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THE FACTOR OF TIMING IN THE EMERGENCE OF DISTINCTIVELY HUMAN CHARACTERS

by

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(With six text figures)

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INTRODUCTION

Any assessment of Darwin's *Origin of Species* must take into account evidence from the whole world of biology, and that will necessarily come mainly from non-human sources. Nevertheless, we are all human and at some stage inevitably comes the query: " how does this affect me? Darwin's (1859) modest hint that " Light will be shed upon the origin of man and his history " set the pattern from the outset. However detached we feel ourselves to be the personal implications of evolutionary theory inevitably inject an anthropocentric bias into our thinging, and that is my excuse for talking about man tonight.

Darwin's supporters followed up his hint in the then fashionable direction of seeking forms intermediate between man and the other primates. Every ancient skull was closely scrutinized for such features as smaller brain, bigger jaws, large brow ridges, retreating forehead—anything that might link it a little closer to the ape. The greater the antiquity the better, of course; but any modern-looking human skull in an ancient stratum was almost automatically rejected as a recent intrusion. Those people knew what to look for, and they found it.

Not all were indifferent to objective appraisement of the evidence, however. So long ago as 1863 T. H. Huxley (Huxley, 1894) pointed out that the Neanderthal skull—the then prize " missing link "—showed no features that could not be matched from modern skulls, citing the Australian Aborigine among others. His warning was either ignored or it was misrepresented as a claim that the Aborigine was a surviving representative of Neanderthal Man. In any case, subsequent discoveries of *Pithecanthropus, Sinanthropus et omnia sic alia* seemed to dispose effectively of such academic quibbles.

Thus a nicely graded series from *Pithecanthropus* up to modern man was set up on purely morphological grounds, although some serious discrepancies existed (Abbie, 1952a). But when it came to arranging these forms in a convincing chronological order the system foundered badly. Most inconsiderately, the proven oldest skull is none of these—it is the Swanscombe skull, which cannot be distinguished from modern skulls (Le Gros Clark 1938). *Pithecanthropus* and *Sinanthropus* were no older than Swanscombe and might be much younger; Neanderthal Man appeared only yesterday. This inconvenience was countered by the claim that *Pithecanthropus* and Co. were simply specialized terminal offshoots of the common evolutionary line leading to man. That could be so but supporting evidence has yet to be produced: the onus of proof clearly falls upon whose views require this argument.

Attention has lately been attracted to the Miocene apes of East Africa and the *Australopithecinae* of South Africa as an evolutionary line possibly ancestral to man (Le Gros Clark and Leakey, 1951). The possibility cannot be denied (see, e.g., Broom, 1946; Dart, 1940; Le Gros Clark, 1950a) but while the *Australopithecine* teeth and posture seem to foreshadow the human the brain is still within the range of the ape (Robinson, 1960). And again, there are chronological difficulties.

On every present indication there has been only one kind of man who has always been much as we know him today in all his variety. And he seems to have appeared fairly suddenly between the beginning and middle of the Pleistocene—i.e., from 1,000,000 to 500,000 years ago (Le Gros Clark, 1950b).

If we provisionally dismiss from our minds all the traditional views on human evolution by gradual modification the problem can be approached from a completely different aspect. In particular, we shall be free to ask what known biological factors could have produced the human species fairly suddenly from some other animal: preferably, but not necessarily, from some other primate.

