

mathematicians have been applying entropy definitions to ever more general classes of stochastic processes and obtaining limit theorems on sums of independent random variables. This work really is much closer to probability theory than to information theory.

The concepts and results of information theory, together with those of Fourier series theory, have now become the basic themes of most work in communication theory today.

The only other applications I shall mention are two attributable to Mandelbrot (30). One lies in the field of statistical thermodynamics; in it he exploited a suggestion of Szilard's to apply various statistical concepts to thermodynamics. The other lies in the field of linguistics and concerns, in particular, stochastic properties of language. Mandelbrot considered discourse as a sequence of letters and words with various Markoff-type chain relationships between them. This leads to some quite unusual theorems in probability that have received empirical verification.

There have also been applications of information theory to biology, psychology, science, and statistics, but space

does not permit me to go into these. Fortunately, however, books are available on these subjects, by Attneave (31), Brillouin (32), Kullback (33), and Quastler (34).

References and Notes

1. F. L. Stumppers has compiled a very complete bibliography on information theory, which has been published in various years in the *IRE Transactions on Information Theory* ["A bibliography of information theory," *IRE Trans. on Inform. Theory* **PGIT-2**, 1 (1953); **IT-1**, 31, 40 (1955); **IT-3**, 150 (1957)]. Forthcoming books by W. W. Peterson and J. Wolfowitz will have quite up-to-date bibliographies on the entire subject.
2. L. Szilard, *Z. Phys.* **32**, 753 (1925).
3. C. E. Shannon, *Bell System Tech. J.* **27**, 379, 623 (1948).
4. R. A. Fisher, *Proc. Cambridge Phil. Soc.* **22**, 700 (1925); *Contributions to Mathematical Statistics* (Wiley, New York, 1950).
5. M. P. Schutzenberger, *Compt. rend.* **232**, 925 (1951).
6. P. Elias, *IRE Trans. on Inform. Theory* **PGIT-4**, 29 (1954).
7. J. von Neumann, "Probabilistic Logics and the Synthesis of Reliable Organisms from Unreliable Components," *Automata Studies, Annals of Mathematics, Study No. 32* (Princeton Univ. Press, Princeton, N.J., 1956).
8. C. E. Shannon and E. F. Moore, *J. Franklin Inst.* **262**, 191, 281 (1956).
9. R. W. Hamming, *Bell System Tech. J.* **29**, 147 (1950).
10. D. Slepian, *ibid.* **35**, 203 (1956).
11. R. C. Bose and D. K. Ray-Chaudhuri, *Information and Control* **3**, 68 (1960).
12. A. Feinstein, *Foundations of Information Theory* (McGraw-Hill, New York, 1958).
13. I. A. Khinchin, *Uspekhi Math. Nauk* **8**, No. 3, 3 (1953) [translated in *Mathematical Foundations of Information Theory* (Dover, New York, 1958)].
14. J. Wolfowitz, *Illinois J. Math.* **1**, 591 (1957).
15. D. Blackwell, L. Breiman, A. J. Thomasian, *Ann. Math. Statistics* **29**, 1209 (1958).
16. B. McMillan, *ibid.* **24**, 196 (1953).
17. N. M. Abramson, *IRE Trans. on Inform. Theory* **IT-5**, 150 (1959).
18. P. Fire, "A Class of Multiple-Error-Correcting Binary Codes for Non-Independent Errors," *Sylvania Rept. No. RSL-E-2* (1959).
19. J. E. Meggitt, *IBM J. Research Develop.* **4**, 329 (1960).
20. D. E. Muller, unpublished work.
21. W. W. Peterson, *Error Correcting and Error Detecting Codes* (Wiley, New York, in press).
22. C. M. Melas, *IBM J. Research Develop.* **4**, 58 (1960).
23. P. Elspas, *IRE Trans. on Circuit Theory* **CT-6**, 45 (1960).
24. P. Elias, *IBM J. Research Develop.* **2**, 346 (1958).
25. G. D. Birkhoff, *Proc. Natl. Acad. Sci. U.S.* **17**, 656 (1931).
26. J. von Neumann, *ibid.* **18**, 70 (1932).
27. A. N. Kolmogorov, *Doklady Akad. Nauk S.S.S.R.* **124**, 754 (1959); see also V. A. Rohlin, *ibid.* **124**, 980 (1959); Y. Sinai, *ibid.* **124**, 768 (1959).
28. Y. V. Linnik, in *Theory of Probability and Its Applications* (1959).
29. I. M. Gelfand and A. M. Yaglom, *Uspekhi Math. Nauk* **12**, No. 1, 3 (1957).
30. L. Apostel and B. Mandelbrot, *Logique, Language et Théorie de l'Information* (Presses Universitaires de France, 1957); B. Mandelbrot, "Role of Sufficiency and of Estimation in the Statistical Structure of Thermodynamics," *IBM Research Rept. No. RC-235* (1960).
31. F. Attneave, *Applications of Information Theory to Psychology* (Holt, New York, 1959).
32. L. Brillouin, *Science and Information Theory* (Academic Press, New York, 1956).
33. S. Kullback, *Information Theory and Statistics* (Wiley, New York, 1959).
34. H. Quastler, *Information Theory and Biology* (Univ. of Illinois Press, Urbana, 1953); *Information Theory in Psychology* (Free Press, Glencoe, Ill., 1956).

Chromosome Cytology and Evolution in Primates

Study of chromosomes adds to our knowledge of evolutionary relationships among primates.

E. H. Y. Chu and M. A. Bender

Since the chromosomes of higher organisms are characteristic of a species, they are of obvious value in taxonomic and evolutionary studies. The chromosomes of members of a given species are usually the same in number and form, but those of members of different species are frequently different. Thus the karyotype—the number of chromo-

somes, their lengths, their relative arm lengths, and other features—is a valuable morphological character, particularly because of its intimate association with the genetic makeup of the species.

