Anatomy. — *The influence of the cephalization coefficient and body size upon the form of the forebrain in mammals.* By C. U. ARIËNS KAPPERS.

(Communicated at the meeting of October 24, 1927).

In the following pages I give some figures concerning the general form of the forebrain in less and more cephalized mammals of the same orders, and some data concerning the influence of the body size upon this form in different varieties of the same species, or in different, but equally cephalized species of the same family.

As only the forebrain is concerned here, my indices should not be confused with those obtained by measuring the length-width index of the endocranial cavity, since in this cavity the cerebellum also is included. Whereas in the anthropoids (also in several other monkeys) and in man, the length-width index of the endocranial cavity corresponds with that of the forebrain, which in these animals and in man covers the cerebellum entirely, it is different with lower mammals, where the forebrain covers the cerebellum only partly or not at all (Fig. 1) and its length therefore is not the same as that of the endocranial cavity.

As a standard for the greatest length of the forebrain I did not take the greatest horizontal measurement (*b*—*b'*) but the greatest possible distance between the front- and hindpole (*a*—*a'* in Fig. 1), which in most animals is an inclining line. The accompanying figure explains my intention. I did this because it gives a better expression of the size of the brain and its increase in length.

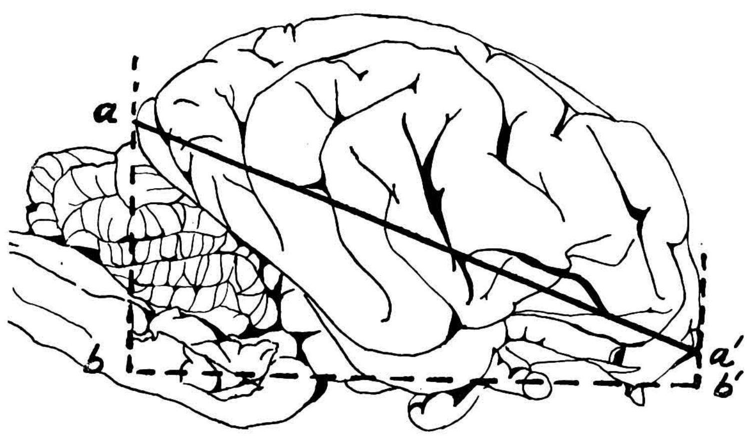

Fig. 1. Felis leo (nat. size).

In the following tables are given the greatest length and width of the forebrain and the index resulting therefrom in more and less cephalized species of the same orders and in some differently cephalized species of the same families. In these animals consequently, the cephalization coefficient k of DUBOIS' [1]) formula, $E = kP^r$, is obviously different.

I noted also the total weight of the brain up to 2—3 mm beyond the calamus. *The material used was weighed without meninges* [2]) after preservation in formaline 10 % [3]). In foot notes the brainweight found by others [4]) is mentioned.

MARSUPIALS.

Animal	Forebr. length	Forebr. width	Forebr. index	Total brainweight
Metachirus opossum (S.Am.)	2.7 cm	1.9 cm	70.4	3.75 gr.
Macropus cervinus	5.— „	4.6 „	92.—	61.— „
Macropus robustus	5.4 „	5.— „	92.6	64.— „
Phascolomys latifrons	4.2 „	4.4 „	105.—	37.5 „

Among marsupials (table 1), according to DUBOIS, a difference in the cephalization coefficient occurs between the North American (Virginian) opposum [5]) and the Macropodidae, that of the latter being about $1\frac{1}{2} \times$ as large as that of the opossum. This apparently corresponds with a greater forebrain index, a distinct brachencephaly in the Macropodidae.

1) DUBOIS. The proportion of the weight of the brain to the size of the body in mammals. Verhandelingen der Kon. Akad. v. Wetenschappen, Vol. **5**, N⁰. 10, 1897 (the same in Bulletin de la Société d'Anthropologie de Paris 1897 and Arch. f. Anthropologie Bnd. **25**, 1898).

DUBOIS. On the significance of the large cranial capacity of Homo neandertalensis. These Proceedings Vol. **23**, 1921,

DUBOIS. Phylogenetic and ontogenetic increase of the volume of the brain in Vertebrata. These Proc. Vol. **25**, 1922,

DUBOIS. The brainquantity of specialized genera of mammals. These Proc. Vol. **27**, 1924.

2) This may explain the slightly smaller weights of some of my specimens in comparison with those found by others.

3) According to FLATAU the brainweight increases about 1 % after preservation (during 15 months) in 10 % formaline. (Beitrag zur technischen Bearbeitung des Zentral-Nervensystems, Anat. Anzeiger, Bnd. **13**, 1897).

4) Specially the following: KOHLBRUGGE, Zool. Ergebn. einer Reise in Niederl. Ost Indien, Leyden 1891, p. 139 and Natuurk. Tijdschr. v. Ned. Indië, Deel **55**, p. 261, Batavia 1896, Zoogdieren v. d. Tengger. Further: Zeitschr. f. Morph. und Anthrop., p. 43—55, Bnd. **2**, 1890, and Monathschr. f. Psychiatrie und Neurologie, 1901.

WEBER, Vorstudien über das Hirngewicht der Säugethiere, Festschr. f. Carl Gegenbaur, Leipzig 1896 and these Proceedings 1896.

ZIEHEN, Anatomie des Zentralnervensystems, Fischer, Jena, 1899.

SPITZKA, Brainweight of Animals etc. Journ. of Comp. Neurol., Vol. **13**, 1903.

