

**Palæontologie.** — *On the gibbon-like appearance of Pithecanthropus erectus.*

By EUG. DUBOIS.

(Communicated at the meeting of May 25, 1935).

The abundant evidence, given since 1932 by five thigh bones, on the organismal distinctness of *Pithecanthropus erectus*, furnishes proof, at the same time, of the close affinity with the Gibbon group of anthropomorphous Apes <sup>1)</sup>. Indeed various remains, now on hand, of the so-called Ape-Man point to that affinity, notwithstanding its ability to walk erect and the one degree higher cephalization, an affinity shown most directly by the rightly understood femur, but most conclusively by the calvaria.

However, far more than the seemingly too perfectly human femur, it was the surprising volume of the brain, as betrayed by the size of the calvaria, very much too large for an anthropomorphous ape, very small only in comparison with the average of man, that led to the presently almost general opinion that the "Ape-Man" of Trinil was really a very primitive Man.

That ambiguous brain volume is indeed the most conspicuous distinctive feature of *Pithecanthropus erectus*, and it was to obtain a better insight into this new organism that, soon after the discovery, I undertook the search for laws which regulate cerebral quantity in Mammals, a study which indeed furnished evidence as to the place of *Pithecanthropus* in the zoological system, and with which I am still intensively occupied, on account of its great biological significance.

Unnecessary to repeat here the line of argument of these researches. It may be remembered only that in every species the volume of the brain is obviously proportionate to the degree of organization, the complexity of the animal functions of the organism, which is determined by the number of nerve-cells, but as a matter of course and of daily observation it is, in some way, related also to the size of the body.

Thus comparing, in a number of different cases, the brain quantity in two species of mammals, having the same organization ("nearly related species"), but different body weight, I found (in 1897) that the functional degree could be expressed, in every case, by the formula  $K = \frac{E}{S^{5/9}}$ , where  $E$  is the weight of the brain and  $S$  the weight of the body;  $K$  the coefficient of cephalization (or factor of animal organization) appeared to arrange the Mammal groups in good systematic order, generally in accordance with what we know of their animal organization. Thereupon LOUIS LAPICQUE and his collaborators (in 1905) found the same law to

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<sup>1)</sup> Proceedings, Vol. XXXV, pp. 716—722 (1932); Vol. XXXVII, pp. 139—145 (1934). With two plates.

hold good for Birds; I confirmed it for Reptiles and Fishes (in 1913). It thus holds good for Vertebrates in general.

It soon appeared that properly this law of the quantitative relation of brain and body applies to the functionally most central part of the brain, the **psychencephalon**, chiefly the cerebral hemispheres.

Armed with this knowledge it was possible to detect a second law (in 1924), the law of the autonomic phylogenetic progression of the psychencephalon, which law has a direct significance for the taxonomy of *Pithecanthropus* and is highly important with respect to biology in general. By comparing nearly related groups of Mammals it appeared in not a few cases, that the coefficient *K*, concerning the psychencephalon, increases by doubling and redoubling, thus according to a geometrical progression with the ratio 2.

Very strikingly this law appears (without any calculation) by comparing the brains of nearly related animals of equal size, such as the Polecat and the Stone Marten, the great difference of the brain volumes is very impressive, indeed the one of the former animal being half that of the latter. Likewise the Upper-Miocene *Procamelus gracilis* and the present-time Lama resemble each other closely and are of equal size, however the volume of the psychencephalon of the precursor is exactly half that of the recent species.

But also the Stoat and the Weasel, belonging to the same group with the Polecat, have half the cephalization coefficient of the Marten group. In the same relation are the Shrew and the Mole, the Marmot and the Squirrel, the Kanchil and the True Ruminants; etc.

The common Small Bats (the majority of the *Microchiroptera*), however, are two degrees below the Large Bats (*Megachiroptera*), the values of the cephalization coefficient being in the relation 1 : 4. The link here is supplied by the Leaf-nosed Small Bats (*Phyllostomidae*), with a coefficient half that of the Large Bats and double that of the common Small Bats. In the same relation again are the Monkey genera *Callithrix*, *Saimiri* and *Cebus*, the relative values of the cephalization coefficient being 1 : 2 : 4.

Recently (in 1934) the law of the autonomic phylogenetic progression was confirmed for Birds by LAPIQUE<sup>1</sup>). Undoubtedly also this law holds good for Vertebrates in general.