Although the evolution of the primates has been a subject of great interest to biologists, it is only relatively recently that any attempt has been

made to determine the interrelationships of these animals by comparative studies of their chromosomes. The main reason for this situation has probably been that technical difficulties are involved. Since most mammalian species possess a large number of small chromosomes, counting and observing individual chromosomes are very difficult. The recent development of techniques for the culture of diploid somatic cells, as well as the improvement of cytological procedures, has made it possible to determine not only the chromosome numbers but also the morphology of the chromosomes of a great variety of animals which have not been previously studied. These technical advances led to the discovery by Tjio and Levan (1) of the correct chromosome number of man, and stimulated a great many descriptive and experimental studies of mammalian, and especially human, cytogenetics.

The karyotypes of relatively few primates other than man have been deter-

The authors are members of the staff of the Biology Division of Oak Ridge National Laboratory, Oak Ridge, Tenn.

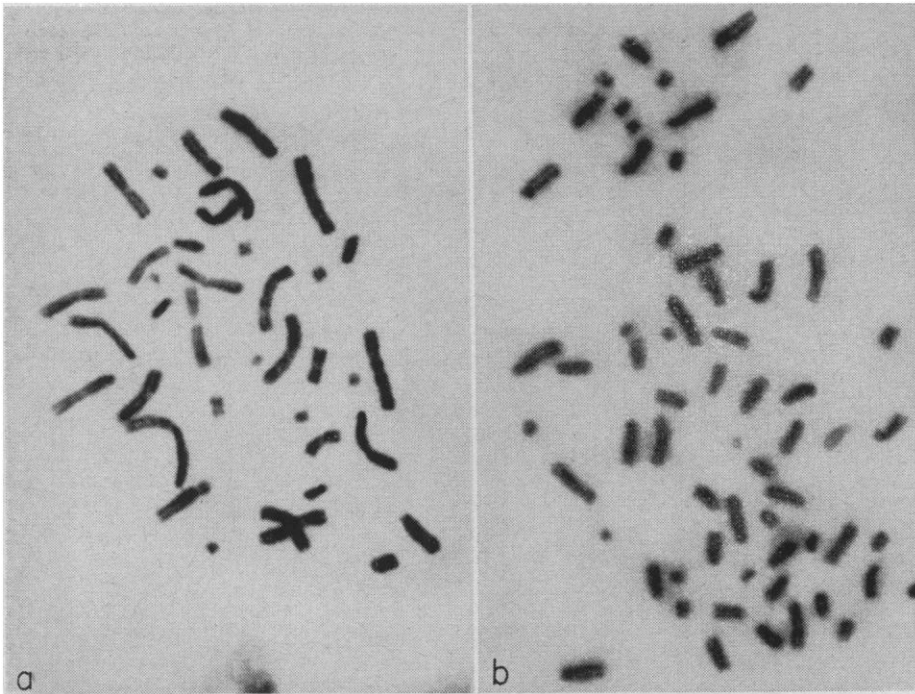


Fig. 1. Chromosomes of cells from tissue-cultured skin biopsies of two species of the genus *Galago*. (a) *Galago senegalensis* ♂; (b) *Galago crassicaudatus* ♂ (about $\times 1450$).

mined by the modern cytological techniques now available (2-5). The need for additional studies is apparent, especially since many primate species are diminishing in number and are in danger of becoming extinct.

For a systematic survey of karyotypes in primates, it has been found feasible to utilize small pieces of tissues, derived either by biopsy or necropsy from captive animals, for in vitro cultivation and cytological examination. Successful cell cultures have been established even after the tissue specimens have been transported over long distances, a factor which involved considerable delay before culturing.

In the present article (6) we review the available information on the chromosome cytology of the order Primates. In addition, some recent data on the karyotypes of several species of primates are presented. These studies have revealed a notable variation, in both chromosome number and morphology, among all groups of primates so far examined. Detailed karyotypic comparisons also suggest some possible mechanisms of chromosome evolution. Comparative cytological studies make at least certain conclusions about species relationships possible; the use of criteria other than gross morphological or anatomical characters serves to supplement the present taxonomic evidence.

Most taxonomists agree that the order

Primates may be divided into three major subgroups. The first, the Prosimiae, includes all the nonsimian primates, such as lemurs, lorises, tarsiers, and the tree shrews. The simian primates fall into two groups: the Platyrrhina or New World monkeys, and the Catarrhina, which include the Old World monkeys, anthropoid apes, and man. We consider each subgroup separately.

Prosimiae

Of prosimian primates, only five genera (six species) have been studied cytologically (Table 1). Of the Tupaiidae, only one specimen of *Urogale everetti* (Philippine tree shrew) has been examined. Dodson (7) has made tentative counts on cells from testis and corneal epithelium and has found that the diploid chromosome number ($2n$) is 26.

Lemur macaco (the black lemur) represents the only species of Lemuriformes that has been examined. Somatic cells grown in culture from skin of a young male and an adult female animal were used for chromosome analysis. The diploid chromosome number is 44. The chromosome complement is readily classified into two separate size-groups. All but one of the 11 pairs of macro-

chromosomes, ranging from 0.8 to 1.2μ in length, are acrocentric. The X chromosome is about 5μ long with a terminal centromere. The Y chromosome is the smallest, and it is acrocentric.

