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EMERGENCE OF PERMANENT FIRST MOLARS IN THE MONKEY (*MACACA MULATTA*). ASSOCIATION WITH OTHER GROWTH PHENOMENA‡§

INTRODUCTION

The main purpose of the present report is to examine emergence data on the permanent first molars of the macaque against the background of similar data on the entire deciduous dentition. In addition to this an attempt will be made to link the phenomenon of odontiasis with other expressions of growth and development in the same primate. The ultimate objective of these investigations is to obtain clues which might be of value in designing better studies of the human dentition in the future.

Very little is actually known about the subject matter with which this paper deals. Over one hundred years ago Youatt[34] found the inspection of the dentition useful in estimating the ages of calves and cows, and soon thereafter Saunders[23] exhorted members of the English Parliament to use the teeth as a criterion of age to remove certain difficulties in the application of the child labor law.

The ranges of variation normally encountered in dealing with erupting teeth are quite wide. Until the variations and correlations occurring normally in the course of development are known, there is no satisfactory frame of reference for interpreting observations on odontiasis in experimental animals. Some of the problems that confront the investigator who wishes to construct reasonably reliable statistical standards for estimating the chronological age of an infant macaque are discussed at length in a previous paper by the authors.[13] The present report can be looked upon as a continuation and expansion of the aforementioned study.

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‡ This investigation was supported in part by a research grant (PHS C-2304) from the National Institutes of Health, of the National Institutes of Health, Public Health Service, to Yale University.
§ Preliminary reports were given at meetings of The International Association for Dental Research in Chicago, Illinois, on March 20, 1955, and The American Association of Anatomists in Philadelphia, Pennsylvania, on April 6, 1955.
Received for publication September 27, 1955.

TABLE 1. AGES OF EMERGENCE OF ALL DECIDUOUS TEETH AND OF THE PERMANENT FIRST MOLARS IN 26 TO 27 MALE MACAQUES
Figures for deciduous teeth represent averages for a tooth and its antimere. The data are in terms of years after birth.

Number of animal	*Maxilla*							*Mandible*						
						M_1							M_1	
	di_1	di_2	dc	dm_1	dm_2	*Rt.*	*Lt.*	di_1	di_2	dc	dm_1	dm_2	*Rt.*	*Lt.*
603	.01	.03	.10	.13	.30	1.19	1.17	.01	.01	.10	.13	.29	1.08	1.04
728	.00	.05	.16	.16	.34	1.35	1.35	.01	.01	.16	.16	.30	1.23	1.23
642	.01	.06	.13	.16	.40	1.40	1.40	.01	.01	.13	.16	.40	1.28	1.32
590	.04	.10	.13	.13	.39	1.33	1.31	.02	.05	.13	.14	.39	1.18	1.18
719	.03	.10	.12	.16	.37	1.37	1.37	.03	.07	.15	.16	.33	1.30	1.30
712	.05	.09	.16	.16	.40	1.30	1.30	.03	.05	.15	.17	.33	1.16	1.16
625	.03	.09	.18	.18	.41	1.48	1.42	.03	.04	.16	.19	.43	1.32	1.32
484	.00	.09	.17	.20	.40	1.47	1.47	.00	.01	.20	.25	.39	1.41	1.41
510	.07	.09	.21	.21	.36	1.32	1.32	.02	.05	.22	.21	.36	1.20	1.17
665	.04	.09	.16	.20	.44	1.54	1.54	.03	.06	.18	.20	.40	1.29	1.36
288	.06	.09	.17	.13	.48	1.52	1.52	.05	.07	.20	.15	.43	1.42	1.44
612	.03	.11	.16	.21	.43	1.49	1.49	.07	.07	.16	.20	.42	1.37	1.37
449	.04	.07	.15	.17	.40	1.92	1.90	.01	.04	.17	.21	.40	1.90	1.90
706	.07	.13	.25	.19	.39	1.28	1.28	.05	.08	.26	.23	.42	1.26	1.26
717	.07	.15	.20	.21	.46	1.63	1.63	.05	.08	..	.20	.41	1.38	1.38
521	.06	.12	.19	.21	.49	1.51	1.51	.06	.12	.19	.21	.41	1.43	1.43
718	.08	.13	.22	.18	.49	1.61	1.71	.07	.07	.19	.17	.43	1.54	1.54
525	.07	.11	.20	.22	.45	1.53	1.53	.07	.08	.21	.24	.40	1.38	1.38
553	.10	.13	.21	.19	.50	1.42	1.52	.07	.07	.22	.19	.50	1.27	1.27
556	.08	.13	.22	.22	.46	1.47	1.47	.05	.09	.22	.22	.46	1.36	1.36
477	.07	.10	.23	.23	.50	1.67	1.71	.06	.07	.17	.23	.44	1.55	1.60
286	.07	.14	.18	.20	.56	1.79	1.83	.10	.10	.20	.25	.46	1.52	1.56
440	.05	.15	.20	.28	.58	1.63	1.63	.05	.05	.20	.30	.52	1.63	1.55
660	.09	.15	.26	.28	.54	1.62	1.71	.06	.09	.23	.26	.54	1.47	1.47
578	.10	.15	.30	.28	.60	...	...	.08	.10	.30	.28	.52	1.58	1.56
686	.12	.18	.31	.26	.54	1.61	1.61	.12	.14	.35	.27	.51	1.36	1.36
483	.15	.23	.28	.30	.57	1.71	1.71	.09	.16	.30	.28	.48	1.51	1.51

MATERIAL AND METHODS

The material studied consists of the dental records of 27 male and 42 female macaques born and reared in the monkey colony of the Department of Obstetrics and Gynecology at the Yale University School of Medicine. Only records on presumably normal animals were included, as it is known that certain pathological conditions, such as rickets[3, 10, 16, 27, 32] and certain types of hormonal interference, for example, treatment with testosterone propionate,[30] may affect tooth eruption. As the dental effects of castration are not known with certainty, the records on several castrated males were excluded also. A pseudohermaphrodite female likewise was left out of the series.

TABLE 2. AGES OF EMERGENCE OF ALL DECIDUOUS TEETH AND OF THE PERMANENT FIRST MOLARS IN 40 TO 42 FEMALE MACAQUES
Figures for deciduous teeth represent averages for a tooth and its antimere. The data are in terms of years after birth.

Number of animal	*Maxilla*							*Mandible*						
						M_1							M_1	
	di_1	di_2	dc	dm_1	dm_2	Rt.	Lt.	di_1	di_2	dc	dm_1	dm_2	Rt.	Lt.
582	.03	.04	.11	.14	.38	1.40	1.40	.00	.00	.11	.14	.34	1.26	1.25
404	.01	.09	.15	.15	.33	1.46	1.46	.01	.04	.15	.15	.31	1.19	1.15
591	.03	.09	.15	.15	.31	1.28	1.32	.03	.04	.14	.16	.33	1.15	1.21
615	.03	.08	.17	.13	.32	1.35	1.35	.02	.03	.18	.16	.32	1.20	1.18
442	.03	.08	.17	.16	.34	1.28	1.35	.04	.06	.14	.14	.29	1.24	1.24
641	.01	.07	.17	.15	.38	1.32	1.30	.02	.04	.18	.17	.34	1.27	1.23
730	.02	.08	<.16	<.16	.44	1.35	1.35	.01	.03	<.16	.18	.40	1.23	1.23
441	.04	.14	.15	.14	.34	1.39	1.33	.04	.06	.15	.16	.32	1.25	1.23
705	.04	.08	.17	.12	.41	1.27	1.29	.03	.05	.19	.16	.41	1.27	1.27
617	.05	.09	.16	.16	.42	1.32	1.32	.06	.07	.16	.15	.32	1.22	1.22
485	.03	.11	.20	.14	.39	1.42	1.40	.03	.09	.20	.20	.29	1.24	1.24
589	.06	.09	.17	.17	.38	1.36	1.36	.05	.05	.19	.19	.36	1.21	1.32
651	.07	.10	.18	.20	.43	1.34	1.41	.01	.03	.19	.19	.37	1.34	1.34
272	.06	.09	.17	.18	.43	1.32	1.32	.04	.07	.18	.19	.41	1.24	1.20
482	.04	.10	.17	.17	.42	1.50	1.50	.02	.04	.17	.21	.35	1.37	1.37
568	.03	.10	.17	.17	.41	1.29	1.40	.04	.04	.17	.27	.41	1.27	1.27
474	.03	.08	.20	.20	.41	1.39	1.41	.03	.04	.23	.23	.41	1.32	1.32
289	.04	.12	.21	.19	.48	1.49	1.47	.04	.07	.22	.19	.32	1.37	1.37
518	.05	.11	.20	.19	.41	1.47	1.49	.03	.06	.26	.20	.38	1.34	1.34
638	.09	.14	.18	.16	.48	1.29	1.29	.02	.10	.18	.19	.44	1.39	1.27
656	.07	.13	.22	.15	.42	1.37	1.37	.06	.07	.22	.20	.38	1.26	1.26
659	.08	.11	.20	.18	.40	1.37	1.37	.06	.08	.20	.21	.41	1.21	1.21
520	.05	.10	.23	.21	.42	1.53	1.49	.05	.06	.23	.21	.40	1.31	1.31
563	.07	.14	.21	.16	.37	1.32	1.32	.09	.09	.21	.21	.37	1.32	1.32
285	.05	.07	.21	.19	.57	1.52	1.56	.06	.07	.18	.18	.47	1.39	1.43
291	.06	.11	.20	.18	.49	1.58	1.56	.05	.07	.19	.21	.44	1.41	1.44
736	.08	.11	.25	.19	.44	1.38	1.38	.06	.07	.26	.22	.40	1.29	1.29
292	.06	.11	.20	.20	.51	1.54	1.54	.05	.08	.20	.20	.45	1.37	1.37
507	..	..	..	..	.48	1.49	1.49	..	..	..	..	.46	1.37	1.37
652	.07	.13	.23	.20	.44	1.46	1.56	.05	.07	.23	.21	.44	1.46	1.38
731	.09	.14	.21	.23	.46	1.49	1.49	.06	.09	.22	.22	.39	1.22	1.29
567	.09	.12	.21	.27	.44	1.42	1.44	.06	.08	.21	.27	.40	1.31	1.31
456	.06	.15	.23	.25	.47	1.62	1.60	.04	.08	.25	.25	.43	1.56	1.56
451	.05	.15	.25	.25	.52	1.65	1.67	.05	.07	.28	.22	.44	1.48	1.48
452	.04	.12	.31	.21	.52	1.56	1.56	.06	.07	.27	.23	.51	1.50	1.50
527	..	..	..	..	.48	1.66	1.66	..	..	..	..	..	1.45	1.40
470	.09	.14	.29	.19	.55	1.54	1.56	.07	.09	.29	.19	.49	1.40	1.40
733	.09	.12	.27	.25	.51	1.55	1.63	.06	.10	.29	.23	.43	1.41	1.41
448	.08	.14	.28	.25	.55	1.64	1.64	.08	.08	.32	.25	.37	1.33	1.37
580	.10	.18	.26	.22	.45	1.53	1.55	.10	.12	.26	.24	.43	1.39	1.38
732	.09	.15	.29	.26	.52	1.55	1.55	.09	.15	.30	.26	.44	1.41	1.41
447	.12	.16	.22	.25	.55	1.61	1.61	.10	.16	.28	.24	.48	1.48	1.46

