

Elephant brain

Part I: Gross morphology, functions, comparative anatomy, and evolution

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Received 22 September 2005; received in revised form 21 March 2006; accepted 24 March 2006

Available online 18 April 2006

Abstract

We report morphological data on brains of four African, *Loxodonta africana*, and three Asian elephants, *Elephas maximus*, and compare findings to literature. Brains exhibit a gyral pattern more complex and with more numerous gyri than in primates, humans included, and in carnivores, but less complex than in cetaceans. Cerebral frontal, parietal, temporal, limbic, and insular lobes are well developed, whereas the occipital lobe is relatively small. The insula is not as opercularized as in man. The temporal lobe is disproportionately large and expands laterally. Humans and elephants have three parallel temporal gyri: superior, middle, and inferior. Hippocampal sizes in elephants and humans are comparable, but proportionally smaller in elephant. A possible carotid rete was observed at the base of the brain. Brain size appears to be related to body size, ecology, sociality, and longevity. Elephant adult brain averages 4783 g, the largest among living and extinct terrestrial mammals; elephant neonate brain averages 50% of its adult brain weight (25% in humans). Cerebellar weight averages 18.6% of brain (1.8 times larger than in humans). During evolution, encephalization quotient has increased by 10-fold (0.2 for extinct *Moeritherium*, ~2.0 for extant elephants). We present 20 figures of the elephant brain, 16 of which contain new material. Similarities between human and elephant brains could be due to convergent evolution; both display mosaic characters and are highly derived mammals. Humans and elephants use and make tools and show a range of complex learning skills and behaviors. In elephants, the large amount of cerebral cortex, especially in the temporal lobe, and the well-developed olfactory system, structures associated with complex learning and behavioral functions in humans, may provide the substrate for such complex skills and behavior.

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Keywords: *Elephas maximus*; *Loxodonta africana*; Evolution; Encephalization quotient; Memory

1. Introduction

Despite the attention of the public to elephants and popularity of these animals, many aspects of elephant biology have been incompletely studied. In particular, detailed studies of the nervous system have been limited, notwithstanding a literature dating from the early 19th century. A recent paper brought to light the paucity of information on elephant brain research and provided a stimulus to publish our findings [22]. In the present

investigation, we provide a summary of findings on the gross anatomy of elephant brains.

We studied elephant brains and compared them to other mammalian brains, with the objective to collect data on elephant brain gross morphology. Evolutionary inferences were made based on our examination of ontogenetic stages of elephant brains, from endocasts, and from structures preserved in cranial cavities of extinct proboscideans.

2. Materials and methods

Our data are based on direct observations of seven elephant brains, three Asian and four African elephants, *Elephas maximus* and *Loxodonta africana*, respectively (Table 1A). Elephant brains listed in Table 1A were obtained within 12–24 h after death. They were removed with tools, such as chain saw, chisels,

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and hammers for adult elephants, or with a Stryker electric handsaw or a hacksaw for a newly born elephant (Fig. 1A and B). Specimens were originally fixed in formaldehyde or formaldehyde/phenol solutions. Our investigation focuses on macroscopic descriptions of the brain surface and of brain slabs.

Sources of comparative elephant material obtained from the literature are summarized in Table 1B and C, in which we list only papers that included data, illustrations and description of whole brains. Brains from other species used for comparative purposes included preserved brains of humans, sheep, and other mammals (Table 1E). Many of these specimens are kept at the Natural History Museum, Wayne State University in Detroit. All specimens are preserved in 10% formaldehyde.

3. Results

3.1. General observations

Six of the seven captive elephant brains available for our study (Table 1A) were females. African elephants (*L. africana*) brains comprised 13/22 of all the brains listed in Table 1A and B; the

remaining eight brains were of Asian elephant (*E. maximus*), plus one of unknown genus.