To the interpretation of both laws different researches have contributed, chiefly on the relation of body weights of individuals, belonging to one and the same species, to brain quantity, and of body weights of Mammals in general to volume of homologous nerve-cells. Those researches taught

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<sup>1</sup>) LOUIS LAPIQUE, Sur le développement phylogénétique du cerveau (d'après les travaux récents d'Eugène Dubois). Annales des Sciences Naturelles. Zoologie. — 10e Série. — T. XVII — 1934. Paris 1934.

that the second law is a consequence of the fact that the number of the nerve-cells increases by bipartition, in the phylogenetic as well as in the ontogenetic growth of the brain. Nature threw light on this point by putting this, with respect to the latter growth, as it were to the test in human microcephalia.<sup>1)</sup>

Consequently the series of values of  $K$  in the different Mammal groups is not constituted by numbers which are irregularly dispersed along the scale of variations, but discontinually in successive degrees, the value of each degree being half the one above and double that below. This signifies that in the phylogeny of the psychencephalon the quantitative progression occurs by abrupt great mutation. The number of the nerve-cells doubles, without transition; thus the mutation is due to one bipartition more.

It is, therefore, possible to arrange all the groups of Mammals existing at present in a geometrical series of progressive coefficients of cephalization, in which series there are no gaps (even when fossil groups are not taken into account), with one sole exception. There is also little deviation from the mean terms. Putting the cephalization of Man equal to 1, we find exactly  $\frac{1}{4}$  for the *Anthropomorphae* inclusive Gibbons; about  $\frac{1}{8}$  for the majority of our large Mammals: Ruminants, Cats, Dogs etc.; about  $\frac{1}{16}$  for Kanchils, Civet-Cats, Hares, Large Bats (*Megachiroptera*) etc.; about  $\frac{1}{32}$  for Mice, Moles, Leaf-nosed Bats (*Phyllostomidae*) etc.; about  $\frac{1}{64}$  for Shrews, common Small Bats (*Microchiroptera*) etc. The previously supposed gap or void space between the *Megachiroptera* and the *Microchiroptera* I found filled up by the *Phyllostomidae*.

The only real void space in the series is between Man and the anthropomorphous Apes (incl. Gibbons). This void space marks the place of *Pithecanthropus* according to the following computation.

With fair approximation to accuracy we can calculate the volume of the entire cranial cavity by comparing the conserved calvarial part (570 cm<sup>3</sup>), — which was once filled by the largest part of the psychencephalon, from near the roof of the orbits horizontally to the cerebellum, — with the corresponding part of the cranial cavity of Apes and Monkeys (*Hylobates*, *Gorilla*, *Pongo*, *Pygathrix*, *Pithecus*), constructed in similar proportion, taking into account the transformations of minor importance which necessarily result from the differences in the relative size of the cranial and orbital cavities as a consequence of different size of the body. In this way the entire cranial cavity was estimated at 908 cm<sup>3</sup>.

To calculate from this the corresponding brain weight, we cannot put this volume on a par with the capacity of an ordinary dried skull, for the calvaria as a part of the dead body was deposited under water and petrified in humid state. In consequence the capacity remained exactly the same with the volume of the encephalon, enveloped by its membranes, during

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<sup>1)</sup> See: R. BRUMMELKAMP, On Microcephalia Vera. Psychiatrische en Neurologische Bladen. Jaargang 1935, N<sup>o</sup>. 2. Amsterdam 1935.

life. Deducting from this volume that of the membranes, calculated according to the human proportionality, we obtain the brain volume, and by multiplying this by the specific gravity of brain substance, the brain weight 880 g, further from this the weight of the psychencephalon 766 g.

In order to calculate from this fairly exact psychencephalon weight a coefficient  $K=1.25$ , equal to half the human coefficient (2.5), and double that of the *Anthropomorphae* (0.625), the body weight must have been 104 kg. We may accept this weight as highly probable, from the relation existing between the chief dimensions of the femur: the length of the mechanical axis and the circumference of the shaft, and body weight in similar organisms.

Now, in the whole suborder *Anthropoidea* we do not meet with any type of femur more closely resembling the *Pithecanthropus* femur in respect of the chief dimensions of mechanical character than that of the Gibbons, apart from the difference of the condyles as a consequence of the acquired ability to walk erect, of no importance in this respect, as this does not affect those chief dimensions. Moreover the similarity in the form of the lower shaft end and the peculiar internal structure of the shaft in *Pithecanthropus erectus* point to similarity in function.

