

Anatomy. — *The Proportion of cerebellar to total brain weight in Mammals.* By IRMARITA KELLERS PUTNAM ¹⁾ M.D. (Communicated by C. U. ARIËNS KAPPERS).

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There are few data available upon the proportion between the weight of the cerebellum and that of the whole brain in mammals. Perhaps this is partly because there are few large collections of mammalian brains in existence. Moreover figures which do exist in the literature coming from different sources are not comparable as the cerebella have been removed in no standard fashion and the weighing of the brain has been done under varying conditions and generally with the meninges, at the least with the pia mater and parts of the arachnoid ²⁾).

Material and Methods.

A hundred mammalian brains of the collection at the Central Institute for Brain Research, Amsterdam, were used for this investigation. The body weights and the ages of the animals were not noted. The collection included old and young animals, but no foetal brains nor brains of new born animals were included. The brains mentioned below had all been preserved, without meninges, for varying lengths of time in 4 % formaldehyde (10 % formaline). Brains in 10 % formaline (4 % formaldehyde), according to FLATAU (1897), the first month of preservation increase from one to two per cent of their original weight.

Between the first and fifth months they loose some of this initial increase, so that at the fifth month they are only one per cent heavier than their original weight and remain so for the following months (FLATAU's observations covered 15 months). Most of the brains in this series were preserved for a still longer period. As however in the last ten months of a fifteen months preservation the then obtained increase of 1 % does not change, there is little reason to believe that it should increase later.

There is a slight percentage difference between weight changes in brain and spinal cord during similar preservation. Whether there is a difference between the change of the cerebellar weight and the rest of the brain we do not know. We can assume however that this is very slight.

¹⁾ Holder of the Vassar Alumnae Fellowship for graduate study, 1925—1926.

²⁾ Weighing the brain with the pia (and part of the arachnoid) includes a source of errors, as this tissue may keep a fairly great deal of the preservation fluid.

In alcohol on the other hand brains lose large amounts of weight and the loss is continuous, so that at the end of fifteen months a brain has lost thirty four per cent of its original weight. We have listed only one brain preserved in this way (cf. p. 162).

The hypophysis, which was often allowed to remain in the sella turcica, when the brain was removed from the skull in the zoological garden, was dissected off those brains where it was still attached in order to equalize conditions. *All meningeal tissue was carefully removed* ¹⁾.

The cerebellar peduncles were severed just above the emergence of the seventh and eighth nerves tangential to the brain stem, care being observed to leave the posterior corpora quadrigemina and the fourth nerve intact. The brain stem was cut 3 mm below the calamus scriptorius. Pains were taken to perform these manipulations as nearly as possible in the same way, as it is obvious that each one of them involves a source of error.

Of some of the brains only one half was available the other half being cut in microscopical sections. In these cases the *hemisection* is mentioned in my tables. They were only used for this statistic if it appeared that the hemisection was accurately made, and thus did not influence the percentage relation.

Weighing was done on a chemical balance sensitive to a milligram. The brains were removed from formaldehyde, dried with a soft towel (so that there was no more draining of fluid) and weighed directly, exposed to the air during the process. Very little time was required for this, since preliminary weighings had been made on the previous day to facilitate the final weighing.

It was found that one individual could so standardize the amount of drying and that there was less variation between two weighings of the same brain on successive days by this method than by either of the methods described in the next paragraph. Also it was found that the variations for small brains were less than for large brains which was the reverse with the other two methods. This is important because very slight changes in the weights of the small brains cause large percentage variations, while the reverse is the case for the large brains. However, these variations also constitute a source of error.

Dr. RICHARD S. LYMAN of Rochester University, New-York to whom I am indebted for much help, determined during his sojourn in the Central Institute for Brain Research the rate of loss of moisture when brains were allowed to dry in the open air, and found that a constant state of dryness was not reached at any point. As was to be expected the rate of loss was proportional to the surface area so that the cerebellum lost weight more rapidly than the rest of the brain and small brains more rapidly than large ones. An attempt was also made to bring the brains to a constant state of moisture by keeping them in a moist chamber.

