Histology. — *The different structures of the cyto-architectonic fields of the cerebral cortex as different manifestations of a general scheme, each being mainly indicated by the value of one varying property, called the field exponent.* By S. T. BOK. (Communicated by Prof. M. W. WOERDEMAN).

(Communicated at the meeting of November 25, 1939.)

The microscopic appearance of the cytoarchitectonic fields of the cerebral neocortex suggests that all these fields are different manifestations of a common scheme of structure. The question arises whether the differences seen between the fields are due to changes of only one property of the underlying structural principle. In that case all the other properties of that principle would be constant over the whole neocortex and the structure of each special architectonic field would be determined by the special value of the variable one. The other possibility is, that the structural principle contains many variable properties changing independently of each other. In that case at the border between two special fields a change might occur in a number of these properties and at the border between two other fields changes might occur in another combination of properties.

In my paper "A quantitative analysis of the structure of the cerebral cortex" (Royal Academy of Science, Amsterdam, XXXV, 2, 1936) the results were described of a series of measurings of the size of the ganglion cells at the various distances from the pia mater in one field, the area temporalis superior posterior of man. The size of the nerve cells — expressed by the volume of their nucleus — proved to be dependent upon the depth below the pia in such a way, that a fairly simple scheme could be given of the mutual relations between these volumes and depths.

The above problem can be studied by executing the same type of measuring in other fields of the human neocortex: do the relations between nucleus volume and depth in these other fields correspond to analogic schemes and, if so, what are the differences between these schemes? Do they depend upon one property that has a different value in the different fields, or must we describe the differences between two special schemes as different values of the one property and those between two other schemes as the variation of another property?

By plotting the nucleus volumes and depths measured in the area temp. sup. post. into a rectangular scheme (Fig. 5 l.c.) a correlation diagram was obtained that in two aspects differs from those common in literature.

In the first place the relation points (each indicating the two values of one cell) are distributed in two fields, called the upper and the lower main group. The upper group is built up by the nerve cells of the 2d and 3d layer and by some larger ones in the 4th layer, the lower group by the other (small) nerve cells of the 4th layer and those of the 5th and 6th. The two fields touch each other in a part where the density of the points is low. The boundary between them, in consequence, is rather sharp.

In the second place the density of the points in the different parts of each group is very unequal: at the side of the small values (of the nucleus volumes as well as of the depths) the points are found very close together, their density greatly decreases towards the opposite side of the field. If the logarithms of the values measured are plotted in the same way this dissymmetry disappears, however. This remarkable fact shows that the distribution of the values is not based upon an arithmetic progression (each nucleus volume presented being a constant amount larger than the former one in size) but upon a geometric progression (each volume presented being a constant number of times as large as the former in size).

By this peculiarity the correlation of the logarithms is easier to read than that of the values measured themselves. In each of the two groups it happens to be a simple one showing remarkable relations.

Both fields are oval in shape.

In the diagram shown in fig. 6 l.c., the volumes were plotted horizontally and the depths vertically. A number of horizontal straight lines at equal distances from each other was imagined, the mean of the *log* nucleus volumes between each pair of lines was reckoned and plotted as small circles (fig. 9 l.c.). In the upper zone these circles proved to be situated very near to a straight line with a gradient of 45° (tangent = 1): *in the upper zone the mean nucleus volume increases proportional to the depth.*

The nerve cells with a nucleus volume equal to the mean nucleus volume of their depth, thus, have the same quotient of their nucleus volume and depth. If the logarithms of these quotients are plotted against the logarithms of their depths, the relation points of these mean cells will be situated along a straight vertical line (small circlets in fig. 10 l.c.), so that one regression line in this new diagram is exactly vertical. The other regression line (through the mean depths of the cells with the same nucleus volume) is horizontal. *This means that the quotient nucleus volume divided by depth varies independently of the depth.*

In this diagram, moreover, the upper field is found to be a circle: its horizontal diameter is equal to its vertical diameter. The logarithms of the quotient, thus, vary as much as the logarithms of the depths. *This means that the quotient nucleus volume divided by depth varies as many times as the depths.*

The logarithms of these quotients show a normal distribution (frequen-

cy curve of GAUSS). The extension of the variations, thus, can be described accurately by one value, the standard variation (being equal to 0.155).

