

BRAIN ORGANIZATION IN *PLATANISTA GANGETICA*

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ABSTRACT

The quantitative composition of the brain of a young individual of *P. gangetica* is presented both in simple percentages and with progression indices referring to a basal mammalian type. The neocortical development is emphasized as well as the hippocampal reduction. This species ranks low among Odontoceti and even among Platanistids, which may be considered in agreement with its life-habits. Qualitative features of transverse sections are also presented.

INTRODUCTION

A detailed study of dolphin brains is not easy because the size of that organ in most species makes it difficult to prepare histological sections. We have, however, been able to carry out a gross and microscopical examination of one such brain belonging to a young individual of the Ganges dolphin (*Platanista gangetica indii*), collected by the first author in the Indus River in Pakistan. We present here our observations of the most important quantitative characteristics of the composition of that brain with an appendix on some of its external and internal features. We hope that, although the animal was not an adult, a basic description of its brain will be useful as a reference type for those having to identify the main characteristics of bigger, more unwieldy specimens.

MATERIAL AND TECHNIQUES

An individual of *Platanista gangetica* measuring 106.5 cm and weighing 17.5 kg was collected from the Indus River in Pakistan. It is assumed to have been about one year old at the time of death. The weight of its brain was 170 g. That brain was fixed in 1/6 formalin solution. One sagittally cut half of it was embedded in paraffin, sectioned at 10 μ m and Nissl stained. Photographs of 108 sections from front-end to back-end were prepared. The above laboratory operations took place in Montreal (collection number P285) while the final study was carried out in Tokyo. The photographs were used to estimate the volumes of nine main components of

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the brain according to the technique explained elsewhere (e. g. Stephan, Bauchot and Andy, 1970).

ABBREVIATIONS

Here are the abbreviations used throughout this paper for the brain components. N=neocortex; Rh=rhinencephalon or paleocortex (P); S=septum; D=diencephalon; St=striatum including the area of the capusula interna that is spread out considerably; H=hippocampus; M=mesencephalon; C=cerebellum including pontine fibers; O=medulla oblongata.

RESULTS AND COMMENTS

We shall report here on the quantitative aspects of the brain of *P. gangetica*, leaving for the appendix a few remarks on its qualitative morphology. In fact, quantitative comparisons are not easy in this case because few biometrical data have been published on dolphin brains. We do not know of any analysis of such material carried out with a method similar to the one applied in the present paper. Therefore, we shall have to refer to studies of other animals. We will consider especially some Primates since it is classical to insist on the high degree of both encephalization and corticalization in the two orders Cetacea and Primata. For comparison purposes, we have selected a small number of data from Stephan, Bauchot and Andy (1970—see their Tables 1 to 6 for more details).

A. *Percentage composition*

Table 1 presents the absolute and percentage composition of the brain of *P. gangetica* while Table 2 shows the percentages of its telencephalic parts only. An approximate idea of brain structure can be gained by looking at those simple ratios; however, these do not indicate the comparative evolutionary trends since they do not take into account the allometrical correlation between brain and body. They only provide a general picture of the subdivision of the brain, the functional significance of which must be interpreted if comparisons are made. We picked up about a dozen Prosimians and as many Simians from the Tables in Stephan, Bauchot and Andy (1970) and made approximate estimates of some proportions of brain-parts in those Primates.

We can offer the following brief comments.

a) The absence of an olfactory bulb is well known in Odontoceti, as is the case for *P. gangetica*.

b) The most important component of *P. gangetica*'s brain is the neocortex. The abundance of sulci and gyri in many cetaceans has been observed since long, just like the increasing complexity of cortical folding in an ascending series of Primates.

c) The second largest component is the cerebellum. One could possibly expect this on the assumption that agile swimmers need a well developed cerebel-

lum in order to steer their complicated movements through their environment. Breatnach (1960) mentions that Mysticeti have a slightly larger cerebellum (20%) than Odontoceti (15%) and our specimen stands even a little lower (12.77%). That author also questions the direct relationship often established between aquatic manoeuvring and cerebellar size (o.c. p.221). Other ecological situations and types of locomotion, especially flying and climbing, are also expected to require an important cerebellum, as the common belief goes. We may note that the cerebellum may range quantitatively from 11 to 16% of total brain in Prosimians of all sizes and from 8 to 15% in Simians and man. In Megachiroptera, it varies from 12 to 16% approximately and in Microchiroptera from 15 to 22% (Pirlot and Pottier, 1977).