5) Didelphis virginiana has a brainweight (ZIEHEN) of 3.9—4.5 gr.

The remarkable brachencephaly of the Wombat is not a result of a greater cephalization compared with the Macropodidae, but is due to flatness of the front part of its skull, which gave it the epithet "latifrons".

In Rodents with various cephalization coefficients the following proportions were found :

RODENTIA.

Animal	Forebr. length	Forebr. width	Forebr. index	Total brainweight
Cavia cobaya	2.24 cm	2.10 cm	93.7	4.3 gr.
Dasyprocta aguti	3.44 „	3.35 „	97.4	17.5 „ [1])
Hydrochoerus capybara	5.69 „	5.69 „	100.—	58.— „ [2])
Dolichotis patagonica	3.8 „	4.55 „	120.—	31.5 „

Here also, the increase of brachencephaly in animals with a greater cephalization coefficient is obvious, since in Hydrochoerus and Dolichotis this coefficient is more than twice as large as in Cavia aperea, the wild form of Cavia cobaya.

The same is observed if we compare the poorly cephalized artiodactyle, Sus scrofa, with the more cephalized artiodactyles, the giraffa and dromedary, and with the perissodactyle horse. The cephalization coefficients of the giraffa, dromedary and horse are twice as large as that of Sus. It is obvious that the last three have also a higher index. Upon the very high index of the dromedary, the youth of this specimen also has influence (compare page 76).

UNGULATES.

Animal	Forebr. length	Forebr. width	Forebr. index	Total brainweight
Sus scrofa dom.	7.28 cm	5.68 cm	78	112.— gr. [3])
Bos taurus	10.6 „	10.09 „	95.2	403.— „ [4])
Camelopard. giraffa	13.5 „	11.96 „	88.6	665.— „ [5])
Camelus dromed. (young sp.)	9.8 „	10.— „	102.—	478.— „ [6])
Equus caballus	10.79 „	10.17 „	94.2	549.— „ [7])

[1]) SPITZKA found variations of 16—21 gr. WEBER found 20 gr.
[2]) A specimen weighed by WEBER (apparently larger) showed 75 gr.
[3]) ROGNER (quoted from ZIEHEN) found variations from 111—120 gr.
[4]) BISCHOF found variations from 400—500 gr.
[5]) WEBER's largest specimen had a brainweight of 680 gr.
[6]) LAPICQUE weighed a dromedary cerebrum of 650 gr., ZIEHEN one of 655 gr.
[7]) WEBER found 615 gr., SPITZKA only 519.5 gr. COLIN 593—640 gr.

The brachencephaly of the *elephant* is striking, especially if we compare this animal with its nearest relative among living ungulates, *Procavia dorsalis*, but also in comparison to the Tapir. This is again in accordance

Animal	Forebr. length	Forebr. width	Forebr. index	Total brainweight
Procavia dorsalis	3.92 cm	3.1 cm	79.—	19.7 gr. [1]
Tapirus indicus	8.— „	7.7 „	96.2	204.9 „ [2]
Elephas indicus	23.— „	28.5 „	124.—	5474.— „ [3]

with the greater cephalization of the elephant which, according to DUBOIS, is about 4 × greater than its nearest living relative, the ungulate Procavia, and also more than the tapir.

If we now study the Carnivora, Viverridae, Mustelidae, Procyonidae and Ursidae and among the Cetacea an Odontocete and a Mysticete, it is obvious that here again the more cephalized forms are more brachencephalic. So the Viverridae generally have the smallest cephalization coefficient.

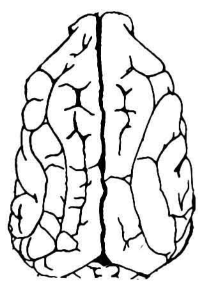

Fig. 2. Paradoxurus musanga, adult (nat. size)

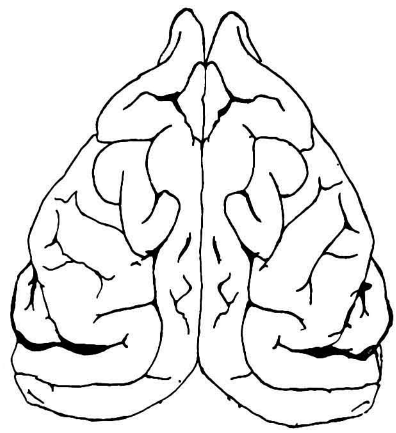

Fig. 3. Lutra vulg. adult, (nat. size)

CARNIVORES.

Animal	Forebr. length	Forebr. width	Forebr. index	Total brainweight
Mungos mungo	3.4 cm	2.5 cm	73.5	12.— gr. [4]
Paradoxurus musanga	4.2 „	3.2 „	76.2	23.5 „ [5]
Arctitis binturong	5.— „	3.9 „	78.—	37.— „

[1]) WEBER found with related Hyrax capensis variations of 19.2 gr. to 21 gr.

[2]) WEBER found 265 gr.

[3]) The heaviest specimen of CRISP had a brainweight of 5430 gr.

[4]) Herpestes mungo by WEBER: 10.9 gr.

[5]) WEBER: 22 gr.

CARNIVORES (*Continued*).