To express these relations more clearly a circle is drawn in the second diagram round the upper field. The borders of the field not being sharp, this circle has not a quite exact meaning, but nevertheless it illustrates the equality of the range of variation in the horizontal and vertical direction and it indicates in a simple way the practical extension of that variability. The oval drawn round the upper field in the first diagram (fig. 9 l.c., demonstrating the relation between *log* nucleus volume and *log* depth) is the transformation of this circle, and so is the curve round this field in the diagram of the nucleus volumes and depths themselves in fig. 5 l.c.

The conclusions drawn above probably have a very simple morphological basis. The depth of a nerve cell under the pia is the length of its main dendrite, being the dendrite that rises from the cell body and ends in the pia glia membrane. And in a cats brain the basal dendrites of a cortical neuron were found to be proportional to the volume of its nucleus. The quotient nucleus volume divided by the depth, thus, is proportional to the quotient of the length of the basal and the main dendrites, it is a value directly related to the shape of the dendrite field of the neuron: the relation between the height and the breadth of the dendrite field is a constant number of times that quotient. The conclusions drawn above, in consequence, may be formulated as follows: *in the upper group the shape of the dendrite fields varies normally, independently of and as many times as the length of the main dendrites* (with normal variation of the shape a normal distribution of the logarithm of the quotient breadth: height is meant).

The lower group shows two differences with the upper one.

In the diagram of *log* nucleus volume and *log* depth the regression line through the mean volumes has not a gradient with a tangent equal to 1 but nearly equal to 2: the mean nucleus volume increases proportional to a higher power of the depth. The second difference will be discussed later. The field takes the form of a circle when *log* (nucleus volume divided by the higher power of the depth) is plotted against the logarithm of the higher power of the depth. The radius of the circle is equal to that of the upper zone described above.

The neuron with a nucleus volume and a depth equal to the values of the centre of the circle may be called the central neuron of the field. The central neurons of both fields have exactly the same nucleus volumes: the centres were found to be lying exactly on the same vertical line (standard error of the measuring smaller than 5 %). The depth of the lower central cell is 3,16 $\times$ that of the upper one.

Since then measurements of other fields of the same specimen of cerebral cortex have been made. The various Nissl preparations were made simultaneously and ample precautions were taken that the various

parts cut from the cortex were under the same conditions during fixation, embedding, slide cutting and colouring.

The logarithms of the nucleus volumes and depths measured in 6 fields are shown in the figs. 3—8. All the relations described above can be found in these diagrams of the other architectonic fields, three dimensions only differ: the radius of the circle, the nucleus volume of the central neuron and the gradient of the regression line in the lower group. In all the architectonic fields this nucleus volume and the tangent of the gradient being proportional to that radius, these three varying values are dependent upon each other. The diagrams of these various architectonic fields, thus, differ in the value of one property only, indicated by the length the said radius.

In order to demonstrate this conclusion in an easy way the transformed circles (according to this conclusion) are drawn in the diagrams and a glance at the figures will demonstrate, that these lines describe in a fairly exact way all the fields of measuring points, notwithstanding the great differences between the architectonic fields studied.