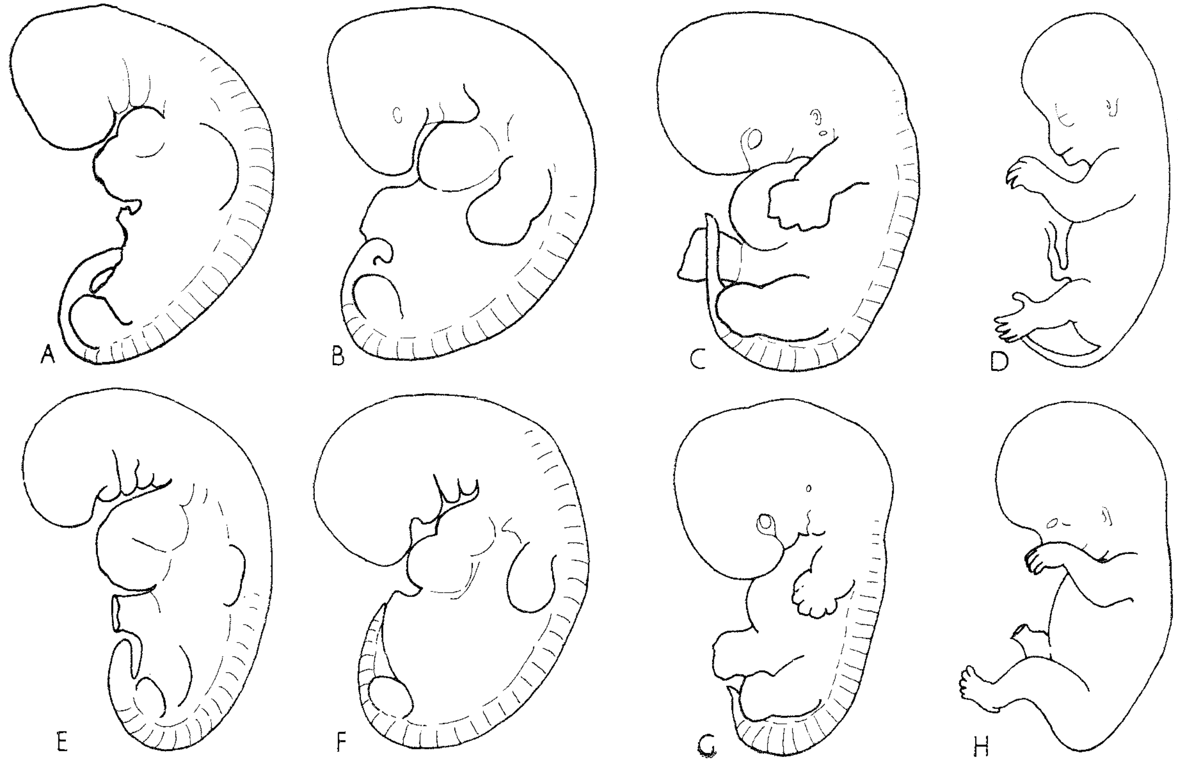

FIG. 1.—Comparative embryonic stages: A-D, macque; E-H, human (from Abbie, 1958a).

One such factor is the element of time. This has been largely neglected in most discussions on human evolution. Tonight I hope to show that timing in onset, speed, duration and cessation of development of many features has largely determined the physical bias that distinguishes man from what seem to be his nearest relations, and further, distinguishes some ethnic groups of men from others.

Before I start I should explain two terms I propose to use: one is "paedomorphism" (more or less synonymous are "foetalization" and "neoteny") which implies a tendency to retain embryonic, foetal or infantile standards of physical development; the other is "gerontomorphism" which implies a rushing on to physical maturity. In paedomorphism development and differentiation are retarded, in gerontomorphism they are accelerated (see Bolk, 1926; de Beer, 1940; Abbie, 1952a, 1958a; Hardy, 1954; and others).

TIMING

The Body as a Whole

In common with other animals (see Child, 1915) man shows a cephalo-caudal gradient of differentiation. Early evidence of this is the large head, tapering trunk and initial absence of limbs in the embryo (Fig. 1). Then the trunk differentiates and in succession the upper and lower limbs appear, enlarge and gradually assume their proper proportions. Thus as each region approaches developmental satisfaction the peak of the gradient gradually shifts distally in both trunk and the limbs. To describe this distal shift I have borrowed the botanical term "acropetalism" (Abbie, 1958a).

At the time of birth the human head occupies about one quarter of the total body length, the trunk about half and the inferior extremities approximately the remaining quarter (Fig. 2A). By the sixth year the head has dropped to only one-sixth of the stature and in the adult it is just over one-eighth. Growth in the trunk and superior extremities proceeds meanwhile at a moderate pace, but distal shift of the gradient peak causes the inferior extremities to extend with accelerating vigour so that they occupy more and more of the total stature and push the trunk progressively further from the ground (Fig. 2). In adult European males, in the outcome, the inferior extremities occupy nearly half the total stature, having doubled their relative proportions in some 20 years of differentiation.

These proportions may be affected in various ways. Whatever precipitates early maturation or retards growth—malnutrition, hypergonadism, hypothyroidism, achondroplasia, &c.—hampers extension of the lower limbs which end up shorter