While the daily variations of these brains were less than the hourly variations which Dr. LYMAN obtained, they were still greater than the variations obtained by the method

¹⁾ This may explain that the brain weight of several animals is less than the figures mentioned in the current literature.

described in the paragraph above, which was therefore chosen for the series. Comparative results of the three methods applied to a brain of a young *Nasua narica* (preserved in formaline 10%) are recorded below to establish the justification of this choice. (Table I).

I. Brain exposed to air during five hours (Determinations by R. S. LYMAN).

Moment of weighing	Cerebellar w.	Cerebral w.	Total brain w.	Cerebel. perc.
Aug. 13th 11.35 AM.	2.83 gr.	20.73 gr.	23.56 gr.	12.00%
" " 12.00 M.	2.79 "	20.59 "	23.38 "	11.93 "
" " 12.30 PM.	2.75 "	20.46 "	23.21 "	11.84 "
" " 1.00 "	2.73 "	20.37 "	23.10 "	11.82 "
" " 1.30 "	2.70 "	20.20 "	22.96 "	11.76 "
" " 2.30 "	2.65 "	20.09 "	22.74 "	11.64 "
" " 3.30 "	2.60 "	19.93 "	22.53 "	11.53 "
" " 4.30 "	2.55 "	19.77 "	22.32 "	11.42 "

II. Brain kept in moist chamber.

Sept. 5th	2.78 gr.	20.22 gr.	23.00 gr.	12.20%
" 6th 11.00 AM.	2.745 "	20.155 "	22.90 "	12.0 "
" " 4.00 PM.	2.74 "	20.04 "	22.78 "	12.05 "
" 7th	2.72 "	20.00 "	22.72 "	11.99 "
" 12th	2.67 "	19.72 "	22.39 "	11.96 "
" 14th	2.64 "	19.58 "	22.22 "	11.88 "

III. Brain removed from formaldehyde softly dried and weighed directly

Sept. 15th	2.73 gr.	20.53 gr.	23.26 gr.	11.73%
" 16th	2.74 "	20.57 "	23.31 "	11.70 "
" 17th	2.73 "	20.54 "	23.27 "	11.73 "

The method of weighing under water might be still more accurate. However, this method was not tried as it was thought too elaborate for this purpose. The temperature of the water influencing the specific gravity of the particular water used, movements in the water must all be carefully controlled, if this method is to be as accurate practically for our purpose as it is theoretically.

The results of the weighings are given in the accompanying table, which shows the weight of the cerebellum, that of the cerebral hemispheres and stem, the total brain weight and the proportion between the weight of the cerebellum and that of the total brain, expressed as a percentage of the latter.

The classification of the animals is essentially that of OSBORN (1910). The primates however, are listed according ELLIOT (1913).

ORDER RODENTIA.

	Wt. cereb.	Wt. cerebr.	Wt. together	% cereb.
<i>Sciuridae.</i>				
<i>Pteromys nitidus</i>	1.39 gr.	7.50 gr.	8.89 gr.	15.62 %
<i>Cynomys ludovicianus</i>	1.5 ..	9.95 ..	11.45 ..	13.10 ..
<i>Echinosciurus aureogaster</i>	.96 ..	5.24 ..	6.20 ..	15.45 ..
<i>Heterosciurus notatus</i>	.65 ..	3.63 ..	4.28 ..	15.18 ..
<i>Leporidae.</i>				
<i>Lepus cuniculus</i>	.94 ..	6.07 ..	7.03 ..	13.4 ..
<i>Hystriidae.</i>				
<i>Hystrix cristata</i>	2.9 ..	16.3 ..	19.2 ..	15.00 ..
<i>Hystrix javanica</i> (hemisect.)	1.39 ..	8.23 ..	9.62 ..	14.45 ..
<i>Coendu prehensilis</i>	2.57 ..	16.26 ..	18.83 ..	13.62 ..
<i>Chinchillidae.</i>				
<i>Lagostomus trichodactylus</i>	1.9 ..	13.48 ..	15.38 ..	12.35 ..
<i>Dasyproctidae.</i>				
<i>Dasyprocta aguti</i>	2.32 ..	17.58 ..	19.90 ..	11.65 ..
<i>Dasyprocta aguti</i>	2.08 ..	13.73 ..	15.81 ..	13.12 ..
<i>Octodontidae.</i>				
<i>Myopotamus coipu</i>	1.13 ..	10.33 ..	11.46 ..	9.80 ..