The principle used in constructing these transformed circles is demonstrated in fig. 1, being a theoretical diagram of the logarithms of the

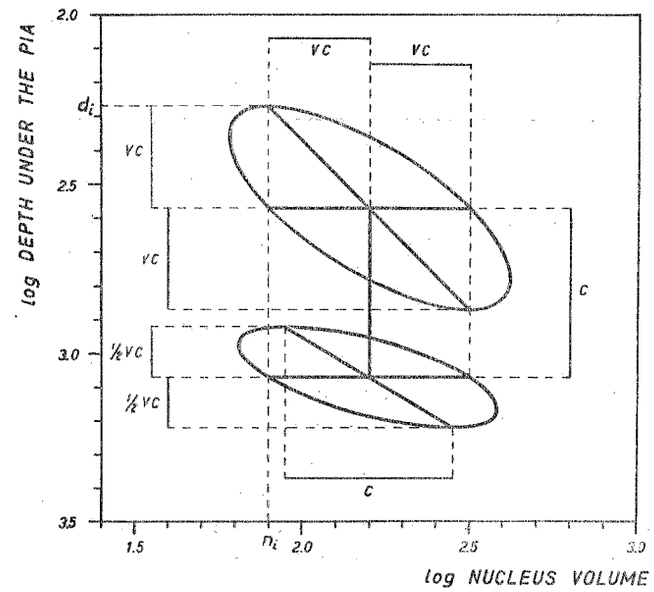

Fig. 1. General scheme of the size of the ganglion cells at the different depths of the cerebral neocortex. The value of the field exponent v varies from ½ to 1 and characterizes each cyto-architectonic field. The values of c, d_i and n_i are nearly constant in the whole human neocortex.

nucleus volumes and depths in a random architectonic field of the human cerebral cortex.

The regression line of the upper group starts at a depth of 168 μ

(*log* 168 = 2,25) and a nucleus volume of 83 μ (*log* 83 = 1,92). (The table p. 953 and fig. 2 show that in all the architectonic fields the upper group begins — at the border between the first and second layer — with almost the same mean nucleus volume and at about the same distance from the pia. In the table the proportion of the measured values of that depth and volume and the constant values of the scheme are expressed by their logarithms p and q; these are small and they do not show a

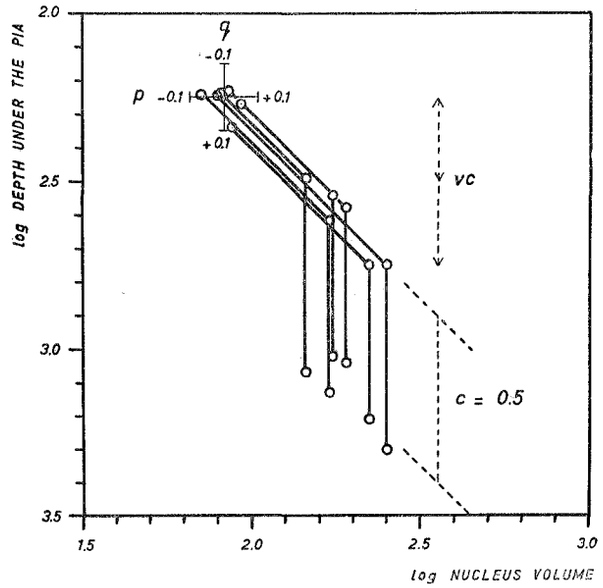

Fig. 2. The starting points of the upper regression line, the upper and the lower centre of the architectonic fields represented in figs. 3—8.

correlation to the field exponent, described below). The regression line has a gradient of exactly 45°. The centre of the upper field, therefore, lies at equal distances more to the right and lower down. This distance is the radius of the circle spoken of above and it varies in the various architectonic fields.

In the vertical line drawn through the upper centre the lower centre is found. In nearly all the architectonic fields studied the distance between these centres is found to be nearly the same (0,50). This means that in all the architectonic fields the central neuron of the lower group has the same nucleus volume as that of the upper group and a depth about 3,16 times larger than the upper one (*log* 3,16 = 0,50). In other vertebrates this factor has a different value. It thus being characteristic for the neocortex of a definite species of animal, it may be called the *cortex factor* (C). In man this cortex factor is 3,16.

