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Chromosome Studies of Primates

The application of new culture and cytological techniques should help solve some puzzles of evolution.

Michael A. Bender and Lawrence E. Mettler

Although the evolution of the primates is a subject which has long interested biologists, it is only relatively recently that any attempt has been made to determine their relationships through a study of their chromosomes. The main reason for this situation is the notorious difficulty of studying mammalian material, which is amply illustrated by the long dispute over the chromosome number of man. It is difficult to make accurate counts by means of the standard techniques of sectioning or by making smears of tissue removed at necropsy, while to obtain detailed karyotypes from such material is virtually impossible.

The recent development of new techniques for the culture of diploid somatic cells in monolayers on glass surfaces, as well as the development of new cytological techniques, has made it possible to determine not only the chromosome numbers but also the chromosome morphology of a great variety of animals which have not been previously studied. Making use of such techniques, Hsu (*1*) and Tjio and Levan (*2*) have published detailed karyotypes of man, while Chu and Giles (*3*) have recently published chromosome counts for five genera of catarrhine or Old World monkeys. Only one count for a platyrrhine or New World monkey is available (*4*), and so far as we know there have been no counts reported for any prosimian primate.

Karyotype analyses of other groups of animals and of plants, such as those of Patterson and Stone (*5*) on the genus *Drosophila* and those of Babcock (*6*) on the genus *Crepis,* have been extremely successful in elucidating the evolution of these groups. Within the order Primates there exist many cases in which the classical anatomical approach has been unable to clarify relationships. An example is the quandary in which taxonomists find themselves when attempting to classify the genus *Callimico.* Various authors have assigned this genus to the family Cebidae or to the family Hapalidae, or have erected a new family, Calimiconidae, to contain it. With the hope that a cytological survey might clear up such puzzles, we have undertaken to investigate the order Primates, paying special attention at present to the infraorder Platyrrhina. The work discussed here (*7*) includes study of one prosimian, three genera of Catarrhina, and four of Platyrrhina.

Materials and Methods

Primate material has been obtained from several sources. Recently dead animals have been obtained from the Bal-

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timore Zoo (*8*). Many live specimens, especially of the rarer genera, have been obtained from dealers (*9*). In all cases the tissue cultures were made from kidney. This was done mainly because this organ can easily be removed from the living animal, which can then be used for other purposes.

The tissue was prepared for culture by the trypsin digestion technique of Younger (*10*). Mass cultures were made in a modified Chang's medium (*11*) consisting of Hanks' balanced salt solution (70 percent), adult human serum (25 percent), and beef embryo extract ultrafiltrate (5 percent). This medium also contained 100 units of penicillin, 0.1 milligram of streptomycin, and 2.5 units of Mycostatin per milliliter. The kidney cells cultured in this medium were predominantly epithelioid. They were maintained in serial culture for a maximum of three passages. For the preparation of a new passage, and also for the preparation of cover-slip cultures, the cells were digested free from the glass surface and from each other with 0.05-percent 1:250 trypsin solution made up in Puck's "saline A" (*12*). The resulting cell suspension was added to fresh culture medium and placed in appropriate culture vessels. For cultures intended for cytological examination, the cover slips were placed in the bottom of 1-ounce ointment jars with plastic screw caps. These cultures were maintained in an atmosphere of 5 percent CO_2 in air. The usual initial inoculum was about 2×10^4 cells in 5 milliliters of medium per ointment jar.

When a relatively confluent sheet of cells had grown on the cover slips (this usually took about five days), the cultures were used for cytological preparations. Two days before the cells were to be fixed, the old medium was replaced with fresh medium. This procedure usually results in an increase in mitotic activity after a lag period of 24 to 36 hours. Ten to fifteen hours before fixation, colchicine was added to some of the cultures to yield a final concentration in the medium of $10^{-7}M$. The hypotonic pretreatment method of Hsu and Pomerat (*13*) was used for all preparations. Ten to twenty minutes before the cells were to be fixed, the medium was replaced with a 20-percent balanced salt solution in water. The cells were fixed in Darlington and LaCour's 2BD. After washing they were stained by the Feulgen method. The cover slips bearing the stained cells were inverted on slides in 45-percent acetic acid and flattened with moderate pressure in a bibulous book. The slides were dehydrated by the Dry-Ice technique of Conger and Fairchild (*14*) and mounted in euparal.