Comparing the *Anthropomorphae*, we see the femur, with increasing body weight of the genera, becoming less slender, in the sequence; small Gibbon species, Siamang, Chimpanzee, Gorilla. *Pithecanthropus*, however, although certainly comparable in weight with the heavier Apes, agrees in the relative thickness exactly with the much lighter Siamang.

In a certain, entirely full-grown and large male siamang the mechanical axis of the femur is very nearly exactly half as long and the shaft half as thick (measured by the minimal circumference) as the mechanical axis and the shaft of the femur of the *pithecanthropus*.

It appears, that in the two Gibbon genera, although in the genus *Hylobates* the femur is very much slenderer than in the genus *Symphalangus* (the Siamang), the body weight is proportionate to the product of the length of the mechanical axis and the square of the mean diameter of the smallest circumference of the shaft. Thus the *Pithecanthropus* femur is comparable with any Gibbon femur.<sup>1)</sup>

The human femur is incomparable, in this respect, with that of *Pithecanthropus*, on account of the different form, especially the strongly thickening of the shaft at its lower end; here only the volumetric comparative method of MOLLISON could be applied, if it did not appear to be unapplicable even for the Gibbons among each other. The volume of the femur of *Pithecanthropus* (without the exostosis) is 463 cm<sup>3</sup>; the mean volume

<sup>1)</sup> Comparable in the same manner is also the Gorilla with the Chimpanzee, and are Cat species of large size with those of small size, Rat with Mouse. The relation in all those cases is properly one of muscle volume, as consequently is the proportionality with body weight.

of 9 male australian femora (measured by HAUGER), calculated to *Pithecanthropus* length, is 431 cm<sup>3</sup>, of 10 male european femora (measured by HAUGER) and calculated in the same manner, 596 cm<sup>3</sup>. Between these two types of the human femur, but nearer to the australian type, the comparable human femur should therefore be found, if the different form of the shaft were no impediment to an exact comparative determination of the body weight. This can only be approximative.

Certainly the different form of the human femur shaft in comparison with that of the Gibbons is connected with the very great difference between Man and the Gibbons (and likewise all the other *Anthropomorphae*) in the proportion of the lower and the upper limb. The relative weight of the arm, estimated from the volume of the three large long bones, to the leg, estimated from the volume of the three large long bones, is in Man only  $\frac{1}{4}$  from the relative weight of the arm to the leg in the Siamang. This striking difference is evidently the consequence of the total exemption of the upper limb in Man from locomotive function, whereas in the Siamang the upper limb is particularly active in this way. A further consequence is the relatively much heavier upper part of the body, above the legs, in the Siamang than in Man.

In this we find a sharp test of the proportion of the upper limb and the trunk to the lower limb in *Pithecanthropus*.

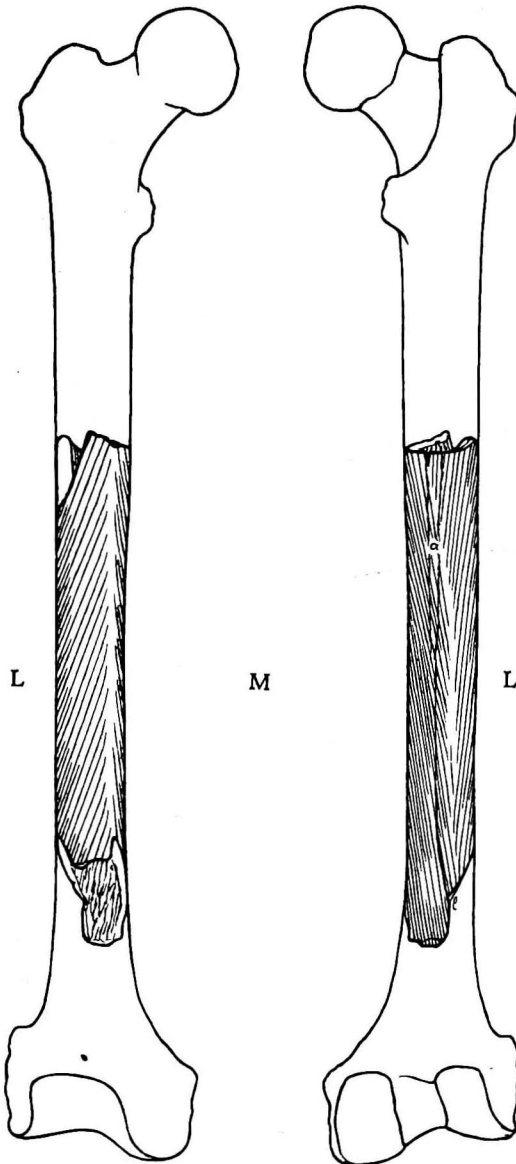
How matters stand here is clearly evident from this that the body weight of the *Pithecanthropus erectus* 104 kg, calculated from the psychencephalic coefficient equal to half the human or double the anthropomorphous coefficient, in accordance with the law of autonomic phylogenetic progression of the psychencephalon, is quite the same as the body weight calculated by comparing the femur of the *Pithecanthropus erectus* with that of our large male siamang, whereas a comparison in accordance with human proportions of the body would only have given a body weight of about 60 kg.