Encased in the bony braincase, the brain of an adult elephant is well protected (Fig. 1A, top). In adult elephants, the sidewalls and roof of the braincase are not all solid bones; they are pneumatized, extensively sacculated with air pockets [13,36]. All air cells are interconnected and also contain perforations for the blood vessels. In a newborn, the air cells are not developed (Fig. 1A, bottom), thus the brain is protected by the cranial bones, which are about 5–10 mm thick. In adult elephants, bone thickness (including air cells) on the dorsal side can reach up to 250 mm. In Fig. 1C, we depict structures inside the braincase of a stillborn *L. africana* (specimen G in Table 1A), such as foramina for cranial nerves and arteries and meninges. A similar illustration with these foramina for adult *L. africana* was reported previously (see Ref. [121]).

Table 1
Brains and endocasts of proboscideans and other taxa examined or were available for comparison in this study^a

Sample no.	Taxon	Specimen letter code or source ^b	C or W ^c	Age ^d	Sex ^e	Body ^f	Weight of (g)		Dura mater ⁱ	EQ ^j
							Brain (B), with brain-stem ^g	Cerebellum (C)/ratio (%) of C/B ^h		
(A) Elephant specimens examined in this study ^a										
1	<i>Elephas maximus</i>	A	C ^{c1}	34	F	3216000 ^{f1}	5220 ^{g1}	960 ^{h1} /18.4	–	2.02
2	<i>Elephas maximus</i>	B	C ^{c2}	33	F	3450400 ^{f2}	5000 ^{g2}	1000 ^{h2} /20	630 ⁱ¹	1.84
3	<i>Elephas maximus</i>	C	C ^{c3}	46	F	2267430 ^{f3}	4550 ^{g1}	858 ^{h3} /19	608 ⁱ²	2.21
4	<i>Loxodonta africana</i>	D	C ^{c4}	14	F	2477000 ^{f4}	Part brain	–	–	–
5	<i>Loxodonta africana</i>	E	C ^{c5}	46	F	3505000 ^{f5}	4420 ^{g3}	735 ^{h4} /16.6	–	1.61
6	<i>Loxodonta africana</i>	F	C ^{c6}	24	F	1793.300 ^{f4}	4050 ^{g4}	–	–	2.3
7	<i>Loxodonta africana</i>	G	C ^{c7}	0	M	159000 ^{f5}	1724 ^{g5}	858 ^{h5} /19	203 ⁱ³	NA ^{j1}
(B) Adult elephant specimens on which data were obtained from the literature ^a										
8	<i>Elephas maximus</i>	Ref. [48]	C ^{c8}	?Ad.	F	197540 ^{f6}	7475 ^{g6}	–	–	[18.5]
9	Elephant (no genus)	Ref. [22], p. 220	–	?Ad.	–	No data	6500 ^{g7}	–	–	–
10	<i>Elephas maximus</i>	Ref. [125], p. 21	C ^{c9}	50	F	3190098.5 ^{f5}	6075 ^{g8}	–	–	2.36
11	<i>Elephas maximus</i>	Ref. [66], p. 247	?C ^{c10}	?Ad.	–	3048000 ^{f7}	5430	–	–	2.17
12	<i>Elephas maximus</i>	Ref. [21], p. 1093	?C ^{c11}	?Ad.	–	3048000 ^{f7}	4717	–	–	1.88
13	<i>Elephas maximus</i>	Ref. [21], p. 1093	?C ^{c11}	?Ad.	–	2047000 ^{f4}	4048	–	–	2.11
14	<i>Loxodonta africana</i>	Ref. [104], p. 134	W ^{c12}	30	M	4380100 ^{f8}	9000 ^{g9}	–	–	[2.83]
15	<i>Loxodonta africana</i>	Ref. [120], p. 74	W	Ad.	M	–	6000	–	–	–
16	<i>Loxodonta africana</i>	Ref. [23], p. 259	W ^{c13}	Ad.	M	6654000 ^{f5}	5712 ^{g3}	–	–	1.36
17	<i>Loxodonta africana</i>	Ref. [117], p. 183	W ^{c14}	Ad.	M	5550000 ^{f5}	5300 ^{g3}	–	–	1.42
18	<i>Loxodonta africana</i>	Ref. [106], p. 611	W	Ad.	–	2750000	4480	–	–	1.92
19	<i>Loxodonta africana</i>	Ref. [62], p. 8	?C	Ad.	?	4000000	4210	–	–	1.4
20	<i>Loxodonta africana</i>	Ref. [117], p. 183	W ^{c14}	Ad.	F	2160000 ^{f5}	4100 ^{g3}	–	–	2.06
21	<i>Loxodonta africana</i>	Ref. [117], p. 183	W ^{c14}	Ad.	F	2537000 ^{f5}	4000 ^{g3}	–	–	1.80
22	<i>Loxodonta africana</i>	Ref. [104], p. 134	W ^{c12}	40	M	5174400 ^{f5}	4000 ^{g3}	–	–	1.13
(C) Elephant whole brains or only cerebellum, illustrated by other investigators, listed chronologically by taxon ^a										
23	<i>Elephas maximus</i>	Ref. [81], plates XIII–XIV	–	–	–	–	–	Cerebellum	–	–
24	<i>Elephas maximus</i>	Ref. [87], plt VIII	–	–	–	–	–	Brain	–	–
25	<i>Elephas maximus</i>	Ref. [32], plates I and II	–	–	Calf	–	–	Brains	–	–
26	<i>Elephas maximus</i>	Ref. [72], p. 513	–	–	–	–	–	Brain	–	–
27	<i>Loxodonta africana</i>	Ref. [10], plates XXII–XXIII	–	–	Yg.	M	–	Brain	–	–
28	<i>Loxodonta africana</i>	Ref. [62], p. 19	–	–	–	–	–	Brain	–	–
29	<i>Loxodonta</i> and <i>Elephas</i>	Ref. [76], plts XXXIV–XXXVIII	–	–	–	–	–	Brains	–	–
(D) Endocasts of extinct proboscideans that we examined or specimens that were available for study (data were obtained by us or from the literature) ^a										
30	<i>Moeritherium lyonsi</i>	Ref. [4], pp. 105–6; Ref. [66], pp. 342–3	–	–	–	1000000	240	–	–	[0.2]
31	<i>Mammuth americanum</i>	Ref. [4], p. 107; Ref. [66], pp. 342–3	–	–	–	2300000	4600	–	–	[2.2]
32	<i>Mammuth americanum</i>	MCZ 11106	–	–	–	–	–	–	–	–
33	" <i>Hesperoloxodon antiquus italicus</i> "	Ref. [94], pp. 1251–2	–	–	–	3,049,760 or 4,250,000	5446	–	–	[2.18 or 1.75]