d) Among cortical structures, the rhinencephalon (paleocortex with amygdaloid area) is notably small in *P. gangetica*. This agrees, of course, with the loss of olfactory bulb and nerve. However, the amygdala complex is still present and constitutes most of the volume and probably almost all of the functions of that component (strictly speaking, the name *rhinencephalon* for that region in a dolphin is hardly appropriate if it is true that most or all of the olfactory function has disappeared). Note that the relative size of that component remains fairly large in some Primates although, in the course of evolution, it has regressed in many of them more than in our dolphin.

TABLE 1. VOLUMES AND PROGRESSION IN THE BRAIN OF *P. GANGETICA*

Components	Volumes (mm ³)	Percentages of total brain	Progression indices
N	107,504.73	67.98	3,903
Rh	3,599.59	2.27	123
S	332.90	0.21	132
D	9,893.12	6.25	719
St	5,743.82	3.64	739
H	1,161.10	0.73	99
M	3,564.35	2.25	432
C	20,193.24	12.77	671
O	6,171.96	3.90	325
	158,164.90	100.00	—
Total brain	170 g with body-weight 17.5 kg		842

TABLE 2. TELENCEPHALIC COMPOSITION (%)

	<i>P. gangetica</i>	Prosimians	Simians
N	90.85	Max. 80	Up to 88~95
Rh	3.04	4~10	<4, even <1
S	0.28	—	—
St	4.85	5~8	2~3
H	0.98	5~10	<5, even <1
	100.00	—	—

e) The relative smallness of the hippocampus is amazing. This fact is also mentioned for cetaceans in general and in particular for *Tursiops truncatus* but without any figure by Kruger (1966). We would also agree up to a point with Breatnach and Goldby (1954, p.280) who point to the "indefiniteness of the boundary" of the hippocampus, resulting in the introduction of "quite a large uncertainty into the estimate of the sectional area" of that component. We did experience difficulties in drawing some hippocampal demarcations from Nissl stained sections but we believe that our method was not grossly inaccurate.

f) The septum as demarcated in our dolphin brain cannot probably be compared with other published data because we have restricted our demarcation to a minimal area including the nuclei in strictly paraseptal location, which probably is not the case in other works. We follow Jacobs, Morgane and McFarland's (1971) practice of including the diagonal band within the olfactory area (o.c. p. 206) whereas other authors prefer to pool it with the septal nuclei (Stephan, Bauchot and Andy, 1970, p. 295).

In conclusion, the quantitative composition of the brain in the young *P. gangetica* is characterized by an overwhelming predominance of the neocortex that approaches that found in higher Primates. Most components are relatively small mainly because the neocortex and, to a lesser but also significant degree, the cerebellum are enormously developed. The oversizing of the neocortex can be demonstrated to take place in early prenatal life already while the fast growth of the cerebellum seems to occur mainly in late prenatal life (PirLOT and Kamiya, in preparation).

B. *Evolutionary progression*

The method of progression indices proposed firstly by Stephan to describe the evolutionary level attained by mammals, then applied by him and other authors (e. g. Stephan, 1967; PirLOT and Stephan, 1970; Stephan and PirLOT, 1970; PirLOT and Pottier, 1977) to various species, has also been used here. A summary of its principles can be found in PirLOT and Stephan (1970) and the relevant technique is described in Stephan, Bauchot and Andy (1970). In brief, comparisons are made between the volumes of the brain (or brain-component) in the species under investigation and the volumes of the brain (or brain-components) in an idealized primitive type ("basal Insectivore") that would have *the same body-weight* as the animal being studied. So, the allometrical relationship between brain and body is taken into account, which allows to describe and compare *evolutionary stages* in animals with various overall sizes. The basal value is 100 so that any figure above 100 indicates evolutionary progression while any figure below 100 betrays evolutionary regression.

From that viewpoint, it can be seen that *P. gangetica* stands rather low among dolphins. Its encephalization index (brain-to-body progression) is 842 and this is not high for its order. Still it is probably a little higher than it would be if the individual investigated were not a young but a fully adult individual. An average index found from a sample of 8 individuals was 675 (PirLOT and Kamiya, 1975).