ORDER EDENTATA.

<i>Myrmecophagidae.</i>				
<i>Myrmecophaga jubata</i>	8.67 gr.	43.4 gr.	52.07 gr.	16.52 %
<i>Bradipodidae.</i>				
<i>Choloepus didactylus</i>	5.27 ..	25.68 ..	30.95 ..	13.84 ..
<i>Choloepus didactylus</i>	4.5 ..	24.31 ..	28.81 ..	15.55 ..
<i>Choloepus didactylus</i> (hemisection)	2.3 ..	12.16 ..	14.46 ..	15.90 ..
<i>Dasypodidae.</i>				
<i>Dasypus villosus</i>	2.19 ..	12.86 ..	15.05 ..	14.53 ..

ORDER UNGULATA.

Sub Order Artiodactyla.	Wt. cereb.	Wt. cerebr.	Wt. together	% cereb.
<i>Dicotylidae.</i>				
<i>Dicotyles labiatus</i>	7.67 gr.	58.98 gr.	66.65 gr.	11.55 %
<i>Camelidae.</i>				
<i>Camelus dromedarius</i>	57.5 ..	420.— ..	477.5 ..	12.05 ..
<i>Auchenia glama</i>	20.23 ..	128.85 ..	149.08 ..	13.60 ..
<i>Giraffidae.</i>				
<i>Camelopardalis giraffa (young)</i>	53.3 ..	433.— ..	486.3 ..	10.90 ..
<i>Cervidae.</i>				
<i>Cariacus nemoralis</i>	13.7 ..	114.4 ..	128.1 ..	10.70 ..
<i>Alces machlis</i>	27.8 ..	232.5 ..	260.3 ..	10.65 ..
<i>Cervulus muntjac (young spec.)</i>	4.45 ..	39.5 ..	43.95 ..	10.12 ..
<i>Rusa hippelaphus</i>	19.37 ..	116.15 ..	185.52 ..	10.4 ..
<i>Rusa hippelaphus</i>	19.7 ..	166.2 ..	185.52 ..	10.6 ..
<i>Rucervus Eldi</i>	21.9 ..	179.7 ..	201.6 ..	10.86 ..
<i>Dama dama</i>	14.9 ..	146.5 ..	161.4 ..	9.22 ..
<i>Ovidae.</i>				
<i>Ovis tragelaphus (small spec., hemisect.)</i>	12.1 ..	107.15 ..	119.25 ..	10.1 ..
<i>Ovis tragelaphus</i>	19 ..	173.— ..	192.— ..	9.87 ..
<i>Capra hircus (small spec.)</i>	10.35 ..	73.6 ..	83.95 ..	12.32 ..
<i>Antilopes.</i>				
<i>Antilope cervicapra (hemisect.)</i>	5.35 ..	44.5 ..	49.85 ..	10.75 ..
<i>Antilope borea</i>	6.3 ..	53.95 ..	60.25 ..	10.45 ..
<i>Oreas Livingstoni</i>	37.2 ..	395.4 ..	432.6 ..	8.65 ..
<i>Catoblepas gnu (small spec., hemis.)</i>	7.26 ..	66.3 ..	73.56 ..	9.86 ..
<i>Anoa depressicornis</i>	18.7 ..	163.3 ..	182.— ..	10.26 ..
Sub Order Perissodactyla.				
<i>Equidae.</i>				
<i>Equus caballus</i>	57 gr.	446 gr.	503 gr.	11.3 %
<i>Equus asinus</i>	36.5 ..	298.2 ..	334.7 ..	10.92 ..
<i>Tapiridae.</i>				
<i>Tapirus indicus</i>	27.77 ..	213.12 ..	240.89 ..	13.00 ..

ORDER PROBOSCIDAE.

	Wt. cereb.	Wt. cerebr.	Wt. together	% cereb.
<i>Elephas indicus</i> (small specim.)	923.— gr.	2816.—gr.	3739.—gr.	24.68 %

ORDER ODONCETI.