The radius of the upper circle is found to be different in the various architectonic fields. It is maximal in the motoric area giganto-pyramidalis

	area striata	area parastriata	area orbitalis granulosa	area postcentralis granulosa	area paracentralis	area praecentralis gig. pyram.
exponent of the field (v)	0.50	0.54	0.70	0.76	0.82	1.00
log factor of the field ($vc = 0.5\ v$)	0.25	0.27	0.35	0.38	0.41	0.50
mean log nucleus volume at the upper border of upper group (n_i)	1.91	1.97	1.93	1.85	1.94	1.90
correction of volume ($p = n_i - 1.92$)	−0.01	+0.05	+0.01	−0.07	+0.02	−0.02
log nucleus volume central neurons (n_c) (equal to $1.92 + vc + p$)	2.16	2.24	2.28	2.23	2.35	2.40
log depth of upper border upper group (d_i)	2.24	2.27	2.23	2.24	2.34	2.25
correction of depth ($q = d_i - 2.25$)	−0.01	+0.02	−0.02	−0.01	+0.09	0.00
log depth of upper central neuron (d_I) (equal to $2.25 + vc + q$)	2.49	2.54	2.58	2.62	2.75	2.75
log depth of lower central neuron (d_{II})	3.07	3.02	3.04	3.13	3.21	3.30
$d_{II} - d_I$	0.58	0.48	0.44	0.51	0.46	0.55
tangent of upper regression line	1.00	1.00	1.00	1.00	1.00	1.00
tangent of lower regression line (equal to v)	0.50	0.54	0.70	0.80	0.82	1.00
number of neurons counted in upper group (under 0.01 mm² pial surface)	484	328	354	446	398	324
item in lower group	696	336	392	474	324	302
the proportion of these numbers	0.70	0.98	0.90	0.94	1.23	1.08

of the gyrus centralis anterior. In this area with the largest cells the radius measures 0,50, being equal to *log* C (the logarithm of the cortex factor). It is found minimal in the optic area striata, the field with the smallest cells. In this area it is 0,25 or ½ c (if $c = log\ C$). In the other areae studied its value lies between ½ c and c. The radius, therefore, can best be expressed by the formula vc, in which c is the constant distance between the two centres, that is the logarithm of the cortex factor C. In the various areae the value of v varies from ½ to 1.

What is the exact meaning of this v? Owing to the fact that it defines the size of the circles (the size of the correlation fields) it characterizes to a great extent the structure of each special architectonic field.

In the first place it defines the nucleus volume of the two central neurons. In the general scheme of fig. 1 the upper centre lies vc more to the right than the starting point of the upper regression line. In each area this starting point representing the same nucleus volume of 83 μ^3, the log

nucleus volume of the central neuron is $log\ 83 + vc = log\ 83 + v\ log\ C = log\ 83 + v\ log\ 3{,}16$. The nucleus volume of the central neurons, in consequence, is $3{,}16^v \times 83\ \mu^3$.

The central nucleus volume being nearly equal to the geometrical mean nucleus volume of the upper main group, the value of v of an architectonic field determines the mean size of its ganglion cells: a larger value of v is found in an area with larger cells. As in the formula $log\ N_c = 3{,}16^v \times 80\ \mu^3$ the v is an exponent, v can be called *the exponent of the architectonic field*.

In the second place v defines the depth of the two central nerve cells. In fig. 1 the centre of the upper field lies vc lower than the starting point of the regression line. The starting point lying at a depth of 168 μ, the depth of the upper central nerve cell is $3{,}16 \times 168\ \mu$. In an area with larger nerve cells the upper central neuron has a larger main dendrite than in an area with smaller cells.

In each area the depth of the lower central neuron being 3,16 times the depth of the upper one, the depth of the lower central cell is $3{,}16 \times 3{,}16^v \times 168\ \mu$ or $3{,}16^{v+1} \times 168\ \mu$.

In the third place it defines the thickness of the two main groups.