Since one of the purposes of the investigation was the establishment of statistical norms for the emergence of permanent first molars in the monkey, the selection of laboratory data was limited to the records which supplied information on these teeth, in addition to data on the deciduous dentition. The records of one male and two females without complete deciduous tooth data were added to the above material in order to obtain the largest possible number of individual items for the calculation of permanent first molar statistics. The basic first molar data will be found in Tables 1 and 2, in columns M_1.

Although seven generations are now represented in the colony, in which breeding for replacement was begun in 1935,[31] only about half of these contained animals that were old enough to supply data for the present study. The tooth population sample available may be regarded as a sufficiently random one, since the monkeys included in the series analyzed were members of a large number of genetically unrelated families.

The rôle of personal factors in making and recording the observations is negligible, considering that during the 20-year period under consideration all details pertaining to this phase of the investigation were attended to by one and the same individual.* For information on the procedural details followed in preparing the data for statistical analyses the reader is referred to the earlier work of the authors.[18] Only one exception need be noted, namely, that to insure the employment of the most probable ages of emergence in the calculations, 0.01 yr. was subtracted from laboratory entries based on weekly inspections and 0.04 yr. from those based on monthly examinations.

Some of the procedures followed in the analyses have been described elsewhere.[12, 18] Due to the fact that chronological asymmetry in the emergence of permanent teeth is not at all uncommon, the numerical values for a tooth and its antimere were never averaged, as was done in dealing with the deciduous dentition. It is worth emphasizing that the available data represent a random sampling from the universe of erupting teeth; they are the result of serial observations of such duration that no information has been excluded by commencing the study after some teeth already had emerged, or by terminating it before the completion of this process in some animals.

As the data obtained supply information on both ends of a range of distribution, cumulative percentages can be calculated for all age levels that appear in a series. After this the percentages can be plotted on ordinary arithmetically ruled graph paper. As a rule the arrangement of the plotted points is such that it is not difficult to draw a cumulative percentage ogive freehand in order to establish the line which furnishes the simplest graphic generalization of the location of the points. This line which is, in reality, a special type of regression curve, is drawn through as many individual points as possible; if difficulty is experienced in completing the ends of the line, recourse may be had to visualizing the universally occurring pattern that characterizes all graphic representations of similar data, based on a quantitatively adequate number of observations.

The freehand curve described above provides what appears to be a fair approximation to the hypothetical curve that would be obtained if an infinitely large population of

* All laboratory examinations were meticulously carried out by Mr. Joseph Negri, technical assistant. Prior to September, 1948, he made weekly inspections for emerging permanent first molars and monthly examinations after the date mentioned. The criterion of odontiasis was always the same, namely, the first appearance of a tooth crown, or any part thereof, above the oral mucosa.

these monkeys were available for study. The statistical expressions of variability that can be derived by suitable analyses of this curve have a high degree of stability and are surprisingly independent of the number of field or laboratory observations utilized for plotting the graphic scaffolding of the curve, provided, of course, that the basic data are not excessively limited in quantity.

The computations required for a mathematical description of chronological scattering in the emergence of permanent first molars can be based either directly on the values recorded in Tables 1 and 2, or indirectly on them by utilizing the freehand ogives mentioned above. Since the technique employed may be a matter of personal preference, the results obtained by the second technique were included in Table 3 for purposes of comparison.

The standard errors given in Table 3 were calculated by assuming that the two observations per animal were not independent, i.e., *N-1* was considered established by the number of tooth pairs.

RESULTS

A. *Emergence of permanent first molars and the influence of sex.* Some of the statistical data on the permanent first molars have been condensed into compact graphic form for more convenient presentation. Figures 1 to 4 present the authors' concept of the cumulative frequency curves that can be derived from the original data given in Tables 1 and 2, in columns M_1. The percentage values summarized by the smoothed curve are shown by small circles; the hypothesized extremes of the curve are indicated by small arrows.

Determination of the exact location of these terminals is extremely difficult in all cases and would require repeated examination of thousands of animals for the attainment of a high degree of reliability. The ends of the curves shown in Figures 1-4 are merely for the purpose of designating the most likely limits of distribution for the vast majority of normal animals. The points on the curves indicate where the latter are intersected by vertical lines that represent the limits of age intervals of 0.04 of a year; they may be helpful in translating the graphs into numerical values.

Estimates of the percentile distribution of emerging first molars may be made from the curves shown in Figures 1 to 4. It is evident that the degrees of asymmetry are not large; in all four instances a slight degree of skewing in the positive direction can be observed. It was not deemed necessary to make formal tests for normality.

The most important statistical values are shown in Table 3. In addition to the means, modes and medians were calculated also, but since they were only slightly below the first-mentioned measures of central tendency, they were not included in the table. As for the means and standard deviations, it

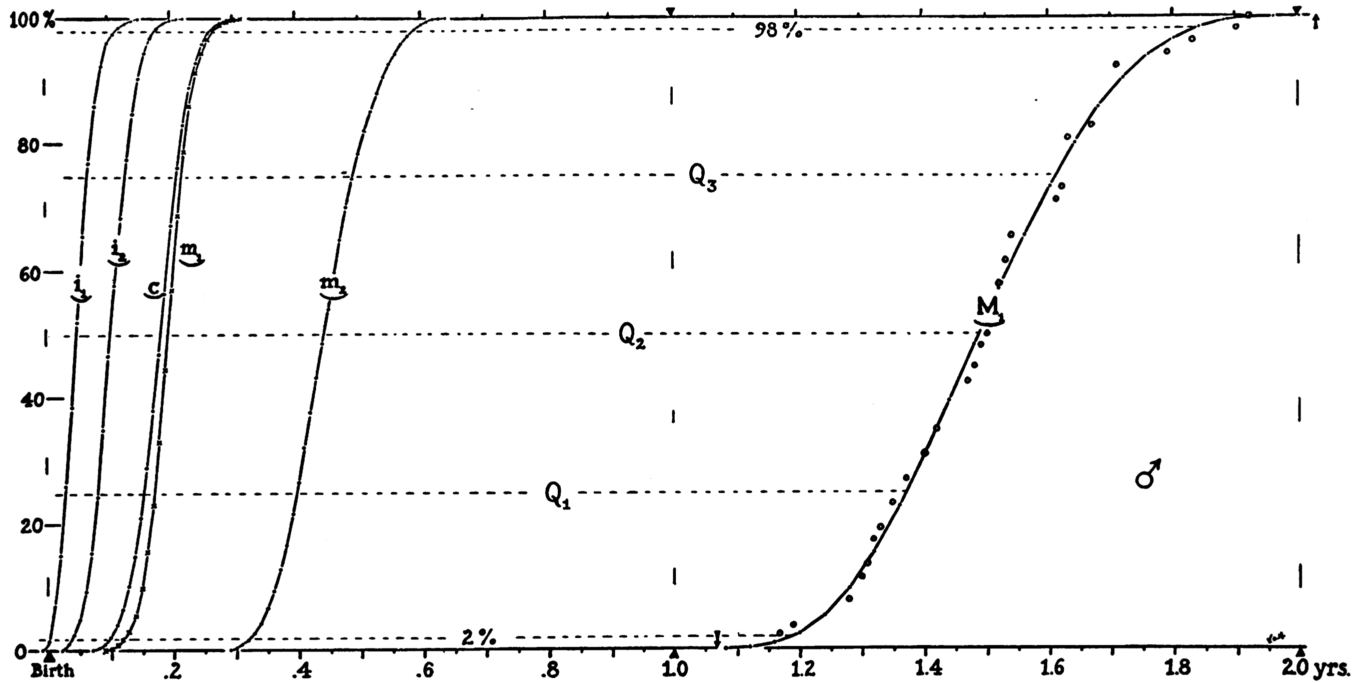

FIG. 1. Cumulative percentage ogives for the emergence of the permanent maxillary first molar (M_1) and the five classes of deciduous maxillary teeth of male macaques *(Macaca mulatta)*.

The percentages obtained from original data are shown by small circles; the ends of the M_1 curve are indicated by arrows.

The points on deciduous tooth curves are 0.01 of a year apart; those on M_1 curve 0.04 of a year apart.