Indeed an imaginary giant Siamang, possessing a femur twice as long and twice as thick as a large real Siamang, would have weighed eight times as much, assuming the same bodily proportions. Now the relative weights calculated from a comparison of the *Pithecanthropus* femur with that of our quite full-grown and large male siamang are as 8.083:1, and  $\frac{104}{8.083} = 12.866$  kg. This calculated weight is almost exactly the weight observed of such a large siamang<sup>1)</sup>.

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<sup>1)</sup> C. J. CONNOLLY, Brain Indices of Anthropoid Apes. American Journal of Physical Anthropology, Vol. 17, July-September, 1932, N<sup>o</sup>. 1. Compare p. 67, Table VI. The body weight of a large adult male siamang is given as 12.476 kg, corresponding with a brain weight of 138 g. Our large male siamang has a cranial capacity of 141 cm<sup>3</sup>. The length of the mechanical axis of the femur is 415 mm in the pithecanthropus and 210 mm in the siamang, the circumference of the shaft 90 mm in the pithecanthropus and 44.5 mm in the siamang.

From this we may conclude that *Pithecanthropus*, although having acquired the ability to walk erect, possessed a proportion of weight of



Diagrams of the fifth *Pithecanthropus* femur, from before (left diagram) and from behind (right diagram). The fragmental shaft located in the outlined entire right femur  $\frac{1}{3}$ . *M* medial side, *L* lateral side, *a* linea aspera, *i* its divergent Labium laterale.

the lower limbs and the upper limbs (with the trunk) little different from that of the Siamang and the other Gibbons, and we may, further, infer that the upper limbs still exerted locomotive functions, at least habitually, in a similar manner as in the Gibbons.

This, at the same time, furnishes an interpretation of the particularities of the *Pithecanthropus* femur, especially of the very striking internal structure of its shaft, which I described in 1934 (Proceedings, Vol. XXXVII, pp. 139—145) and of which I reproduce the annex diagrams.

Evidently *Pithecanthropus* was not only superior to the Gibbons by the real erect locomotion on the ground, but also by the perfected use of the leg in arboreal locomotion, in consequence of the acquired faculty to stiffen the leg in the kneejoint, in every state of flexion and rotation.

It altogether confirms the opinion, which MARCELLIN BOULE expressed already in 1921, that *Pithecanthropus erectus* may have been a relatively gigantic species allied with the Gibbon group, which particularly

was superior to its congeners by the large brain volume, "caractère de tout premier ordre", thus truly approaching Man.

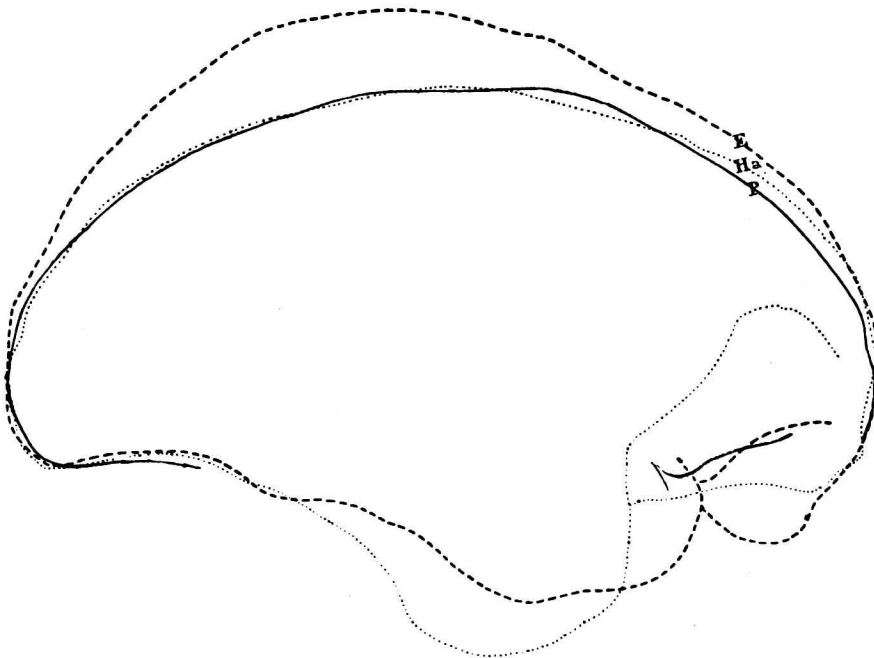
So *Pithecanthropus* appears indeed as a case of ascent to a higher level