In many cases the chromosome arm indices of each individual chromosome were calculated, by the system of Tjio and Levan (1). The chromosomes are classified arbitrarily into three groups: M chromosomes (median-submedian centromeres), S chromosomes (subterminal centromeres), and A chromosomes (acrocentric, with nearly terminal centromeres). Thus, in *Lemur macaco*, there are 12 M chromosomes, 8 S chromosomes, and 22 A chromosomes. Both the X and Y chromosomes are of the A type. It should be pointed out, however, that because of variability in arm length it is sometimes difficult to assign a particular chromosome pair to a particular class. We have attempted to assign the chromosomes of most of the species studied, but have indicated some of the uncertain cases by placing the numbers in brackets in the tables. Also, in a number of instances, such as *Nycticebus* and *Perodicticus*, the quality of the cytological preparations, while permitting counting, did not lend itself to karyotype analysis.

In the Lorisiformes, two genera (one species each) of the family Lorisidae have been studied. The diploid chromosome number of *Nycticebus coucang* (slow loris) is 50 (2); that of *Perodicticus potto* is 62.

Of the family Galagidae, two species of *Galago* (the bush babies) have recently been examined. The diploid chromosome number of *Galago senegalensis* is 38, confirming an earlier finding, reported by Matthey (8), who had studied its chromosomes in spermatogenesis. The chromosome morphology, as illustrated in Fig. 1a, agrees with Matthey's results. Both macro- and microchromosome types are present in this species. Most of the macrochromosomes have either median or submedian centromeres. However, two pairs of microchromosomes also have median centromeres. The X chromosome is a medium-sized (6μ in length) subtelocentric; the Y is acrocentric, and it is the smallest element in the complement (1μ in length).

Most interesting is the karyotype of *G. crassicaudatus*, as shown in Fig. 1b.

The diploid chromosome number is 62. In both chromosome number and morphology, this species is strikingly different from *G. senegalensis*. In *G. crassicaudatus*, the chromosomes are in general shorter than the macrochromosomes of *G. senegalensis*. There seems to be no discontinuity in the range of chromosome lengths. The chromosomes of the longest pair are about 3.5 μ long, and the shortest, the Y chromosome, is 0.8 to 1 μ long. Most of the chromosomes have nearly terminal centromeres, with the exception of three pairs which clearly possess subterminal centromeres. The X chromosome is subterminal and approximately 2 μ long.

Despite the obvious karyotypic differences between *G. senegalensis* and *G. crassicaudatus*, detailed karyotypic comparisons reveal interesting relationships. First, the total metaphase chromosome lengths of these two species are approximately equal. Second, there is close agreement in the number and length of chromosome arms between the two species.

Platyrrhina

Prior to 1958, only one count was available for the Platyrrhina. Painter (9) reported that a specimen of an unknown species of the ringtail, *Cebus*, had a diploid chromosome number of 54. To date, karyotypic analyses have been made of four genera of the family Cebidae (2), of two genera of the family Callithricidae, and of the unique genus *Callimico* (Goeldi's marmoset) (3). In addition, tentative counts have been made on single specimens of four additional genera of Cebidae (10).

In contrast to the prosimian *Galago* and the catarrhine *Cercopithecus*, no difference in number has been found between species of the same genus in the Platyrrhina. A summary of chromosome numbers and karyological characteristics of platyrrhine primates is presented in Table 2.

In the family Cebidae, a wide range in chromosome number has been encountered. Forty-six is the commonest diploid number. In the four genera for which detailed karyotype analyses have been made, a wide variation in the number of acrocentric chromosomes is found. Thus, *Cebus* has 13 acrocentric pairs, while *Ateles* (spider monkey) has only one. *Ateles* has one pair of chromosomes with a fairly prominent secondary constriction, and *Saimiri* (squirrel

Table 1. Mitotic chromosome numbers and types of prosimian primates. The classification used in this and the following tables is that of Fiedler (35). Numbers in brackets are tentative. M, metacentric; S, subterminal; A, acrocentric.

Scientific and common name	No. of individuals examined		Chromosomes							Reference citation
	Male	Female	2n	M	S	A	X	Y		
Family Tupaiaidae										
<i>Urogale everetti</i> —Philippine tree shrew	1		[26]							(7)
Family Lemuridae										
<i>Lemur macaco</i> —Black lemur	1	1	44	12	8	22	A	A		*
Family Lorisidae										
<i>Nycticebus coucang</i> —Slow loris		1	50							(2)
<i>Perodicticus potto</i> —Potto		1	62							*
Family Galagidae										
<i>Galago senegalensis</i> —Lesser bush baby	1 2		38				S	S		(8)
<i>Galago crassicaudatus</i> —Grand or thick-tailed bush baby		2	38	20	10	6	S	A		*
	2	2	62	0	6	54	S	A		*

* Data of Chu and Bender, this report.

rel monkey) also has one pair with a constriction. Neither *Cebus* nor *Calli-
cebus* (*titi*) has a constricted pair. This is in contrast to the situation in the Catarrhina, which are discussed in the next section. The presence of a smallest, acrocentric autosomal pair is a constant feature of the cebid karyotype, as is the presence of a next-to-smallest metacentric pair. The Y chromosome of all the Cebidae studied appears to be acrocentric and is the smallest chromosome in the complement. The X chromosome, on the other hand, varies; it ranges from acrocentric (*Cebus*) to metacentric (*Ateles*). One specimen of *Ateles* differed slightly in karyotype from the others (11). One member of the smallest, acrocentric pair in this animal possessed a small second arm,

possibly the result of an inversion. In vivo studies of the bone marrow of this specimen established that the aberration was present in the animal and did not arise during the culture of cells for cytological examination.