Table 1 (Continued)

Sample no.	Taxon	Specimen letter code or source ^b	C or W ^c	Age ^d	Sex ^e	Body ^f	Weight of (g)		Dura mater ⁱ	EQ ^j
							Brain (B), with brain-stem ^g	Cerebellum (C)/ratio (%) of C/B ^h		
(E) Non-elephant specimens that were available for study (data were obtained by us or from the literature) ^a										
34	Human	Lab specimens	— ^{c15}				1450 ^{g10}	150/10.3	~124	7.51
35	Chimpanzee	Zoo specimen	C ^{c16}				347.4 ^{g11}	43.32 ^{h6} /12.4	?	2.31
36	Talapoin monkey	Zoo specimen	C ^{c17}				32.7 ^{g12}	2.5 ^{h7} /7.64	?	j ³
37	Sheep	Lab specimens	C ^{c18}				104	10 ^{h8} /9.6	~5	0.54
38	Greater kudu	Zoo specimen	C ^{c19}				Brain			j ⁴
39	Grevy zebra	Zoo specimen	C ^{c20}				Brain			j ⁵
40	Rock hyrax	Lab specimens	C ^{c21}				Brains			0.9
41	Maned wolf	Zoo specimen	C ^{c22}				Brain		~4	j ⁶
42	Domestic cat	Lab specimens	C ^{c23}				Brains			j ⁷
43	Chinchilla	Lab specimen	C ^{c24}				Brain			1.34
44	Guinea pig	Lab specimens	C ^{c25}				Brains			0.95