From the latter publication, it can also be seen that several other dolphins have much higher encephalization indices, up to 2,308. It may be noted that, from Stephan, Bauchot and Andy's tables (1970), a progression index of about 2,900 can be obtained for *Homo sapiens*.

As could be expected from the simple percentages, whatever progression there is in the total brain of *P. gangetica* is due mainly to its neocortex being so large (3,903). That figure stands higher than those for a number of Primates but remains much lower than those for several monkeys and, of course, for apes and man (see a selection in Table 3).

TABLE 3. COMPARATIVE PROGRESSION INDICES

	Br	N	Rh	C
<i>Homo sapiens</i>	2,881	15,576	142	1,872
<i>Pan troglodytes</i>	1,132	5,858	54	780
<i>Cercopithecus ascanius</i>	872	4,448	100	551
<i>Colobus badius</i>	688	3,353	59	536
<i>Cobus albifrons</i>	1,205	6,065	87	921
<i>Tarsius syrichta</i>	507	2,148	78	514
<i>Galago senegalensis</i>	417	1,485	85	490
<i>Platanista gangetica</i>	842	3,903	123	671

Br=total brain; other abbreviations as above. Figures rounded.

The rhinencephalic cortex *sensu lato* (paleocortex) is low but progressive whereas it may be very regressive in Primates. As already suggested above, if olfaction has been lost altogether in this dolphin, some other not unimportant activity may have been taken up by that brain region (amygdaloid area in particular).

Septum development probably follows Rh to some extent. However, one must keep in mind the remark made before that we have pooled the diagonal bands together with Rh, not with S.

The striatum and diencephalon are less progressive than in *Homo* but they probably yield "average" values for higher mammals.

The hippocampus' lack of progression is puzzling (its value lies practically at the neutral level 100). In percentage of the telencephalon, its value is close to man's own (about 0.95), but in the latter the evolutionary progress is around 400 (rough estimate from figures in Stephan, Bauchot and Andy, 1970). We have referred earlier to other authors who seem to be as unable as we are to propose an explanation for the hippocampus of the delphinids being very small. True enough, we are surprised to find it *so small*. That fact suggests both an evolutionary functional regression as well as a relative undersizing (influenced by the relative enlargement of the cortex). Contrary to our observations and those of Kruger (1966) and other authors apparently (through Kruger), Pilleri (1972) finds the amygdala and hippocampal gyrus ". . . comparatively" large (o.c. p. 51). Pilleri does not give any measurement and thus we wonder what his words "comparatively large" may mean. The gyrus hippocampi is present on but a few sections from our animal.

The mesencephalon can probably be considered fairly progressive (cf. Primates, Chiroptera, etc.) and so can the oblongata.

The cerebellum, often expected to be very progressive in skilled swimmers such as dolphins, is not remarkably high by Primate standards, however. It is much more progressive than in bats (range 200~400), on the other hand, and the bats that are highest in that respect are those performing complex and accurate slow movements such as vampire, rather than the fast straight-line flyers that catch insects on the wing.

CONCLUSION

Although showing a great development of its brain and some of its brain components, *P. gangetica* appears as a rather modest dolphin from that viewpoint. The relative size of its neocortex, by comparison with other mammals including other dolphins, may look impressive but, when referred to body-size, probably remains among the most lowly of the family. We do not, unfortunately, possess accurate data for such apparently "smarter" genera as *Tursiops*, *Delphinapterus*, *Phocoena* and even *Inia* among the Platanistidae. But knowing the general size parallelism between total brain and neocortex in advanced mammals (Primates, Cetaceans), we may expect those other genera to possess more progressive cortices than *Platanista*. The idea almost immediately arises that, in a general way, a river dwelling and only modestly sociable dolphin like *P. gangetica* (Pilleri, 1970) has remained "in-

