Anatomy. — *"On the slope of the Foramen magnum in Primates"*. By Prof L. BOLK.

(2nd Paper on the Comparative Craniology of Primates).

In the first paper on the anatomy of the Primate-skull, the position and shifting of the occipital Foramen in Primates was treated. This paper will be devoted more especially to the consideration of the inclination of this plane.

All the writers who have dealt with this subject have pointed out that these two features: position and inclination, stand in a certain relationship to each other, in so far as the closer the Foramen lies to the occipital pole the more vertical a position does it assume, while as it gradually approaches the middle of the cranial base the tendency is towards a horizontal position. This variation in the slope, like the shifting, has been connected with the erect gait of the human body. In the typical quadruped, where the skull more or less hangs from the spinal column, the Foramen lies at the occipital pole of the skull, and the plane is vertical; in human beings, where the longitudinal axis of the body runs vertically, the occipital Foramen lies in the middle of the cranial base, while the plane is almost horizontal. Thus it is seen that this plane is disposed to take up a position perpendicular to the longitudinal axis of the body. Another point of view, first fully developed by HUXLEY, concerns the connection which is said to exist between the slope of the plane of the Foramen magnum and the degree of prognathism [1]). The more pronounced the prognathism — i. e. the longer the face-skull — the more perpendicular would the Foramen magnum stand. If now a rough comparison be made of an animal's skull with a human skull, the parallelism between these two features is at once noticeable. HUXLEY, however, believed he could show it even in the skulls of different races of men. From the superposition of the mediagrams of the highly prognathous skulls of an Australian and a Negro on the skull of a Tartar, it was seen that "the plane of the occipital Foramen forms a somewhat smaller angle with the basiscranial axis in those particular prognathous skulls than in the orthognathous".

WELCKER [2]) holds a somewhat similar opinion, though he does not express it as being a connection between prognathism and the slope of the Foramen magnum, but between prognathism and the position

[1]) T. HUXLEY, On some fossil remains of man. Collected Essays. VII, p. 198.

[2]) H. WELCKER, Untersuchungen über Wachsthum und Bau des menschlichen Schädels. Leipzig 1862.

of this opening, which, however, comes practically to the same thing, if a connection between position and slope be assumed. "Biegt am Vorderschädel", he says (l. c. p. 50), "der Oberkiefer des Menschen mehr nach vorn (Prognathismus) so rückt zugleich am Hinterschädel das Foramen medullare mehr nach rückwärts". AEBY[1]) does not agree with HUXLEY: "HUXLEY glaubte die Neigung mit dem Prognathismus in Verbindung bringen zu können. Die Steilheit der Stellung sollte in gleichem Masse wie die letztere wachsen. In unseren Tabellen findet sich keine Bestätigung dieser Ansicht" (l. c. p. 17). AEBY himself sees a connection between the degree of development of the occiput and the slope of the Foramen magnum: "Die Abflächung des Hinterhauptes fuhrt eine Erhöhung des Foramen magnum im Gefolge." This opinion does not really differ in principle from WELCKER's, for if the occiput be markedly flattened the Foramen magnum will lie further back, and thus the opinions of WELCKER and AEBY coincide after all with the opinion already expressed by DAUBENTON, that the For. magn. is the more perpendicular in proportion as it is pushed further backwards. The connection which HUXLEY believed he had shown was, however, of another kind, and AEBY is therefore not correct in representing his opinion as being in contradiction to HUXLEY's. For it is not impossible that the slope is proportional on the one hand to the degree of prognathism, and on the other to the position. Is then the relation between position and slope of such a constancy as TOPINARD made it appear originally when he said[2]): "qu'il suffit de mesurer l'un des deux termes par exemple l'inclinaison du trou occipital pour connaître l'autre, c'est à dire la quantité du déplacement du trou"? This seems à priori improbable, since TOPINARD's method of determining each of the two phenomena possesses merely a very relative degree of accuracy. Indeed TOPINARD himself saw this later[3]), and then expressed himself more cautiously: "Toutefois il n'y a pas un parallélisme rigoureux entre les deux phénomènes."