^a Elephant brains specimens 1–22 are listed by taxon and then by decreasing brain weights; specimens 23–29 are listed chronologically by taxon; specimens 30–33 are listed by geological age of the taxon, oldest first; specimens 34–44 are listed by decreasing EQ values within mammalian orders and by the availability of data for the last four columns. Among specimens 30–33, *Moeritherium* lineage originated at about early to middle Eocene (52–42 million years ago = Ma), *Mammuth* lineage originated at least during the late Oligocene to early Miocene (26–24 Ma) and “*Hesperoloxodon*” lineage originated close to Miocene/Pliocene boundary (7–5 Ma) [111,114]. The endocast of *Mammuth americanum* (MCZ 11106) exhibits major brain features, including the olfactory bulb that protrudes anterior to the frontal lobe as depicted in Fig. 20. Osborn [94] provided additional data for brain and body weights; however, based on current knowledge, the estimates he provided for some of the taxa are too high or too low, giving skewed EQ values. For this reason, we did not include these data. None of the data for the extinct species (specimens 30–33) are included in calculating the averages for brain weights or EQ values.

^b Given names for specimens and their sources are listed in footnotes c1–c7.

^c C = captive held individual; W = elephant from the wild.

c1–c7: The sources for the seven elephant brains are given as: specimen code, name of owners (all in the USA), date of death, and cause of death.

^{c1} Specimen A (Tulsa), Bucky Steele, Seagoville, Texas, March 9, 1981, euthanized.

^{c2} Specimen B (Missy), Detroit Zoological Institute, Detroit, Michigan, October 18, 1997, euthanized.

^{c3} Specimen C (Iki), Ringling Brothers and Barnum & Bailey Circus, Virginia, July 8, 1980, endometritis.

^{c4} Specimen D (Loren), Toledo Zoological Gardens, Toledo, Ohio, December 21, 1994, intestinal torsion.

^{c5} Specimen E (Nancy), National Zoological Park, Washington, DC, August 22, 2000, euthanized.

^{c6} Specimen F (Kenya), Chris Hamblen, Kountze, Texas, January 14, 1997, euthanized.

^{c7} Specimen G (unnamed), Toledo Zoological Gardens, Toledo, Ohio, December, August 16, 2002, stillborn. Term of gestation, 642 days.

^{c8} From Calcutta, India; data from [48], as presented in Ref. [11], pp. 108–9.

^{c9} This elephant, “Alice”, lived in Luna Park, New York.

^{c10} Ref. [66], p. 247, cited Ref. [139] as the source for this elephant.

^{c11} After Ref. [16], also cited in Ref. [21].

^{c12} Culled in Zambia (formerly Northern Rhodesia).

^{c13} From “Maji Moto Camp, Africa”.

^{c14} From “East Africa”.

^{c15} Human (*Homo sapiens*, family Hominidae, order Primates)—one complete and one sagittally sectioned brain, on loan from N.J. Mizeres (School of Medicine, Wayne State University, WSU, Detroit, Michigan, USA), plus archived specimens in Department of Pathology, WSU, Detroit.

^{c16} Chimpanzee (*Pan troglodytes*, family Hominidae, order Primates)—right hemisphere, from Detroit Zoological Institute (DZI), Royal Oak, Michigan, USA; DZI Sample no. 97-3340.

^{c17} Talapoin monkey (*Miopithecus talapoin*, family Cercopithecidae, order Primates)—whole brain, DZI no. 97-0017.

^{c18} Domestic sheep (*Ovis aries*, family Bovidae, order Artiodactyla)—five specimens from Carolina Biological Supplies, used in Biology 0471 course, WSU.

^{c19} Greater kudu (*Tragelaphus strepsiceros*, family Bovidae, order Artiodactyla)—left hemisphere, DZI no. 97-0036 “2nd brain”, partly sectioned.

^{c20} Grevy zebra (*Equus grevyi*, family Equidae, order Perissodactyla)—left hemisphere, DZI no. '96.

^{c21} Rock hyrax (*Procavia capensis*, family Procaviidae, order Hyracoidea)—whole Brain, DZI no. 97-0015. Also a specimen from private collection of J. Shoshani.

^{c22} Maned wolf (*Chrysocyon brachyurus*, family Canidae, order Carnivora)—left hemisphere, DZI no. 97-4918.

^{c23} Domestic cat (*Felis catus*, family Felidae, order Carnivora)—a specimen from Carolina Biological Supplies, used in Biology 0471 course, WSU.