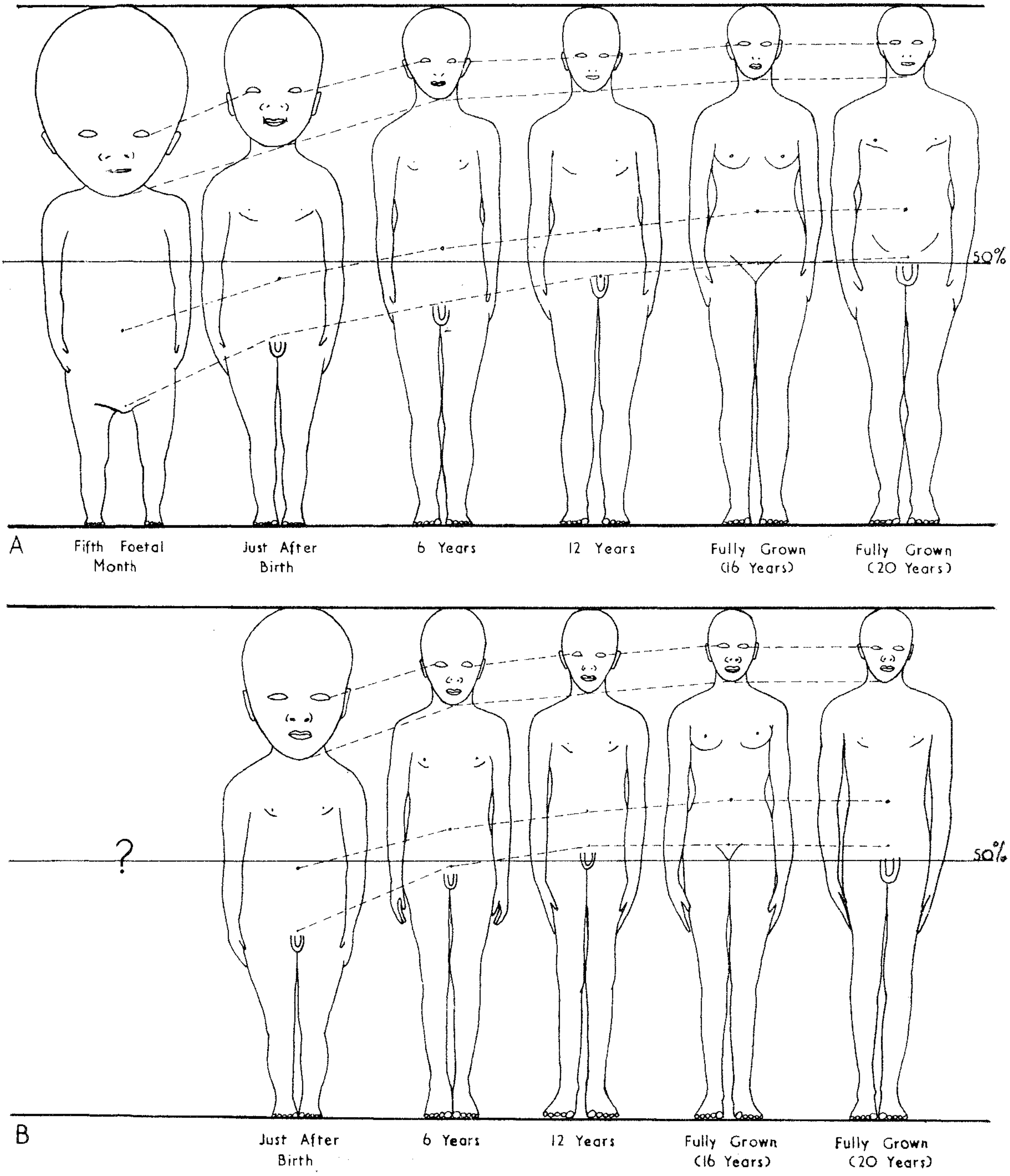

FIG. 2.—Progressive growth pattern in A. Europeans; B. Australian aborigines (from Abbie, 1958a).