In general the above writers determined the slope of the Foramen magnum by determining the angle which was formed between the base-line adopted by them, and the line which connects basion and opisthion. The base-line in these researches connected the basion with the nasion or typhlon, and therefore ran through the skull-base. This method has been contested by BROCA, and quite justly, for the size of the angle which is formed by these two lines is

[1]) C. AEBY, Die schädelformen der Menschen und Affen. Leipzig 1867.
[2]) P. TOPINARD. L'Anthropologie. 4me Edition.
[3]) P. TOPINARD. Éléments d'Anthropologie générale.

not dependent merely on the direction of the Foramen magnum because the direction of the base-line, i. e. one of the legs of the angle, depends on several factors, e.g. the angles of the basis cranii, the length of the skull, the length of the clivus, the position of the nasion, etc. To avoid this difficulty BROCA determined the slope of the For. magn. by an angle made by the plane of this opening with a plane which is entirely independent of the cranial base, viz. that which connects the axes of the two orbitae. He constructed his "angle orbito-occipital" [1]). BROCA here was proceeding from the postulate that the orbital-plane, in Primates at least, is the natural horizontal plane of the skull, as, in the case of normal sight, these animals look straight before them and the orbitae in this circumstance therefore will have the same direction. The correctness of this opinion will be discussed in a following paper.

RAUBER [2]) in a recently published treatise, returns to the old, disused method, takes as base-line again the nasion-basion, and even says that: "eine Beziehung der Neigung des Foramen occipitale auf eine andere Linie als auf die Basallinie fuhrt sehr leicht zu Unverständlichkeiten und entbehrt zugleich der morphologischen Bedeutung".

SCHWALBE, also, lately expressed as his opinion regarding the value of AEBY's base-line as follows: "So rationell auch die von AEBY gezogene Grundlinie ist, ist sie doch nicht geeignet über die Ausbildung der verschiedenen Teile des Schädelraumes Auskunft zu geben."[3])

There is a certain contradictoriness in this criticism. A rational base-line of a craniometrical system must be able to serve as basis for at least a primary division of the skull. I have already briefly stated my objections to base-lines which are drawn through the skull-base, and will come back to this subject in a following paper. Such a line may have a certain value as boundary line between the cerebral- and facial-skull, but as basis of a craniometrical system it is absolutely useless.

HUBER [4]) finally has determined the slope of the For. magn. in Hylobates with regard to the so-called German horizontal, a method which when the skulls to be examined cannot be halved medially is preferable to those of other investigators. The probable error will here be less than by the use of the basal line and certainly likewise less than by employing the horizontal auxiliary line made use of by

[1]) P. BROCA. Sur l'angle orbito-occipital. Revue d'Anthropologie 1897.

[2]) A. RAUBER. Der Schädel von Kegel. Int. Monatsch. f. Anat. und Phys. 1906.

[3]) G. SCHWALBE. Kritik zu KOHLBRUGGE's: Morphologische Abstammung des Menschen. Globus 11 Juni 1908.

[4]) L. HUBER. Vergleichung des Hylobates und Menschenschädels. München 1902.

LISSAUER [1]), running from the protuberantia occipitalis externa to the point where the ala of the vomer is joined to the rostrum sphenoïdalis.

By the method I have adopted in determining the slope of the For. magn. I have proceeded from the base-line which was described in the first paper, and in so-doing have answered the question as to what angle is made by the plane of the occipital foramen with this line. To express this angle in all Primates always as a positive value it is not possible to measure the angle directly. For in the Primates 3 conditions occur: *a*. the opisthion lies higher than the basion, the For. magn. looks backwards, and the angle is therefore an acute one closed at the back; *b*. basion and opisthion lie at equal distances from the base-line, the For. magn. looks downward, is parallel to the base-line, and the angle $= 0$; *c*. the basion lies higher than the opisthion, the For. magn. looks forward and the angle is an acute one closed in front. To prevent confusion between angles of equal size in cases *a* and *c*, a + or — sign could be used. I think, however, the variations in the inclination might be represented more simply in determining the angle made by the plane of the For. magn. with a perpendicular drawn from the basion to the base-line. In case *a* this angle is always acute, in case *b* it is a right angle, and in case *c* it is an obtuse angle.