Animal	Forebr. length	Forebr. width	Forebr. index	Total brainweight
Putorius putorius [1]	3.1 cm	2.3 cm	74.2	7.7 gr. [2]
Meles taxus	5.46 „	4.5 „	82.4	45.— „
Lutra vulgaris	5.8 „	5.— „	86.2	45.6 „ [3]
Nasua rufa	5.2 cm	3.71 cm	72.0	29.9 gr. [4]
Procyon cancrivorus	7.— „	5.7 „	81.4	93.— „
Ursus arctos (young spec.)	9.—cm	8.— cm	88.8	234.— gr. [5]
Ursus malayanus	9.4 „	8.5 „	90.4	313.— „ [6]
Ursus maritimus (young sp.)	11.— „	10.1 „	92.—	424.— „ [7]

CETACEA.

Balaenoptera sulfurea	22.—cm	29.8 cm	135	5676.— gr. [8]
Phocaena communis	7.8 „	12.4 „	160	389.— „ [9]

Only Paradoxurus and Arctitis have (DUBOIS) a $1\frac{1}{4}\times$ larger cephalization coefficient than the Mustelid Putorius, and among Mustelids Meles and Lutra, have the greatest cephalization coefficient. My table shows that these two are also the most brachencephalic while Putorius is less brachencephalic than the Viverridae.

The largest cephalization coefficient of all carnivora, however, occurs in the Ursidae whose cephalization coefficient on the average is twice as large as that of the Viverridae (DUBOIS l.c. tertio p. 322) and $1\frac{1}{2}\times$ as large as that of the Nasuae. In accordance with this it appears that the Ursidae are also the most brachencephalic.

It is remarkable that Procyon cancrivorus (the crab washbear), which in the zoological system is more related to the Nasuae, also belonging to

[1]) With the small Grison and Mephitis I found broader brains (80 and 82), notwithstanding their small cephalization coefficient. I ascribe this to the smaller size of these animals (Cf. p. 8 and 9).

[2]) DUBOIS: 7.8 gr.

[3]) SPITZKA found with Lutra 39 gr.; HUSCHKE (citated after ZIEHEN) 42—51 gr.

[4]) SPITZKA found variations from 29 to 41 gr.

[5]) SPITZKA found with Ursus Americanus variations from 192 to 248 gr.; WEBER found a cerebrum of Ursus arctos weighing 407 gr.

[6]) WEBER found 325 gr.

[7]) Ursus maritimus may, according to WEBER, reach a fresh brainweight of 530 gr.

[8]) WEBER's specimen of Balaenoptera sibbaldi had a brainweight of 7000 gr.

[9]) ZIEHEN found an average of 512 gr.

the Procyonidae, has a larger cephalization coefficient and accordingly a larger forebrain index than the Nasuae.

Among the Cetacea, the Odontocetes have a greater cephalization coefficient than the much bigger Mysticete Balaenoptera (DUBOIS). And again this corresponds with a greater brachencephaly in Odontocetes.

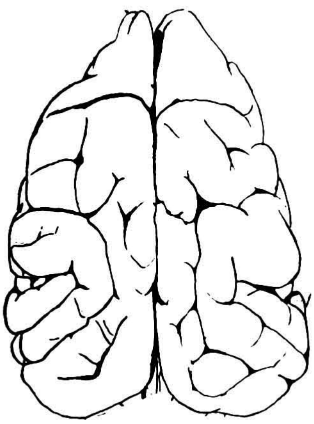

Fig. 4. Nasua rufa, adult (nat. size)

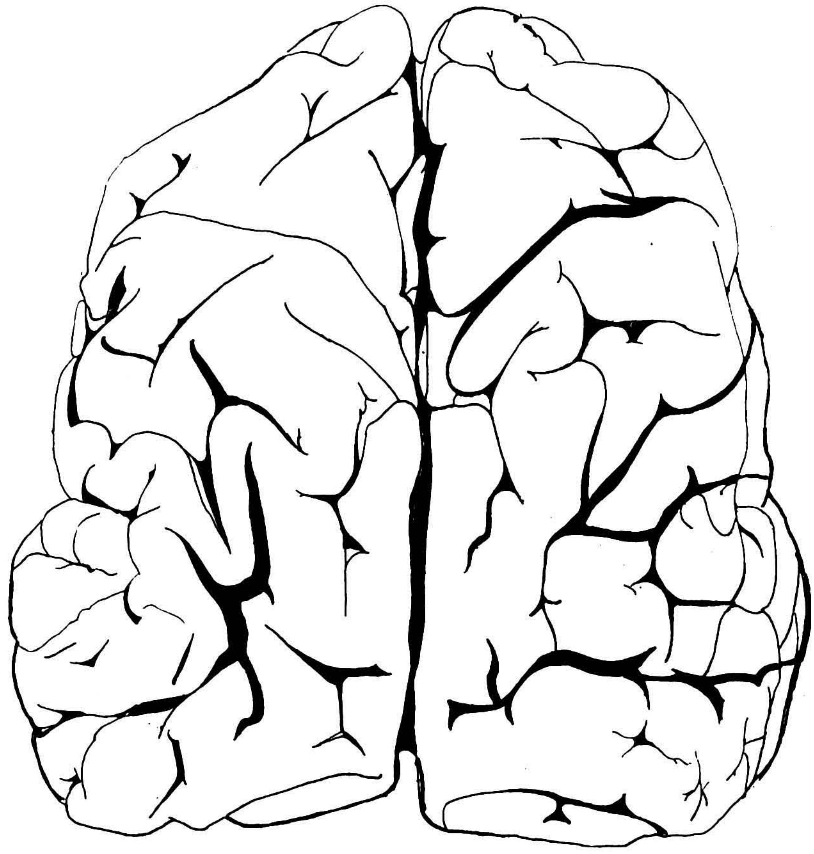

Fig. 5. Ursus maritimus, adult (nat. size)

PROSIMIAE.