<i>Delphinidae.</i>				
<i>Phocaena phocaena</i> (hemisection)	28.85 gr.	157.86 gr.	186.71 gr.	15.49 %
<i>Phocaena phocaena</i>	58.— ..	332.— ..	390.— ..	15.— ..

ORDER CARNIVORA.

<i>Ursidae.</i>				
<i>Ursus arctos</i> (young sp.)	36.— gr.	196.— gr.	232.— gr.	16.30 %
<i>Ursus maritimus</i>	68.8 ..	365.5 ..	434.3 ..	15.75 ..
<i>Heliarctos malayanus</i>	40.7 ..	211.65 ..	252.35 ..	16.10 ..
<i>Mustelidae.</i>				
<i>Lutra vulgaris</i> (hemisection)	2.05 ..	22.— ..	24.05 ..	8.38 ..
<i>Lutra vulgaris</i> (hemisection)	1.94 ..	16.3 ..	18.24 ..	10.69 ..
<i>Putorius putorius</i>	0.61 ..	4.77 ..	5.38 ..	11.30 ..
<i>Mustela erminea</i> (hemisection)	0.3 ..	2.27 ..	2.57 ..	11.66 ..
<i>Mustela erminea</i> (hemisection)	0.22 ..	1.84 ..	2.06 ..	10.65 ..
<i>Mustela foina</i> (hemisection)	0.40 ..	2.81 ..	3.21 ..	12.60 ..
<i>Meles taxus</i>	5.39 ..	38.42 ..	43.81 ..	12.29 ..
<i>Viverridae.</i>				
<i>Paradoxurus musanga</i> (hemisection)	1.22 ..	7.35 ..	8.57 ..	14.28 ..
<i>Arctitis binturong</i> (hemisection)	2.17 ..	12.63 ..	14.80 ..	14.65 ..
<i>Herpestes griseus</i>	1.18 ..	9.38 ..	10.56 ..	11.17 ..
<i>Canidae.</i>				
<i>Canis familiaris</i>	4.55 ..	46.75 ..	51.30 ..	8.9 ..
<i>Canis familiaris</i>	7.— ..	66.93 ..	73.93 ..	9.6 ..
Black and Tan (hemisection)	3.82 ..	33.70 ..	37.50 ..	10.18 ..
Retriever (hemisection)	4.24 ..	42.12 ..	46.36 ..	9.15 ..
Dachshund	5.62 ..	62.81 ..	68.43 ..	8.25 ..
Spaniel	8.57 ..	81.7 ..	90.27 ..	9.50 ..
Airdale Terrier	7.18 ..	72.65 ..	79.83 ..	9.17 ..

	Wt. cereb.	Wt. cerebr.	Wt. together	% cereb.
Wolf Hound (hemisection)	3.81 gr.	35.97 gr.	39.78 gr.	9.60 %
Shepherd Dog (hemisection)	3.18 ..	32.7 ..	35.88 ..	8.85 ..
Gordon Setter (hemisection)	3.80 ..	41.80 ..	45.60 ..	8.46 ..
Collie (hemisection)	4.2 ..	35.66 ..	39.26 ..	10.62 ..
German Dog	10.2 ..	87.42 ..	97.62 ..	10.4 ..
Irish Setter	7.94 ..	73.62 ..	81.56 ..	9.70 ..
Boxer (hemisection)	3.28 ..	32.72 ..	36.— ..	9.02 ..
Canis lupus	5.67 ..	58.43 ..	64.10 ..	8.85 ..
Vulpus lupus opus (hemisection)	1.64 ..	12.11 ..	13.75 ..	11.90 ..
<i>Felidae.</i>				
Zibethailurus pardalis (hemisection)	2.57 ..	22.39 ..	24.96 ..	10.30 ..
Zibethailurus pardalis	6.98 ..	44.51 ..	51.49 ..	13.56 ..
Felis leo	19.65 ..	167.24 ..	186.92 ..	10.52 ..
Felis leo (hemisection)	8.78 ..	86.95 ..	95.73 ..	9.28 ..
Felis concolor (hemisection)	7.53 ..	48.11 ..	55.64 ..	13.05 ..
Felis concolor (hemisection)	5.78 ..	45.11 ..	50.89 ..	11.36 ..
Felis macroscelus nebulosa	6.13 ..	39.03 ..	45.16 ..	13.52 ..
Lynx lynx	5.78 ..	36.31 ..	42.09 ..	13.70 ..
<i>Phocidae.</i>				
Phoca vitulina (small spec.)	26.10 ..	143.40 ..	169.50 ..	15.4 ..
Phoca vitulina	29.5 ..	179.— ..	208.50 ..	14.1 ..