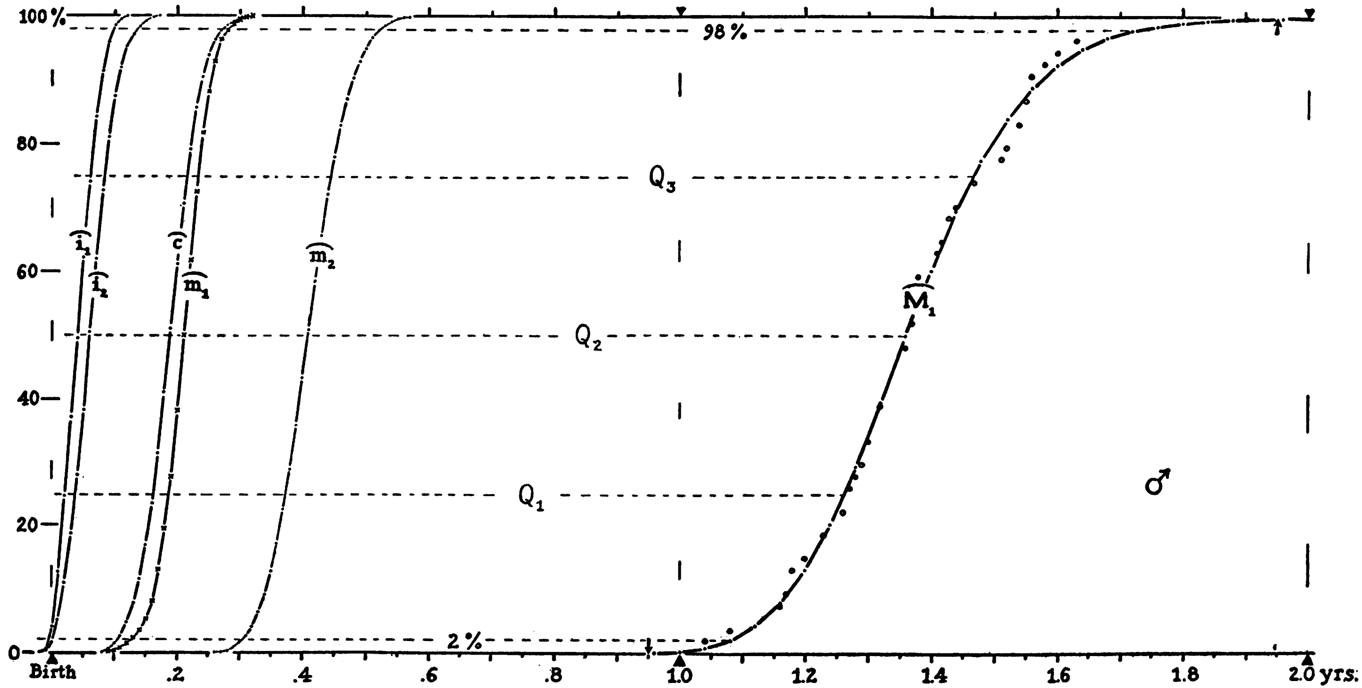

FIG. 2. Cumulative percentage ogives for the emergence of the permanent mandibular first molar ($\overline{M_1}$) and the five classes of deciduous mandibular teeth of male macaques *(Macaca mulatta)*.

For explanation of details, see text under Figure 1.

is worthy of note that the two methods of calculation yield very similar results.

The data at hand indicate much less variability in the emergence of permanent first molars in female macaques than in males. This is a finding which, so far as the authors know, has not been reported before. It has no readily discoverable counterpart in man.[11]

Biometrically speaking there seems to be no doubt about the actuality of the sex difference just mentioned. The narrower range of variability is given by the data on the permanent first molars of females and not by those

TABLE 3. STATISTICAL SUMMARY OF AGES OF EMERGENCE OF PERMANENT FIRST MOLARS
Data expressed to the nearest hundredth of a year

			Computation based on				
		Number of	*Original scores*		*Smoothed ogive*		
Dental arch		*tooth pairs*	*Mean*	σ	*Mean*	σ	$S.E._{\bar{M}}$
Males	Max.	26	1.51	0.17	1.49	0.16	0.03
	Mand.	27	1.39	0.17	1.37	0.16	0.03
Females	Max.	42	1.46	0.11	1.44	0.12	0.02
	Mand.	42	1.33	0.10	1.32	0.10	0.02

of males, although, as a rule, the greater the number of individual items in the series analyzed, the wider is the range of distribution. In this particular instance three additional facts increase the probability of correctness of the statistical finding here reported.

Firstly, although two different methods of statistical analysis were employed, the standard deviation figures obtained indicate a strong contrast between variability in the two sexes regardless of the method used.

Secondly, in each sex there is a strong similarity between the measures of variability for maxillary and mandibular teeth. Were this not the case, one would have some reason for questioning the statistical adequacy of the unprocessed data, and a confirmation of unequal degrees of variability would make it necessary to base the analysis on a larger number of observations.

Thirdly, the discovery of a sex difference in the developmental pattern of permanent first molars is not an unexpected finding in view of the sexual precocity of the female "rhesus" monkey. Several studies of human data have revealed similar positive correlations, especially in girls.[4, 25, 28, 29] Again, had these teeth been found completely unaffected by the general rate of physical maturation, one would have been led to question the sufficiency of the material under investigation.

B. *Variable duration of early phases of odontiasis.* To show how variability increases with advancing chronological age, Figures 1, 2, 3, and 4 have been extended to the left, or toward the neonatal period, to permit the inclusion of cumulative percentage graphs for the five classes of deciduous teeth which precede the emergence of the permanent first molars. The curves for the deciduous teeth have been drawn on the basis of cumulative percentage determinations for every hundredth of a year, starting just prior to birth.

TABLE 4. LENGTH OF FIRST PERIOD OF ODONTIASIS* AND OF INTERVAL OF REST PRECEDING EMERGENCE OF A PERMANENT FIRST MOLAR, FROM DATA ON 69 MACAQUES
All data in decimals of a year

		Emergence of deciduous dentition			*Outwardly quiescent phase*		
Dental arch		*Minimum*	*Average*	*Maximum*	*Minimum*	*Average*	*Maximum*
Males	Max.	0.29	0.39	0.53	0.87	1.06	1.50
	Mand.	0.28	0.37	0.48	0.75	0.96	1.50
Females	Max.	0.28	0.38	0.52	0.81	1.02	1.18
	Mand.	0.25	0.35	0.42	0.79	0.93	1.13

* The period of emergence of the permanent teeth constitutes the second period of odontiasis.

In all four instances the nearly vertical slopes of the midranges of the deciduous incisor curves are in strong contrast with the lesser slopes of the curves depicting the emergence of deciduous second molars and permanent first molars. These contrasts, together with the existence of a relatively long outwardly quiescent period between the completion of the deciduous dentition and the advent of the first permanent tooth, naturally give rise to the question of whether the two major phases of dental growth and development are at all interrelated.

Table 4 summarizes certain information that can be obtained by analyzing the contents of Tables 1 and 2, but only surmised by inspecting Figures 1, 2, 3, and 4. According to this table the outwardly quiescent interval that separates the two major periods of odontiasis is always longer than the active period of emergence of the deciduous teeth which precedes it. It is evident, further, that dental growth processes in the mandible are, on an average, somewhat speedier than those in the maxilla, in both sexes.

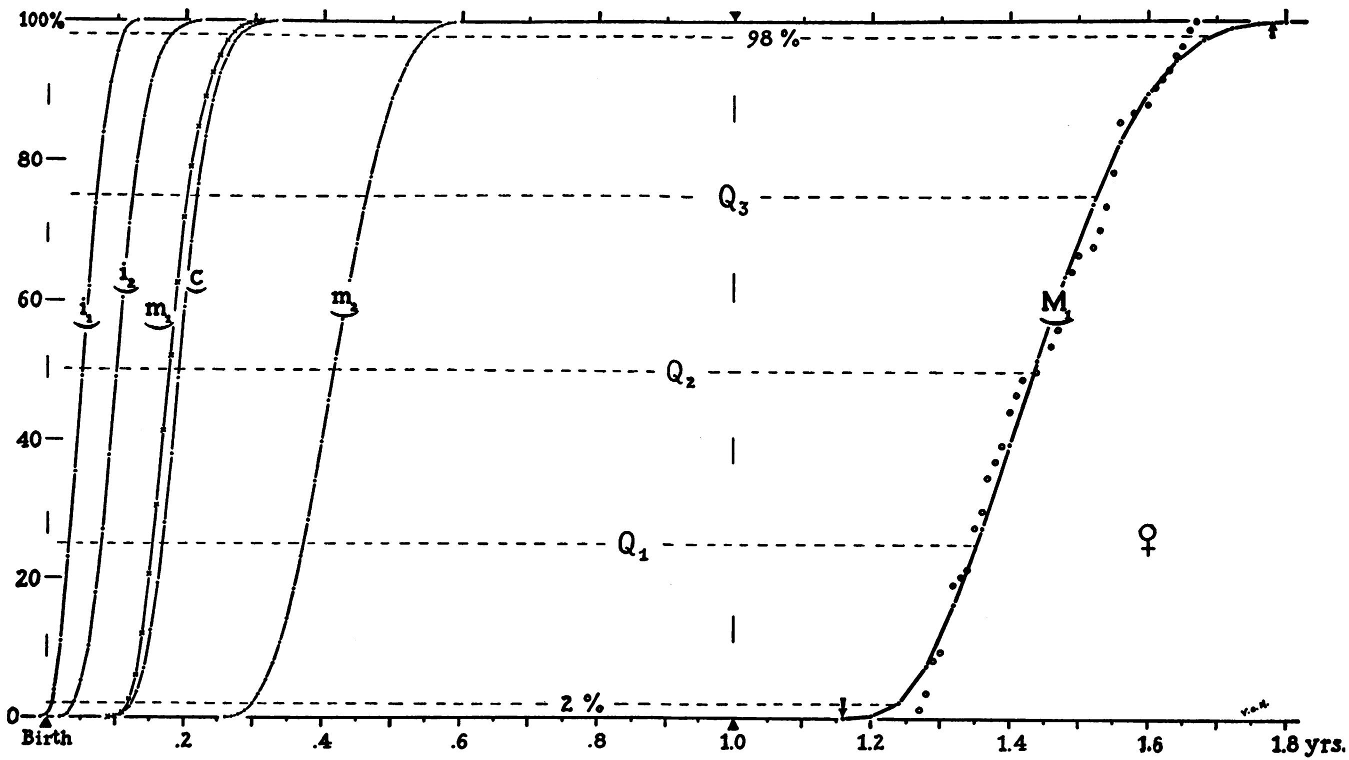

Fig. 3. Cumulative percentage ogives for the emergence of the permanent maxillary first molar (M1) and the five classes of deciduous maxillary teeth of female macaques *(Macaca mulatta)*.