From fig. 1 it follows, that the lower border of the upper group is indicated $2vc$ lower than its upper border (the starting point). The lower border, thus, lies at a depth equal to $3{,}16^{2v} \times 168\ \mu$.

The height of the lower field in fig. 1 is half as large as that of the upper field. Its upper border is drawn $\frac{1}{2}vc$ higher and its lower border $\frac{1}{2}vc$ lower than its centre. The lower main group, thus, starts at a depth of $3{,}16^{\frac{1}{2}v-1} \times 168\ \mu$ and it ends at a depth of $3{,}16^{1\frac{1}{2}v+1} \times 168\ \mu$. The depth of the lower border of the lower group is the same as the total thickness of the cortex. The field exponent v, thus, also defines the thickness of the cortex in the field.

In the fourth place v defines the geometrical mean volume at each depth of the lower group.

In the upper group the mean volume is determined by the depth only: the starting point of the regression line indicates the constant mean nucleus volume of 83 μ^3 at a depth of 168 μ and the mean nucleus volume in the upper group being proportional to the depth, in each area the mean nucleus volume at a depth of d μ in the upper group is $\frac{d}{168} \times 83\ \mu^3$.

In the lower group, however, the nucleus volume increases proportional to a higher power of the depth, the regression line having a smaller gradient than 45°. This gradient differs in the different architectonic fields. Its tangent is found equal to v. In the lower group, thus, the depth increases proportional to the v-power of the mean nucleus volume. The value of v being known, the mean nucleus volume at each depth of the lower group can be calculated from it.

Owing to the height of the lower correlation field in fig. 1 being vc and the tangent of its regression line being v, the endpoint of this regression line lies c more to the right than its starting point: in each area the largest mean nucleus volume of the lower group (lying at the border between cortex and white matter) is 3,16 times as large as its smallest mean nucleus volume (lying at the upper border of the lower group). The total variation range of the mean nucleus volumes in the lower group, expressed in times, thus, is the same in all areae. In the upper group, on the contrary, it differs in the various areae, the endpoint of the regression line lying $2vc$ more to the right than its starting point, the largest mean nucleus volume, in other words, being $3{,}16^{2v}$ times as large as the smallest one.

In the fifth place the field exponent v defines the range of the variation in size of the ganglion cells at each depth in the cortex, the maximal variation at a special depth being determined by the horizontal diameter at that depth of the correlation field, bordered by the transformed circles of fig. 1. (More exactly it follows from the standard deviation spoken of above, which is equal to 0,37 times the radius or equal to 0,185 v.)

In the sixth place the exponent seems to define the number of ganglion cells present in each group under a unit of pial surface. In the upper group this number seems to be fairly constant, in the lower group it seems to vary inversely proportional to v. The numbers of cells measured, however, are to small to make this certain.

The details of the general scheme of fig. 1 described above can be summarized as follows.

In each architectonic area of the human cerebral cortex an upper and a lower main group of nerve cells can be distinguished. The cells of each group can be seen as variations from a mean type, called the central neuron of the group. The upper and the lower central neuron of one area have the same nucleus volume. The main dendrite (= depth under the pia) of the lower one is 3,16 times as long as in the upper one.

In the upper group the quotient nucleus volume divided by depth ($N : D$, probably being a measure of the shape of the dendrite field, in a cat N being found proportional to the length of the basal dendrites and D being the length of the main dendrite) varies normally (for exact meaning see above) and as many times as and independently of the depths (length of the main dendrites). The maximal extension of these variations from the values of the central neuron is $3{,}16^v$ times, in which v is the exponent of the field. In the various fields the value of v varies between $\frac{1}{2}$ and 1.

In the lower group the quotient $N : D^{1/v}$ varies normally and independently of the depth and as many times as $N : D$ in the upper group.

In consequence of these types of variation the mean nucleus volume varies with the depth: in the upper group it increases proportional to the depth, in the lower group proportional to the $^1/_v$ power of the depth.