ORDER PRIMATES.

Prosimiae.

<i>Daubentonidae.</i>				
Cheiromys madagascariensis (sm. spec.)	3.38 gr.	22.23 gr.	25.61 gr.	13.18 %
<i>Lemuridae.</i>				
Lemur catta	1.38 ..	9.03 ..	10.41 ..	13.35 ..
Lemur macaco (hemisection)	1.42 ..	9.— ..	10.42 ..	13.60 ..
Lemur mongoz (hemisection)	1.40 ..	9.17 ..	10.57 ..	13.23 ..

	Wt. cereb.	Wt. cerebr.	Wt. together	% cereb.
<i>Simiae.</i>				
<i>Callitrichidae.</i>				
<i>Callithrix pygmaea</i>	4.66 gr.	37.61 gr.	42.27 gr.	11.— %
<i>Hapale jacchus</i>	.25 ..	2.6 ..	2.85 ..	8.75 ..
<i>Oedipomidas oedipus</i>	.8 ..	6.85 ..	7.65 ..	10.375..
<i>Oedipomidas oedipus</i>				
<i>Cebidae.</i>				
<i>Mycetes laniger</i>	.55 ..	6.03 ..	6.58 ..	8.36 ..
<i>Chrysothrix sciureus</i>	3.76 ..	28.30 ..	32.06 ..	11.70 ..
<i>Nyctipithecus trivirgatus</i>	.38 ..	3.06 ..	3.44 ..	11.06 ..
<i>Ateles ater</i> (hemisect.)	4.15 ..	34.— ..	38.15 ..	10.86 ..
<i>Lagothrix lagotricha</i>	9.7 ..	76.58 ..	86.28 ..	11.22 ..
<i>Cebus hypoleucus</i> (hemisect.)	2.32 ..	23.2 ..	25.52 ..	9.09
<i>Cebus hypoleucus</i> (hemisect.)	2.6 ..	17.92 ..	20.52 ..	12.68
				} 10.88
<i>Cebus fatuellus</i>	2.78 ..	25.10 ..	27.88 ..	9.95 ..
<i>Cebus fatuellus</i>				
<i>Lasiopygidae.</i>				
<i>Cynocephalus hamadryas</i>	10.15 ..	84.50 ..	94.65 ..	10.70 ..
<i>Cynocephalus porcarius</i> (hemisection)	7.8 ..	67.88 ..	75.68 ..	10.30 ..
<i>Macacus rhesus</i>	7.04 ..	70.6 ..	77.64 ..	9.05 ..
<i>Macacus rhesus</i>	6.07 ..	65.3 ..	71.37 ..	8.65 ..
<i>Cercocebus fuliginosus</i>	1.94 ..	16.3 ..	18.24 ..	10.62 ..
<i>Mona mona</i> (hemisection)	2.39 ..	24.8 ..	27.19 ..	8.80 ..
<i>Inuus inuus</i>	7.03 ..	72.53 ..	79.56 ..	8.80 ..
<i>Cercopithecus callitrichus</i>	5.42 ..	50.26 ..	55.68 ..	9.70 ..
<i>Erythrocebus patas</i>	6.93 ..	64.76 ..	71.69 ..	9.66 ..
<i>Semnopithecus entellus</i> (hemisection)	4.17 ..	38.61 ..	42.78 ..	9.75 ..
<i>Anthropoidae.</i>				
<i>Simia satyrus</i>	30.8 ..	191.4 ..	222.2 ..	13.86 ..
<i>Simia satyrus</i> (hemisection)	14.11 ..	92.32 ..	106.43 ..	13.25 ..
<i>Troglodytes niger</i> (hemisect.)	18.1 ..	102.5 ..	120.6 ..	15.—
<i>Troglodytes niger</i> (hemisect, alcohol)	17.27 ..	114.19 ..	131.46 ..	13.11
				} 14.05

Discussion.