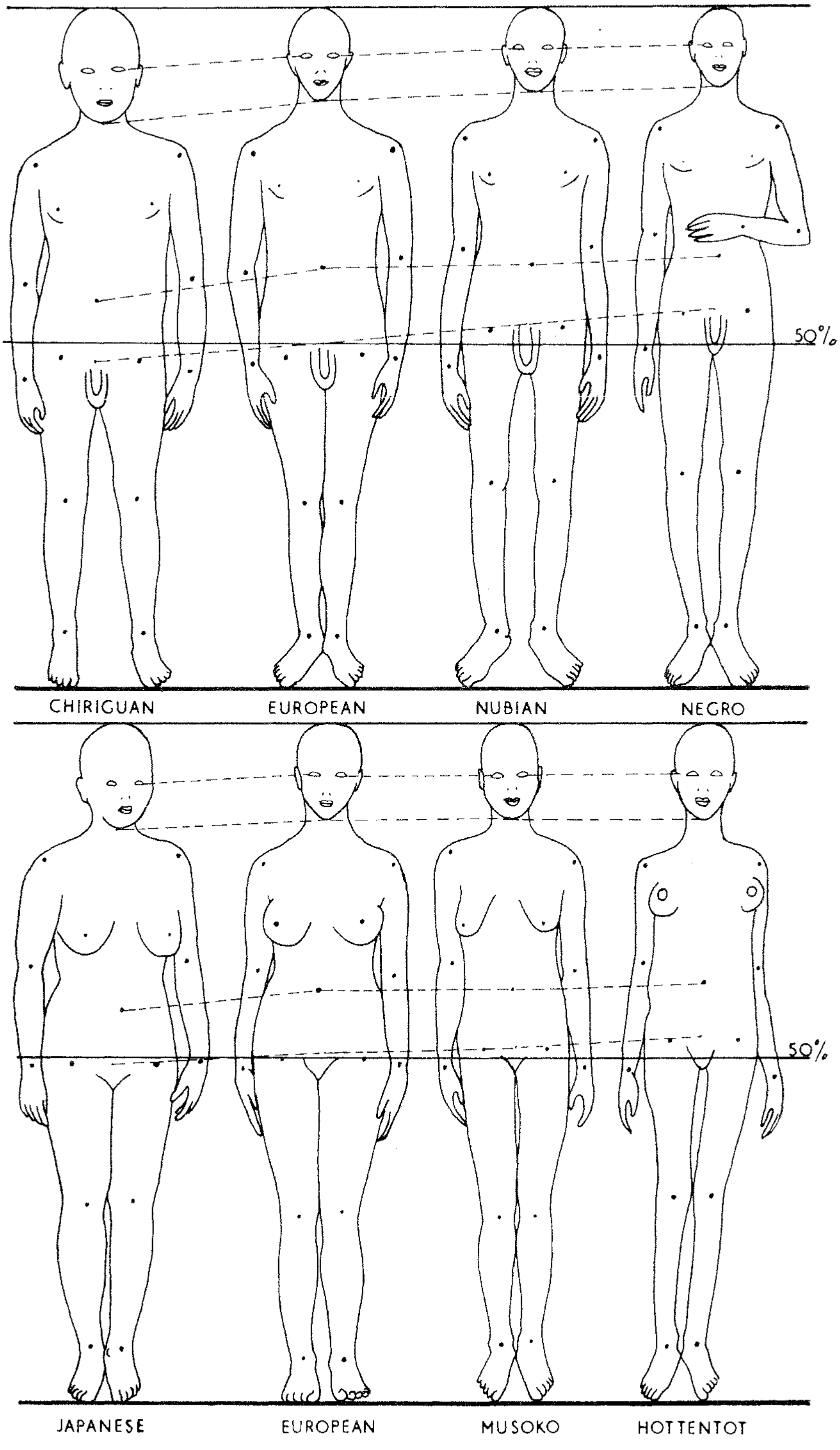

FIG. 3.—Comparison of proportions of various ethnic types drawn from photographs in Martin (1928).

than the norm, as in various kinds of dwarfs. And shorter legs are normal in adult females who stop growing some years earlier than males. It is also normal in some ethnic groups, e.g., mongoloids in China, Japan and the Americas, whose growing period does not seem to be curtailed, yet they retain such paedomorphism that their heads are relatively larger and their inferior extremities relatively shorter than in Europeans (Fig. 3). On the other hand, whatever delays maturation or accelerates growth—hypogonadism (eunuchoidism), hyperpituitarism—favours extension of the inferior extremities which appear disproportionately long. This is found normally in some ethnic groups, notably in Africa (Fig. 3). Keith (1919) has attributed these ethnic differences in proportion to a sort of ethnic hormonal distinction but his views have not received any real support.

One of the longer-legged peoples is the Australian Aborigine (Fig. 4). Up to about the fifth year his physical proportions differ little from those of Europeans then, quite suddenly, the inferior extremities make a spurt that gives the Aboriginal child of six the proportions of a European child of twelve (Abbie, 1957, 1958a). Thereafter the Aborigine stays that much ahead of the European until growth ceases (Fig. 2B). The reason for this sudden spurt is unknown but there is no doubt that the timing of its onset six years earlier than in Europeans is largely responsible for the final difference in proportions that distinguish the Aborigine from the European.

Intra-human ethnic differences in physical proportions can, therefore, fairly be attributed to differences in the timing accorded to the development of various parts of the body. This is more decidedly the case with intra-primate physical differences (Fig. 5). In the great apes differentiation of the body as a whole is considerably more advanced than in humans. Within the Pongid pattern the trunk and superior extremities show a marked relative acceleration in development, i.e., gerontomorphism; the inferior extremities, on the other hand, are relatively retarded, they are paedomorphic in comparison. It is as though the growth gradient is not given enough time to complete its job on the inferior extremities. And in this connexion it is of interest that maturation in the apes occupies only a little more than half the time required in man.