Table 1. Somatic chromosome numbers and chromosome types of eight genera of primates. The classification used here is that of Fiedler (*19*). M, metacentric; S, subterminal; T, telocentric.

Infraorder	Scientific name	Common name	Sex	Chromosomes					
				2*N*	Autosomes			X	Y
					M	S	T		
Lorisiformes	*Nycticebus coucang*	Slow loris	♀	50					
Catarrhina	*Cercopithecus mona mona*	Mona guenon	♂	66			6		
Catarrhina	*C. mona mona*	Mona guenon	♀	66			6		
Catarrhina	*Cercocebus torquatus torquatus*	Sooty mangabey	♂	42			0		
Catarrhina	*Papio sphinx*	Mandrill	♂	42			0		
Platyrrhina	*Cebus apella*	Cinnamon ringtail	♂	54	6	18	28	T	T
Platyrrhina	*C. apella*	Cinnamon ringtail	♂	54	6	18	28	T	T
Platyrrhina	*C. capucinus*	Capuchin ringtail	♀	54	6	18	28	T	
Platyrrhina	*Callicebus cupreus*	Red titi	♂	46	10	10	24	S	T
Platyrrhina	*Saimiri sciureus*	Squirrel monkey	♂	44	16	14	12	S	T
Platyrrhina	*S. sciureus*	Squirrel monkey	♀	44	16	14	12	S	
Platyrrhina	*S. sciureus*	Squirrel monkey	♀	44	16	14	12	S	
Platyrrhina	*Ateles geoffroyi cucullatus*	Hooded spider monkey	♂	34	12	18	2	M	T
Platyrrhina	*A. paniscus chamek*	Black-faced spider monkey	♂	34	12	18	2	M	T
Platyrrhina	*A. paniscus chamek*	Black-faced spider monkey	♀	34	12	18	2	M	

More than 30 good figures were scored for each species, except for *Cebus capucinus* and *Ateles geoffroyi chamek,* in which 25 cells were scored for each species. In no case were less than 12 cells scored for each individual. Freehand drawings were made of all cells to facilitate counting. Some normal and some colchicine metaphases were used for each individual. Wherever available, many slides from all three passages were examined. In order to minimize the chance of counting figures from which some of the chromosomes had escaped, most counts were made on unbroken cells. The figures to be counted were preselected at low magnification for ease of counting. In most instances those cells which were judged before counting to be the best gave completely consistent counts. In spite of this preselection, however, some cells were scored in which the chromosome number could not be determined exactly. Later karyotype analysis allowed most of these cases to be resolved. Except for tetraploids and a few cells which seemed to be the product of tripolar division of tetraploids, the chromosome counts showed very little variation. It is our opinion that there is no real variation in chromosome number in diploid cells from our material. The few counts which differed from those of the modal class were of cells in which some chromosomes overlapped. It is difficult, if not impossible, to be certain of the chromosome number in these cases.

A number of camera lucida drawings were made from each platyrrhine species. The figures used for this purpose were usually colchicine metaphases and were frequently from cells which had broken during the flattening process. Such well-spread figures were found to be the most useful for determining the position of the centromeres. Only those colchicine metaphases were used in which the chromosomes had contracted to about the same degree as those of normal metaphases. Karyotypes were prepared by tracing the chromosomes from the camera lucida drawings. Where possible they were paired according to size and centromere position, but in some instances groups of four or more similar chromosomes had to be paired in arbitrary fashion. Photographs were also made (*15*).

Results

Fifteen individuals were analyzed for chromosome number. These are listed in Table 1, together with the diploid chromosome number. In order to test the possibility that a difference exists between the chromosome complements of cells grown in vitro and those growing in vivo, the bone marrow of the *Ateles paniscus chamek* male was examined. A