The establishment of the percentage variations in individuals is a necessary preliminary to any interpretation of figures involving the larger groups. Unfortunately this collection contains few duplicates. Where more than one individual of a species is present, the maximum difference between the percentage weights is 3.59 as may be seen in the following table.

III. Percentage variation between different individuals of the same species.

Species	Individual	Percentage	Differences in percentage
Ovis tragelaphus	I	10.10	0.23
	II	9.87	
Macacus rhesus	I	9.05	0.40
	II	8.65	
Simia satyrus	I	13.86	0.61
	II	13.25	
Mustela erminea	I	11.66	1.01
	II	10.65	
Felis leo	I	10.52	1.24
	II	9.28	
Phoca vitulina	I	15.4	1.30
	II	14.1	
Dasypsecta aguti	I	13.12	1.47
	II	11.65	
Felis concolor	I	13.05	1.69
	II	11.36	
Rusa hippelaphus	I	10.60	0.20
	II	10.40	
Trogodytes niger	I	15.—	1.89
	II	13.11	
Choloepus didactylus	I	15.90	2.06
	II	15.55	
	III	13.84	
Lutra vulgaris	I	10.69	2.31
	II	8.38	
Zibethailurus pardalis	I	13.56	3.26
	II	10.30	
Cebus hypoleucus	I	12.68	3.49
	II	9.08	

In connection with this percentage variation among individuals, it is profitable to consider the figures reported by ARIËNS KAPPERS (1926), who also found a considerable range of variation amongst man.

The percentages of cerebellar to total brainweight in the brains
of 25 Dutchmen were 8 % to 12.6 % a range of 4.6 ;
of 22 Chinese 8.61 % to 12.22 % a range of 3.61 ;
of 8 Japanese 9.51 % to 11.25 % a range of 1.74.

It is very difficult to tell the cause of these variations and highly improbable that the cause in each case is the same.

For man WEISBACH (1867), who made a similar observation, believed the heavier specimens to have the greater cerebellar percentage.

The question whether body size has any influence on the cerebellar percentage of animals can be best controlled by comparing smaller and larger, though both adult representatives of the same species as enumerated in table III.

Of the animals mentioned there only of the two *Mustela erminea*, the two *Zibethailurus pardalis* and the two *Felis concolor* and two *Simia satyrus*, the largest specimens (according to the total brain weight) had larger cerebella.

On the other hand, however, of the two *Dasyproctae*, three *Choloepus*, two *Ovis tragelaphus*, two *Lutrae*, two *Phocae* and two *Phocaenae*, the specimen with the greatest (total brain) weight had a smaller percentage of cerebellum. From this no evidence can be obtained in favor of a constant influence of the bodysize (or total brainweight) in the percentage of the cerebellum.

Also KAPPERS could not confirm WEISBACH's opinion — that a larger weight should be constantly correlated with a larger cerebellum, although this occasionally occurs.

I have also made a comparison between the different representatives of the same order, suborder or genus wherever more than two specimens were available, just as I did in the cases of species. The advantage of this comparison is moreover that the differences in size are greater and more constant though certainly also other factors come in here (vide infra).

Here also it is evident that WEISBACH's thesis does not hold good as in the majority of cases the smaller genus has a higher percentage. So in the rodent suborder of *Sciuridae* the largest of all, *Cynomys ludovicianus*, has a cerebellar percentage of 13.10 %, whereas the average of the smaller *Pteromys*, *Heterosciurus* and *Echinosciurus* is more than 15.40 %. Amongst Antilopes¹⁾ the large *Oreas Livingstoni* has only 8.65 %, while all the others have about 10 % or more, the small Antilope *cervicapra* even 10.75 %, the highest percentage amongst this suborder.

The same is observed comparing the Camel (12.05 %) with the smaller Lama (13.60 %). The Giraffa, still larger than the Camel, has only 10.90 %.

Amongst the *Ovidae* the smaller *Capra hircus* has a higher percentage than the larger *Ovis tragelaphus*. In the suborder of the *Perissodactyla* the smaller *Tapir* has a higher percentage than *Equus caballus* and *asinus*.

¹⁾ Amongst the *Cervidae* the percentage varies so little that this suborder seems to be less fit for comparison. Its result would not be in favor of any rule in this respect.