of cephalization, and progression of animal functions, in a group, a case similar to those of which I pointed out some above.

According to the law of autonomic phylogenetic progression of the psychencephalon, properly signifying a natural process of growth, this ascent took place in leaps. There was a leap from the anthropomorphous level to the pithecanthropus level and another leap from the pithecanthropus- to the human level, not the gradual, slow ascent presumed by the darwinistic hypothesis.

The apparent gibbon likeness of *Pithecanthropus* is clearly evident also by the place of the gravitation center of the head before the condyles, and by the absence of a parietal vertex of the brain, an anthropomorphous feature, which I described in my paper of 1933, on "The Shape and the Size of the Brain in *Sinanthropus* and in *Pithecanthropus*"<sup>1)</sup>, from which I may reproduce here the upper figure of Plate IV. Both features signify, undoubtedly, that in *Pithecanthropus*, in distinction to Man, the head was not poised on the vertebral column.

Further point of resemblance with the gibbons is the general form



Endocranial casts of *Pithecanthropus erectus* (P)  $\times \frac{3}{4}$ , mesocephalic European Man E, and *Hylobates agilis* (Ha). Made to equal length. Telephotographic contour lines of right norma lateralis views, in subcerebral (orbital-suboccipital) plane orientation.

of the skull. Very striking is the gibbonoid occipital impression for the attachment of the two *rectus capitis posticus minor* muscles, impression

<sup>1)</sup> Proceedings, Vol. XXXVI, pp. 419 et seq. Plates III and IV.

completely absent in the Chimpanzee. The absence of sinus frontales in the gibbons, which are well developed in *Pithecanthropus*, I consider to be a difference of the same character as between *Hippopotamus* and *Choeropsis*. The mandibula also most resembles that of the gibbons, in so far as its features are anthropomorphous. One of these shows that *Pithecanthropus* was devoid of the human power of speech.

The strongest evidence of the gibbonlike appearance of *Pithecanthropus*, however, is that given by the volume of the psychencephalon, exactly doubled in relation to the body weight computed from the gibbonlike chief dimensions of the femur.

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**Physics.** — *A new type of colorimeter.* By J. WOUDA. (Communicated by Prof. L. S. ORNSTEIN).

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The methods, most commonly used in colour measuring, are the trichromatic and the monochromatic. The former consists in the mixing of three well-specified spectral colours in such a way, that the resulting light produces the same colour sensation as the colour to be measured, the latter in the mixing of white light with one spectral colour. Both methods, however, have various disadvantages. For, though the colour sensation, produced by the colour-mixture of the apparatus is the same as that of the colour to be measured, yet the actual composition of these colours may differ widely. This circumstance requires in the first place that the observer should possess a so-called „normal” eye, that is to say an eye for which the sensation curves of the three fundamental colours agree with the standard curves. Further it is necessary to illuminate the colour to be measured with light of the colour temperature, for which one wishes to determine the colour point. This gives also rise to difficulties, when a colour point must be determined for high colour temperatures, as e. g. for daylight. Moreover, the adjustment for equal colour requires an appreciable amount of practice.

On account of these difficulties, Prof. ORNSTEIN requested me to construct an apparatus, which would make it possible to determine the re-emission-, respectively the transmission-curve by means of a monochromatic comparison of brightnesses and which would at the same time abbreviate the lengthy calculations, necessary to obtain the colour point from this curve. To meet these demands, I was led to the construction of the apparatus, described below. Before entering into details, I give here a brief outline of how the instrument works.

It consists of two parts :

1. The part, which, when the apparatus is ready for use, is put in front of a spectroscope and which I shall call the spectroscope front-piece.