The Head

Comparison of the skulls of the major primates at the time of birth discloses that they are all closely similar (Fig. 6). In each case the calvaria is little more than a simple osteo-fibrous membrane for the brain (Abbie, 1947), and a rudimentary facial skeleton is suspended below. Subsequent differentiation proceeds at different rates in different animals. In most non-human primates the jaws enlarge rapidly forwards to occupy a predominant proportion of the total skull. The calvaria does not expand to the same extent so it develops various bony excrescences in the way of brow ridges, and sagittal and nuchal crests which provide additional muscle attachments although they are not necessarily associated with jaw size (Abbie, 1952a). In the human the jaws retain smaller proportions in comparison and the calvaria, being relatively large, has no need for the extra bony muscle attachments seen in the ape and remains pretty smooth. Of them all, the human skull has departed least from the foetal proportions it started out with—it is essentially undifferentiated, or paedomorphic. In most apes, on the other hand, differentiation of the skull as a whole has proceeded much further in half the time.

Apart from such obvious features human paedomorphism is shown in more subtle ways as in the thinner cranial bones, delayed closure of joints, tendency to retain a metopic suture, more forward siting of the foramen magnum, more open speno-maxillary fissure (Hone, 1952), increasing failure of the third molar teeth to erupt and so on. These features are accentuated where growth is arrested, as in dwarfs and in normal adult females.

However, while paedomophism predominates in the human skull it is not the only factor involved. Some features, such as the highly arched nose and prominent chin, must be considered more diffenentiated than in the apes and, therefore, relatively gerontomorphic. A case in point is the mastoid process—this is much better developed in man than in apes for, as Schultz (1957) points out, the human mastoid appears soon after birth and is practically maximal by adulthood while the gorilla mastoid does not begin to develop until after dental maturity and not till old age is it as large as in a young man. Timing has an important part in the development of all these features and, in some cases at least, it could be argued that the difference in timing towards gerontomorphism is adaptive (Abbie, 1958a).

Human cranial capacity and, therefore, brain size far exceeds that of any other primate. The gorilla, though it have three times the bulk of a big man, has a brain only half as large. The human brain is distinguished by both its great absolute size and its great relative weight in comparison with body weight (Abbie, 1958a). Again, timing helps to determine this human distinction. Schultz (1957) has shown that the cranial capacity of the human newborn is about 14 per cent of the body weight and this is much the same in the other major primates. In adult humans after twenty years the brain still accounts for 2.0 per cent of the body weight whereas in adult apes after only eleven years it has fallen to just 0.25 per cent—relatively, a bare tenth. This is another example of paedomorphism since, clearly, the human brain has departed less from the foetal proportion than has the ape: to one-seventh as against nearly one-seventieth.

Other Physical Characters

Table I shows a number of other features in which human distinctions depend upon retardation of development as compared with other primates. The period of gestation, the total growing period and expectation of life, onset and completion of ossification and dentition, development of pigment and hair are all progressively slowed down as we go from monkeys through apes to man. Indeed, a number of developmental features—pigmentation, hair growth, dentition—despite the more pro-