Amongst the carnivorous suborder of the Ursidae we find that the largest representative *Ursus maritimus* has less cerebellum than both others, although in this whole suborder the percentage is very high (vide infra).

In the Mustelidae¹) and Canidae no constant rule can be observed. It is however striking that of *Canis lupus*, *Vulpes lupus* and *Vulpus lupus opus* the latter, the smallest, again has the highest percentage. The same holds good if we compare the average figure of the two *Felis leo*, with the average figure of the two *Felis pardalis* and the average figure of the two *Felis concolor*, the average cerebellar percentage of the lion, which is the greatest animal of this family, being the smallest.

Amongst Prosimiae the smaller Lemurs have a slightly higher percentage than Chiromys.

So we see that if there is any rule, it is certainly not in favor of WEISBACH's conception but more likely in favor of the higher percentage in the smaller representants.

That, however, also this is not constant appears amongst others from the figure of *Myrmecophaga* compared to *Choloepus* and the figure of *Cercocebus fuliginosus* compared to those of *Cynocephalus hamadryas* and Anthropoids. From this results that other factors, than the size of the body exercise a considerable influence on this figure.

Among these factors are the different cephalization coefficient of different animals and some physiological differences that cannot be expressed in matter of cephalization.

Considering the percentages of cerebellar weight, we have to realize that this percentage may change as well by variation in the forebrain development as by variation in the weight of the cerebellum itself.

Variation in forebrain development will chiefly occur between orders and suborders where the cephalization index is very different, as this cephalization index largely depends on the forebrain, since this represents the greater mass of the encephalon.

So it may be explained that the average cerebellar % in man is only 10.5 % (KAPPERS) while in Anthropoids it is 13.72 %.

The question however arises if greater cephalization *necessarily* diminishes the cerebellar percentage. If for this we consider the different orders it appears that although in each order there are considerable variations (see below) some of the *highly* cephalized animals are conspicuous by their *large* cerebellar percentage.

Among these are the Proboscidae, Pinnipedii, Odontoceti and Edentata, compared to their next relatives. In the Proboscidae, Pinnipedii and Odontoceti this fact is the more striking as their cephalization also is very considerable (according to DUBOIS) compared to their next relatives.

We may conclude from this that in these animals the motor synergia has acquired an extraordinary precision. So in the Elephant the ability for complicated movements may be related to the large cerebellar per-

¹) For the Viverridae see below.

centage. This animal possesses very precise independent monolateral movements of its extremities and a very fine adjustment of its trumpet.

In the Pinnipedii and Cetacea it is chiefly the swimming movement that involves a great cerebellar capacity. The agility of sealions is well known as also their equilibric acrobatics outside the water, often shown to the public. In Dolphins, who easily swim around a quickly moving steamer, the motile capacities are equally striking.

Still in both animals the cerebellar organization is very different. In the Pinnipedii, who greatly use their forelegs, the hemispheres of the cerebellum (the center of independent movements of the legs, BOLK) are increased. In the Cetacea, who have no extremities and where the strong tail is the sole moving agent, the pars floccularis is enlarged and the paraflocculus is enormous (BOLK) on account of its pontine connections (R. B. WILSON) and is chiefly responsible for the great size of the cerebellum. Now it is striking that in the whale, *Balaenoptera sulfurea* KAPPERS found a still higher percentage of cerebellum (18.95 %) than I did in *Phocaena* (15 %). Still the motile capacities of *Balaenoptera* are not nearly the same as those of *Phocaena*, as they hardly can follow a fast steamer. So I am inclined to believe that the higher cerebellar index in *Balaenoptera* is influenced by its cephalization index (which according to DUBOIS is only $\frac{2}{3}$ of that of the *Odontoceti*), as it is very probable that this smaller cephalization is largely due to the comparatively smaller forebrain in *Balaenoptera*, which is also more dolichocephalous than the forebrain of *Odontoceti*, whose greater brachencephaly, according to KAPPERS (1927), is also a result of greater forebrain development.

As far as concerns the high cerebellar index in Edentates this fact may be due to the special character of their movements, which though being extremely slow, are highly complicated and require much independency of each extremity.