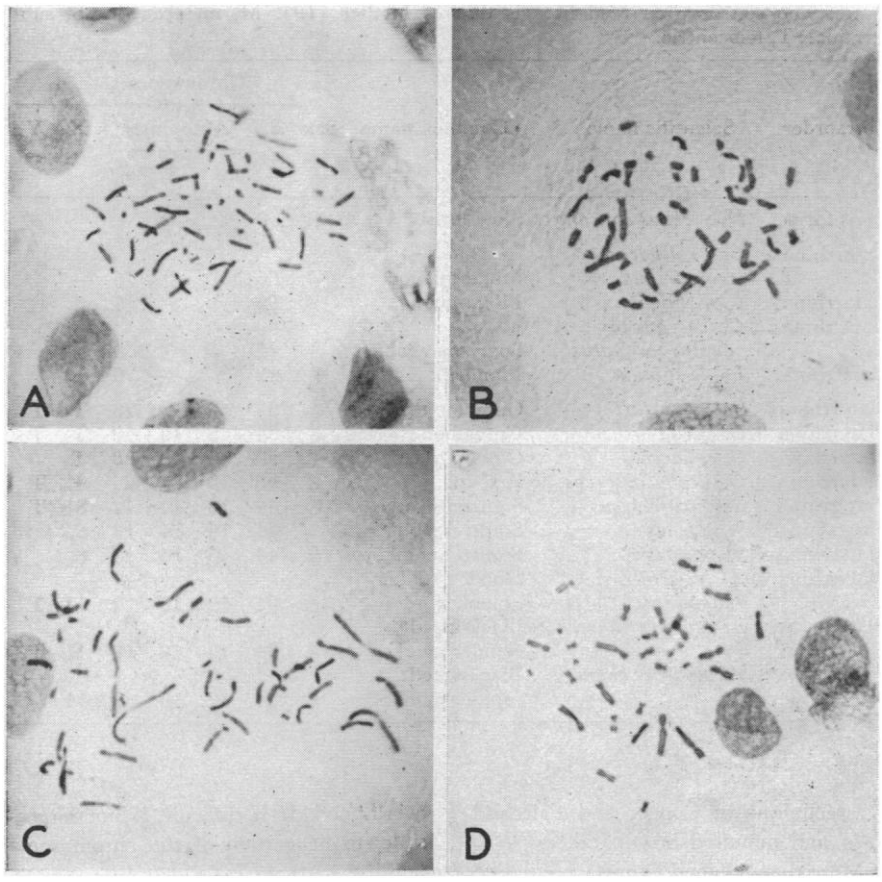

Fig. 1. Diploid figures from tissue-cultured material treated with colchicine. (*A*) *Cebus apella* ♂; (*B*) *Callicebus cupreus* ♂; (*C*) *Saimiri sciureus* ♂; (*D*) *Ateles geoffroyi cucullatus* ♂.

modification of the technique of Ford and Hamerton (*16*) was used. The counts obtained from this material verified the diploid condition (and the chromosome morphology) of the vast majority of the tissue-cultured cells. Most cells not conforming to the diploid condition were tetraploid. An extremely low number of cells with higher ploidy were present, while aneuploidy was not observed. Photographs of representative diploid cells from the four platyrrhine genera are presented in Fig. 1.

The chromosome number listed in Table 1 for the slow loris (*Nycticebus coucang*) is particularly significant, since it represents the first report on a prosimian primate. Unfortunately, the material was such that a detailed karyotype analysis was not possible.

The three genera of the family Cercopithecidae (Old World monkeys) which are reported here have recently been investigated by Chu and Giles (*3*). All are members of the subfamily Cercopithecinae. The chromosome number 66 for *Cercopithecus mona mona* confirms Chu and Giles' count for a different subspecies of this form. Likewise, the count of 42 for *Cercocebus torquatus torquatus* is the same as that reported by Chu and Giles for a different subspecies. The count for *Papio sphinx* is the first for this species, although the number 42 has been reported for other members of this genus by Chu and Giles and also by Darlington and Haque (*17*).

A detailed karyotype analysis was made of four genera of Platyrrhina (New World monkeys), all members of the family Cebidae. A representative male karyotype for each genus is presented in Fig. 2. The chromosomes have been classified into three morphological categories: telocentrics (T), subterminals (S), and metacentrics (M). Chromosomes with approximately equal arms have been designated as metacentric, while those with unequal arms are classified as subterminals. Chromosomes with no visible second arm are considered telocentrics. The autosomes of the four genera have been classified into these three categories in Table 1. The sex chromosomes have been classified separately. No autosomal difference was found either between individuals of the same species or between species of the same genus. In the genus *Saimiri*, a prominent constriction occurs in the centromere region of one metacentric pair, while in *Ateles* one metacentric pair has a prominent secondary constriction. The X chromosome varies all the way from a terminal (in *Cebus*) to a metacentric (in *Ateles*). The Y chromosome, which is the smallest chromosome in all four genera, appears to be a telocentric.