Another consequention of these types of variation is the possibility to express the thickness of the cortex and of the two main groups and probably the number of the neurons as a function of the field exponent v.

The field exponent v, thus, defines the various sizes of the neurons at each depth of the cortex, it thereby describes the structure of the cyto-architectonic field to a great extent.

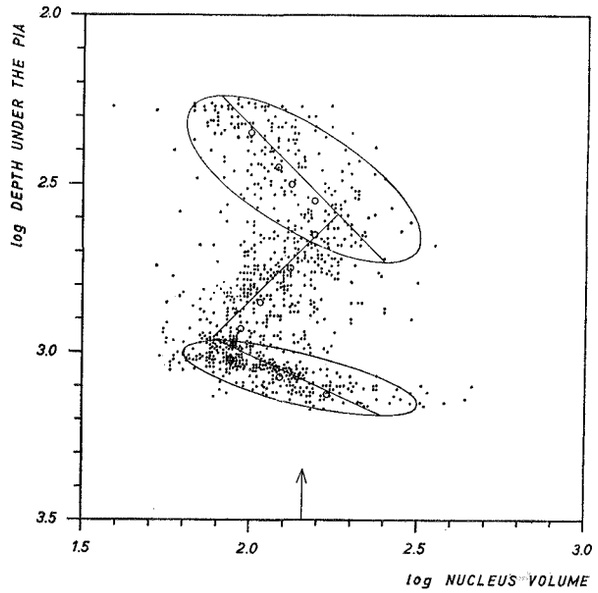

Fig. 3. Area striata ($v = 0.50$).

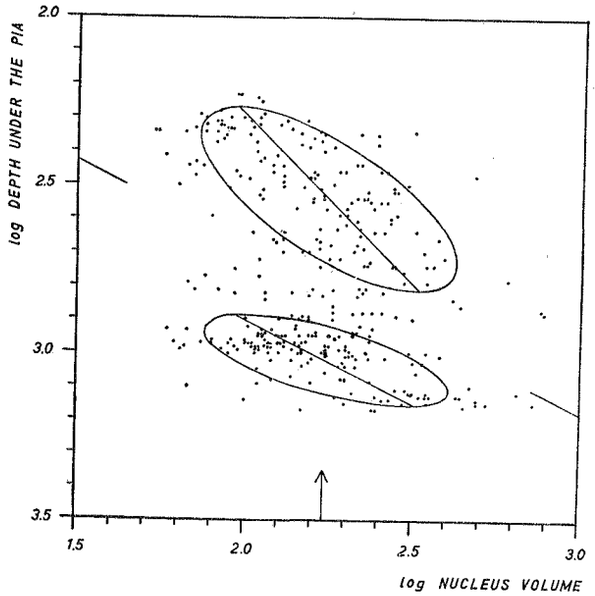

Fig. 4. Area parastriata ($v = 0.54$).

Indeed the cyto-architectonic fields, thus, seem to be different manifestations of one common scheme of structure and by far the most of their differences are due to the variation in size of only one property of that scheme. This size can be expressed by the value of the so called field exponent (v). Differences of smaller size, present in the measurings, could be defined by two other exponents p and q. The size of these extra

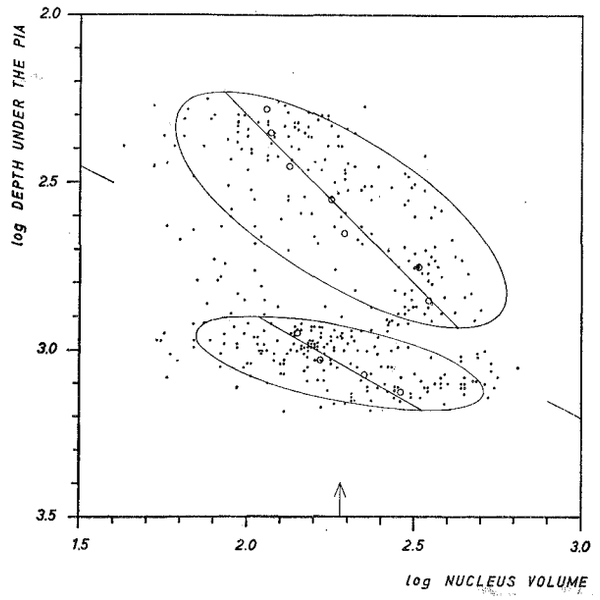

Fig. 5. Area orbitalis granulosa ($v = 0.70$).