^{c24} Chinchilla (*Chinchilla laniger*, family Chinchillidae, order Rodentia)—a specimen from private collection of J. Shoshani.

^{c25} Guinea pig (*Cavia porcellus*, family Caviidae, order Rodentia)—three specimens from private collection of J. Shoshani.

^d Age in years; Ad. = adult individual; Yg. = young individual.

^e F = Female, M = Male.

^f Some body weights were converted from lbs., others are estimated weights.

^{f1} Body weight of 3,216,000 g ([116], p. 78) was converted from 7090 lbs.

^{f2} Specimen B's heart weighed approximately 38 lbs (17.252 kg). From this heart weight we estimated the body weight to be 3,450,400 g (according to Ref. [11] elephant heart weighs nearly 0.5% of body weight, thus (17,252 g × 100%)/0.5% = 3,450,400 g, the estimated body weight of specimen B).

^{f3} Ref. [116], p. 35, gave the weight of this elephant as 2156.16 kg. Errors were found at a later date (weights of the lungs were originally taken as pounds not kilograms, and the weight of the head and trunk were not included) therefore the total weight had to be adjusted to 2267.43 kg.

^{f4} Estimated weight.

^{f5} Actual weight.

Table 1 (Footnote Continued)

^{f6} See footnote g6.

^{f7} It appears as though this elephant [66] is the same individual as noted by Ref. [21], p. 1093, as it has the exact same body weight. Note, however, that the brain weights in the two sources are different (5430 g in Ref. [66] versus 4717 g in Ref. [21]), for this reason, we kept both specimens in our data.

^{f8} Weights were converted from lbs to kg or vice versa; see also footnote g8.

^g All our data on brain weights include parts of the dura mater and variably long portions of the medulla oblongata (a part of the brainstem).

^{g1} Brain weight from Ref. [116], p. 51.

^{g2} Extrapolated from 4785 g of brain (of Specimen B, without dura mater) because some tissues were missing.

^{g3} Actual weight.

^{g4} Estimated weight.

^{g5} The brain of the stillborn (specimen G) was partly autolyzed; the left cerebral hemisphere was completely autolyzed, whereas only about one quarter (25%) of the right cerebral hemisphere (RCH) was autolyzed. The cerebellum was better preserved, only about 10% was autolyzed. Based on these estimates, we obtained the brain weight as follows: 540 g (weight of the RCH) + 180 g (estimate loss 25% of tissue) = 720 g (estimate for the RCH). Therefore, $720 \text{ g} \times 2 = 1440 \text{ g}$ estimate for the entire cerebrum. Cerebellum weight $340 \text{ g} + 38$ (estimate 10% tissue loss) = 378 g cerebellum estimate. Therefore, the conservative estimated total brain weight for the stillborn (about 22 months old) without dura mater is: 1440 g (cerebrum) + 378 g (cerebellum) = 1818 g. See also footnote i3. The average brain weight of six near-term and neonate elephants is 2551 g. This average is based on these data: 1818 g (specimen G), 1650 g ([106], p. 611), 2040 g ([32], pp. 137, 277), 2700 g ([117], p. 183), 3000 g ([117], p. 183), and 4100 g ([117], p. 132).

^{g6} The brain weight for this specimen [48], cited in Ref. [11], p. 109, is the largest recorded weight for an Asian elephant; it appears to be too large for such a small elephant. The body weight is small implying that the animal was either sub-adult or lost much weight before death. The EQ of this specimen was not included in our average calculations.

^{g7} This brain weight appears to be outside of the range of other brains we studied; it was excluded from our average brain weight calculations.

^{g8} Brain weight is without dura matter.

^{g9} Based on Ref. [104], pp. 134–5; it appears that the weight of 9000 g is a rough estimate and probably too large for an elephant whose body weight is 4,380,100 g (another elephant reported by Ref. [104] had a body weight of 5,174,400 g and a brain weight of 4000 g). The 9000 g brain weight is the largest recorded elephant brain weight; it was excluded from our average brain weight calculations. The EQ of this specimen was also not included in our average calculations.

^{g10} Range weight of human brain, females and males, is 1130–1680 g [134].

