanism underlying their isolation and differentiation can be determined. This last condition is not easy to realize among animal forms.

The group of forms which would seem to meet all these exacting requirements is to be found in the genus *Drosophila*. It is for this reason, perhaps, that several different workers have recently become interested in this line of investigation, especially Sturtevant, Dobzhansky, Spencer and our own group here in Texas.

It seems surprising that work of this nature on the genus has been so long delayed, but this is due undoubtedly to a failure to secure fertile hybrids at an earlier time. As late as 1934 only two cases of hybrids had been reported. The first of these was found by Sturtevant in 1920 and involved crosses between *D. melanogaster* and *D. simulans,* two closely related species. Unfortunately the hybrids from this cross are completely sterile. The second case of interspecific hybridization in the genus was not found until nearly a decade later (1929), when Lancefield reported that *D. pseudoobscura* was represented by two races or physiological species. He found that crosses between these two races produce partially fertile females and sterile males. Since then, and especially during the last few years, the number of cases of fertile hybrids in the genus has gradually been increased, so that the lack of such hybrids is no longer a handicap.

Drosophila in the Southwest

We had reasons for supposing that southern United States, and especially the southwestern area and northern Mexico, would be an excellent region in which to collect *Drosophila* species for use in the study of this problem. Accordingly, in 1938 we began collecting the wild strains in Texas, and since then have covered most of the southern states and parts of northern Mexico. To date this region has yielded a total of 97 species of the subfamily *Drosophilinae.* Twelve of these species belong to non-Drosophila genera and will not be considered further. Of the 85 species belonging to the genus *Drosophila,* 81 came from the Southwest and northern Mexico.

A detailed morphological study of these 85 species makes it possible to arrange a large majority of them into natural groups or "species groups," each composed of two or more closely related forms. Through such studies we have established twelve species groups which include 67 species. Thus far we have not found a closely related form for any of the eighteen unassigned species, but it is probable that further collecting in this and other areas will bring to light some such forms.

I am emphasizing the groups because they constitute the material units within which the tests for species origin must be made. Indeed, it is within the group that one may expect to find the production of hybrids. Cross tests carried out between species selected from different groups have thus far failed to produce hybrids, and this is true even when the forms used for the test come from groups obviously closely related. Moreover, various types of population are to be found in different species groups, such as those with dense populations as compared with those having sparse populations. Again, the members of some groups have small, dense populations with wide-spread distribution. All these different types must be thoroughly studied if faulty conclusions are to be avoided.

The groups are also important for purposes of chromosome analysis. The fact has long been known that the basic diploid number for the genus is twelve, consisting of five pairs of rod-shaped elements and a pair of small chromosomes which are usually referred to as dots. One notable characteristic in some groups is that the X chromosomes are distinctly longer than the autosomes, and that the Y chromosome may vary in size and shape—from a short to a long rod, or from a J to a V. Within the groups, variations in the number of arms in metaphase have been found to be due either to a fusion of two rods, or to an inversion or insertion which has shifted the centromere from its position close to the end to one nearer the middle. This results in changing the chromosome from a rod to a J- or V-shaped element. My coworker Griffen has found that this is true for all cases thus far examined for any given group.

Within the group, where hybrids are obtainable, the salivary chromosome furnishes the only means whereby a highly detailed analysis and comparison of chromosome organization can be made between different species. The structural features of these elements make it possible to use them as tracers in following out the distribution of a particular chromosome or its parts within the population, like the use of radioactive tracer atoms in following out the distribution of substances within the body. This method has been used by Sturtevant and Dobzhansky in their studies on *pseudoobscura* and *miranda* and we have extensively employed it in our own work.

Some of the twelve species groups have been investigated in other laboratories. We have been working on seven of them, and they furnish considerable material upon which to base some general conclusions concerning the origin of species in the genus Drosophila. To make this clear it will be necessary to refer again to some of the facts given in my symposium address, but these repetitions will be reduced to the minimum.