In the family Callithricidae, the karyotypes of *Callithrix* (marmoset) and *Leontocebus* (tamarin) are virtually identical. The karyotype of *Callimico* is markedly different from that of the marmoset, even though the chromosome numbers differ only by 2. Of particular interest is the fact that *Callimico* has eight pairs of acrocentric chromosomes, whereas the marmosets have only five. None of the three genera possesses a pair with secondary constrictions. The Y chromosome of the marmosets is remarkable, since it is apparently meta-

Table 2. Mitotic chromosome numbers and types of platyrrhine primates. Numbers and letters in brackets are tentative.

Scientific and common name	No. of individuals examined		Chromosomes							Reference citation
	Male	Female	2n	M	S	A	X	Y		
Family Cebidae										
<i>Ateles geoffroyi</i> —Hooded spider monkey	1		34	12	18	2	M	A		(2)
<i>Ateles paniscus chamek</i> —Black-faced spider monkey	1	1	34	12	18	2	M	A		(2)
<i>Ateles belzebuth</i> —Golden spider monkey	5	6	34	12	18	2*	M	A		†
<i>Saimiri sciureus</i> —Squirrel monkey	1	2	44	16	14	12	S	A		(2)
<i>Callicebus cupreus</i> —Red titi	1		46	10	10	24	[S	A]		(2)
<i>Cebus</i> sp.—Ringtail	1		54				S	A		(9)
<i>Cebus apella</i> —Cinnamon ringtail	2		54	6	20	26	A	A		(2)
	2		54							†
<i>Cebus capucinus</i> —Capuchin ringtail	2	1	54	6	20	26	[A]			(2)
			54							†
<i>Alouatta seniculus</i> —Red howler	1		[44]							†
<i>Aotes trivirgatus</i> —Owl monkey	1		[54]							†
<i>Cacajao rubicundus</i> —Uakari	1		[46]							†
<i>Pithecia pithecia</i> —Saki		1	[46]							†
<i>Callimico goeldii</i> —Goeldi's marmoset		1	48	2	30	16				(3)
Family Callithricidae										
<i>Callithrix chrysoleucos</i> —Golden or silky marmoset	1	2	46	4	30	10	S	M		(3)
<i>Leontocebus illigeri</i> —Red-mantled tamarin	2	2	46	4	30	10	S	M		(3)

* In one animal, there was one metacentric and one acrocentric, instead of a pair of acrocentrics (see text).

† Data of Chu and Bender, this report. ‡ Data of Bender and Mettler, unpublished.

centric, which is in contrast to the other Platyrrhina studied. It is unfortunate that the only specimen of *Callimico* studied was a female, as it is obviously quite important to determine the form of the Y chromosome in this species.

Catarrhina

In Table 3, the chromosome numbers and karyological characteristics of Old World primates, including five genera (17 species) in the subfamily Cercopithecinae (*Macaca*, *Papio*, *Cercocebus*, *Erythrocebus*, and *Cercopithecus*) and one in the subfamily Colobinae (*Presbytis*) of the family Cercopithecidae, as well as one each of the families Hylobatidae and Pongidae, are listed. Most notable is the variation in

chromosome number among various genera, and even within a single genus, *Cercopithecus*. Diploid chromosome numbers of 42, 44, 48, 50, 54, 60, 66, and 72 have been found in the Catarrhina.

The chromosomes of all the species in the subfamily Cercopithecinae have a number of morphological characteristics in common. First, sex-chromosome dimorphism (an X and a Y) has been found in all species. The X chromosomes are generally of medium size, with submedian centromeres. The submetacentric Y chromosome is the smallest element in each complement; it is smaller than the human Y (4, 12). Second, there is a single autosomal pair having a marked secondary constriction, which may carry nucleolus organizers, in each species. They are all

morphologically alike in the sense that their secondary constrictions are of similar lengths and are located close to the centromere. However, the total length of this particular chromosome pair appears to differ in different species (4). Third, with the exception of *Erythrocebus* and *Cercopithecus*, there are no truly acrocentric autosomes in this family.

The most detailed description of primate chromosome morphology (exclusive of human chromosomes) is probably that of the rhesus monkey (*Macaca mulatta*) by Rothfels and Siminovitch (13). Painter (14) had reported a diploid chromosome number of 48 for this species; but Shiwago (15) counted 42, and this number was later confirmed by several workers (4, 12, 13). According to Rothfels and Siminovitch (13), the Y chromosome is the smallest element in the complement and is acrocentric; Chu and Giles (4), however, found that it was metacentric. The X chromosome ranks eighth in decreasing order of size and typically has an arm ratio of 1.4. The autosomes form a graded size series of metacentric chromosomes, 3 to 15 μ long in early metaphase, and with arm ratios from 1.1 to 3.3. On the basis of relative length, arm ratio, and occurrence of secondary constrictions, most chromosomes of the complement can be individually identified.

The karyotype of *Macaca irus* is probably identical with that of *M. mulatta*. The same diploid number of 42 has been reported for both *M. nemestrina* (12) and *M. cyclopis* (16).

Among the baboons, *Papio papio* and *P. doguera* were found to have the same karyotype. Although the diploid chromosome number is the same as in *Macaca*, the chromosomes in general are shorter in length and the karyotypes differ in relative numbers of M and S chromosomes (Table 3).

Three species of *Cercocebus* (mangabeys) have been examined so far. The karyotype of *C. torquatus* differs from those of *Macaca* and *Papio*. Tentative counts on *Cercocebus albigena* and *C. galeritus* indicate the same chromosome number, 42 (17).

The diploid chromosome number of *Erythrocebus patas* (patas monkey) is 54. It has 18 M and 24 S chromosomes, and 10 A chromosomes. Three different diploid numbers, 60, 66, and 72, have been found in the single genus *Cercopithecus* (guenons). It is particularly interesting to note that there are

Table 3. Mitotic chromosome numbers and types of catarrhine primates. Numbers and letters in brackets are tentative.