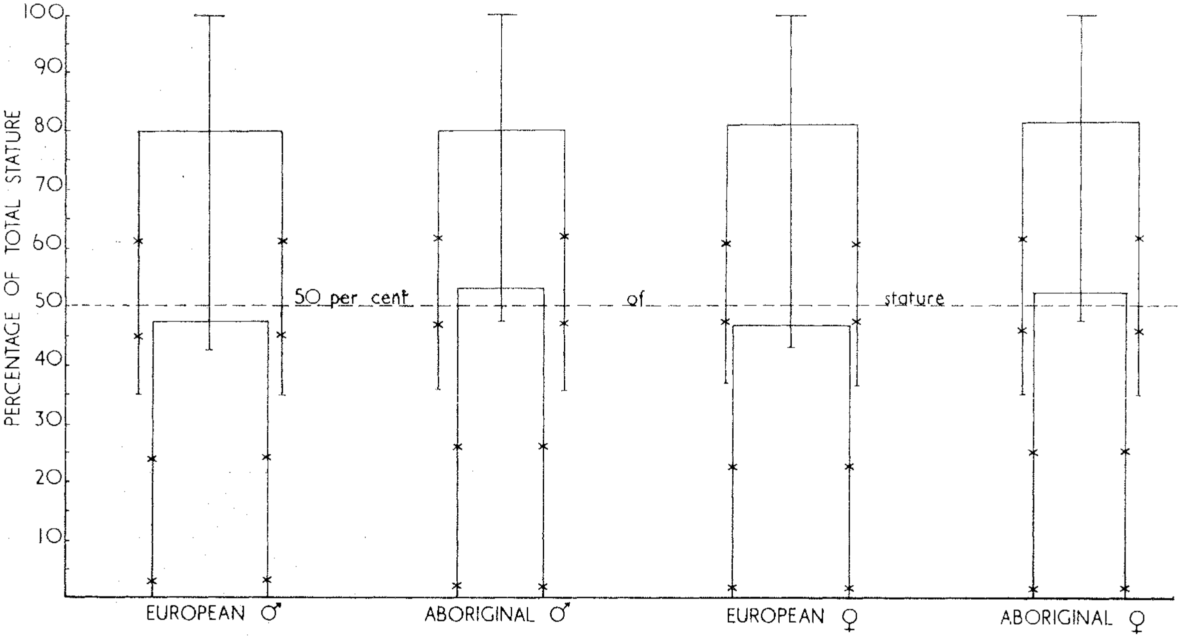

FIG. 4.—Comparison of proportions of adult male and female Europeans and Australian aborigines (redrawn from Abbie, 1957).

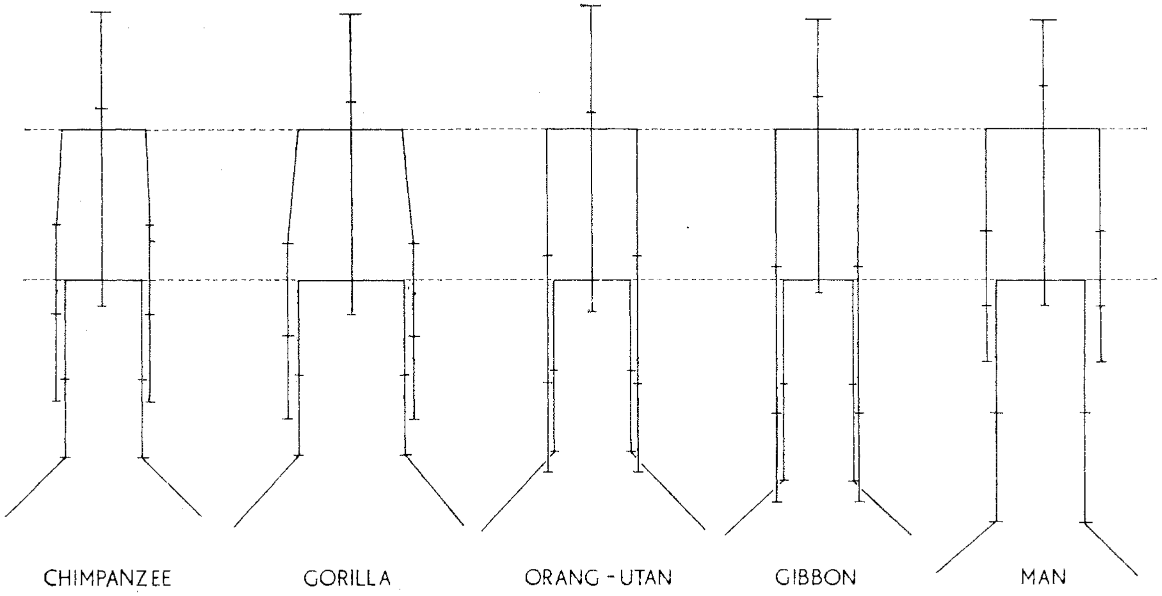

FIG. 5.—Comparison of proportions of man and other primates, taking trunk length as a common basis (redrawn and modified from Martin, 1928).

tracted growing period, may never reach completion at all in man. I must add that while pigmentation does become complete in some human groups this should (provisionally) be attributed to natural selection, not to alleged sub-human affinities—in many Aborigines completion of pigmentation is delayed until adolescence or later (Abbie and Adey, 1963.

TABLE 1

Primate	Gestation (Weeks)	Pigmentation	Hair Covering	Carpal Ossification Centres at Birth	First Dentition (Months)	Second Dentition (Years)	Growing Period (Years)	Life Span (Years)
Macaque	24	Completed early in gestation	Completed during gestation	All centres	0.6-5.9	1.6-6.8	7	25
Gibbon	30	Onset during gestation, completed after birth	Onset during gestation, completed after birth	2-3	1.2-?	?-8.5	9	33
Orangutan	39			2-3	4.0-13.0	3.5-9.8	11	30
Chimpanzee	34			2	2.7-12.3	2.0-10.2	11	35
Gorilla	37			?	3.0-13.0	3.0-10.5	11	35
Man	40	*Coloured,* Onset mainly after birth. *White,* Never	Never completed	0	6.0-24.0	6.0-20.0	20	70+

Data from Bolk, de Beer and Schultz (slightly modified).