Animal	Forebr. length	Forebr. width	Forebr. index	Total brainweight
Lemur mongoz	4.53 cm	3.8 cm	83.8	23.5 gr. [1]
Chiromys madagascariensis	4.7 „	4.5 „	95.8	34.6 gr. [2]

Of the Prosimiae, Chiromys has a cephalization coefficient twice as large as the Lemurs. Correspondingly its forebrain is more brachencephalic.

[1] WEBER found variations of 21—28 gr.

[2] WEBER found a brainweight of 43 gr.

WESTERN APES

Animal	Forebr. length	Forebr. width	Forebr. index	Total brainweight
Callithrix jacchus	3.5 cm	2.46cm	70.3	10.— gr. [1]
Cebus apella	7.— „	5.5 „	78.5	69.— „ [2]

In the Platyrrhine apes, the coefficient of Cebus is four times as large as that of Callithrix. Accordingly we see that its forebrain index is less dolichencephalic than that of Callithrix, although the latter has a smaller body and consequently one might expect a larger index in Callithrix (see p. 72, 73, 74).

In Katarrhine monkeys and in Anthropoids I found the following indices.

EASTERN APES.

Animal	Forebr. length	Forebr. width	Forebr. index	Total brainweight
Cercopithecus pygerythrus	6.8 cm	5.5 cm	80.9	76.— gr.
Macacus nemestrinus	7.5 „	6.— „	80.—	103.8 „ [3]
Symphalangus synd. (small spec..)	7.6 cm	6.—cm	80.—	107.— gr. [4]
ANTHROPOIDS.				
Pan (Troglodytes) Schweinf.	10.8 „	9.1 „	84.2	374.— „ [5]
Simia sat. (small spec.)	9.8 „	8.6 „	87.7	295.— „ [6]

The cephalization coefficient of these Anthropoids appears to be twice as large as that of the Katarrhine monkeys (DUBOIS) and accordingly they are more brachencephalic [7]). The Gibbon (Symphalangus syndac-

[1]) SPITZKA found variations of 7—9 gr. in Jacchus vulg.

[2]) For Cebus capucinus WEBER also found 69 gr.

[3]) SPITZKA found in Mac. nemestrinus an average brainweight of 110 gr.

[4]) KOHLBRUGGE found variations from 102 to 130 gr.

[5]) The Troglodytes of WEBER varied from 340—348 gr. One specimen of SPITZKA weighed 380 gr.; that of MÖLLER 391 gr.; one of MARSHALL 412 gr.

[6]) The statements of WEBER vary from 306—339 gr. DENIKER and BOULART reported a cerebrum of 400 gr., just as MILNE EDWARDS. R. FICK, one of even 440 gr. (quoted from ZIEHEN).

[7]) The index of the Gorilla brain and the endocranium varies very strongly. Two young cerebra of Madelle COUPIN gave me an average of 84.4, two endocranial casts received from ELLIOT SMITH 79,2. BOLK (these Proceedings 1925) found variations between 80.6 and 85.9 (an average of 83.25) and besides on specimen with an index of 72.2. HARRIS, having investigated the greatest number of endocrania, found variations from 72.1 to 86.8. (American Journal of physical anthropology, 1926).

tylus), which usually is considered as a transition between Cercopitheci and Anthropoids, stands closer to the first in this respect.

From these comparisons it appears that generally the more highly cephalized species of an order tend to brachencephaly. Their forebrain has a rounder instead of a longer form. Deviations of this rule are discussed p. 78—80. This tendency must be explained by the fact that if a brain increases more than in the usual proportions with the body, its volume increases more than its surface, the latter being limited by the skull. Consequently it approaches the form of the globe, since a globe contains the greatest volume with the smallest surface.

As the more highly cephalized species in my tables are also generally larger animals, one might be inclined to consider body size as a factor, causing brachencephaly. That this is not so, however, clearly appears from the following tables, in which smaller and larger, but equally cephalized representatives of the *same species*, or of the *same family*, are compared, so that the influence of body size can be traced separately.

From these tables it appears that the larger Canidae, Felidae, Nasuae, Pinnipedia and Odontoceti are *less brachencephalic* than the smaller ones, so that the brachencephaly cannot be the result of a larger body. The same appears with the Giraffidae, Antilopes, Cervidae (excepted Cephalobus and Capreolus) and Equidae. And again this is observed in monkeys, if we compare equally cephalized species of different size.

In the following groups the cephalization coefficient k is about the same. The species differ only in size. It is obvious that in nearly all cases an *increase in body size* is accompanied with a *decrease of*

Influence of body size.

CANIS. [1]

Animal	Forebr. length	Forebr. width	Forebr. index.	Total brainweight
Griffon	5.6 cm	5.05 cm	90.2	55.2 gr.
Spaniel	7.1 „	5.75 „	81.—	90.— „
St. Bernard	7.4 „	5.70 „	77.—	97.— „ [2]
German dog	7.7 „	5.70 „	74.—	97.5 „

[1]) The weights which I found for these dogs are nearly all lower than those found by CORNEVIN (Études sur le poids de l'encéphale dans les diverses races des espèces domestiques. Journ. de Médicine vétérinaire et de Zootechnie, Année 1899 p. 248) and RÜDINGER, Ueber die Hirne verschiedener Hunderassen (Verhandl. der Anat. Gesellsch. in Strassburg 1894 p. 173). I presume that they made the weighings with the meninges (see note 2, p. 66).

[2]) A very large specimen examined by WEBER had even a brain weight of 123 gr.