If mutational changes lie at the basis of organic diversity, it should be possible to demonstrate the mechanism involved through suitable tests and careful cytological observations. Unless the genetic mechanism of organic evolution is to remain a mere hypothesis, it will be necessary to do this on wild populations. Various questions have been raised concerning the nature of this mechanism. Our own studies afford answers to some of these questions.

One of the essential differences between animal species is the fact that they usually do not attempt to cross. This reluctance or refusal to mate has been termed sexual isolation. Our results show that this type of isolation is due to genetic factors which operate both between species and within a species. In the single species, *Drosophila repleta,* Wharton has made cross tests with strains collected at different points in Texas, Eagle Pass, Elgin, Fredericksburg and Galveston, and with stocks from New Haven, Connecticut, Guatemala, Central America, and Ankara, Turkey. Her results show that while matings between certain strains either fail to go or go very rarely, yet the reciprocal crosses are very successful, producing offspring which are highly viable and fully fertile. A few examples may be cited.

The cross between Ankara males and either Fredericksburg or Guatemala females is practically sterile, while the reciprocal crosses are highly fertile. Again, New Haven males are sterile to Fredericksburg and Guatemala females, but fully fertile to Eagle Pass and Elgin females. In the reciprocal crosses, New Haven females are fully fertile to Fredericksburg and Eagle Pass males, slightly fertile to Guatemala males and sterile to Elgin males.

The failure to produce offspring in many of these crosses is due to sexual isolation. This was proved by examinations of the reproductive tracts of the females, which in no case of cross-sterile matings contained sperm. If successful mating has occurred, sperm can always be detected. A study of the salivary-gland chromosomes of the F_1 larvae shows that the sterility is not associated with major chromosomal rearrangements. The complexity of the cross-sterility relations indicates that sexual isolation depends on different factors in the several strains. These factors are autosomal recessives because the heterozygotes are fully fertile and exhibit hybrid vigor. Despite this isolation, the different strains can not be regarded as separate species. This same type of isolation has been encountered in all the species groups which we have studied, and in the virilis group at least some of them are also due to autosomal recessive factors.

While sexual isolation must play an important rôle in species differentiation, yet it is doubtful whether it alone would be a sufficient mechanism. There is always the possibility that this barrier to crossing might occasionally break down and thus permit an exchange of genes within the population. It was therefore not surprising to find additional isolating mechanisms present within differentiating species groups.

THE MACROSPINA GROUP

A very fine example of multiple mechanisms in operation is to be seen in the macrospina group. There are at least four detectable mechanisms present in this group. These are sexual isolation, hybrid sterility, a sex chromosome unbalance and the passive factor of geographical separation. Geographically, the several forms may be separated into three divisions. In California there is a single species which has been described by Spencer as *Drosophila subfunebris.* The second divisional group is composed of a series of strains taken in Sonora, Mexico, southern Utah, Arizona, New Mexico and west Texas. The numerous strains probably all belong to a single subspecies of *D. macrospina* which is known as *limpiensis.* The third divisional group is composed of another series of strains which have been taken from central Texas eastward to Florida and northward to Ohio. These strains may also constitute a single subspecies known as *D. macrospina macrospina,* although Spencer regards the Ohio strains as different from the type material from Texas and has designated them as the subspecies *ohioensis.* The three groups will be referred to as *subfunebris, limpiensis* and *macrospina.*

If a series of cross tests be carried out between the different members of this group by starting with *subfunebris* of California and progressing eastward, a very interesting set of facts become revealed. The cross between *subfunebris* and its nearest *limpiensis* neighbor in Utah goes rather readily in both directions, producing fertile female hybrids and sterile male hybrids. In matings of *subfunebris* to a New Mexico strain of *limpiensis* the cross again goes both ways, but owing to the operation of sexual isolation, it takes twice the normal time of ten days for the larvae to appear in the culture when *subfunebris* is used as the female parent. The cross between *subfunebris* and a strain of *limpiensis* from west Texas goes but one way, producing only a few progeny and requiring from twenty-five to thirty-five days for the larvae to appear. Finally, in the cross between *subfunebris* males and *macrospina* females from central Texas, a small number of the mated pairs produce offspring, with about thirty days required for the larvae to appear in the culture.