For explanation of details, see text under Figure 1.

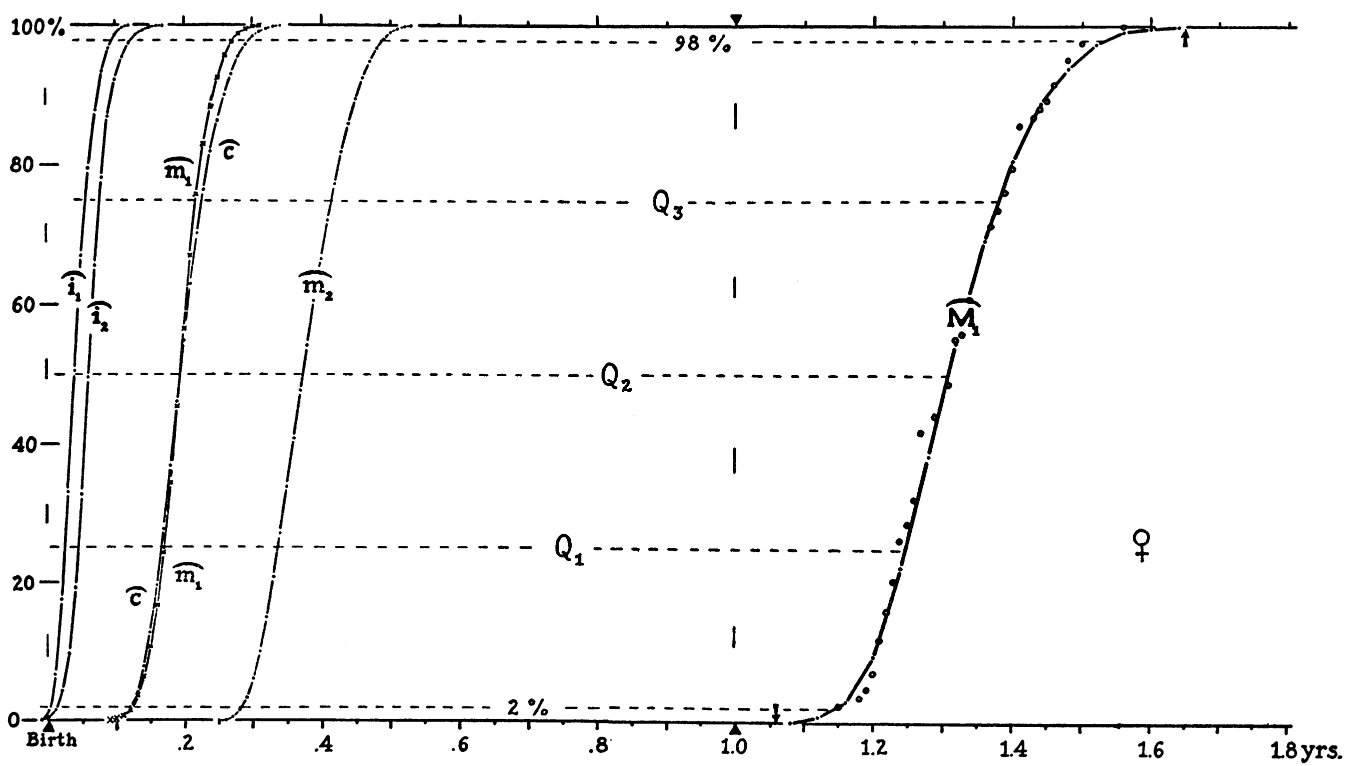

Fig. 4. Cumulative percentage ogives for the emergence of the permanent mandibular first molar ($\overline{M_1}$) and the five classes of deciduous mandibular teeth of female macaques *(Macaca mulatta)*.

For explanation of details see text under Figure 1.

C. *Dental interrelations.* Mutual relationships between the growth and development of the many individual organs which collectively make up the dentition of a mammal such as the monkey—not to mention the human species—are still a virtual *"terra incognita"* to biology. There seems to be no literature at all on the interrelationships between the eruption of the deciduous and permanent teeth. If the reports by Nissen and Riesen[20] and Hurme and van Wagenen[18] are not considered, only a small number of articles by other writers can be cited as containing any documented information on the subject.

The data by Schultz[24] on monkeys are too limited to enable one to draw any definite conclusions, while those by Spiegel[26] merely *suggest* that early emergence of deciduous second molars is likely to be followed by earlier-than-average emergence of the permanent first molars.

After a study of 8 to 12 children Baldwin and Smith[1] concluded, in 1925, that "there was a tendency for children who began dentition early to finish early," and vice versa. The graphs which accompany the report by Camescasse[2] corroborate this finding, although they reveal considerable variability in individual instances. In one way or another the findings or tabulations of several other authors[6, 7, 9, 14, 15, 18, 25, 27] are in harmony with the concept of Fujita[8] who in 1947 stated explicitly that "there is an interrelationship between the eruption times of the teeth of an individual."

A recent article by Clements, Davies-Thomas, and Pickett,[5] however, contains an assertion to the effect that the times of eruption of certain teeth in man are "independent of each other," or "distributed at random." This generalization appears too sweeping in the form in which it is stated and may be due to the fact that the British study was based on cross-sectional material, analyzed by utilizing techniques which differ considerably from those employed in the present investigation, and that it attempted no review of the scanty literature available.

Having at their disposal many long-term records of serial observations, which are ideal for studies that deal with such complex phenomena as the development of the dentition, the present authors made an effort to find out—without too much sacrificing of detail—whether the analysis of a larger body of data would confirm the findings reported by them earlier.[18] It was desired particularly to throw some light on the possible interrelationships between the emergence of the deciduous teeth, individually and collectively, and the initiation of the process for the succedaneous dentition. The first permanent tooth cut by *Macaca mulatta* is a first molar, which is also ordinarily the first in man. This tooth is of special interest to dentists and odontologists, many of whom, rightly or wrongly, regard it as "the keystone" of a dental arch.

To prepare the ground for an assault upon the problem just discussed, the actual ages of emergence (see Tables 1 and 2) of all deciduous teeth and of all four permanent molars in the 26 males and 40 females (whose dental records were adequate for the purposes of this special study) were converted into so-called "Z" score readings. Following this average standard scores for all 12 tooth pairs in each of the 66 macaques were computed and arranged in rank order in two series, one for males and one for females. High negative values were placed at the beginning of each series and high positive values at the end.

The results were plotted on graph paper to construct the rather complex scatter diagrams reproduced here as Figures 5 and 6. Standard scores for a given animal were plotted along the same ordinate, the location of which was determined by the rank order of the average value. The plotting was done with care so that the diagrams would preserve, indirectly, the numerical values that determined the placement of the symbols.

The symbols used are explained under the word *Legend* at the bottom of each figure. With one exception, they have been selected with the possibility of a need for superimposition in mind, and a few examples of three signs combined can be found. Where superimposition would have resulted in too much confusion, the symbols have been arranged along the same horizontal line, or in a tight cluster, both to save space and to keep the identity of the vertical rows distinct. Also, to avoid excessive complexity of the graphs, no separate signs were used for the five morphological classes of deciduous teeth in each jaw; it was deemed sufficient only to make a distinction between maxillary and mandibular teeth. For the same reason right and left teeth were not differentiated either, but the average for a tooth and its antimere was used.

More data were available on female monkeys than on males. Therefore, in order to make mutual comparison of the two "scattergrams" easier, their horizontal dimensions were made approximately the same, while the vertical "Z" scales were kept constant, a procedure which necessitated wider spacing of the vertical rows of symbols for the males than for the females.

Figures 5 and 6 may be said to speak for themselves. They show, with great clarity, that eruption times are not completely independent of each other, in spite of fairly wide limits of variability. The symbols are not scattered evenly all over the diagrams, each of which shows them forming a wide zone which rises gradually from the lower left quadrant to the upper right quadrant. No statistical calculations are needed to prove that a given tempo of development does not affect the teeth as isolated units, but rather as integral parts of a larger unit—the dentition—which maintains its essen-