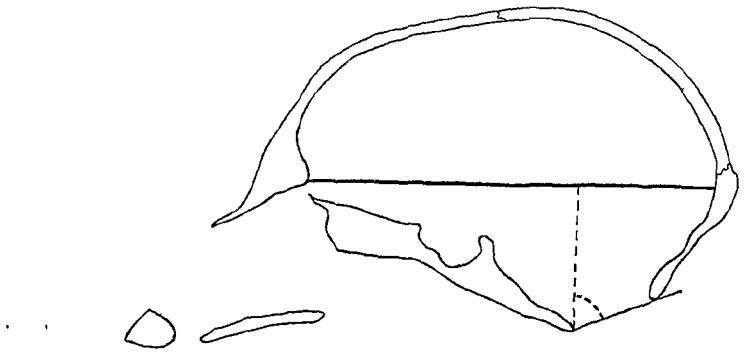

Fig. 1.
Mediagram of an Ateles skull, illustrating the method of determining the slope of the For. magn. ($^3/_4$ natural size).

In Fig. 1 this method is clearly seen on the mediagram of an Ateles skull. The following table gives the results of the researches on the skulls of full-grown monkeys.

[1]) LISSAUER. Untersuchungen über die sagittale Krümmung des Schädels. Arch. f. Anthrop. XV Bnd. Suppl.

Lemur. 40. Propithecus 42.
Mycetes. (18). 33. 45. 53. 59. Average **47.5.**
Pithecia. 54. 56. 60. 64. Av. **58.5.**
Hapale. 61. 61. 63. 64. 69. 72. Av. **65.**
Chrysothrix. 60. 61. 63. 65. 66. 69. 70. 70. 71. 71. Av. **66.6.**
Cebus. 63. 64. 64. 65. 67. 67. 68. 72. 73. 75. Av. **67.8.**
Ateles. 66. 67. 68. 71. 77. 79. 82. Av. **72.7.**
Cynocephalus. 63. 64. 66. Av. **64.2.**
Inuus. 66. 68. 70. 76. 76. Av. **71.2.**
Macacus ♂. 68. 70. 70. 74. 79. Av. **72.2.**
Macacus ♀. 67. 73. 75. 78. 84. Av. **75.4**
Cercopithecus. 74. 80. 81. 82. Av. **79.2.**
Colobus. 64. 72. Av. **68.**
Semnopithecus. 60. 61. 61. 64. 68. Av. **62.8.**
Siamanga. 55. 56. 56. 56. 58. 61. 63. 63. 67. 68. Av. **60.2.**
Hylobates. 52. 60. 66. 73. 75 Av. **65.1.**
Chimpanzee. 64. 79. 80. Av. **74.3.**
Gorilla. 63. 63. 66. 70. 76. 77. 80. 80. Av. **71.8.**
Orang. 58. 62. 68. 70. 72. 75. 79. 80. Av. **70.3.**

These figures show in the first place that the slope of the Foramen magnum varies greatly in individual cases, a fact which is apparent by merely looking at the skulls. This individual variability is especially noticeable in the large skulls such as those of the Anthropoids. And yet the general configuration of the skull is but little influenced by these great variations in the slope of the Foramen. As a proof