All of the figures used in preparing the karyotypes were colchicine metaphases, which were selected so that the amount of contraction was about the same as that at full metaphase in a normal mitosis. Although the four karyotypes are of the same magnification, the over-all size difference is not necessarily indicative of the natural state. Absolute and relative lengths can vary from cell to cell. For example, the absolute size of the largest telocentrics in the *Callicebus* material ranged between 6.8 and 8.0 microns. The relative lengths of the two largest pairs in *Callicebus* differ to the extent that in a few cells the second, or subterminal, pair is longer than the first, or telocentric, pair. Occasionally a size difference exists between the homologs, especially among the very long chromosomes. Thus, in the cell used for the *Saimiri* karyotype, the two members of the second pair of chromosomes are not of the same length. It is believed that this is the result of differential stretching due to the spreading technique used.

Discussion

The results of the present study, together with those of Chu and Giles (*3*), reveal a large variation in chromosome number among representatives of three major groups of primates. The numbers range from $2n = 34$ to $2n = 66$, and in such a way that their only common denominator is 2. This fact makes it very unlikely that polyploidy could have been a factor in the evolution of the primates; this is not surprising, since polyploidy must be an extremely rare evolutionary mechanism in species, such as those recorded here, which have a well-differentiated pair of sex chromosomes.

There are several other mechanisms which can lead to an evolutionary change in chromosome number. Of these, fusion has been most clearly demonstrated. Patterson and Stone (*5*), for instance, have suggested that centric fusions account for the reduction in chromosome number and the origin of metacentric and subterminal chromo-

somes in the genus *Drosophila,* in which the most primitive species are characterized by rod-shaped chromosomes. Makino (*18*) showed that the chromosome number of the domestic sheep is 54, and that, of these chromosomes, six are metacentrics, the rest telocentrics. He found that the goat, on the other hand, has 60 telocentric chromosomes. Makino suggests that 12 of the chromosomes of the goat correspond to the 12 arms of the six metacentrics in the sheep.

The four karyotypes presented here for the family Cebidae strongly suggest that centric fusion has played an important role in the evolution of this group. Of the four genera, *Cebus* is morphologically the least specialized, while *Ateles* is obviously highly specialized for an arboreal existence, having a well-developed prehensile tail, a shortened trunk, elongated limbs, and (usually) no thumb. The other two genera, *Callicebus* and *Saimiri,* are both moderately specialized for a squirrel-like existence, although they are not considered to be very closely related to each other.

The four genera thus form a series of increasing specialization. The chromosome numbers of these genera show a correlation with their degree of specialization. It is clear from Table 1 that a reduction in chromosome number is correlated with a relative decrease in the number of telocentric chromosomes. This is expected if the reduction in number has been accomplished by means of centric fusions. The karyotypes strongly suggest that *Cebus,* with 14 pairs of telocentric chromosomes, is the most primitive of the four genera studied, although this in no way implies that *Cebus* is ancestral, or even that this genus is the most primitive in the living Platyrrhina.

It is obvious that other mechanisms of karyotype evolution must also have been important in the Cebidae. Tandem fusions and pericentric inversions must have occurred to produce the longer chromosomes in each set, particularly chromosomes like the longest pair in *Callicebus.* Such processes would account for the difference in karyotype between the genus *Callicebus* and the genus *Saimiri.* It is interesting to note that if one arbitrarily decides how many small telocentrics it would have taken to make each chromosome in each of the four genera, the total for each genus is close to 70. A plausible speculation, therefore, is that the basic primitive karyotype for the Platyrrhina, and perhaps even for the order Primates, might have been about 70 small telocentrics.