FELIDAE.

Animal	Forebr. length	Forebr. width	Forebr. index	Total brainweight
Felis bengal. minuta	3.7 cm	3.5 cm	94.6	23.5 gr. [1]
Felis domestica	4.2 „	3.9 „	93.—	34.— „ [2]
Felis nebulosa	5.2 „	4.8 „	92.3	46.— „
Felis pardalis	5.7 „	5.18 „	91.—	72.— „
Felis concolor	7.4 „	6.25 .	84.5	149.5 „ [3]
Felis leo (small spec.)	8.3 „	7.3 „	88.—	195.— „ [4]
Felis tigris	8.8 „	7.4 „	84.1	202.— „ [5]

NASUA.

Animal	Forebr. length	Forebr. width	Forebr. index	Total brainweight
Nasua narica	4.6 cm	3.6 cm	78.3	23.3 gr.
Nasua rufa	5.2 „	3.71	72.—	29.9 „

PINNIPEDIA.

Phoca vitulina (small spec.)	7.1 cm	8.3 cm	116.9	205.— gr [6]
Otaria jubata	9.7 „	10.1 „	104.—	268.— „ [7]
Zalophus californianianus	10.1 „	10.1 „	100.—	347.— „ [8]

ODONTOCETI.

Animal	Forebr. length	Forebr. width	Forebr. index	Total brainweight
Phocaena communis	7.8 cm	12.4 cm	160	389.— gr. [9]
Tursio tursiops	12.85 „	16.85 „	132	± 1350.— „ [10]

[1] WEBER: 23.6 gr.

[2] WEBER found an average of 31 gr.

[3] A specimen of WEBER had a brainweight of 137.5 gr.

[4] WEBER found as average brainweight 216 gr.

[5] WEBER: 246 gr.

[6] WEBER found variations of 242—290 gr.

[7] These measures have been made on the drawing of MURIE (who gives also this weight) in his descriptive anatomy of the sealion (Otaria jubata). Transactions of the zool. Society of London. Vol. 8, 1874.

[8] SPITZKA found with this animal 335 gr. brainweight, WEBER 347—399 gr.

[9] ZIEHEN found an average brainweight of 512 gr.

[10] WEBER weighed a cerebrum of 1886 gr. It is remarkable that my specimen of Balaenoptera sulfurea (a Mysticete) has a somewhat larger index than Tursio. Possibly the heavy cerebrum of my Balaenoptera is a little broadened by lying on its basis.

ANTILOPES.

Animal	Forebr. length	Forebr. width	Forebr. index	Total brainweight
Gazella dorcas	6.1 cm	5.5 cm	90.1	78.— gr.
Gazella soemmer.	7.5 „	6.7 „	89.3	128.5 „
Cephalophus maxwelli	*5.35* „	*4.7* „	*87.8*	*47.—* „ [1]
Damaliscus albifrons	9.12 „	7.87 „	86.3	254.5 „
Taurotragus oryx liv.	12.2 „	10.3 „	84.4	437.— „
GIRAFFIDAE.				
Ocapia Johnstoni	10.6 cm	10.— cm	94.—	450 gr.[2]
Camelopard. giraffa	13 5 „	11.96 „	86.6	665 „

brachencephally or an increase of *dolichencephali*. This corresponds with the phenomenon found by KLATT [3]) that larger animals of the same family have longer skulls.

Consequently the greater brachencephaly in more cephalized species is a result of their greater cephalization only.

The elongation of the brain in larger animals of the same species is a phenomenon analogous to what is seen in onto-

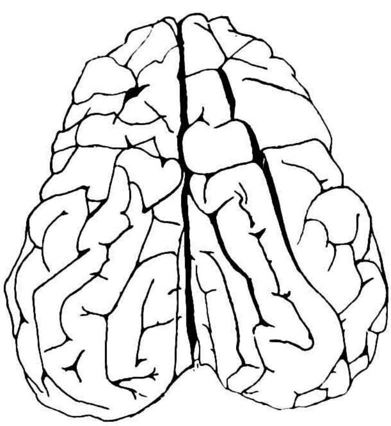

Fig. 6. Cervulus muntjac adult (nat. size).

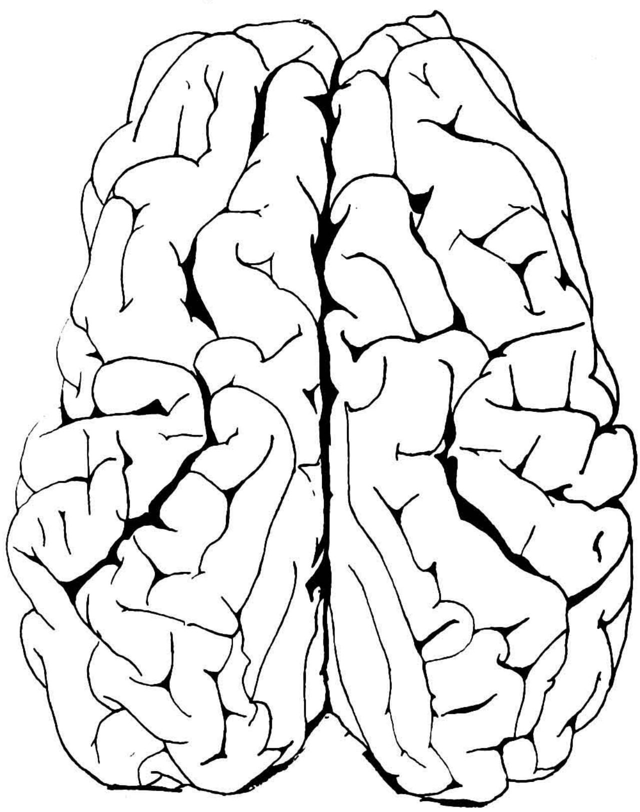

Fig. 7. Rucervus duvauc. adult (nat. size).