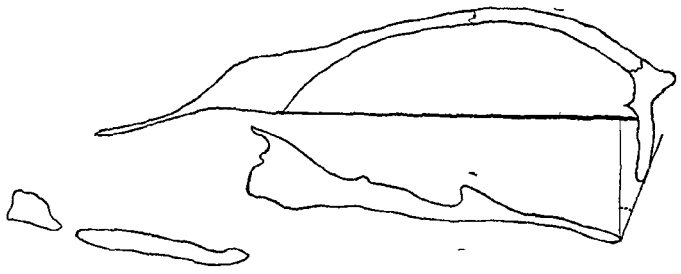

Fig. 2.
Mycetes. ($^3/_1$) Angle of inclination of the For. magn. 18°.

of this, I have given in Figs. 2 and 3 the mediagrams of two Mycetes skulls, with slope-angles of 18° and 59° respectively.

From the figures it can also be seen that a slight shortening of the Clivus is of great influence on the angle of the slope. Now

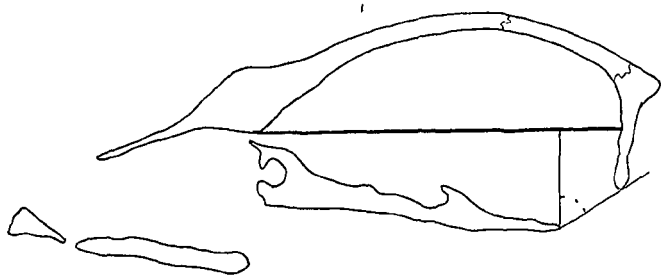

Fig. 3.
Mycetes. (3/4) Angle of inclination of the For. magn. 59°.

Mycetes occupies a foremost place in the variability of the inclination as in that of the position of the Foramen magnum for reasons fully given in the previous paper. For the other skulls, however, the same holds good. Another cause of the individual variations is the striking difference in sagittal measurement of the For. magnum especially in Anthropoids. In the Orang-outang skulls, for instance, which I used, this measurement varied from 25 to 41 mm.

Nevertheless, in spite of these individual variations some remarkable features are to be detected between the different primate-genera, especially if the series be compared as a whole with one another. It is noticeable that Chrysothrix does not seem to occupy the place attributed to this family in the literature on this subject. Among the Plathyrhines, Cebus, and more especially Ateles, have greater angles, that is to say, in these genera the For. magn. lies more horizontally. In this respect the Chrysothrix is inferior even to most of the families of the Catarrhines. On an external observation, however, the For. magn. seems in this monkey's skull to lie horizontally in consequence of the enormous development of the occiput, and the large share that the squama occipitalis occupies in the formation of the cranial base. (See Fig. 4).

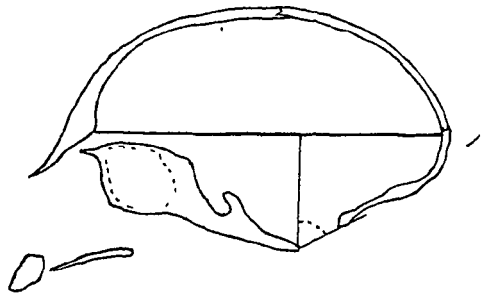

Fig. 4.
Mediagram of the skull of Chrysothrix. (1/1).

Among the Catarrhine monkeys, the greatest angles, 80° and more, occur among the Anthropoids and the genus Cercopithecus. This genus thus, also as regards the slope of the Foramen magnum, takes the high place which we have already awarded to it in the previous paper on account of the position. And similarly the genus Siamanga takes again the lowest place among this group of Primates. In this otherwise so highly developed monkey the Foramen magnum is inclined more vertically than in any other family of monkeys of the Old World, although it is closely followed by the genus Semnopithecus. A study of the skull base will afford us the opportunity of pointing out more particularly what a quite distinct place the Siamanga takes in the group of Primates, as regards the general form of the cranium. In the first paper I have already mentioned that it is difficult to believe that original conditions have been here persistent.