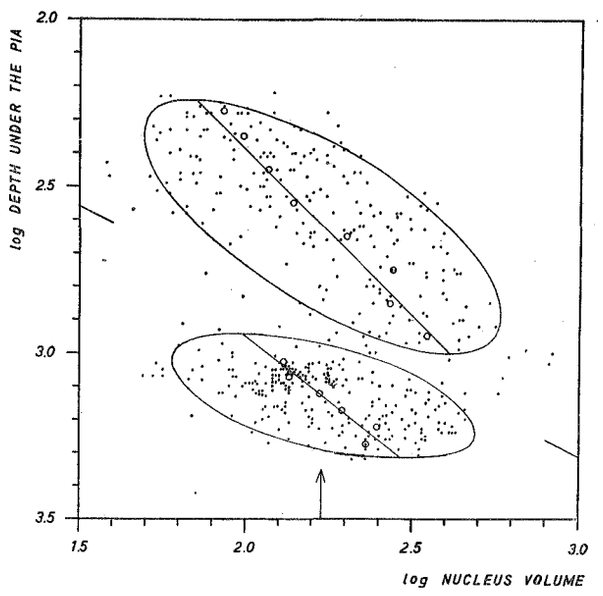

Fig. 6. Area postcentralis granulosa ($v = 0.76$).

exponents, however, is so small that it is not certain if they express real architectonic differences between the fields. If so, the differences indi-

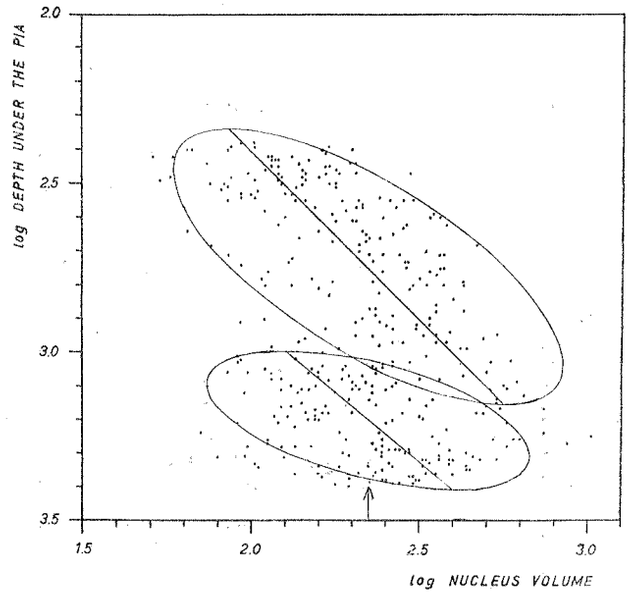

Fig. 7. Area paracentralis ($v = 0.82$).