The tail, so well developed in monkeys, is suppressed almost to extinction in man and the apes. This suppression is manifest in early foetal life (Fig. 1) and must be attributed to paedomorphism.

The longer inferior extremities in man are gerontomorphic as a whole but the feet show exceptions. In all non-human primates the great toe is widely separated from the others, like the thumb in the hand, and this is evident early in pre-natal life (Fig. 1). In man the great toe is not only closely apposed, its metatarsal is firmly attached to the other metatarsals by the deep transverse ligament of the sole (Wood Jones, 1944)—an attachment found in no other primate. Separation of the toes is determined by a series of radial splits around the periphery of the footplate (Fig. 1G). In non-human primates the split for the big toe extends deeply, producing a highly mobile organ. In man the splitting is partly suppressed, a further example of paedomorphism. Suppression of development is also apparent in the other human toes which do not grow so long relatively as in the apes (Schultz, 1957). However, not all foot developments in man are paedomorphic: the strong specialization in the talus and calcaneum (astragalus and os calcis) to form the human heel is markedly gerontomorphic. This gerontomorphism in the heel is adaptive and permits man to walk upright; the apes are essentially quadrupedal.

I have no space here to consider other human adaptions to the upright posture but there are many (see Schultz, 1957).

CONCLUSION

Acceleration of development may lead to high differentiation, i.e., gerontomorphism; prolonged growth at a lesser speed could finally produce the same result: but prolonged growth is simply retention of the foetal tendency to grow, i.e.,paedomorphism. Since two such diverse processes may have a similar outcome it is essential to try to avoid confusion over which is involved. This may be done by considering how much is achieved in a given time. The gorilla, for example, attains far more total differentiation than does the human in twice the time; that is overall gerontomorphism. The ape's inferior extremities are paedomorphic in comparison with the human but it must be conceded that apes have only half the time in which to extend their inferior extremities. Were it not for the total gerontomorphic trend in apes we might be in doubt over how to class the development of their lower limbs. On the other hand, ethnic groups which end up with shorter inferior extremities than Europeans *in the same time* are relatively paedomorphic, those with longer inferior extremities are gerontomorphic.

A factor to be taken into account also is the environment. This is loosely recognised in the term " adaptation " but, while most animals are very well adapted to their environment, we must note that man is changing his and this is reflected in his physique. Not only has improved environment, in the way of improved nutrition for example, affected such characters as stature, body weight, &c., it is actually producing more profound changes, e.g., in head form (Boas, 1940; Abbie, 1947; Kaplan, 1954). When we have some idea of how the perfect genetic make-up can respond to the ideal environment (if either exists) we shall have some way of measuring more precisely the true effects of timing in differentiating man from other primates.