In the foregoing paper it was also pointed out that during the infantile and juvenile period the For. magn. shifts towards the occiput. It appears now that also the slope of the Foramen changes during growth. *For in the skull of a young ape the Foramen magnum lies more horizontally than in that of a full-grown one.* The following may serve as a proof of this. Whereas in a full-grown Siamanga the angle varied between 55° and 68°, I found in a juvenile skull (mixed dentition) an angle of 70°, and in an infantile skull (complete lactal dentition) an angle of 81°. In a Chimpanzee, with a complete set of milk teeth, the For. magn. lay almost horizontally with a angle of 88°. In three infantile Orang-outang skulls I found angles of 78°, 85°, and 86°, while finally a juvenile Gorilla skull had a angle of 87° and an infantile one even of 95°. In the case of this last skull, thus, the For. magn. looked forwards as in that of man. We shall soon see that as regards human beings also the plane of the For. magn. turns during infantile and juvenile periods in the same manner as with the Anthropoids, though I must here point out that this turning is much more pronounced in Anthropoids and Siamanga than in human beings.

Thus both in the position and the slope of the For. Magn. the young Anthropoid agrees more with the human conditions than the full-grown one.

In respect to the slope of the For. magn., man occupies a distinct place among all Primates, as in him the opening is not turned towards the back but towards the front. This fact, which has already been alluded to by DAUBENTON, and after him by all the writers on this subject, is illustrated by the figures below. I call to mind that

an angle of 90° obtained by my method agrees with a position of the For. magn. parallel to the base-line, i. e. a horizontal position.

Angle of the For. magn. in full-grown human skulls.

Papuans:	96°, 99, 99, 99, 100, 101, 103, 107, 107, 108,	Av. **101,9°.**
Negroes:	92°, 96, 07, 98, 99, 100, 100, 101, 103, 106,	„ **99,2°.**
Frisians:	86°, 89, 90, 94, 95, 99, 100, 103, 103, 103,	„ **96,2°.**
Zeelandians:	93°, 97, 99, 100, 101, 103, 104, 105, 109, 112,	„ **102,3°.**
Javanese:	92°, 92, 97, 99, 100, 100, 103, 103, 103, 105,	„ **99,4°.**

The averages of three of the groups lie comparatively near each other, and the existence of a difference between dolichocephalic skulls (the first three groups) and brachycephalic cannot be assumed on the ground of these figures, although the difference between the long dolichocephalic Frisian skulls and the short strongly brachycephalic Zeelandian skulls is very remarkable. It is also peculiar that among the Frisian skulls there were two in which the For. magn. looked slightly backwards (angles of 86° and 89°) and one where it lay exactly horizontal. This was caused by the particularly long clivus in these objects. That the degree of development of this part of the cranial base in human beings has a great influence on the slope of the For. magn. is proved by infant skulls. On an average the For. magn. in young human skulls has without exception a more considerable inclination towards the front than in full-grown ones, as will be seen from the following figures.

Angle of the For. magn. in children's skulls.

0—1	year. 110, 110, 109, 105, 104, 103, 102, 101, 100, 100, 92.
1—2	years. 100, 110, 110, 108, 106.
2	years. 107, 107, 106, 106, 103, 101, 95.
3	years. 110, 110, 108, 107.
4	years. 114, 109, 106, 105, 100.
5—6	years. 114, 113, 109, 107, 105, 103, 96, 96.
7	years. 108, 100, 100, 99, 98.
8—9	years. 104, 103, 101, 97.
10—11	years. 110, 104, 104, 101, 100 92.

The average angle of the human full-grown skulls can from the preceding table be set at 100°. And now it is seen that of the 31

skulls of children under 5 years of age only 2 have a smaller angle while of the 23 skulls of children between 5 and 12 years of age this is so in 6 cases. From this it may be inferred that during infancy when, as has been shown in the 1st paper, a shifting of the position of the occipital foramen takes place in man, also the plane of the For. magn. turns, and in the same direction as with the Anthropoids. Yet, as has been said, this turning, like the accompanying shifting of position is more marked in Anthropoids than in human beings.