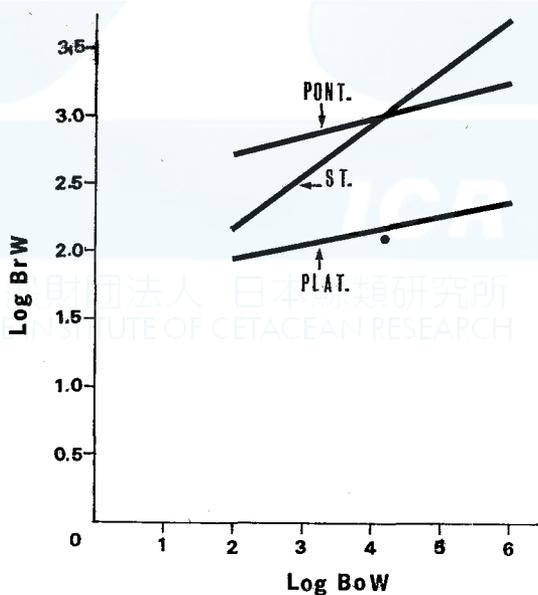


Fig. 1. Log regression for brain-to-body growth in *Stenella*, *Pontoporia* and *Platanista*. The black dot represents the specimen used for brain analysis in this study.

ferior" in neocortical performances to species that are open-sea dwellers, live in large schools and are said to maintain refined social communications between individuals (*Stenella*, *Tursiops* etc.) In order to illustrate the relative encephalization of *P. gangetica* by comparing it with *Pontoporia* (coastal dolphin) and *Stenella* (high sea dolphin), we have reported the position of our specimen of *P. gangetica* on a graph showing average regression BrW/BoW straight lines for those three genera (Fig. 1). In all likelihood the stronger increase in relative brain-size observed in *Stenella* is to be related with the postnatal "training" that seems to occur in that social species (Pirlot and Kamiya, 1975).

On the other hand, structures directly concerned with accousti functions, such as the subcortical components O and especially M, do show a strong progression in *Platanista*. This fact appears quite remarkable if one compares dolphins with bats which yield indices in the 200~250 range for M and in the 100~200 range for O (Stephan and Pirlot, 1970; Pirlot and Pottier, 1977). Considering that dolphins, like bats have simplified optic but highly sophisticated acoustic functions, those figures are particularly significant in *Platanista* (432 and 325).

The basic quantitative findings reported in this paper clearly suggest that further and more detailed investigations on the structure of each brain component in this dolphin and in higher types are likely to be rewarding. Studies of the quantitative composition of the brain in bats and in other mammals already pointed to the same idea. As for dolphins, there has been a fashionable excitement in the last few years about those aquatic mammals being almost as intelligent, in several respects, as man itself, or even "smarter" than *Homo sapiens* in some. It will take a lot more data on both the qualitative and the quantitative aspects of the dolphin brain to "relocate" such claims into reality, and many, many more observations of their behaviours.

APPENDIX

ON SOME QUALITATIVE FEATURES OF *P. GANGETICA*'S BRAIN

This appendix is made of short remarks A) on a sample of 8 low magnification photographs of the brain sections used for the above quantitative analysis, B) on the gross external morphology of 4 views of another brain of *P. gangetica* and C) on the most obvious features in 9 sections of the brain-stem of the same specimen. The animal used for B) and C) was a female individual 120.5 cm long with a brain weighing 236 g. It was thus a little older and larger only than the specimen P285 mentioned above. It was collected together with the former by the first author in the course of his expedition to Pakistan.

A. Sections for quantitative analysis

Demarcations of main areas have been made by following the few photographs published on dolphin brain and, in the absence of relevant pictures from dolphins, by resorting to atlases for various Primates. Photomagnification $\times ca. 2$.

Fig. 2. Front part of the right hemisphere with distended ventricle. Section

1061.

Fig. 3. Plane of emergence of a little distinct paleocortical region, in caudad direction. Section 1506.

Fig. 4. Septal plane. Ventral P reduced. Section 1856.

Fig. 5. Caudad to commissura anterior. P reduced to small lateral area. Tuberculum olfactorium visible ventrally. Section 2206.

Fig. 6. Pontine fibers plane. Emergence of H and a few fimbriae visible. Colliculus superior. Section 2906.

Fig. 7. Colliculus inferior and cerebellar peduncle plane. Nucleus cochlearis. Section 3356.

Fig. 8. Plane at caudal edge of H. Caudal part of colliculus inferior. Maximum extension of O. Section 3506.

Fig. 9. Caudal N. Typical outline of Cetacean C with developed paraflocculus in particular. Section 3956.