Scientific and common name	No. of individuals examined		Chromosomes							Reference citation
	Male	Female	2n	M	S	A	X	Y		
Family Cercopithecidae										
<i>Macaca mulatta</i> —Rhesus monkey	{	2	2	48				A	A	(14)
		2		42						(15)
		1		42						(12)
		3	1	42	18	22	0	M	M	(4)
		Not stated		42	18	22	0	M	A	(13)
<i>Macaca irus</i> —Cynomolgus or crab-eating macaque		1		42	[18	22]	0	[M	M]	*
<i>Macaca nemestrina</i> —Pig-tailed macaque		1		42						(12)
<i>Macaca cyclopis</i> —Formosan macaque		1		42						(16)
<i>Papio papio</i> —Guinea baboon	{	1		42						(12)
			42	[30	10]	0				(4)
<i>Papio doguera</i> —Olive baboon		2		42	[30	10]	0	S	M	(4)
<i>Papio sphinx</i> —Mandrill		1		42			0			(2)
<i>Cercocebus torquatus lunulatus</i> —White-crowned mangabey		2		42	[14	26]	0	S	M	(4)
<i>Cercocebus torquatus torquatus</i> —Sooty mangabey		1		42			0			(2)
<i>Cercocebus albigena</i> —Grey-cheeked mangabey		1		[42]						(17)
<i>Cercocebus galeritus</i> —Crested mangabey		1		[42]						(17)
<i>Erythrocebus patas</i> —Patas monkey		1	3	54	[18	24]	10	S	M	(4)
<i>Cercopithecus aethiops sabaeus</i> —African green monkey		1		60	[18	34]	6	M	M	(4)
<i>Cercopithecus aethiops tantalus</i> —African white monkey		2	1	60	[18	34]	6	M	M	(4)
<i>Cercopithecus diana roloway</i> —Diana monkey		1	1	60			6			(4)
<i>Cercopithecus neglectus</i> —De Brassa's guenon		1		[60]						(17)
<i>Cercopithecus mona Campbelli</i> —Campbell's guenon			2	66			12			(4)
<i>Cercopithecus mona mona</i> —Mona guenon		1	1	66			[6]			(2)
<i>Cercopithecus mona (denti)</i> —Guenon		1		[66]						(17)
<i>Cercopithecus nictitans buttkoferi</i> —White-nosed or spot-nosed guenon			3	66	[28	24]	12			(4)
<i>Cercopithecus l'Hoesti</i> —l'Hoest's guenon			1	72	[28	24]	18			*
<i>Presbytis entellus</i> —Langur		1		50				M	A	(16)
Family Hylobatidae										
<i>Hylobates hoolock</i> —Hoolock gibbon			1	44	38	6	0			*
Family Pongidae										
<i>Pan troglodytes</i> —Northern chimpanzee	{	1		[48]						(18)
			5	48	38	10	0			†
		7	2	48				[M	M]	(5)
Family Hominidae										
<i>Homo sapiens</i> —Man		over 200		46	16	18	10	M[S]A		(20)

* Data of Chu and Bender, this report. † Data of Bender and Mettler, unpublished.

three pairs of acrocentric chromosomes in the 60-chromosome species, six pairs in the 66-chromosome species, and nine pairs in the 72-chromosome species.

There is only one count for a species of the subfamily Colobinae. Makino (16) has reported that the diploid chromosome number of *Presbytis entellus* (langur) is 50. The X chromosome is described as submetacentric and the Y as acrocentric.

The cytology of surprisingly few anthropoid apes is known. The karyotypes of one species of gibbon, *Hylobates hoolock*, has been recently investigated by cell-culture techniques with skin and kidney biopsies. The chromosomes of a kidney cell from *H. hoolock* are shown in Fig. 2. The diploid chromosome number is 44. There are 38 M, 6 S, and no A chromosomes. A single pair of chromosomes with conspicuous secondary constrictions, similar in morphology to those in Cercopithecidae, could be easily recognized.

The chromosome number of *Pan troglodytes* (chimpanzee) was investigated by Yeager *et al.* (18), who made a tentative count of $2n = 48$ from the spermatogonia of one specimen. This has recently been confirmed by Young *et al.* (5) and by Bender and Mettler (19). The female karyotype consists of 19 pairs of M chromosomes, 5 pairs of S chromosomes, and no A chromosomes. The X is a moderately large metacentric chromosome, and the Y is probably a very small metacentric chromosome (5, 19).

The diploid chromosome number of man is 46. There are five pairs of acrocentric chromosomes. The X is submetacentric and ranks about sixth in decreasing order of size. The Y is one of the smallest chromosomes, and it is acrocentric (20).

Discussion

This survey of primate chromosome cytology is an attempt to summarize available information, thus bringing up to date the earlier tabulations by Tobias (21) and Chiarelli (22). Classical studies and recent findings on human cytology have not been included since the subject has been well discussed elsewhere (see 23). However, a detailed karyotypic comparison between man and other primates, especially the anthropoid apes, should prove to be of particular interest.