We have now seen twice over that a shifting of the For. magn. and a change in the angle go hand in hand during the individual development. For in human beings as well as in Anthropoids the shifting backwards diminishes the angle of inclination. To what degree this relation between these two features exists in comparative anatomy will be apparent from the following table. The 2nd column gives the average of the angle, while the first column shows the average basal-index as determined in the 1st paper. I may here call to mind that the greater this index is, the further backwards does the For. magn. lie.

	Index basalis.		*Angle of inclination of the For. magn.*	
Lemur albifrions	87	(1)	40°	(1)
Propithecus diadema	80	(2)	42°	(2)
Mycetes	86	(3)	47.5°	(3)
Pithecia	74	(6)	58.5°	(4)
Hapale	71	(8)	65°	(8)
Cebus	67	(10)	67.8°	(11)
Ateles	64	(13)	72.7°	(16)
Chrysothrix	59	(18)	66.6°	(10)
Inuus	65	(12)	71.2°	(14)
Cynocephalus	65	(12)	64.2°	(7)
Macacus	64	(14)	73.8°	(17)
Cercopithecus	57	(19)	79.2°	(19)
Semnopithecus	74	(7)	62.8°	(6)
Colobus	75	(5)	68°	(12)
Siamanga	76	(4)	60.2°	(5)
Hylobates	71	(9)	65.1°	(9)
Chimpanzee	64	(15)	74.3°	(18)
Gorilla	61	(16)	71.8°	(15)
Orang	61	(17)	70.3°	(12)

In brackets after the figures of both series is given the place number which each of the genera would take in a regular classification. A comparison of these place numbers shows at a glance in how far the position and the slope of the For. magn. go hand in hand. In general there appears to be a decided parallelism between these features in monkeys, and only in a few cases there is a fairly marked difference between position and slope. This is, for instance, the case in Chrysothrix where the angle is small in comparison to the position, and in Colobus where the reverse is the case.

At the beginning of this paper mention was made of the opinion held by HUXLEY, viz. that the slope of the For. magn. is in proportion to the degree of prognathism. In a following communication, which will deal with the prognathism of the primate skull, this view will be discussed at greater length.

Physics. — "*A short reply to* Mr. VAN LAAR'S *remarks.*" By Prof. PH. KOHNSTAMM. (Communicated by Prof. J. D. VAN DER WAALS).

In the proceedings of the preceding meeting of this Academy Mr. VAN LAAR made some remarks suggested by a paper by Mr. TIMMERMANS and me. Though these remarks do not call in question in any point the validity of our results, but exclusively deal with the question whether we have done sufficient justice to the share Mr. VAN LAAR has had in the construction of the theory, I think that both politeness to Mr. VAN LAAR and deference to the communicator of these remarks forbid me to leave them unanswered. So I shall try to state as shortly as possible the reasons why I still think I have done full justice to that share.

1. Mr. VAN LAAR writes in point *a* of his remarks:[1]) "Here I must remark that I have *never*[2]) represented the special case $a_{12} = \sqrt{a_1 a_2}$ as the general case.".

In writing this Mr. VAN LAAR had certainly forgotten that he wrote in These Proc. Sept. 1906 p. 227: "In the *third* paper in These Proceedings (June 24, 1905) the equation:

$$\Delta = \frac{1}{T_1}\left(\frac{dT}{dx}\right)_0 = \theta \sqrt{\frac{1}{\pi}}\left[\theta \sqrt{\frac{1}{\pi}}\left({}^3/_2 - {}^1/_2 \sqrt{\frac{1}{\pi}}\right)^2 - 1\right] \quad . \quad . \quad . \quad (3)$$

was derived . . . for the *quite general*[2]) case $a_2 \lessgtr a_1 \quad b_2 \lessgtr b_1$", etc.

And on the same page: "Now the restricting supposition $\beta = 0$

[1]) These Proc. XII p. 455.

[2]) Mr. VAN LAAR'S italics.