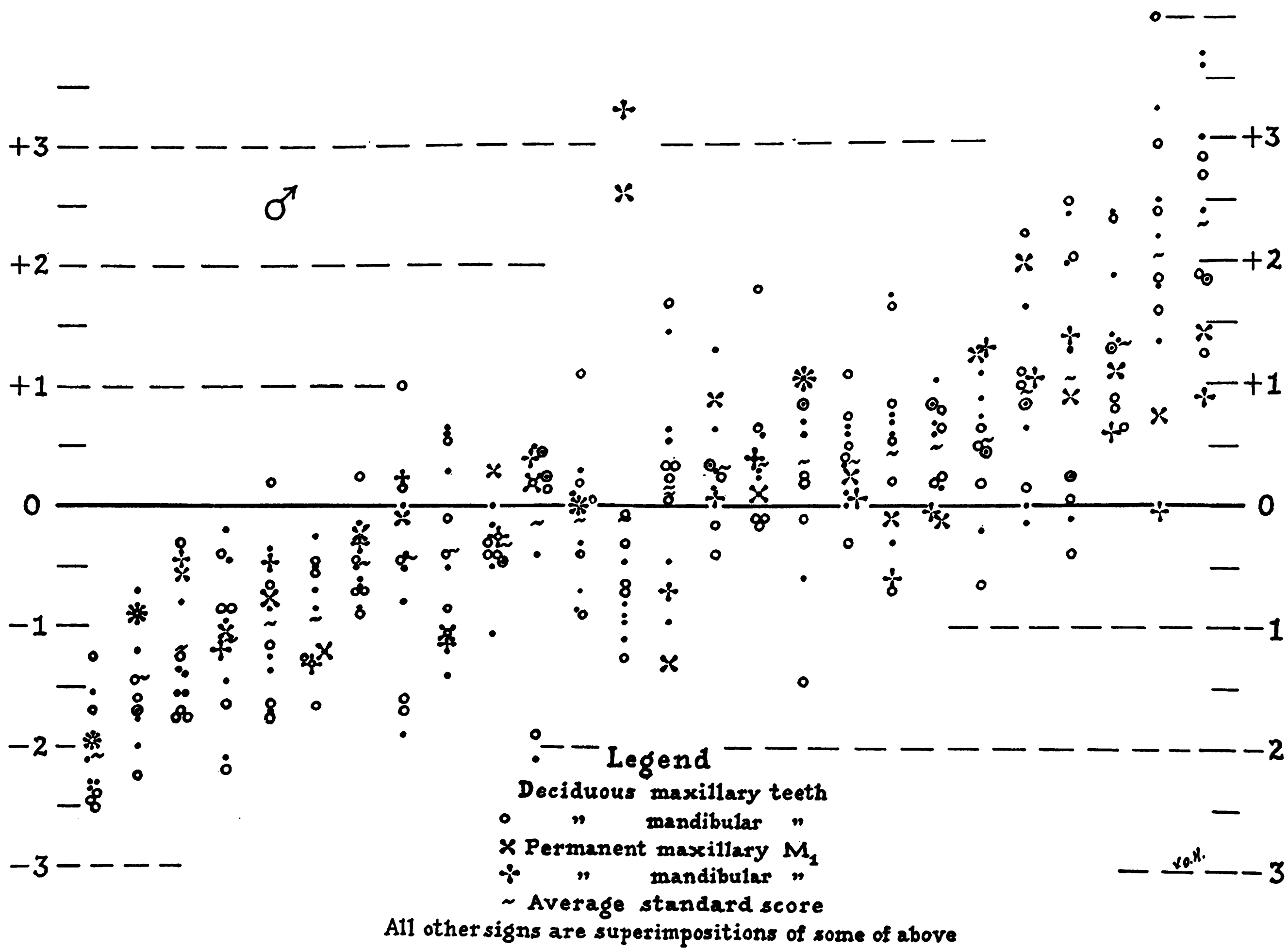

Fig. 5. Scatter diagram showing emergence ages of all deciduous teeth and of the permanent first molars in 26 normal male macaques. The data were converted into standard scores prior to plotting; the sequence of vertical rows of 12 signs is based on rank order of average values (~) for individual animals.

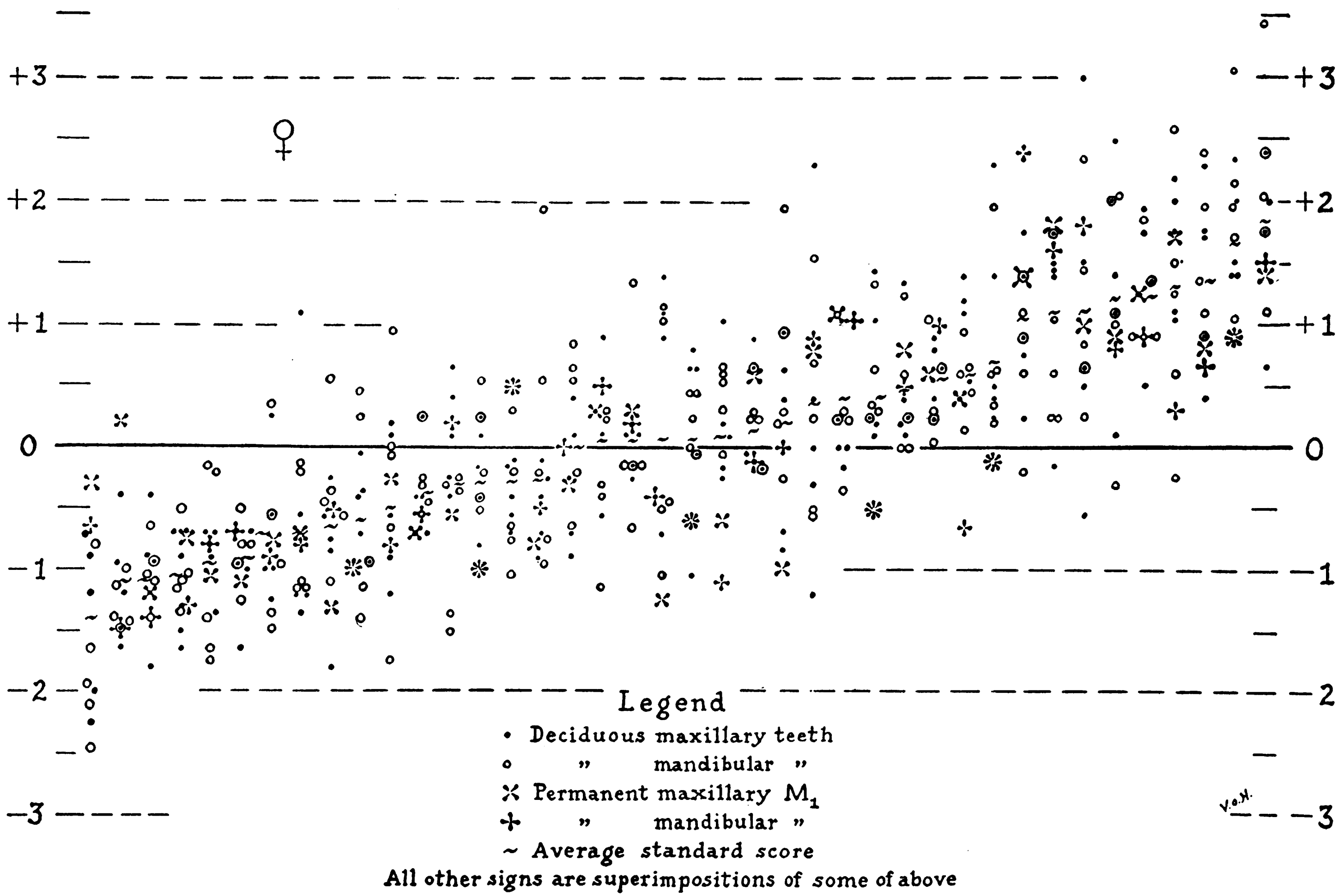

FIG. 6. Scatter diagram showing emergence ages of all deciduous teeth and of the permanent first molars in 40 normal female macaques. Plotting is in terms of standard score units above or below the zero line; sequence of vertical rows is determined by rank order of average values (~).

tial characteristics regardless of how rapidly or slowly the process of odontiasis takes place. If the first few deciduous teeth are early in their emergence, then the teeth that follow are also more or less early, and vice versa. A study of the contents of Tables 1 and 2 will confirm this generalization.

The permanent first molars do not behave in a manner that would indicate any perceptible degree of nondependence upon the same growth mechanism which brought about the emergence of the entire deciduous dentition that predates their much later arrival. (However, just as a reminder of Nature's ability occasionally to break a firm-appearing rule, the 13th item in Figure 5 shows exceedingly late eruption of the permanent teeth in a male whose entire deciduous set emerged relatively early.) The position of the permanent first molar symbols in Figures 5 and 6 varies as much and within the same limits as does the position of any of the other plotted signs, suggesting that in the vast majority of instances these teeth are part and parcel of the same picture, with distinctly limited autonomy.

The scatter diagrams also fail to reveal any clear segregation of the symbols which differentiate the maxillary and mandibular teeth. This is further evidence of the nonlocal character of the physiological mechanism which controls the growth and development of the dental organ complex.

It must be recognized, however, that Figures 5 and 6 do not completely solve the question of intercorrelations between various teeth in the same animal. Experimental studies might reveal that the separate units of a dentition have little or no *direct* influence on each other's development. The biometrician, moreover, will bear in mind the fact that although two variables are uncorrelated, it is possible to obtain a marked correlation if the data consist of mixed groups in which the means are correlated.

No one class of teeth was found definitely more prone to extreme deviations than another. The maxillary and mandibular first incisors and the mandibular second incisors of the deciduous set were, perhaps, slightly more erratic than the other teeth, in both sexes, while the permanent maxillary first molars displayed the greatest relative stability in each sex.

One additional fact may be noted after a study of Figures 5 and 6: chronological variability increases, on an average, which each degree of delay in dental maturation. The number of superimposed or closely clustered signs is more at the beginning of each series than at the end. This finding is in harmony with the previously discovered positive skewness of the frequency distributions.

It is apparent that in attempts to ascertain the velocity pattern of dental emergence in an individual case one's success will be the better, the more one knows about the emergence times of *different* classes of teeth in the same mouth. Dependence on information on a single tooth (or tooth pair) could be misleading, since that one tooth may be the most nonrepresentative member of the entire dentition. The dispersal of signs in Figures 5 and 6 is additional proof of the validity of this contention.

The findings described so far prompted the authors to examine the phenomenon of multiple emergence against the background of general over-all rates of odontiasis. It did not seem reasonable to dismiss completely the question of the order of eruption simply because it had not been convenient to initiate the study of dental interrelations by concentrating on this special feature first.

Among the deciduous teeth those most frequently exhibiting departures from the usual order of emergence are the canines and first molars, as is well known. The mean eruption ages of these teeth are close together and the ranges of variation quite similar, so that irregularity in the sequence of their development should cause no surprise.

Figure 7 shows, by the heavy step-like line, the average "Z" scores for 25 normal male monkeys. Eight of these animals had either simultaneous (difference < 0.01 yr.) or nearly simultaneous (difference $= 0.01$ yr.) emergence of the deciduous first molar and canine in one to four quadrants of the mouth, the time of their emergence being indicated by the level of the quadrant symbols measured against the left-hand scale.

Six out of the eight instances of some degree of multiple emergence are to be found in the first half of the series, which indicates that one may expect to find multiple emergence far more often among male macaques with accelerated dental maturation than among those with a slower rate of development.

Among males the canines usually precede the first molars in eruption, the ratio being about 3.5 to 1. By assuming slight delay of canine development and equally slight hastening of that of the adjoining first molar, the simultaneous emergence of these teeth is easily explained in monkeys with a relatively rapid over-all rate of odontiasis.