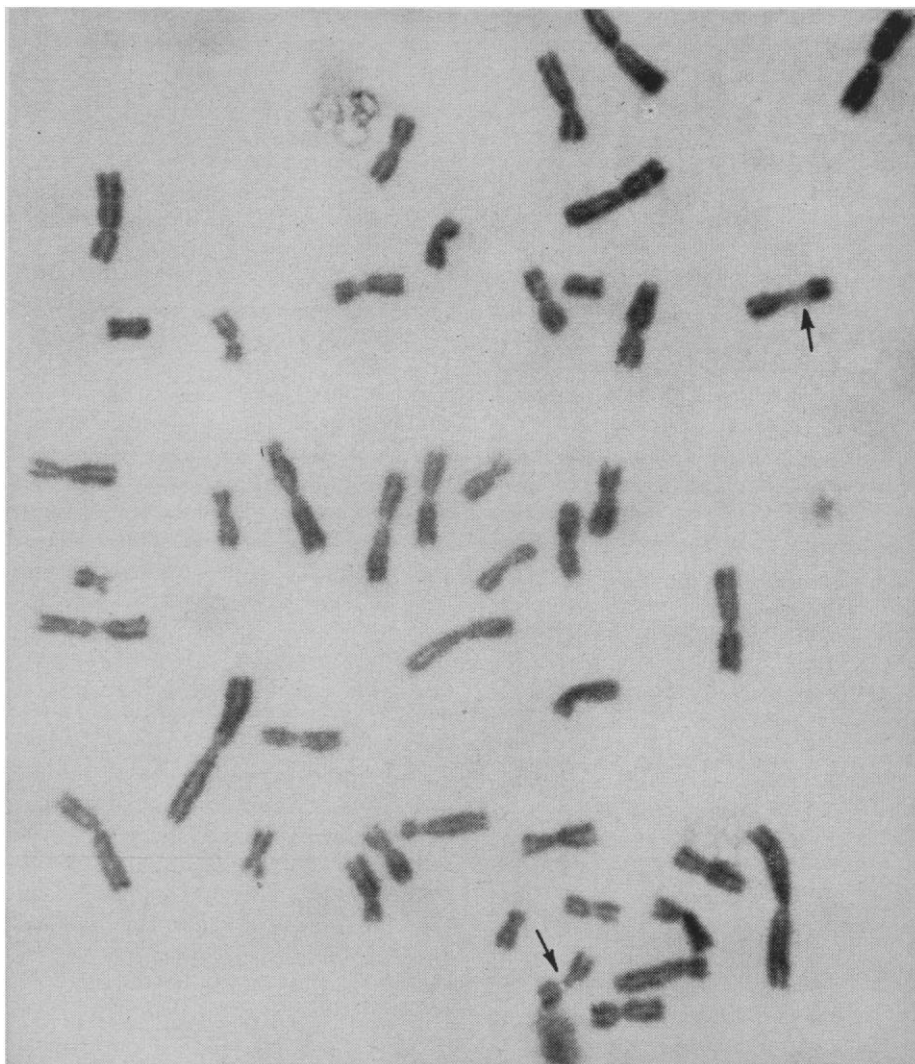


Fig. 2. The chromosomes of a tissue-cultured cell from the kidney of a *Hylobates hoolock* ♀. Arrows indicate the positions of secondary constrictions (about $\times 2100$).

The cytological results here summarized have indicated that the use of tissue culture, coupled with the application of suitable modern cytological techniques, can provide useful information on chromosome number and morphology in various species of primates. It should be emphasized, however, that meiotic chromosomes remain important as sources for comparison and verification. Furthermore, for a definitive establishment of chromosome homology between species the meiotic chromosome behavior in accidental and experimental interspecific hybrids must be studied.

These studies indicate a great diversity in chromosome number and morphology among representatives of the three major groups of the order Primates. The numbers range from $2n = 34$ to $2n = 72$, and in such a way that their only common denominator is 2. In the subfamily Cercopithecinae of the family Cercopithecidae, the fact that

the numbers of all five genera are multiples of 6 leads to a consideration of polyploidy as a possible evolutionary mechanism. However, several lines of evidence have been presented (4) for believing this interpretation to be improbable. One objection is that polyploidy will create difficulties in the sex-determination mechanisms in mammals. Another is that in each species there is only one pair of chromosomes having a clear secondary constriction. Also, the total chromosome length, with the possible exception of the genus *Papio*, is about the same. Finally, spectrophotometric measurements (24) of Feulgen-stained nuclei of three representative species (*Macaca mulatta*, $2n = 42$; *Erythrocebus patas*, $2n = 54$; *Cercopithecus aethiops*, $2n = 60$) show that despite differences in chromosome number the diploid deoxyribonucleic acid values are essentially identical.

It appears more likely that in the pri-

mates differences in chromosome number have arisen from alterations in the chromosomes of a basic set, giving either larger numbers of chromosomes or, more probably, smaller numbers of chromosomes with little loss or gain of chromosomal material.

Patterson and Stone (25) have suggested for the genus *Drosophila*, where the most primitive species have rod-shaped chromosomes, that centric fusions account for the reduction in chromosome number and the origin of metacentric and subterminal chromosomes. Makino (26) showed that the chromosome number of the domestic sheep is 54, consisting of 48 acrocentrics and 6 metacentrics. He found that the goat, on the other hand, has 60 acrocentric chromosomes. Makino suggested that 12 of the chromosomes of the goat correspond to the six metacentrics of the sheep. Such a pattern of fusion has been found in grasshoppers (27), snails (28), shrews (29), the rodent subfamily Microtinae (30), and gerbils (31).

The karyotypes of many of the primates studied demonstrate a marked correlation between low chromosome number and a low number of acrocentric chromosomes, and, conversely, a frequent correlation between high chromosome numbers and a large number of acrocentrics. As has been pointed out before by Matthey (8) and by Bender and Mettler (2), these correlations suggest that a Robertsonian type of chromosome evolution, by means of centric fusion, may also have played an important role in the primates. Thus, in the genus *Galago*, *G. senegalensis*, with only 38 chromosomes, has only three pairs of acrocentrics, while *G. crassicaudatus*, which has 62 chromosomes, has 27 pairs of acrocentrics. In the genus *Cercopithecus*, where three different chromosome numbers occur, those species with 60 chromosomes have six acrocentrics, those with 66 chromosomes have six pairs, and the one species with 72 chromosomes has nine pairs. In this case, the numbers of acrocentrics suggest that centric fusion can account quantitatively for the difference in chromosome number.