Several features of the karyotypes for the Cebidae are of particular interest. While the Y-chromosome has the same morphology in each of the genera, the X-chromosome, which is a simple telocentric in *Cebus,* is a subterminal chromosome in *Callicebus* and *Saimiri* and a metacentric in *Ateles.* Constant features of the cebid karyotype seem to be a small metacentric pair, which is the next-to-last pair in all of the genera but *Cebus,* and a small telocentric pair which is present even in *Ateles.* A pair of chromosomes with a prominent secondary constriction, which has been reported by Chu and Giles (*3*) to be a constant feature in the Cercopithecidae, is not present in all of the Platyrrhina investigated, although the present study confirms its presence in the genera *Cercocebus, Papio,* and *Cercopithecus.* Neither *Cebus* nor *Callicebus* possesses a pair of chromosomes with such a constriction, while the constriction in *Saimiri* does not appear to be secondary. It is possible, of course, that if the constriction noted by

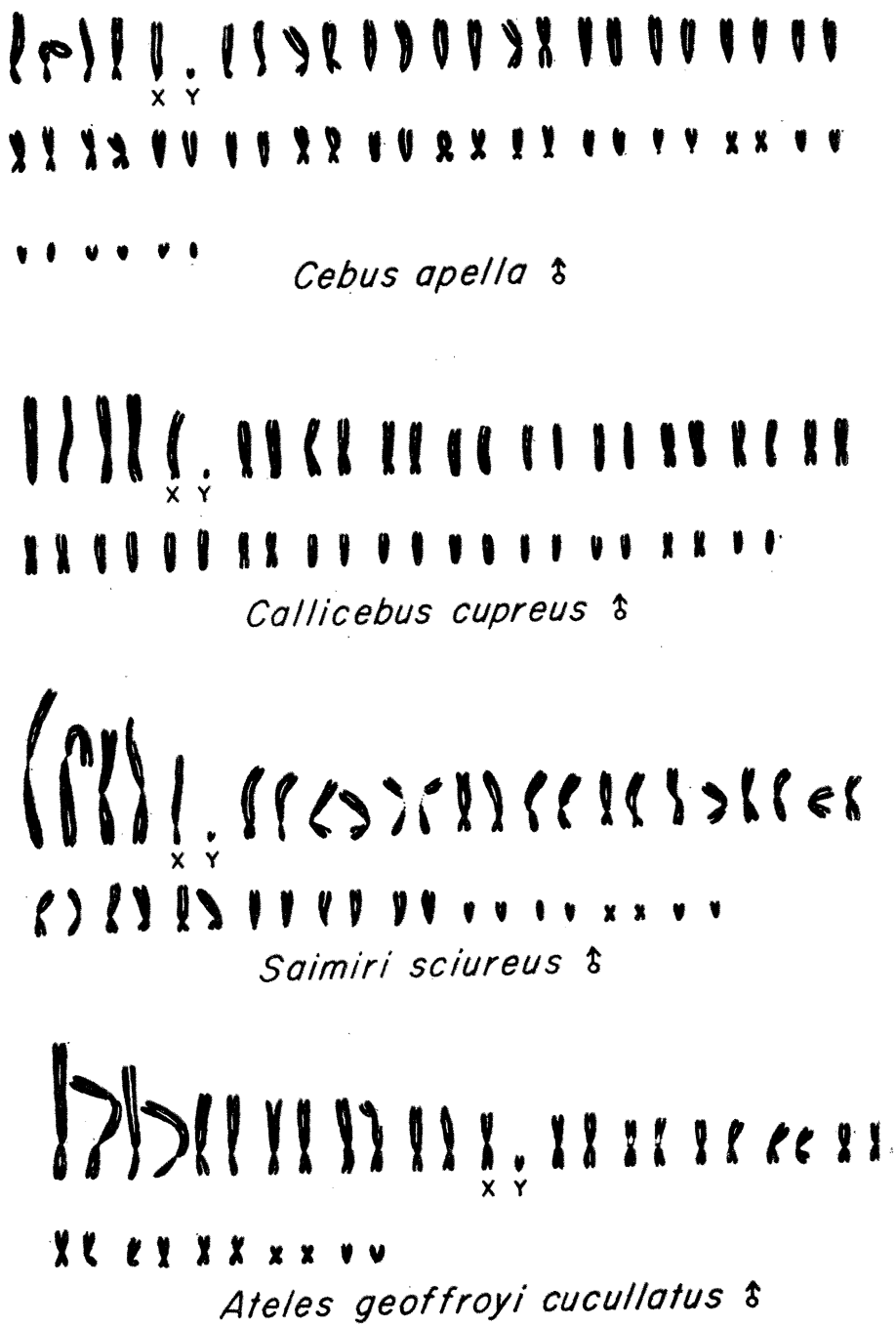

Fig. 2. Mitotic chromosomes of representative species of four platyrrhine genera. The chromosomes are arranged by paired homologs and in order of size.