Figure 8 is a visualization of similar factual material on 39 females. The mean ages of emergence of the deciduous canines and first molars of the female are much closer together than those of the male. More frequent instances of multiple emergence of these teeth should therefore be expected in the female of the species, and Figure 8 shows that this is, indeed, true; only the end section of the series—the last 6 out of 39—is free of symbols indicating multiple emergence. Among females the first molars usually precede the canines in a ratio of about two to one.

Reversals of the usual order of emergence of the deciduous canines and first molars present an interesting distribution among the males. The first molars do not pierce the gingiva ahead of the canines among any of the

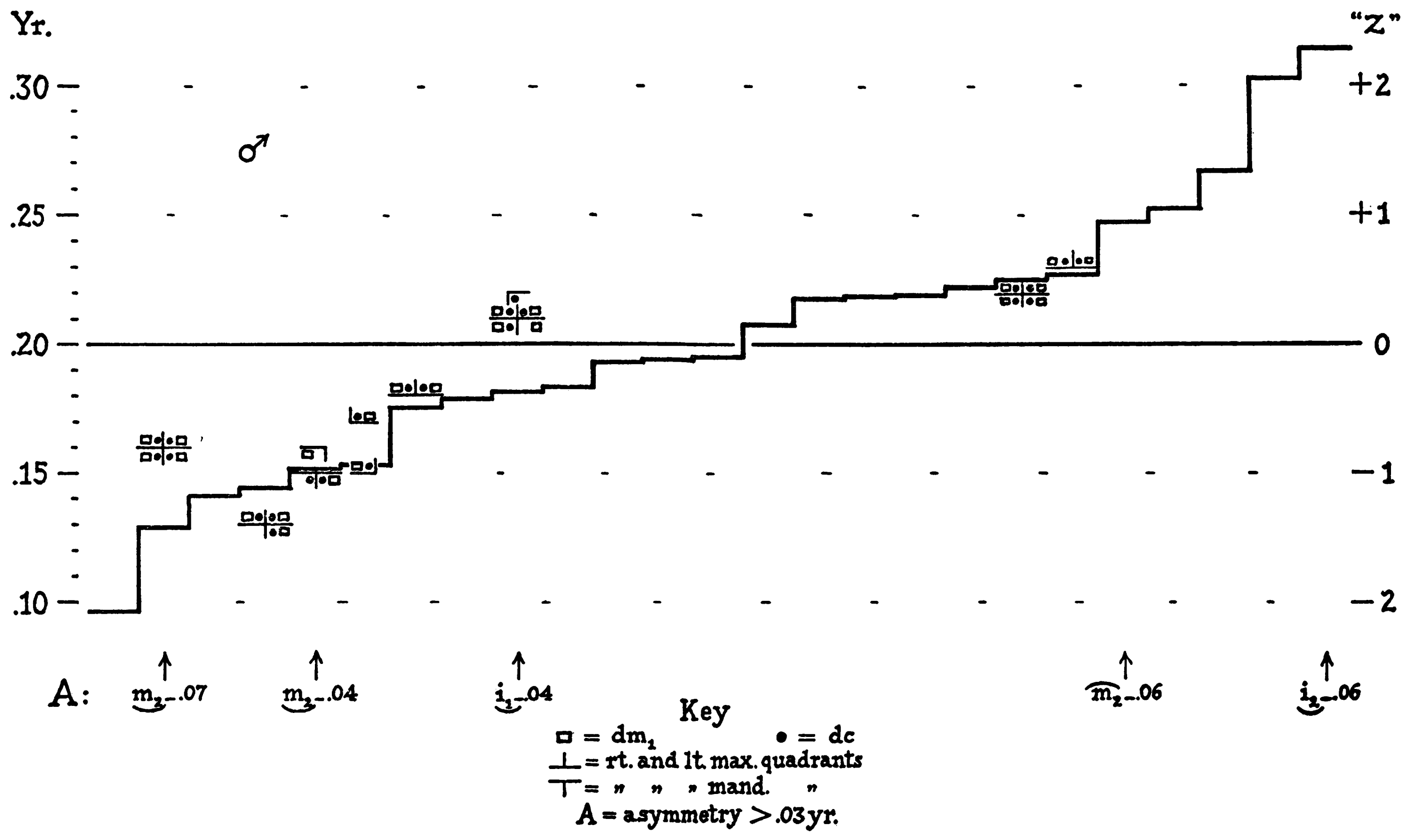

FIG. 7. Distribution of instances of multiple emergence of deciduous canines and first molars in 25 normal male macaques.

Average "Z" scores are shown by the heavy step-like line. Instances of marked chronological asymmetry (> 0.03 yr.) in the emergence of various deciduous teeth are noted along the bottom line. (See p. 557).

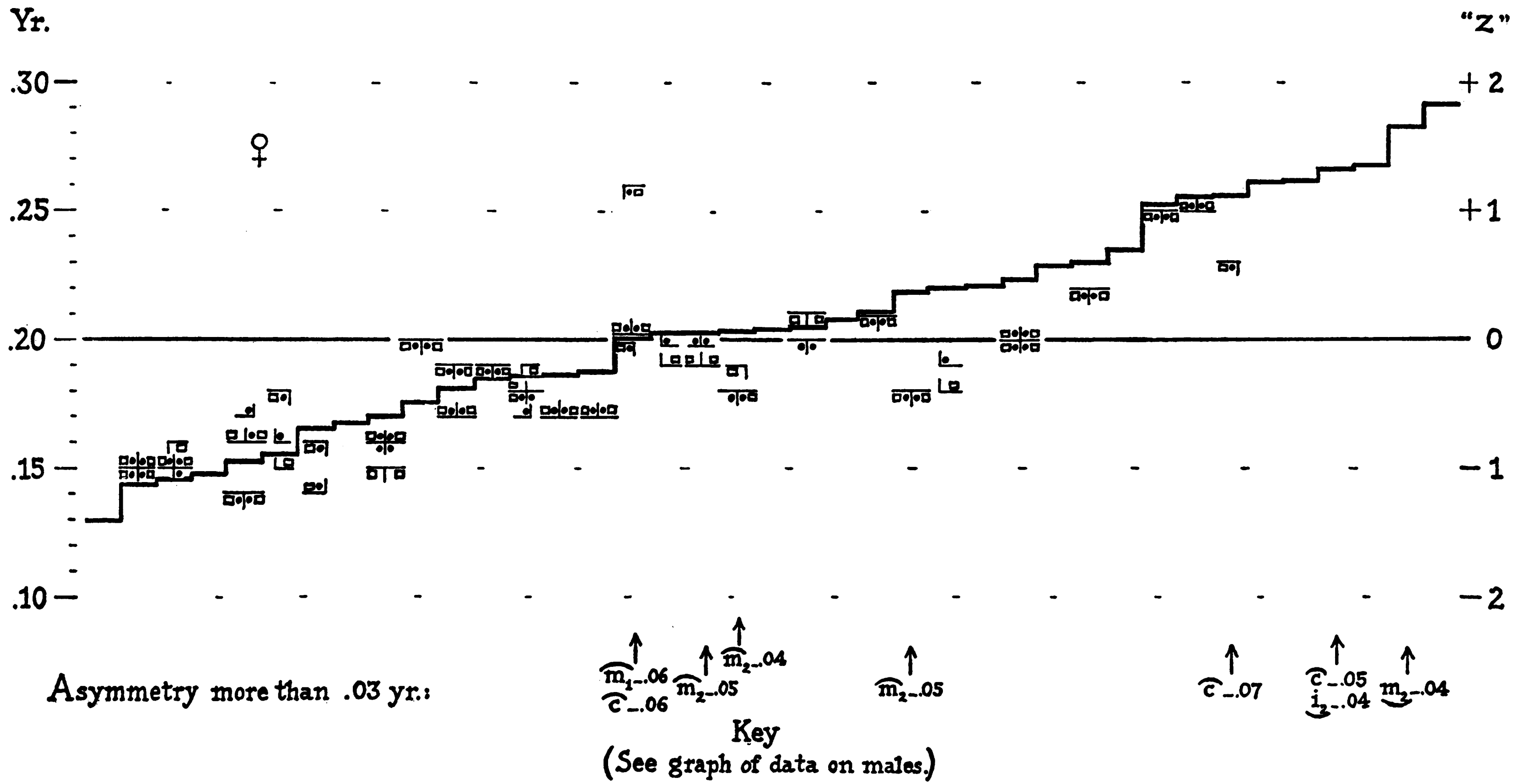

Fig. 8. Distribution of instances of multiple emergence of deciduous canines and first molars in 39 normal female macaques. For explanation of details see text under Figure 7.

animals at the beginning of the series; only among those with slower rates of dental development does this reversal occasionally take place. Its occurrence is suggestive of a tendency of some of the more slowly maturing males to adopt the normal female pattern of first molar precedence.

At the bottom of Figures 7 and 8 are some notes on the occurrence of more marked asymmetries in the emergence of deciduous teeth. It will be noted that, apart from asymmetries involving the deciduous second molar, those involving other units of the primary dentition seem to occur least often among the animals with speediest dental development.

D. *Physical-dental interrelations.* On most of the animals whose dental records had furnished the subject matter of the present study there were other growth data that had been collected in a uniform, systematic manner. The availability of these additional data provided the writers with an opportunity to test the correctness of some of the conclusions already reached and, coincidentally, to demonstrate the astonishing scope of the relationships that exist between the teeth and physique of a young primate.

(a) Growth rates and ageing. The tieup between general metabolic activity and the growth and development of the masticatory organs has been revealed already by the analyses showing several distinct contrasts between the dental data on male and female monkeys. Perhaps the most striking of these is the sex difference in the variability of emergence of the permanent first molars, which suggests the domination of local dental phenomena by the general physiological activities of the entire body.

Another piece of evidence of the interrelations just mentioned is the increase in the variability of tooth emergence which is seen when the latter is related to ageing. As the metabolic processes of the body gradually slow down, the mechanism that initiates the process of tooth emergence also slows down, with the result that positive standard score deviations for various teeth become greater and greater (or the negative deviations smaller and smaller), and the chances for multiple emergence fewer and fewer.