In the Platyrrhina, where thus far no differences in number between species of the same genus have been reported, we again see a suggestion that centric fusion may have been an important evolutionary mechanism. In the Cebidae, a rough correlation between chromosome number and degree of specialization is evident; *Cebus* is certainly a

Table 4. Mean chromosome number ($\pm$ standard deviation) and *nombre fondamental* of the three subgroups of primates.

Subgroup	Mean diploid chromosome number	Approximate <i>nombre fondamental</i> (N.F.)
Prosimiae (6 species)	47.0 $\pm$ 14.1	62-70
Platyrrhina (11 genera)	46.2 $\pm$ 5.3	66-82
Catarrhina (21 species)	49.8 $\pm$ 10.0	84-132

fairly generalized animal, while *Ateles* is quite specialized for a brachiating existence. *Cebus*, with $2n = 54$, has 13 pairs of acrocentrics (not counting the sex chromosomes), while *Ateles*, with $2n = 34$, has only one. The genera with intermediate chromosome numbers have intermediate numbers of acrocentrics.

It may be argued, of course, that the same correlations between chromosome number and number of acrocentrics could theoretically be caused by either centric fusion or centric fission. There are, however, several arguments against the centric fission mechanism. While the loss of a centromere, through fusion, can come about by a simple translocation, gain of a centromere requires an apparently less frequent mechanism, such as centrometric misdivision or, possibly, trisomy. Furthermore, more specialized forms must, as a general rule, have evolved from less specialized ancestral forms. And there may be a selective advantage for a specialized form in having fewer chromosomes, since this may lead to the creation of blocks of genes which are less likely to reassort at meiosis, and hence to a greater probability that offspring will be sufficiently like the parents to survive in the narrow ecological niche to which they are adapted. It is interesting to note that centric fusion has occurred in at least one case in man without any obvious phenotypic alteration (32).

The lack of an exact correlation between chromosome number and number of acrocentrics in the primates does not, of course, argue against the fusion mechanism. Fusion may occur not only in such a way as to yield a metacentric (centric fusion) but it may also occur in such a way as to yield a longer acrocentric (by tandem fusion). Tandem fusions may also yield larger subterminals from metacentrics and acrocentrics. In addition, pericentric inversions which occur after centric fusion may convert metacentrics into acrocentric or sub-

terminal chromosomes. It is clear that such events may have occurred in the evolution of groups, like most of the Cercopithecidae, where there are no acrocentric chromosomes, and in animals, such as *Saimiri*, which have very long chromosomes.

Matthey (33) has calculated the average chromosome number for a large number of mammalian species. He found that the mean diploid number was close to 47, with a standard deviation of about 11. For seven primate species, including man (at $2n = 48$), Matthey found the mean to be 47.4, and the standard deviation to be about 4.5 (8). We have calculated these values for all of the primate species available to us. Our calculations have been made on a per species basis, except for the Platyrrhina, where we have used the number for each genus since no variation between species has been found. Table 4 presents the mean diploid chromosome number and the number of major chromosome arms of the subgroups of primates. It can be seen that our values do not differ significantly from those of Matthey.

As pointed out by Matthey (34), the number of major chromosome arms (the *Nombre Fondamental*, or N.F.) is just as significant in the study of chromosome evolution as the mean number of chromosomes. The range of N.F. for the species in each subgroup for which such determinations can be made is also presented in Table 4. The ranges for the Prosimiae and the Platyrrhina are similar to those reported by Matthey (8) for four primate species, but the range for the Catarrhina is much greater.

Finally, the small amount of work that has been done so far already suggests that karyotype analysis can be of use to the primate taxonomist. The marmosets are a case in point. While Fiedler (35) places the marmosets and tamarins in only two separate genera, other taxonomists believe that the family Callithricidae is composed of many genera. The absence of any karyotypic difference between *Leontocebus* and *Callithrix* lends weight to Fiedler's view of a lower number of genera, although more species of each genus must be examined before any final conclusion can be drawn. Unfortunately, there are also cases where karyotypic analysis has not been very helpful. As an example, we may cite the case of *Callimico*. This genus has been placed both in the Callithricidae and in the Cebidae; it has even been proposed that it should oc-

cupy a separate family of its own. The karyotype of *Callimico* is intermediate between the marmoset karyotype and that of the cebid genus *Callicebus*. It can only be said that in this case the chromosomal evidence is in agreement with the idea, expressed by Hill (36), that the Callithricidae are a specialized, rather than a primitive group, and that *Callimico* is more primitive (and unspecialized) and is hence probably closer to the ancestral cebid stem.