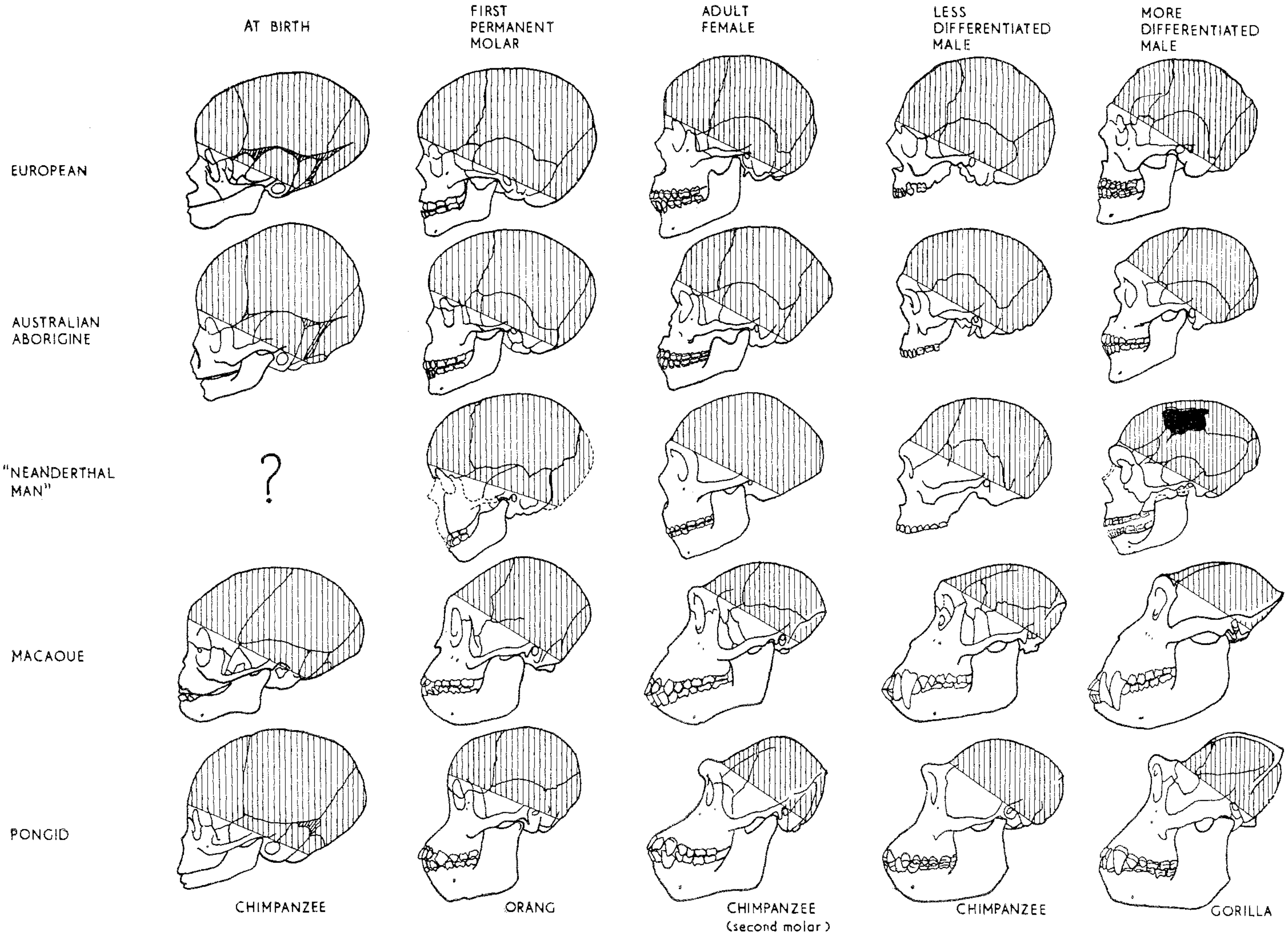

FIG. 6.—Comparison of the growth pattern of skulls of some humans and other primates (redrawn and modified from Abbie, 1952a). Hatching indicates approximate proportion given to the brain.

In tracing the development of different primates we are, really, watching different expressions of what is essentially the same process—variations on a common theme. All start off at about the same point and their differences appear only when differences in the timing of secondary developments become apparent.

Development is like a cinematographic film that comprises the whole of differentiation and can be run slow or fast as desired, or at different speeds at different times. In gerontomorphism the film—wholly or in part—is run through fast: development is accelerated, parts rush to completion, details may become exaggerated, blurred over or completely lost. But more film can be run through in the time available, and much more can be achieved in differentiation. In paedomorphism the film is run through slowly, the whole process is drawn out, features are unfolded in greater detail and hitherto unsuspected aspects show up. However, much less film can be run through in the time available: even when the time is doubled, as it is in man, the final achievement in differentiation may still fall short of extremes if the running rate is very slow. At present we have no idea of the proper speed of the film or even its length, although reference to primate morphology and human developmental variations is beginning to give us some idea of how the picture can be changed under different conditions.

To revert to our original theme: we may conclude that in the development of all primates there is a mixture of paedomorphism and gerontomorphism and that the features that distinguish man peculiarly from the others are, on balance overwhelmingly the outcome of paedomorphism—of delayed timing that imposes a distinctive human bias upon an assemblage of characters that are basically alike for all primates. The factor of timing is, itself, part of the specific heritage of every primate and it determines in what order, at what rate and to what extent any character shall unfold. To put it differently, the germ-plasm of each primate is—as electronic engineers would say—" programmed " from the outset to determine the onset, sequence and the rate of unfolding.

Clearly, then, when we are seeking for man's relations and his line of evolution we shall profit little from studying the end products—the adults—too closely. We must seek for relationships in embryos, and the earlier we look the closer the relationship will be. More specifically, we must look for the germinal timing mechanism that regulates the progress of any primate along its predetermined course of development. It is quite conceivable that a minor genetical twist in the timing mechanism of any primate could have determined the course of development that led to man. That could have happened quite suddenly and at any time—even very recently. Moreover, as Hardy (1954) has pointed out, neotenous changes afford an avenue of escape from ancestral specializations that would otherwise preclude any progress along more generalized lines—this applies especially to man (Abbie, 1952b).

To sum up, the view put forward here as a working hypothesis has several advantages:—

(*a*) it involves nothing unknown in biological mechanisms;
(*b*) it shows how man could have emerged quite suddenly and within relatively recent times;
(*c*) it disposes of the problem created by the absence of satisfactory " missing links "—they are not required.

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