(b) Menarche. The age at menarche had been recorded for 39 of the 42 normal female macaques included in the present study. This made it possible to study the relationship, if any, between an obvious physical sign of sexual maturation and the over-all rate of tooth emergence, and to determine whether the latter phenomenon is directly correlated with the functioning of the sex organs. It could not be assumed, on the basis of statistical sex differences in the eruption of teeth, that the teeth were in any extended sense of the term secondary sex characteristics in the "rhesus" monkey, for it was equally easy to assume that their development simply reflected the development of the body generally, quite apart from the activity of the ovaries. Or, to phrase the above thought differently, it was possible that dental maturation was not correlated with sexual maturation, but merely *associated* with it, as a rule, and only *indirectly* influenced by the hormones that have something to do with sex.

The beginning of menstrual function in the macaque shows no chronological constancy in different females. The range of variation is quite wide, extending from 1.43 to 2.67 years, with an average at 2.00 years. For this reason, although a cursory examination of the data revealed no association, positive or negative, between rate of odontiasis and age at menarche, the coefficient of correlation for the two variables was computed. The exceedingly low value of r that was obtained—+0.02—certainly strengthens the argument that the two variables are only casually interrelated, as suggested by Shuttleworth.[25]

(c) Length of gestation. Long before either physicians or dentists had paid any serious attention to the connection between the time of emergence of the first deciduous teeth and the length of the gestation period, cattle growers had noted that the two events were not altogether isolated from each other. Youatt, in his remarkable treatise on the management of cattle, published in 1834, wrote as follows: "The mouth of the newly-born calf presents an uncertain appearance, depending on the mother having exceeded or fallen short of the average period of utero-gestation," but without attempting to document this assertion.[34] He is, perhaps, the first observer to make a written record of the above mentioned relationship, although the possibility of some other author predating him has not been ruled out.

Even much more recent works that deal with factors controlling the time of eruption of the primary teeth generally do not include any reference to the length of the prenatal period of life. The one exception to the above rule is the teeth of premature children; a few authors, like Ledé,[17] Neu,[19] and Campini and Urquijo[8] have recorded evidence of their retarded emergence, if measured in terms of postnatal age.

Hurme and van Wagenen[18] probably have done the most so far to substantiate Youatt's observation. Although the proof offered by them, based on an analysis of data on the monkey, is fairly conclusive, it appears possible to improve on it further by re-examining the problem in another manner, utilizing the standard score technique employed earlier in other analyses mentioned in this report.

The length of fetal life was known for 23 male macaques out of the 27 included in the present study, and for 31 females out of 42. After arranging the average standard score values computed for the 12 pairs of emerging teeth in each animal in rank order—as had been done previously in prepar-

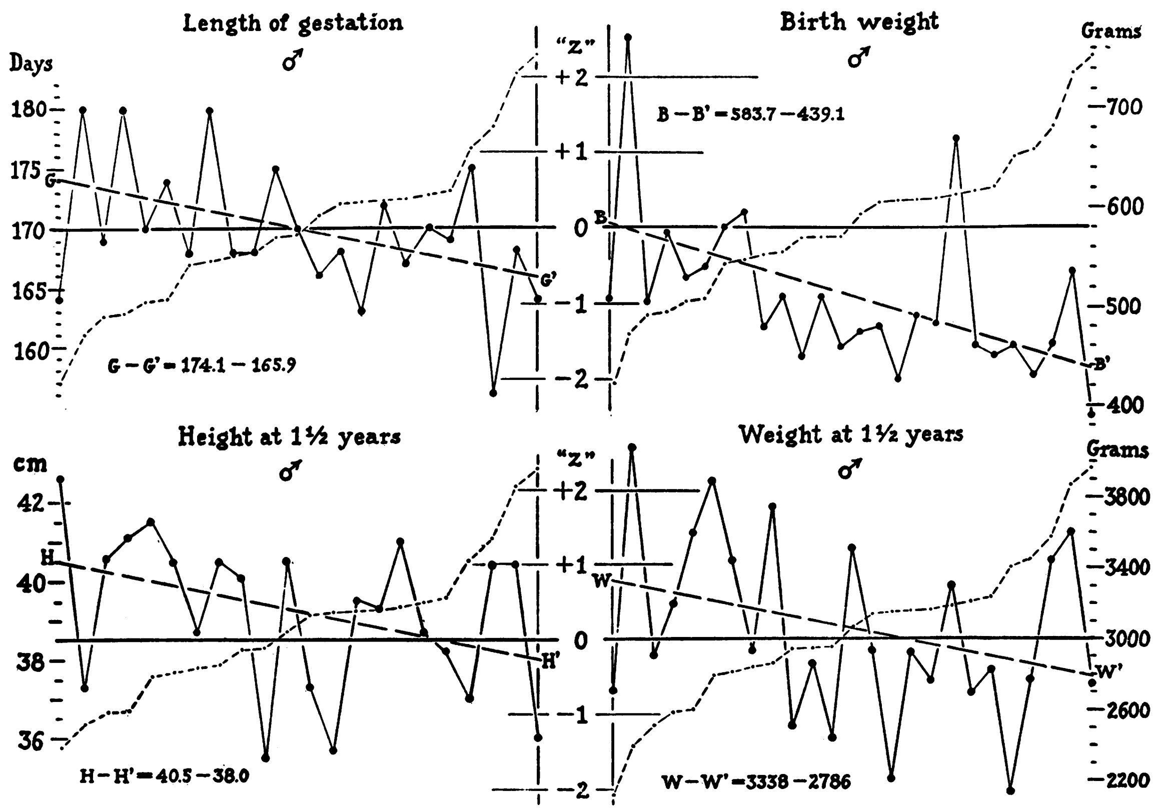

FIG. 9. Relationship between rate of odontiasis, length of gestation, and three measurements of physical size in 22 to 26 normal male macaques.
For explanation of details, see text on p. 561.

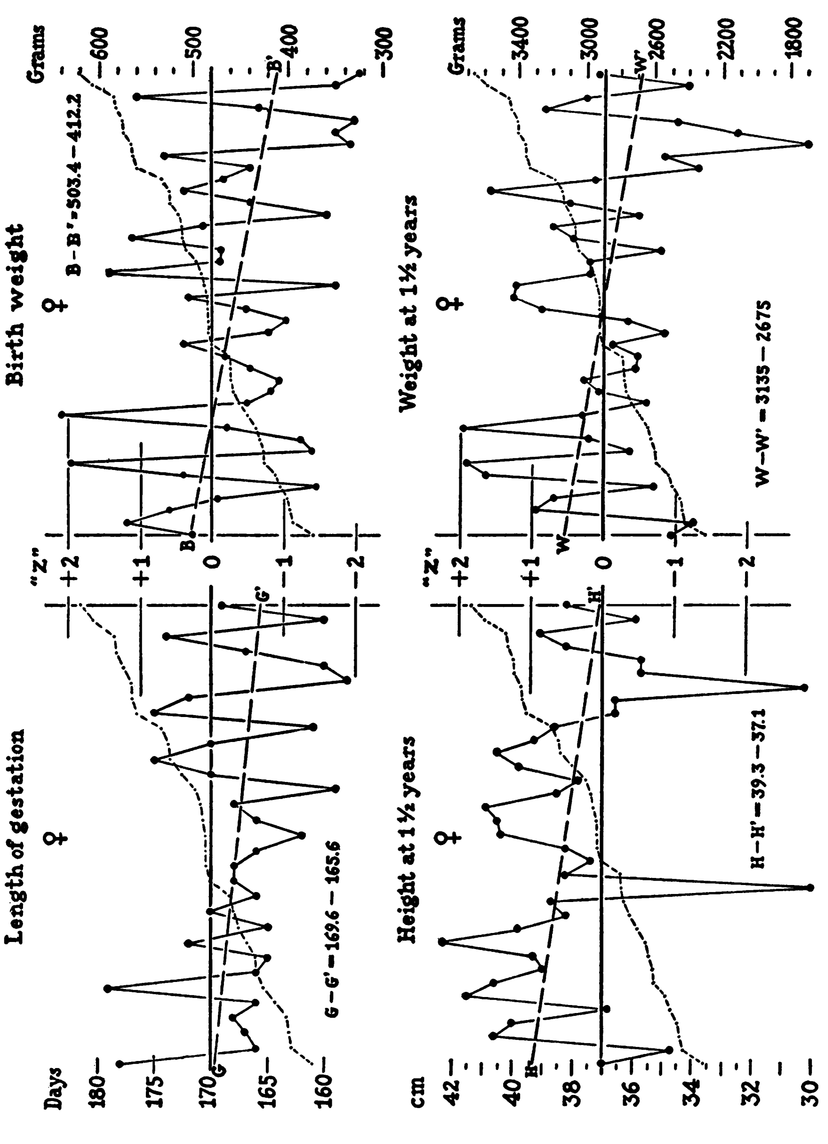

FIG. 10. Relationship between rate of odontiasis, length of gestation, and three measurements of physical size in 31 to 40 normal female macaques.

For explanation of details, see text on p. 561.

ing Figures 5 and 6—corresponding gestation ages were placed in the sequence determined by the average standard scores. The trends shown by the gestation ages—after arrangement in the order just mentioned—were then analyzed statistically.

Again, in order to conserve space and to present the findings in a readily assimilated form, the data were incorporated in a graph, this being done with sufficient care to permit extraction of original numerical values from the graphs if desired later by a reader. The material pertaining to the analysis of dental data versus gestation data is presented in the left upper quadrants of Figures 9 and 10. In each of these figures the fine broken line ascending from left to right represents the average standard score (or "Z") values, the heavy black dots (connected by solid lines), the length of gestation periods, and the heavy broken line slanting down from left to right, the mathematical summarization of the trend indicated by the heavy black dots, considered collectively. The exact numerical values corresponding to the ends (G — G′) of this trend—or regression—line are also given in each diagram.

An examination of the graphs leads one to conclude that as the length of the gestation period decreases, on an average, the speed of odontiasis decreases.