Chu and Giles is the nucleolus organizer, it may exist as an undetected second arm in one of the telocentric chromosomes of *Cebus* and of *Callicebus*.

The mechanism of chromosome evolution suggested for the Cebidae does not apply in any obvious way to the Cercopithecidae. If centric fusions have any importance in the latter family, the evidence has been obscured by further specialization of the karyotypes through such mechanisms as pericentric inversion. It is significant, however, that while the genera *Papio* and *Cercocebus* do not appear to have any telocentric chromosomes, there are three pairs of telocentrics in *Cercopithecus mona mona* (see Table 1). If the $2n = 60$ species of *Cercopithecus* have no telocentrics, as appears to be the case from the photograph of Chu and Giles (*3*), then the number difference in this genus may well be explained by the centric fusion mechanism.

Although the studies of the chromosomes of the Primates which have been made to date have only scratched the surface, so to speak, it is already obvious that such studies can be of great help in the analysis of the problem of the evolution of this group. Studies are now in progress in our laboratory on the chromosome numbers and karyotypes of a second family of the Platyrrhina, the Callithricidae. Preliminary work is also in progress on the rather puzzling genus *Callimico*. It is hoped that these studies will both clear up the question of the taxonomic position of *Callimico* and answer the question of whether the Callithricidae are truly primitive primates or have evolved their seemingly primitive characters secondarily.

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8. We are indebted to Mr. Arthur Watson, director of the Baltimore Zoo, for his kind cooperation.
9. Miss Trudie Jerkins, of the Tarpon Zoo, Tarpon Springs, Fla., has been extremely helpful in obtaining New World monkeys for this study.

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News of Science

Survey of Physics Teaching

A nationwide survey by the American Institute of Physics discloses a shortage of physics teachers in United States colleges and universities, overloaded teaching schedules, and a discouraging outlook for the immediate future. One result of the survey was the revelation that college and university administrators in the academic year 1957–58 provided sufficient funds for 403 new appointments of Ph.D. physicists, but the departments concerned estimated they would be able to appoint only 254 new Ph.D. physicists from the available supply.

Some of the findings of the survey, which was conducted by William C. Kelly, director of education at the AIP and former University of Pittsburgh faculty member, are as follows:

1) Of the 536 American colleges and universities that have a 4-year undergraduate major program in physics, 490 —or 91 percent—took part in the survey. Some 451 institutions reported that their needs for physics teachers are not being met in some degree and that they have had to resort to various substitutes for the services of full-time qualified teaching personnel. Only 39 educational institutions report that their needs for physics teachers are now being met.

2) Almost half of the institutions replying, or 49 percent, said that their physics teachers are carrying teaching "overloads." Another 30 percent reported that graduate or undergraduate assistants are being relied upon to an "undesirable degree" in teaching. Most of these assistants have had little previous teaching experience.

3) Forty-six percent of the colleges and universities responding said that the time available to physicists for research and other scholarly activities has been "markedly reduced" as a result of heavy teaching loads. It is recognized as important for all physicists to do scholarly work—research, writing of technical articles and books, and participation in the work of scientific societies—if they are to be effective educators.

4) Class teaching situations need improvement. Twenty-one percent of the physics departments report that they have had to cancel classes because of inadequate staff, another 36 percent report an increase of class size to an "undesirable degree," and one-third state that teaching duties have been assigned to part-time, although qualified, teachers from outside the institution's physics department.

5) Departmental chairmen estimate that approximately 688 Ph.D. physicists are needed to correct the shortages in these colleges and universities. The total number of Ph.D. degrees granted in 1956–57 amounted to 444 in the U.S. More than half of the 444 did not go into teaching because they took full-time research jobs.

6) The situation in the small physics department is disturbing. Half the shortage of physics teachers occurs in physics departments with staffs of six or less people, and half of the bachelor's degrees in physics in 1957 were granted by these same physics departments.

Nuclear Propulsion

A study of the feasibility of employing controlled nuclear explosions for propulsion has been authorized by the Air Research and Development Command, it was announced on 2 July by Roy W. Johnson, director of the Advanced Research Projects Agency. The authorization is for a contract with the General Dynamics Corporation's General Atomic Division, San Diego, Calif.