If the tests are to be extended beyond central Texas, crosses between *limpiensis* and *macrospina* must be used, because *subfunebris* is completely sterile to all strains of *macrospina* coming from east of central Texas. Crosses between all *macrospina* strains and those of *limpiensis* go in both directions and produce the normal number of progeny, although when *limpiensis* is used as the female parent the male hybrids are either sterile or semi-sterile, depending upon the strain used in the cross. Mainland has shown that this particular type of sterility is due to a genic unbalance between the X and Y chromosomes.

In each cross where the two strains selected are from adjacent areas an exchange of genes occurs. Hence, it would be possible to carry this exchange in steps across the country in either direction, and this would bring about an exchange of genes between the otherwise completely isolated species of *D. subfunebris* and *D. macrospina.*

THE MELANICA GROUP

The melanica species group has three known species: (1) *Drosophila melanica,* which occurs principally in the northern states and from which area we have strains from Wisconsin, Ohio, Maryland, Connecticut and Massachusetts; (2) *D. submelanica,* which ranges across southern United States and extends northward into the Ozarks; and (3) *D. nigromelanica,* which is found in both the North and South along with the other two forms. Extensive breeding tests have been carried out on this group by Dr. A. B. Griffen.

Males from the Wisconsin strain of *melanica* are only slightly cross-fertile to *submelanica* females. The reciprocal cross was found to be completely sterile, with but one exception, and that was the cross between Wisconsin females to Ozark *submelanica* males, which goes but slightly. Madison males of *melanica* go slightly with *nigromelanica* females from Texas. Otherwise, among northern forms, the only *melanica* strain which is cross-fertile to *nigromelanica* was one from Maryland of which the females are poorly cross-fertile to the males of the Wooster strain from Ohio. All *submelanica* strains are completely cross-sterile to all *nigromelanica* strains, irrespective of their geographical origin. The metaphase chromosomes of all three species are alike, but the salivary-gland chromosomes of the hybrid larvae show several conspicuous inversions.

The degree of fertility in the intial crosses is always small and usually amounts to less than one per cent. These three species are almost completely isolated, but in contrast to the *macrospina* group, the isolation is between the parent forms and is not due to hybrid sterility, because all hybrids are fertile.

THE MULLERI GROUP

The first species group which we found in Texas was that of *mulleri.* It is especially interesting in that it exhibits at least six different types of isolating mechanisms. In addition to sexual, geographical and ecological isolations, and hybrid sterility, it shows two different types of zygotic mortality. There are probably as many as seven species which belong to this group. Crow has tested five of these species. These are, *Drosophila mulleri* Sturtevant, found mainly in Texas; *D. aldrichi,* which occupies much the same distribution area in Texas as *mulleri; D. mojavensis* from the deserts of California; *D. arizonensis* from Arizona; and *D. buzzatii.* of which single stocks are available from Argentina and Sicily.

Crosses between the several members of the group produce an unusual series of interspecific hybrids, of which only three are fertile. The main results were as follows: *Mulleri* females are cross-fertile with males of the other four species, but the reciprocal crosses are all sterile. The number of hybrids produced in each cross was small and the only fertile hybrids were the F_1 females from the cross with *mojavensis* males. The mating with *buzzatii* males gives highly abnormal flies which almost invariably die in the pupal stage. *Aldrichi* females are cross-fertile with either *mojavensis* or *arizonensis* males, producing sterile females in each case. The cross between *mojavensis* and *arizonensis* goes in both directions, producing fertile male and female hybrids when *mojavensis* is used as the female parent, and sterile male and fertile female hybrids in the reciprocal mating. *Arizonensis* females are also cross-fertile with *buzzatii* males, but the resulting hybrid larvae never develop as far as the pupal stage.

From these facts it is clear that *buzzatii* is almost completely separated from the other four species, with *aldrichi* next in order. *Mojavensis* and *arizonensis* are the most closely related species, and some workers might be inclined to regard these as subspecies.