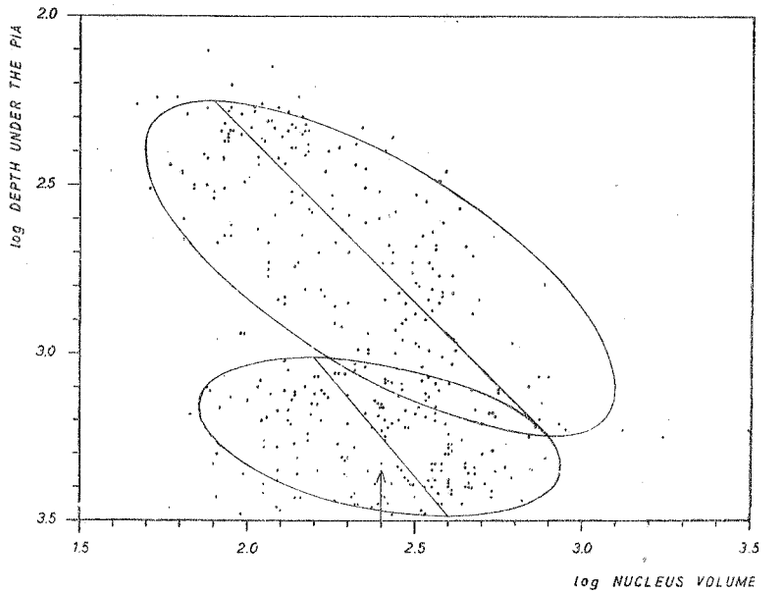

Fig. 8. Area praecentralis giganto-pyramidalis ($v = 1.00$).

cated by p and q are far smaller than those indicated by the field exponent v.

Anthropologie. — *Een onderkaaksfragment van Elephas primigenius met menschelijke bewerking.* Door A. J. P. v. d. Broek. (Communicated by Prof. L. Rutten.)

(Communicated at the meeting of November 25, 1939.)

Uit de zandgraverij te Maarn is een onderkaaksfragment te voorschijn gekomen, dat onze aandacht waard is.

De spoorweginsnijding bij Maarn gaat door den glacialen stuwwal, welks kern uit gestuwd praeglaciaal (prae-Riss) materiaal bestaat. Hij wordt hier en daar door resten van het keizand der Riss-periode bedekt.

Voor zoover uit de mededeeling van de werklieden en uit aanwijzing van de vindplaats is af te leiden, is het onderkaaksfragment afkomstig uit de geplooide lagen van den stuwwal, zoodat deze, naar den tijd, in het praeglaciaal moet worden gesteld, d.w.z. den tijd voorafgaande aan de grootste uitbreiding van de ijsbedekking van den Riss-ijstijd.

Het fragment is een deel van het corpus mandibulae. Aan de voorzijde gaat de breuk vlak langs het foramen mentale internum, aan het achtereinde is een klein gedeelte van den ramus ascendens aanwezig.

In verband met den geologischen ouderdom van de laag, waaruit deze kaak te voorschijn is gekomen, moet de vraag beantwoord worden of wij met de kaak van E. antiquus, dan wel van E. primigenius te doen hebben.

Aan de buitenzijde (fig. 1) komen 3 foramina mentalia voor, aan de binnenzijde (fig. 2) één. De nog aanwezige rest van den ramus ascendens maakt een stompen hoek met den bovenrand van het corpus mandibulae, wat er voor zou pleiten, dat wij met een betrekkelijk jong individu te maken hebben; hoewel in de richting van corpus en ramus ascendens ten opzichte van elkaar, vooral bij E. primigenius, variabele verhoudingen bestaan (Pohlig).

Aan de binnenzijde (fig. 2) zijn de afdrukken van hoogstwaarschijnlijk twee gebitselementen te zien, die wel bewijzen, dat het fragment van E. primigenius afkomstig is.

Vooraan vindt men een diepe, gekromde alveolus, waarvan de doorsnede aan het boveneinde 35 mm. is, de diepte, in rechte lijn gemeten, 95 mm. Daarachter vindt men een trapeziumvormigen indruk, aan den bovenrand ± 145 mm. lang, in 't midden 95 mm. hoog. Duidelijk zijn hier de indrukken van 10 (11?) lamellen vast te stellen, de formule van het desbetreffende element zou dus moeten luiden (x) 10 (11?) (x); met een kroonlengte (gemeten volgens de opgave van Pohlig) van hoogstens 135 mm. De afstand der lamellen is ± 12 mm.

In het onderstaande schema zijn de formules en de maten van enkele