B. *Gross external morphology*

Fig. 10. External aspect of the calve brain. A) Dorsal view. The fissural pattern is one of the simplest found among dolphins. The longitudinal sulcus constitutes the main sulcus. B) Ventral view. Olfactory nerve absent; optic nerve very thin; acoustic nerve well developed. The contrast between the last two nerves is especially noteworthy. C) Lateral view of the left half. We cannot engage here into a rediscussion of sulci and gyri nomenclature. There seems to be very little, if anything, new to contribute from the examination of this specimen. For general surface anatomy of dolphin brain, the reader is referred in particular to Gruenberger (1970). D) Median section of the right half. The high development of the colliculi inferiores can be appreciated.

C. *Sections through the brain-stem*

The internal structure of the brain-stem in *P. gangetica* is illustrated here. The brain-stem was prepared into serial sections which were stained by the Weigert-Par carmin technique (embedding in celloidin, sectioning 30 μ m thick). Microscopical study revealed many remarkable peculiarities in the development of the various component structures. The sectional planes shown here are as follows.

Fig. 11. Section through the inferior end of the medulla (ser. no. 120).

Fig. 12. Section of medulla through the cuneate nuclei (ser. no. 255).

Fig. 13. Section through the rostral portion of the medulla at the exit the pharyngeal-laryngeal fibers to nerves IX, X and XI from nuclei ambigu (ser. no. 450).

Fig. 14. Section through the middle of the trapezoid body at the level of the genu of the facial nerve (ser. no. 555).

Fig. 15. Section through the colliculus inferior at the level of the colliculi inferiores commissure (ser. no. 635).

Fig. 16. Section through the middle of the colliculus inferior at the level of colliculi inferiores commissure (ser. no. 690).

Fig. 17. Section through the colliculus superior, brachium of the colliculus inferior and nuclei for the oculomotor nerve (ser. no. 795).

Fig. 18. Section through the colliculus superior, nucleus ellipticus, nucleus interstitialis and tractus opticus (ser. no. 830).

Fig. 19. Section through the thalamic nuclei (ser. no. 900).