1) WEBER's heaviest cerebrum weighed 41.1 gr.

2) After the statement of BLACK: Journ. of Comp. Neurol. Vol. **25**, 1915.

3) KLATT, Ueber den Einflusz der Gesamtgrösze auf das Schädelbild nebst Bemerkungen über die Vorgeschichte der Haustiere. Archiv für Entwicklungsmechanik. Bnd **36**, 1913.

CERVIDAE.

Animal	Forebr. length	Forebr. width	Forebr. index	Total brainweight
Cervulus muntjac (small sp.)	5.23 cm	4.49 cm	85.8	44.— gr.
Rusa porcinus	8.2 „	7.— „	85.4	143.— „ [1]
Dama dama	8.22 „	6.99 „	85.0	167.— „
Rusa hipp. molucc.	8.34 „	7.1 „	85.1	186.— „
Capreolus caprae	*6.79* „	*5.70* „	*83.9*	*85.—* „ [2]
Rucervus eldi	9.65 „	7.4 „	79.3	202.— „
Rucervus duvauceli	10.7 „	8.3 „	77.5	297.— „
EQUIDAE.				
Equus asinus	9.2 cm	8.74 cm	95.—	334.7 gr. [3]
Equus caballus	10.79 „	10.17 „	94.2	549.— „ [4]
SIMIAE.				
Cercopithecus cynosurus	5.9 cm	4.8 cm	81.3	52.— gr. [5]
Cercopithecus pygerythrus	6.8 „	5.5 „	80.9	76.— „
Macacus rhesus	6.8 cm	5.57 cm	82.—	76.5 gr. [6]
Macacus nemestrinus	7.5 „	6.— „	80.—	103.8 „ [7]

genetic development, as appears from the ontogenetic tables (comp. also fig. 8 with 3 and 9 and 10).

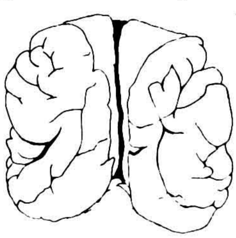

Fig. 8. Lutra vulg. neon. nat. size). Comp. this figure with fig. 3.

The same observation is made by MANOUVRIER and by M^elle^ COUPIN for the Gorilla and by the latter also for the Chimpanzee and Cercopithecus [8]). I have mentioned elsewhere that the same occurs in man [9]).

The fact that the length of the brain generally increases more than the width, in the individual development as well as in the larger representatives

[1]) WEBER: 142 gr.
[2]) WEBER found in Cervus capreolus 98 gr. HUSCHKE (quoted from ZIEHEN) 94 gr.
[3]) COLIN found with Equus asinus (quoted from ZIEHEN) 385 gr.
[4]) WEBER: 615 gr., COLIN: 593—640 gr.; SPITZKA 519.5 gr.
[5]) SPITZKA: 68.5 gr., WEBER: 70.5 gr.
[6]) SPITZKA found with Macacus rhesus an average brainweight of 80 gr. with variations of 71 to 98 gr.
[7]) SPITZKA found with Macacus nemestrinus an average brainweight of 110 gr. with variations of 84 to 128 gr.
[8]) F. COUPIN. Le développement comparé du cerveau chez l'homme et chez les singes. Revue scientifique 1926 p. 9 and fig. 2. It is remarkable that Madelle COUPIN could not state this with Semnopithecus, similarly I did not find it in Bos taurus.
[9]) ARIËNS KAPPERS, Indices for the anthropology of the brain applied to Chinese, dolicho- and brachycephalic Dutch, foetuses and neonati. Proceedings Kon. Akademie. Amsterdam, Vol. **30**, 1926.

of the same species or family cannot be explained only by abscence of necessity of the brain in larger animals to tend to globular form. This appears from the fact that among Cetacea, the brain which in smaller forms is flattened antero-posteriorly, in larger forms approaches the globular form because the index decreases in the direction of hundred.

CARNIVORES.

Animal	Forebr. length	Forebr. width	Forebr. index	Total brainweight
Lutra vulg. neon.	2.6 cm	2.7 cm	104.—	6.6 gr.
„ „ adult.	5.8 „	5.— „	86.2	45.6 „
Felis dom. neon.	2.—cm	2.1 cm	105.—	4.15 gr.
„ „ adult.	4.2 „	3.9 „	93.—	34.— „

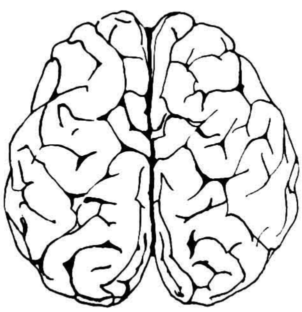

Fig. 9. Sus scrofa dom. neon. (nat. size)

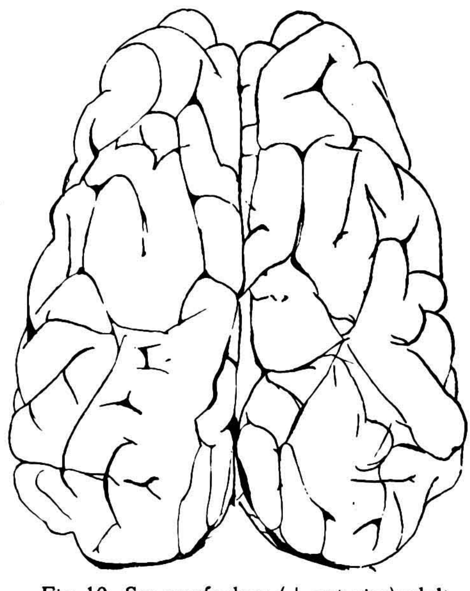

Fig. 10. Sus scrofa dom. (± nat. size) adult.