The accuracy of movements, even if slow, is of importance here as this involves a great deal of inhibition and synergia, which, as we know, are located in the cerebellum (TILNEY and RILEY). That *Myrmecophaga* has a still higher percentage than the other Edentates examined may be explained by the fact that in addition to its extremities it has a very long snout, which is used as a sort of trumpet, for gathering food, as does the Elephant, and certainly has great proprioceptive capacities.

The influence of the character of the motility of an animal is also seen in the Cervidae, which though being quick, have a great simplicity of gait, their extremities acting in a rather monotonous rhythmic collaboration (alternation) of both sides. They have the lowest average of cerebellar percentage.

Among the order of Carnivora, there is a striking and fairly constant difference between the various suborders, the cerebellar percentage being the largest in the Ursidae, next come the Viverridae, then the Felidae, followed by the Mustelidae and finally the Canidae.

It is interesting however, that of the Carnivora the Ursidae also have the highest cephalization index, which might make us expect (cf. p. 165) that their cerebellar index should be smaller, as in the comparison of Odontoceti and Balaenoptera the cerebellar percentage is smaller in Odontoceti.

It is however well known that the capacities in finer adjustment of independent movements of the limbs and in conformity the proprioceptive instrument are very highly developed in bears. As they also have the greatest cephalization (according to DUBOIS *Ursus malayanus* holds a position amongst Carnivora as the anthropoids do amongst monkeys), we have here a case similar to that of the Elephant. As in the latter it is not improbable that in the cephalization of *Ursus* these proprioceptive functions, which are projected both on the cerebrum and on the cerebellum, but which are preponderant for the cerebellum, act the largest part.

On the other hand the relatively high cerebellar percentage of Viverridae is more likely due to the smaller development of their forebrain in comparison to other carnivora, the Viverridae having the lowest cephalization among Carnivora (DUBOIS).

This would also explain their relation to the Mustelidae, which as a rule are more cephalized¹⁾.

A very interesting phenomenon is offered by comparing Canidae and Felidae, two genus in which the coefficient of cephalization is practically the same.

Still we see that the Felidae have a higher average figure for the cerebellar percentage as dogs have. In none of the dogs the % mounts higher than $10\frac{3}{4}$ % whilst in the Felidae the average is far above this figure, rising even to 13.70 %.

This difference no doubt should be explained by the difference in motile abilities in both genus, those of the Felidae being doubtless much more developed than in dogs, specially as far as concerns finer adjustment of independent (unilateral) movements of each of the forelegs.

From the view point attained in this report it is an interesting fact that, just as the Elephants and the sealions (Pinnipedii), also the Ursidae and Felidae belong to those animals to whom tricks of equilibration can be best taught.

In the *Primates* the *Prosimiae* have a greater cerebellar % than the real monkeys. As their forebrain (which does not entirely cover the cerebellum, as it does in most monkeys) is relatively small, this might explain the higher cerebellar %, rather than a difference in motile abilities, that are great in both.

On the other hand the highest cerebellar percentage amongst all *Primates* is found in the *Anthropoids*, who at the same time are more cephalized, so that as in the Elephant, Ursidae, Felidae and Pinnipedii, this high cerebellar

¹⁾ The smaller % in the latter does not necessarily include a smaller development of the cerebellum in relation to the body.

percentage can only be explained by their special cerebellar proprioceptive capacities.

From what is said above it appears that just as the Ursidae, Felidae and the Elephant and Odontoceti, so the Anthropoids, more than other monkeys should be considered as special cerebellar animals, — since in spite of their higher cephalization their cerebellar percentage is greater than that of their next relatives. On the other hand the fact that men have a cerebellar index smaller than Anthropoids should be ascribed by the greater development of the forebrain.

Summary.

10. A comparison of the proportion between the weight of the cerebellum and the total brainweight in a series of mammals shows no constant correlation between the size of the animal and the proportionate weight of the cerebellum.

20. Factors such as cephalization coefficient and capacities of adjustment of the extremities, tail or trumpet have the greatest influence in the relative proportions.

30. Animals, naturally endowed with *special* motile capacities, including those used for special motile tricks such as the elephant, sealions, cats, bears and anthropoids have the greatest cerebellar percentage.

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