The second type of mechanism which causes the death of the hybrid zygote was discovered by Crow while making crosses between *mulleri* and certain strains of *aldrichi.* These two species both have dense populations and occupy a common distribution area in Texas. They are completely isolated from each other by sexual isolation and hybrid sterility, and have a certain amount of ecological isolation. *Aldrichi* is almost entirely dependent on the common prickly pear as a source of food and as a medium for the developing larvae, while *mulleri* can and does feed and breed on various other kinds of fruit.

When *mulleri* females are crossed to males of a certain strain of *aldrichi* the hybrid offspring are predominantly male. This modification of the sex-ratio is due to the lethal effect on the female zygote of a sex-linked gene (or genes) on the X chromosome of *aldrichi.* This factor has no noticeable effect within the species, but acts as a dominant semi-lethal in the interspecific cross. The net effect is the elimination of about one half of the hybrid zygotes. In species already genetically isolated from each other, it could have little advantage to the parent populations other than that of removing the competition from the hybrids.

THE VIRILIS GROUP

In many ways the virilis group is the most interesting which we have studied, and perhaps the most significant. It includes five known species. The first of these is the original form described by Sturtevant in 1916 under the name *Drosophila virilis.* The second is *D. americana* found by Spencer in 1936 in Ohio. The other three, all new to science, have been discovered by us in the last four seasons. These are *D. texana,* first taken in Texas, *D. novamexicana* from southern New Mexico and *D. montana* from the Rocky Mountain system of Colorado, Wyoming, Utah and New Mexico.

These five species show both geographic and genetic isolation to a rather high degree. On the basis of our collection records, *novamexicana* and *montana* appear to be completely isolated geographically from the other three species, and while the distribution ranges of *texana* and *americana* overlap to a certain extent, yet in the main the two species occupy different regions, *texana* being confined to the southern states and *americana* occupying an area centering in Ohio. The main distribution area of *virilis* coincides very closely with that of *texana,* but by virtue of a difference in habitats, the two species have effective ecological isolation. *Virilis* lives and breeds in stores and produce houses in a domestic-type of habitat, while *texana* lives and breeds in the woods in a wild-type habitat.

The question of genetic isolation between the several species has been discussed elsewhere at these meetings and need not be considered further here. I wish, however, to refer briefly to their chromosomes. All five species differ from one another, either in chromosome number or in the inversions present, or in both. These differences are such that one can trace the evolution of chromosome morphology in the population, and by this means we have been able to show that *americana* evolved from hybrids between *novamexicana* and *texana.* The character of the inversions in the different strains indicates that *americana* is not a homogeneous species, for its population still contains several of the possible combinations of chromosomes of the two parent species. This chance to work out the direction of evolution in the origin of this species is striking proof of the efficacy of the salivary-gland chromosome technique. As all the chromosomes differ in gene order from one another in the parent species, recombinations would occur in the descendants of their hybrids. Different strains of *americana* show a limited number of these combinations. The original strain from Smithville, Ohio, for example, has chromosomes 2, 3, 5 and Y of *texana* and X and 4 of *novamexicana,* while another stock from Ohio, known as Pee Wee, differs in having the *texana* type of the male sex-limited fourth chromosome. Still other combinations have been found in different strains.

While it is difficult to determine just where the original hybridization took place, yet there is some evidence to indicate that it occurred here in the Southwest. *Novamexicana* has been found in southern New Mexico and the distribution of *texana* extends from central Texas to the Atlantic seaboard. It is probable that at one time the distribution areas of the two populations overlapped at some point in the intervening region, which would have given the opportunity for the hybridization to occur. Wherever the exact place was, it is clear that once the new species was produced it expanded northeast into a new ecological area in and about the state of Ohio, leaving behind over the trail of its progress some of the combinations which are still to be found associated with *texana.*

DISCUSSION AND CONCLUSION

Most of the investigations of the different workers on these species groups have been concerned with the extent of, and the reasons for, their isolation. As shown above, and especially in my symposium address, various types of isolating mechanisms are present either singly or in combinations among the different groups. Their net effect is the partial or complete elimination of the exchange of genes between populations. Except for simple geographic isolation, these limiting mechanisms are due to gene mutations. Other mutations are responsible for the great variety of morphological and physiological characteristics, and in relation to the isolating mechanisms and the restrictions on gene recombinations imposed by chromosomal rearrangements, form the basis for diversification both within and between species.