In spite of much individual variation, the trends shown in Figures 9 and 10 are clear, the data on males displaying the relationship most convincingly. In this connection one may observe that the repeatedly encountered greater variability of the male macaque is revealed also by the statistics on the length of gestation when these are computed by utilizing more extensive raw data.*

A truly adequate interpretation of the interesting relationship between the length of gestation and the over-all rate of odontiasis is beyond the ability of the writers. What can be said at this point is that when the intrauterine sojourn of a macaque exceeds the average of 168.8 days, it is more likely to arrive into the outer world with a greater potential of growth vigor than is the animal whose prenatal development falls short of the average. Earlier and speedier odontiasis is partial proof of the plausibility of this proposition, which, in itself, is neither new nor revolutionary. It can be said, however, that the aforementioned proposition has never before been put to a test by subjecting dental growth data to a rigorous analysis.

* The means and standard deviations, estimated from data on 42 normal males and 46 normal females, are 168.6 ± 5.6 and 169.0 ± 5.2 days, respectively. Data on four twins were not included in these two "normal" groups. The figures obtained differ slightly from those published earlier.[18]

To rule out the slightest possibility that the delays or prematurities of permanent first molar emergence discussed in this paper would be cancelled off if the ages under consideration were expressed in terms of postconception intervals of time, the data on this class of teeth were placed under scrutiny once more. It was known that the ranges of variability for the permanent first molars were of much greater magnitude than the ranges of variability for the gestation ages of animals born "at term," even if it is assumed that a few born a little before or a little past term are included. Therefore, if the mathematical summation of the ages of emergence of the permanent first molars should yield regression lines that are no steeper than the lines (G — G′) summarizing the data on periods of gestation (in Figs. 9 and 10), it would be self-evident that one should not infer that a decrease in the length of gestation is generally followed by a *real* delay in the time of emergence of the first permanent tooth. Furthermore, should the lines obtained slope down from left to right, like the lines G — G′ in Figures 9 and 10, it would be obvious that the original inference is diametrically opposite to the truth and wholly untenable.

The data on the permanent maxillary first molars of 23 male macaques with gestation periods of known length were selected as a suitable test sample for the analysis mentioned in the preceding paragraph.

The summation of data on their emergence yields a regression line *rising* from 471.6 days (1.292 yrs.) to 589.1 days (1.614 yrs.). The difference of 117.5 days is indisputably greater than that obtained for the ends of the regression line (G — G′) which summarizes the data on the periods of gestation in the same group of animals. (See Figure 9). In the latter case the difference is only 8.2 days, which is much too small to allow an explanation on the basis of chronological variations in length of gestation.

An inspection of the placement of permanent maxillary first molar symbols (X) in Figure 5 is perhaps even more convincing, and the test can be applied with equal success to the data on mandibular first molars, in the same figure, or to the material on female monkeys, shown in Figure 6.

(d) Birth weight and physical size later. One would expect an infant with a longer-than-average prenatal existence to be heavier than average at birth, as a rule. In view of this it is not surprising to find a positive correlation between birth weight and speed of odontiasis in the material at the disposal of the authors.

The heavier the baby, the more likely is it to have early and rapid emergence of its teeth, as is evident from an examination of Figures 9 and 10, wherein the data are shown in the upper right hand quadrants. Although this generalization applies to both males and females, it is particularly true of the males. The female curve of birth weights is characterized by much more kurtosis than the curve for males.

What is rather surprising is the persistence of this association at the age of one and a half years, long after the emergence of all deciduous teeth. Taking the males and females as a group, the heavier animals have earlier eruption of their teeth than the lighter ones. The relationship extends even to the height of the monkeys at 1½ years, although it is not quite as clear-cut as in comparing the rate of dental maturation with weight. The data on which the above inferences were based are shown in the two lower graphs in Figures 9 and 10.

A review of literature discloses the existence of very little confirmatory evidence for the findings just discussed. Baldwin and Smith[1] found the later-born children heavier and taller than those born earlier; they also found "a strong tendency for the children to hold until maturity the rank in height that they held at birth." (Presumably the same could be said about rank in weight.) As regards birth weight and teething, the only report that has come to the attention of the writers is that by Yamada,[88] whose data fully substantiate the findings obtained as a result of the present investigation.

SUMMARY

This paper describes analyses of certain long-term records on the growth and development of 69 normal macaques born and reared in captivity. Particular attention has been paid to permanent first molar emergence and to other growth changes observable in the monkey prior to 2 years of age. Literature dealing with interrelationships of general physical and special dental development has been reviewed.

The findings and conclusions can be summarized under five main headings:

1. *Variability.* The emergence of teeth is characterized by considerable variability, which increases with age, if measured in conventional units of time. The hypothetical extremes of permanent first molar emergence in the macaque are approximately 12 months apart for the teeth of males and 7 months apart for the teeth of females.

Variability does not always affect the two halves of a dentition equally, with the result that chronological asymmetry may appear in the eruption of a tooth and its antimere. Generally speaking, as variability increases with age, so do temporal asymmetries in the emergence of right and left teeth.

Postnatal variability in the ages of emergence is partially accounted for by variations in the length of gestation. The longer the period of intra-

uterine development, the sooner after birth do the teeth appear, as a rule. Nevertheless, the ranges of variation in the emergence of permanent first molars are so wide as to make it obvious that the inequalities must be explained in terms of physiological differences rather than in terms of discrepancies in the chronology of histodifferentiation.

The findings indicate a close association between developmental rates and tendencies to deviations from the biometrician's average. Rapid rates of odontiasis are characterized by lesser degrees of chronological variability than slow rates of dental maturation.

2. *Relative constancy of emergence patterns.* Variability in the times of emergence of individual teeth does not result in much variation in the transitional anatomical patterns of developing dentitions. Although the eruption of one tooth is interlinked with that of another, this linkage is not so rigid as to make observations on the sequence of emergence of various teeth the best method for demonstrating the high degrees of constancy in the developmental patterns of different animals.

The most common order of emergence is given by the mean values obtained for each class of teeth. Only teeth with similar mean values produce frequent deviations from the prevailing pattern. The first molars initiate odontiasis of the permanent series, the mandibular molars usually preceding the maxillary ones.

Observations on variations in the pattern of emergence may furnish evidence of the general rate of development and of sexual maturation in the monkey. This idea is substantiated by the finding that multiple emergence of certain deciduous teeth seldom takes place in a slowly maturing animal, and that a high proportion of males with a slow rate of dental development reveal a transitory anatomical pattern which is generally characteristic of females.

3. *Relative constancy of developmental rates.* The rate of operation of the physiological mechanism that controls the initiation of the process of emergence of various teeth appears to be remarkably constant in the monkey during its first two years of life.

The rôle of velocities of growth and development is all-important in the establishment of whatever dental interrelations can be observed. If these velocities fluctuated very much from one age period to another, the biometrist would not find much statistical orderliness in the processes of tooth eruption.

The present analyses suggest that the rates of odontiasis are causally related, in some manner, either to the length of gestation or to something else which determines the duration of the latter. In either case it is apparent that the basic "rhythm" of tooth emergence is determined prior to birth, and that it is less alterable than the behavior of an individual dental organ. Infants with long gestation periods average earlier and speedier development of their dentition than those with a relatively short prenatal span of existence.

The high degree of constancy of the basic rate of dental development in an individual is revealed most clearly by the finding that it is not altered much by the relatively long outwardly inactive interval of time which separates the two main periods of odontiasis. The time of emergence of the permanent first molars can be predicted with moderate success if the times of emergence of the deciduous teeth are known.

4. *Physiological age.* All findings on physical-dental intercorrelations emphasize the idea that the growth and development of the dental organ complex is dependent on the growth and development of the entire body. It may be said, nevertheless, that although the above idea is not new, rather limited use has been made of teeth as indicators of physiological age, apart from their value as indicators of certain pathological disturbances.

The dentition certainly appears to offer an investigator most valuable clues for appraising the over-all rate of maturation of an individual. This is demonstrated most strikingly by the different degrees of variability in the emergence of the permanent first molars; the earlier maturing female exhibiting markedly less variability than the later maturing, less predictable, male monkey.

5. *Practical implications.* Eruption of teeth serves as an excellent indicator of both physiological and chronological age. It is regrettable that to make use of this indicator requires the keeping of detailed long-term records on a large number of separate dental units.

The results of the present investigation make it appear possible to draw some reasonably reliable conclusions from observations on a limited number of teeth, if suitable statistical standards of reference are available. The authors believe that they have furnished such standards for the normal *Macaca mulatta.* For the sake of convenience in any biological appraisal males and females should be treated as if they represented two different species.

It seems safe to hypothesize that animals which mature at different rates are unequally susceptible to similar environmental stimuli or agents. Attention to rates of dental maturation should enable the experimental biologist to design more critical laboratory studies. The odontologist is in a strategic position for supplying information that is necessary for formulating a theoretical basis for the differentiation of phenotypes and genotypes.

The meaning of minor local variations—affecting only one or a few teeth—can be understood better if the few static, genetically favored anatomical patterns for the species are known. Slight environmentally induced disturbances of growth processes in a semi-autonomous part such as a tooth probably can, under certain circumstances, lead to profound modifications of the anatomical configuration of the dentition and even result in permanently abnormal relationships that are not necessarily of genetic origin.

ACKNOWLEDGMENTS

The location and translation of the Japanese references presented a number of difficulties. That they were solved successfully is due to the help received from several colleagues, including Dr. S. Takahashi of the Orthodontic Department of Tokyo Medical and Dental University, Dr. M. Horiuchi, Clinical Fellow at the Forsyth Dental Infirmary for Children, and Dr. S. Ochiai, Intern during 1954-55 at the latter institution. Miss Dorothy J. Butzko, of the Department of Obstetrics and Gynecology, Yale University School of Medicine, rendered invaluable secretarial assistance many times in the course of the investigation. The contributions of these persons, and of several others not specifically named here, are gratefully acknowledged by the authors.

The speedy completion of the study is largely due to the wholehearted administrative support and encouragement furnished by Dr. H. M. Marjerison, the late Director of the Forsyth Dental Infirmary, to whom the authors are indebted for making this co-operative project possible.

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