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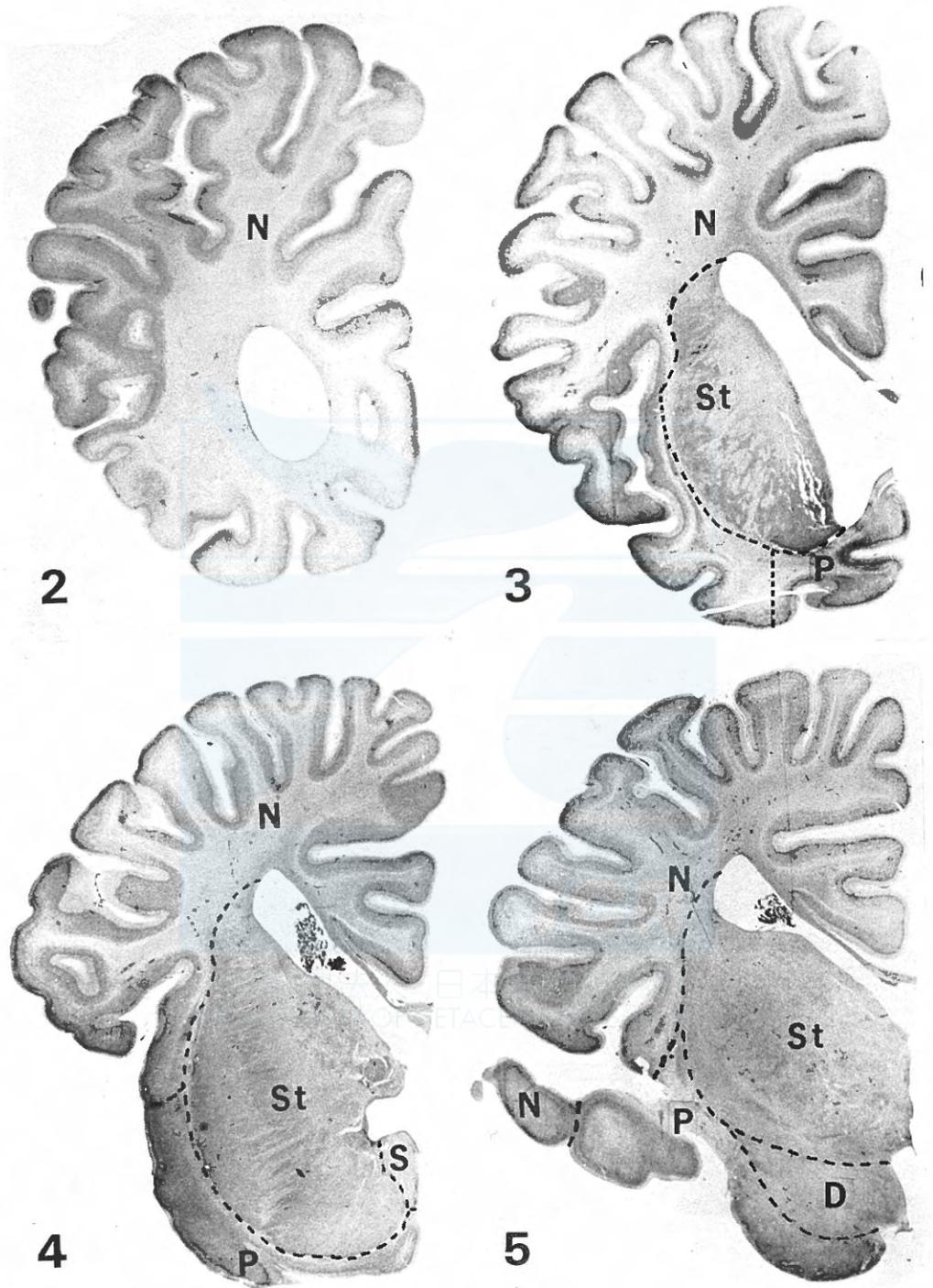
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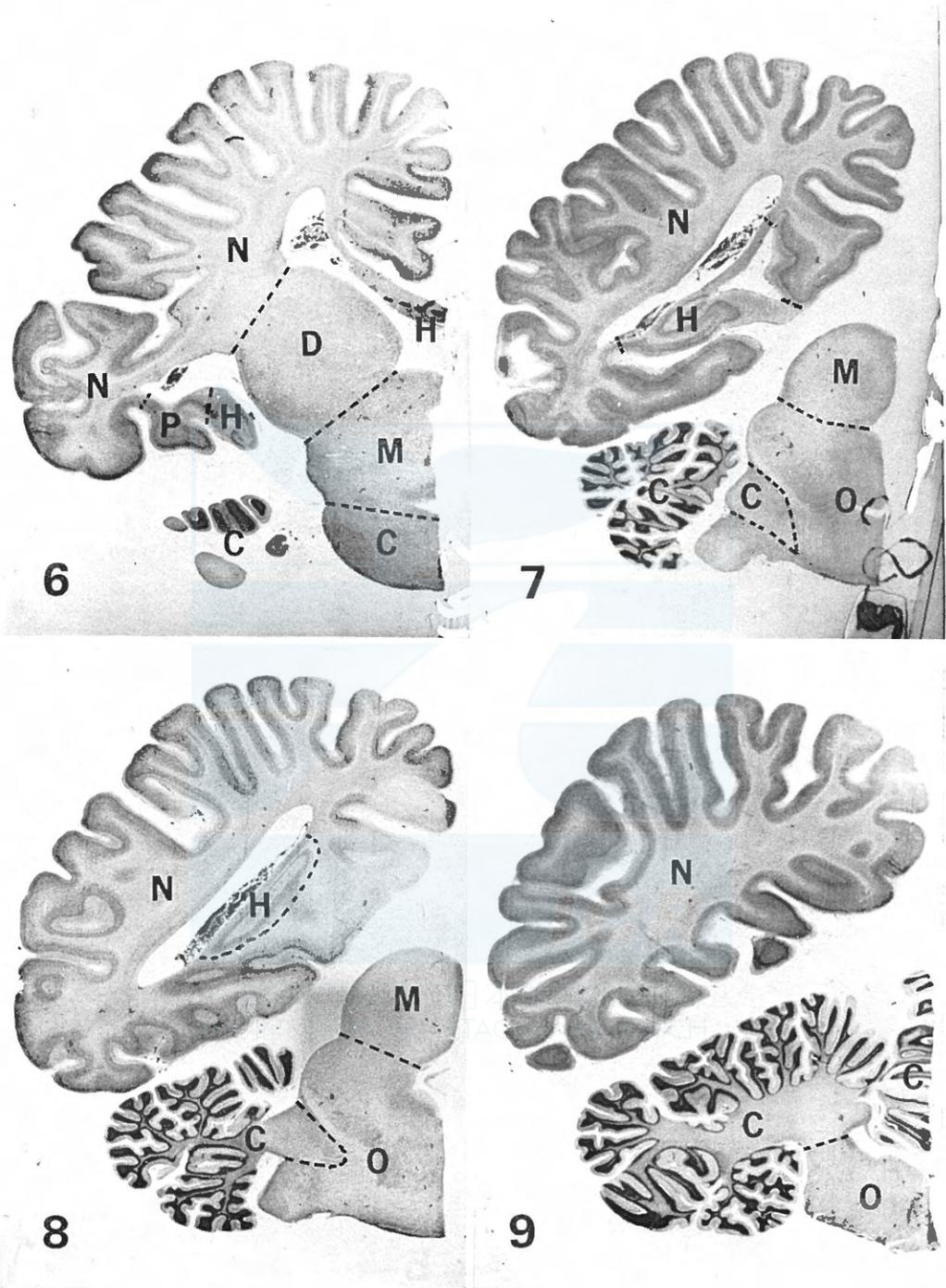