UNGULATES.

Sus scrofa neon.	3.5 cm	3.2 cm	91.4	14.— gr.
„ „ adult.	7.9 „	6.4 „	81.—	112.— „
Rusa porcinus neon.	5.4 cm	5.2 cm	96.3	54 gr.
„ „ adult.	8.2 „	7.— „	85.4	143 „
Camelop. giraf. neon.	10.2 cm	10.9 cm	108.2	466 gr.
„ „ adult.	13.5 „	11.96 „	88.6	665 „

Moreover as the extension of the whole skull (not only the endocranium) takes place especially in antero-posterior direction, we must consider the possibility that the *skull* itself in larger animals of the same family is relatively more lengthened, anteriorly because the insertion of teeth requires more place and posteriorly by the influence of the stronger cervical muscles and ligaments. On the other hand the skull narrows relatively in the larger specimens by the pressure of the larger masticatory muscles.

There is still another question that I want to discuss.

DUBOIS [1]) (l.c.) and LAPICQUE [2]) have shown that the exponent r in the formula $E = kP^r$ between adults of the same species (e.g. various dogs) is smaller ($^5/_{18}$) than in animals of different species ($^5/_9$).

DUBOIS (1922) called the first exponent "ontogenetic", the second, "phylogenetic", presuming that in larger varieties of the *same* species, as in ontogenetic (especially postembryonic) development, the increase of the brain is due merely to an *enlargement of the neurones* [3]). This neurone enlargement according to CONKLIN and G. LEVI, follows an exponent of about $^5/_{18}$ with respect to the body weight.

On the other hand, in more *cephalized* animals of various size in the larger species the enlargement of the neurones is accompanied by a *numeric increase of neurones*, the latter fact according to this anthor being responsible for the higher exponent $^5/_9$.

Is there anything in my tables that may confirm this ? Does the increase of the brain in larger varieties of the *same* species show more conformity with the enlargement of the brain during postembryonic development than it does in larger but not closely related species ?

Comparing the forebrain indices of the different varieties of the species Canis famil., we see that the difference in brainweight of only 42.3 gr. is accompanied by an increase of 18.2 units in the forebrain index.

Comparing members of the family of the Felidae (which is still very homogeneous) we find, with a maximal difference in the brain weight of 78.5 gr., a much smaller index difference, viz. 10.5. In the less homogeneous family of the Cervidae we find with a weight difference of 253 gr. an index difference below 10, (8.3), and in the still less homogeneous group of Antilopes with a still higher weight difference (359 gr.) an even smaller index difference (5.3).

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1) DUBOIS. Ueber die Abhängigkeit des Hirngewichts von der Körpergrösze beim Menschen. Archiv für Anthropologie Band **25**, Heft **4**, **1898**.

2) LAPICQUE. Sur la relation du poids de l'encéphale au poids du corps. Comptes rendus de la Société de Biologie, Paris 1898.

LAPICQUE. Le poids encéphalique en fonction du poids corporel entre individus d'une même espèce. Bulletin de la Société d'Anthropologie de Paris, 1907.

3) This is true for the Norwegian rat and tame albino rat (*Sugita*) compare DONALDSON : The significance of the brainweight. Transactions of the annual meeting of the American neurological Association, Philadelphia, 1924. — Archives of Neurology and Psychiatry, March 1925, p. 385.

If now we consider the index differences during postembryonic development, we find them very large, all above 10; Lutra 15.8, Felis 12, Rusa 10.7, Sus 10.4. The lowest of these still comes in the group of the very homogeneous Felidae. All other index differences are higher and approach varieties of one species (cf. Canis familiaris).

In other words the elongation of the brain in larger animals shows a greater conformity with the ontogenetic elongation if a group is more homogeneous and its elongation resembles the ontogenetic elongation in varieties of the *same* species. This appaıently is in conformity with DUBOIS' supposition.

That the increase of the brain in fullgrown varieties of the same species or of closely related species of one family is only based upon cell enlargement (though this is surely the most important factor) is perhaps too strongly expressed, the more so since we know that some, though not much cell division also occurs during postembryonic development (AGDUHR) [1]).

In regard to the question of ontogenetic brain-body-weight relations I refer to the recent investigations of ANTHONY and COUPIN [2]), on what they call the "indice de valeur cérébrale": $\frac{PE}{PE'}$, in which PE is the real brain weight of a foetus and PE' the calculated brain weight which that foetus would have *if* it were an adult of this size.

We have seen that in animals with a higher cephalization coefficient the greater brachencephaly is a consequence of the greater degree of development of the brain compared to the body, in consequence of which the brain tends to the largest volume with the smallest surface (skull). In very primitive forms, however, particularly the most primitive recent species, the forebrain is very short, and consequently brachencephaly occurs, here also, although now it is not a consequence of the greater volume, but of the shortness of the forebrain.

So Ornithorrhynchus and Echidna have an index of 111.5 and 127.6.