References and Notes

1. J. H. Tjio and A. Levan, *Hereditas* **42**, 1 (1956).
2. M. A. Bender and L. E. Mettler, *Science* **128**, 186 (1958).
3. ———, *Cytologia*, in press.
4. E. H. Y. Chu and N. H. Giles, *Am. Naturalist* **91**, 273 (1957).
5. W. J. Young, T. Merz, M. A. Ferguson-Smith, A. W. Johnston, *Science* **131**, 1672 (1960).
6. This article is based on two papers presented at a symposium on the evolutionary and experimental biology of the primates held during the 29th annual meeting of the American Association of Physical Anthropologists, 12-14 May 1960, Washington, D.C. The specimens of *Lemur*, *Galago*, and *Hylobates hoolock* were obtained through the support of a National Science Foundation grant (G-12331) to Dr. J. Buettner-Janusch, Yale University. Oak Ridge National Laboratory is operated by Union Carbide Corporation for the United States Atomic Energy Commission.
7. E. O. Dodson, personal communication.
8. R. Matthey, *Rev. suisse zool.* **62**, suppl., 190 (1955).
9. T. S. Painter, *Science* **56**, 286 (1922).
10. M. A. Bender and L. E. Mettler, unpublished data.
11. M. A. Bender, in *Immediate and Low Level Effects of Ionizing Radiations*, A. A. Buzzati-Traverso, Ed. (Taylor and Francis, London, 1960), pp 103-118. (Proceedings of a symposium held 22-26 June 1959 in Venice, Italy, published as a supplement to *Intern. J. Radiation Biol.*)
12. C. D. Darlington and A. Haque, *Nature* **175**, 32 (1955).
13. K. H. Rothfels and L. Siminovich, *Chromosoma* **9**, 163 (1958).
14. T. S. Painter, *J. Exptl. Zool.* **39**, 433 (1924).
15. P. I. Shiwago, *Bull. biol. méd. exptl. U.R.S.S.* **8**, 3 (1939).
16. S. Makino, *Cytologia* **16**, 288 (1952).
17. N. Tappen, personal communication.
18. C. H. Yeager, T. S. Painter, R. M. Yerkes, *Science* **91**, 74 (1940).
19. M. A. Bender and L. E. Mettler, unpublished data.
20. J. A. Böök et al., *Lancet* **1**, 1063 (1960).
21. P. V. Tobias, in *Chromosomes, Sex Cells, and Evolution in a Mammal; Based Mainly on Studies of the Reproductive Glands of the Gerbil, and a New List of Chromosomes of Mammals* (Lund, Humphries, London, 1956).
22. B. Chiarelli, *Caryologia* **11**, 99 (1958).
23. E. H. Y. Chu, *Am. J. Human Genet.* **12**, 97 (1960); C. E. Ford, *ibid.* **12**, 104 (1960); C. Stern, *ibid.* **11** (No. 2, pt. 2), 301 (1959).
24. R. Kleinfeld and E. H. Y. Chu, *Cytologia* **23**, 452 (1958).
25. J. T. Patterson and W. S. Stone, in *Evolution in the Genus Drosophila* (Macmillan, New York, 1952).
26. S. Makino, *Cytologia* **13**, 39 (1943).
27. M. J. D. White, in *Animal Cytology and Evolution* (Cambridge Univ. Press, New York, ed. 2, 1954).
28. H. Staiger, *Chromosoma* **6**, 419 (1954).
29. C. E. Ford, J. L. Hamerton, G. B. Sharman, *Nature* **180**, 392 (1957).
30. R. Matthey, *Rev. suisse zool.* **64**, 39 (1957).
31. J. Wahrman and A. Zahavi, *Proc. Intern. Congr. Genet. 10th Congr.* **2**, 304 (1958).
32. P. S. Moorhead, W. J. Mellman, D. M. Batipps, *Genetics* **45**, 1001 (1960).
33. R. Matthey, *Rev. suisse zool.* **62**, 163 (1955).
34. ———, *Caryologia* **6**, 1 (1954).
35. W. Fiedler, *Primatologia* **1**, 1 (1956).
36. W. C. O. Hill, *Trans. Am. Phil. Soc.* **49** (n.s.), pt. 5 (1959).

Human Behavior during the Tsunami of May 1960

Research on the Hawaiian disaster explores the consequences of an ambiguous warning system.

Roy Lachman, Maurice Tatsuoka, William J. Bonk

At 1:05 HST on the morning of 23 May 1960, a great sea wave, or tsunami, caused by an earthquake off the coast of Chile (1), hit the Hawaiian city of Hilo. Despite at least 10 hours of warning, the wave killed 61 persons, injured several hundred more, and completely destroyed an estimated 500 dwellings.

A study group was organized by the Hawaii Division of the Hawaiian Academy of Science to objectively examine the human element in the disaster (2). The objectives of the research, subsequently undertaken, were to study the

subjective interpretations of the warnings and the resulting behavior.

A questionnaire was prepared, to be administered to a cross section of the adult population of the affected areas. The questionnaire was designed on the basis of preliminary observations conducted in the devastated area and of impressions recorded prior to the impact. Pre-testing of the survey instrument was precluded by limitations of time and resources. The prepared questionnaire was explained to the interviewers in an item-by-item discussion of the intent of each question.

Many of the interviewers were close acquaintances of the individuals they were to interview. Hence, open and frank discussions could be initiated almost at once. Also, since the majority

of affected families had not evacuated, failure to evacuate carried no social stigma. There is reason to believe, therefore, that the responses made by the people interviewed give a truthful picture of their impressions of the events.

A large number of those interviewed were at the Red Cross disaster shelter. This group formed a readily available starting point for interviews and also provided leads for locating other displaced individuals. Various church organizations made available the new addresses of their displaced congregations. The Department of Public Instruction required students in displaced families to report their new addresses. Lists of victims were thus compiled, and those to be interviewed were selected in a non-systematic fashion. The interviewing was conducted over a period of seven successive days.

Representativeness of the Sample

The conditions under which the survey was made precluded our drawing a pure random or stratified random sample. No one possessed an exhaustive list of tsunami victims. Neither did we have valid information on the geographic distribution, or other relevant characteristics, of our population before the impact. We therefore sought to achieve, through the means described above, a "quasi-random" sample that

Dr. Lachman is research psychologist at the Johns Hopkins Hospital and School of Medicine, Baltimore, Md. Dr. Tatsuoka and Mr. Bonk are assistant professor of mathematics and science and instructor in anthropology-sociology, respectively, at the University of Hawaii, Hilo.