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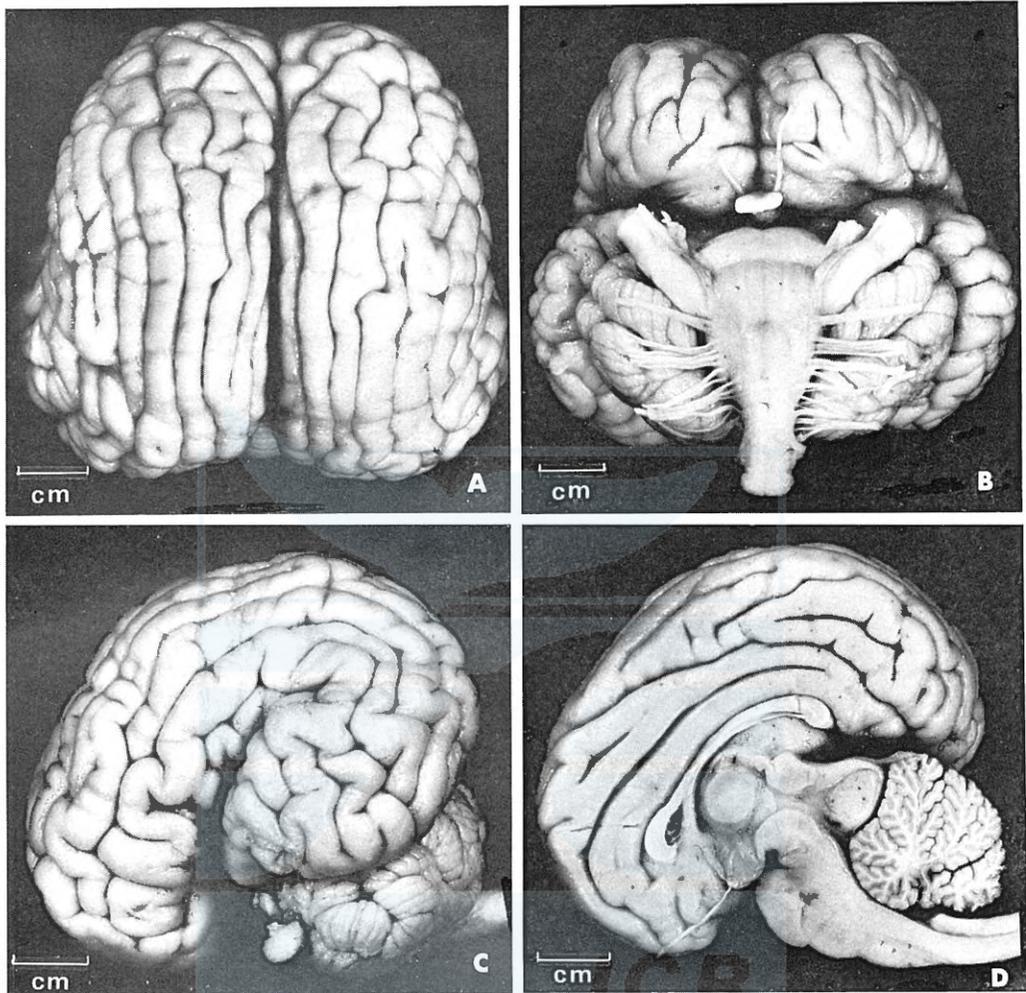


Fig. 10

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