Among Marsupialia the primitive Caenolestes and Orolestes are conspicuous for the shortness of their forebrain, in comparison to the Opossum. In Caenolestes obscurus the forebrain index (measured after a drawing of C. J. HERRICK) [3]) is 125.5; in Orolestes inca (after the drawing of Miss OBENCHAIN) [4]) 137.4. Orycteropus, which is also a primitive animal, has, after a drawing of SONNTAG and WOOLLARD [5]) a

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1) AGDUHR. Is the postembryonic growth of the nervous system due only to an increase in number of the neurones? Proceedings Royal Acad. Amsterdam Vol. **27**, 1919.

2) ANTHONY et COUPIN. Introduction à l'étude du développement pondéral de l'encéphale. l'Indice de valeur cérébrale au cours de l'évolution individuelle. Zagreb. 1925—1926.

3) The brain of Caenolestes. Publications of the Fieldmuseum, Zool. Vol. **14**, 1925.

4) The brains of the South American Marsupials Caenolestes and Orolestes, Publications of the Fieldmuseum, Zool. Vol, **14**, 1925.

5) A monograph on Orycteropus afer: II Nervous system, sense organs and hairs. Proceedings of the Zool. Society of London 1925. WEBER counts this animal among the Ungulates.

PRIMITIVE ANIMALS COMPARED WITH NON-PRIMITIVE (—).

Animal	Forebr. length	Forebr. width	Forebr. index	Total brainweight
Monotremes.				
Ornithorrhynchus	2.6 cm	2.9 cm	111.5	11.— gr.
Echidna	4.— „	5.1 „	127.6	19.— „
Marsupials.				
Caenolestes obscurus	0.954cm	1.2 cm	125.5	—
Orolestes inca.	0.914 „	1.24 „	137.4	—
(Macropus rob.)	5.4 „	5.— „	(92.6)	(64.— gr.)
Orycteropus	4.9 cm	5.4 cm	110.—	—
Ungulates.				
Perissodactyla				
Rhinoceros unic.	12.— „	13.3 „	111.—	864.— gr.
(Equus caballus)	10.79 „	10.17 „	(94.2)	(549.— „)
Artiodactyla				
Hippopotamus	10.3 „	11.— „	107.—	582.— „
Hippopot.; Garrod	—	—	111.6	—
(Sus scrofa dom.)	7.9 „	6.4 „	(81.—)	(138.5 „
Tragulus mem.	3.27 „	3.3 „	101.—	18.5 „
(Cervulus muntjac, small sp.)	5.23 „	4.49 „	(85.8)	(44.— „)
Sirenia.				
Halicore; Dexler [1])	6.9 cm	7.14cm	103.5	282 gr.
Manatus; Garrod	6.9 „	7.3 „	106.—	?
Carnivores.				
Viverra civetta	4.5 cm	4.0 cm	88.—	40.5 gr.
(Paradoxurus musanga)	4.2 „	3.1 „	(73.8)	(23.5 „)

very large forebrain index, viz. 110. The same is observed in Tragulus memmina (total brainweight 18.5 gr.) [2]), which is more primitive than the Antilopes and also has a smaller cephalization coefficient and yet shows a higher index than the latter, viz. 101.

While in the above named cases the small size of these animals might be considered as a factor in the increase of brachencephaly, this is not the

[1]) Das Hirn von Halicore dugong. Morph. Jahrb. Bnd. **45**, 19.

[2]) WEBER 17.1 gr.

case with the Rhinoceros, Hippopotamus and the Sirenia. Yet Rhinoceros sumatrensis in GARROD's drawing [1]) has an index of 119. OWEN's [2]) Rhinoceros unicornis has an index of 111 with a brain weight of 864 gr. A Hippopotamus of my collection has an index of 107 [3]) with a brain weight of 582 gr. (WEBER).

Halicore, calculated after the drawing of DEXLER, has an index of 103.5; Manatus, after that of GARROD [4]), 106.

Among the Viverridae, the most primitive and poorly cephalized Viverra civetta has an index of 88.8, while its relatives Mungos and Paradoxurus, though smaller, have an index of 73.5 and 76.2 respectively.

As stated above, however, the brachencephaly of the forebrain in these primitive animals has a very different character from the brachencephaly in highly cephalized animals, being the result of the shortness of the brain in the first case, whereas in highly cephalized animals it is due to greater width. The latter is a result of increase, the former, of lack of development of the forebrain.

CONCLUSIONS.

1. Higher cephalization within a certain group of animals causes brachencephaly.

2. Larger animals are usually more dolichencephalic than similarly cephalized small animals of the same group [5]).

3. The forebrain of primitive now living [6]) mammals is usually strongly brachencephalic, but this brachencephaly is of an entirely different character.

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1) See GARROD. Transactions of the Zool. Society of London. Vol. **10**, 1877—1879 The brain of the Sumatra Rhinoceros.

2) OWEN. On the Anatomy of the Indian Rhinoceros (unicornis) Ibidem vol. **4**, 1862.

3) GARROD's specimen had even a forebrain index of 111.6, after his drawings in the transactions of the Zool. Society of London Vol. **11**, 1885.

4) GARROD, Ibidem, Vol. **10**, 1877 (see also MURIE, ibidem Vol. **11**, 1879).

5) For the skull, this phenomenon is often stated in man. See KOHLBRUGGE: Tijdschrift v. h. Kon. Nederl. Aardrijksk. Genootschap 2de Serie. Deel **28**, 1911, p. 785.

6) Concerning extinct species, little may be said in this respect, because as a rule only data about the endocranium are available. But these animals are generally less cephalized (DUBOIS) than their present relatives.