It might be well to compare some of these diverse characteristics as they appear in the different members of the species groups. In the *mulleri* group, two of the species live together in the same region and are much alike as to size and color pattern, but differ from each other in the color and size of eyes, in food habits and in length of life cycles, and are completely incapable of exchanging genes. In contrast to this, two other members of the group are separated geographically and differ widely in phenotype, but are readily capable of exchanging genes when brought together.

In the virilis group two distinct types are found, one of which lives in a domestic-type of habitat, the other in a wild-type habitat. The two types are therefore ecologically isolated and otherwise differ from each other in a number of morphological and physiological characters. The different strains of virilis, which represent the domestic-type, etherize very slowly, have clear crossveins, pupate on the sides of the container, have pupae which run the entire gamut of color variation from light-tan to deep black, and are fully cross fertile. The four wild-type species all etherize very quickly, have clouded crossveins, pupate in or at the edge of the food, have pupal color which is basically red, and are not fully cross fertile. Even within the wild-type group there are many character differences. Two of these species live in a region of severe winters in the high elevations of the Rocky Mountains and are readily distinguishable from the other two which live in a warmer climate in low wooded areas.

Some species groups are noteworthy for certain types of variation. For example, in the *pseudoobscura-affinis* complex of species extreme modifications of chromosome structure are common between related forms, but with little difference in phenotype. In the *mulleri* group modifications of phenotype are common, but differences in the chromosomes are absent between two of the genetically isolated species. The virilis group is remarkable among animal forms for having a clear case of hybrid origin of one of the species. The distinctness of the species in this group is in sharp contrast to the conditions found in the macrospina group. In the latter a series of genetic changes have accumulated so slowly across the distribution range that only the extreme ends may be regarded as distinct species.

The first of the fundamental problems propounded by Darwin was the question of the fact of evolution. This has been definitely established by a great variety of evidence from many fields of biology and geology. The second question as to how evolution actually operates is only now being elucidated, and toward the solution of this problem the contributions from the several investigations on the Drosophila species groups are playing an increasing role. It is no longer necessary to explain evolution by analogy, for the application of genetical and cytological techniques in this genus proves that it depends on experimentally measurable gene mutations.

STUDIES OF INFANT CHIMPANZEES

By HENRY W. NISSEN

YALE LABORATORIES OF PRIMATE BIOLOGY

ANNOUNCEMENT was made[1] in April, 1940, of an experimental chimpanzee nursery established at the Yale Laboratories of Primate Biology in Orange Park, Florida. The present report describes in greater detail the aims and methods of this program, and includes a brief account of progress to date.

Our primary general purpose in initiating this project was to provide and utilize infant chimpanzees in relatively large numbers as materials of psychobiological research. Heretofore very few specimens under one year of age have been available. Those few provided by dealers were invariably several months old and had limited scientific usefulness because of only approximately known age and ontogenetic history. Most of those born in captivity were, for obvious practical reasons, left with their mothers during the first year of life or longer and were therefore unavailable for anything but casual observation. The development in these laboratories, over the past decade, of a large and healthy breeding colony, gave the first opportunity, which may not soon be repeated, to undertake a relatively extensive study of young chimpanzees during the critical period starting at birth. Generous support by the Samuel S. Fels Fund, covering the special expenses of the project over a five-year period, made it financially possible to institute the program.

By making possible control and experiment, animal research has almost invariably pioneered in widening our biological horizons. The particular advantages of chimpanzees for investigations of characteristically human phenomena are fairly obvious. The extrapolation of discoveries by analogy and the examina-

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[1] SCIENCE, 91: 336–337, 1940.