^{g11} Computed from data for 1/2 chimpanzee's brain ($173.7 \times 2 = 347.4 \text{ g}$) obtained from the DZI no. 97-002-1.

^{g12} Computed from data for 1/2 Talapoin monkey's brain ($16.35 \times 2 = 32.7 \text{ g}$) obtained from the DZI no. 97-017.

^h Weight of cerebellum is without brainstem.

^{h1} Extrapolated based on cerebellum weight of specimen E. Only 1/2 of cerebellum available (the other half brain is with Darlene Ketten, Harvard Medical School, Boston, MA, USA), the 960 g is a result of $480 \text{ g} \times 2$.

^{h2} Extrapolated based on cerebellum weight of specimen E.

^{h3} Extrapolated based on cerebellum weight of specimen E, after subtracting the estimated weights (200 g) of brainstem and a piece of dura mater.

^{h4} Actual weight.

^{h5} See footnote g5.

^{h6} Computed from data for 1/2 chimpanzee's cerebellum ($21.66 \times 2 = 43.32$) obtained from the DZI no. 97-002-1.

^{h7} Computed from data for 1/2 Talapoin monkey's cerebellum ($1.25 \times 2 = 2.5$) obtained from the DZI no. 97-017.

^{h8} Ref. [79], pp. 423–4, includes data, as composite from different sources, on weights of brains and cerebelli of various mammals at different ages; these may be compared to those presented here.

ⁱ Certain weights of the dura mater are estimates.

ⁱ¹ The dura mater of specimen B weighed 420 g + 210 g (estimated 50% missing dura) = 630 g estimated weight. Dura thickness varies from 1 to 5 mm. A thickness of 3 mm for dura mater at the dorsal cerebral hemisphere was reported for a 25 days-old calf ([32], p. 146).

ⁱ² Specimen C's dura mater weighed 405 g + 203 g (estimated 50% missing dura) = 608 g estimated weight of Specimen C's dura mater.

ⁱ³ The dura mater of specimen G weighed 135 g + 68 g (estimated 50% missing dura) = 203 g.

^j EQ = Encephalization quotient. We followed Ref. [66], p. 61, to calculate the EQ, using this formula: $\text{EQ} = E/[0.12 \times (P \text{ to the power of } 0.666)]$ or $\text{EQ} = E/[0.12 \times (P \text{ to the power of } 2/3)]$, where: EQ = Encephalization quotient; E = brain weight (g); P = body weight (g); 0.12 = a constant. Martin [86] calculated the value of the slope of the line to be 3/4 instead of 2/3 used by Jerison [66]. We realize that certain captive elephants may have lost weight prior to death and thus the value of EQ may be affected. For this reason, we tried to compile as large a data base as possible and to use the average EQ.

^{j1} EQ was calculated only for adult specimens because body weight and brain weights of stillborns, juveniles and sub-adult give skewed EQ values.

^{j2} EQ values or their averages for samples 34–44 were adapted after Ref. [39], pp. 498–502.

^{j3} No EQ available for Talapoin monkey (*Miopithecus talapoin*), but members of the same family (Cercopithecidae), have EQ that ranges from 1.67 to 2.34.

^{j4} No data for Greater Kudu (*Tragelaphus strepsiceros*), but *T. scriptus* (the bushbuck) has an average EQ of 1.07.

^{j5} No data for Grevy zebra (*Equus grevyi*), but *E. zebra* (the mountain zebra) has an EQ of 1.7.

^{j6} No data for Maned wolf (*Chrysocyon brachyurus*), but *Canis lupus* (the wolf) has an average EQ of 1.13.

^{j7} No data for Domestic cat (*Felis catus*), but *F. sylvestrus catus* (the wild cat) has an EQ of 1.14.

3.2. Brain weight

Fig. 2A provides a simplified illustration of an elephant brain and spinal cord viewed dorsally. Fig. 2B depicts the spinal cord in lateral view.

The extrapolated brain weight of the stillborn is 1818 g and the brain weight of six adult elephants we examined ranges from 4050 to 5220 g (Table 1A). All our data on brain weights include parts of the dura mater and variably long portions of the medulla oblongata. One author [125] noted that the weight of the ele-

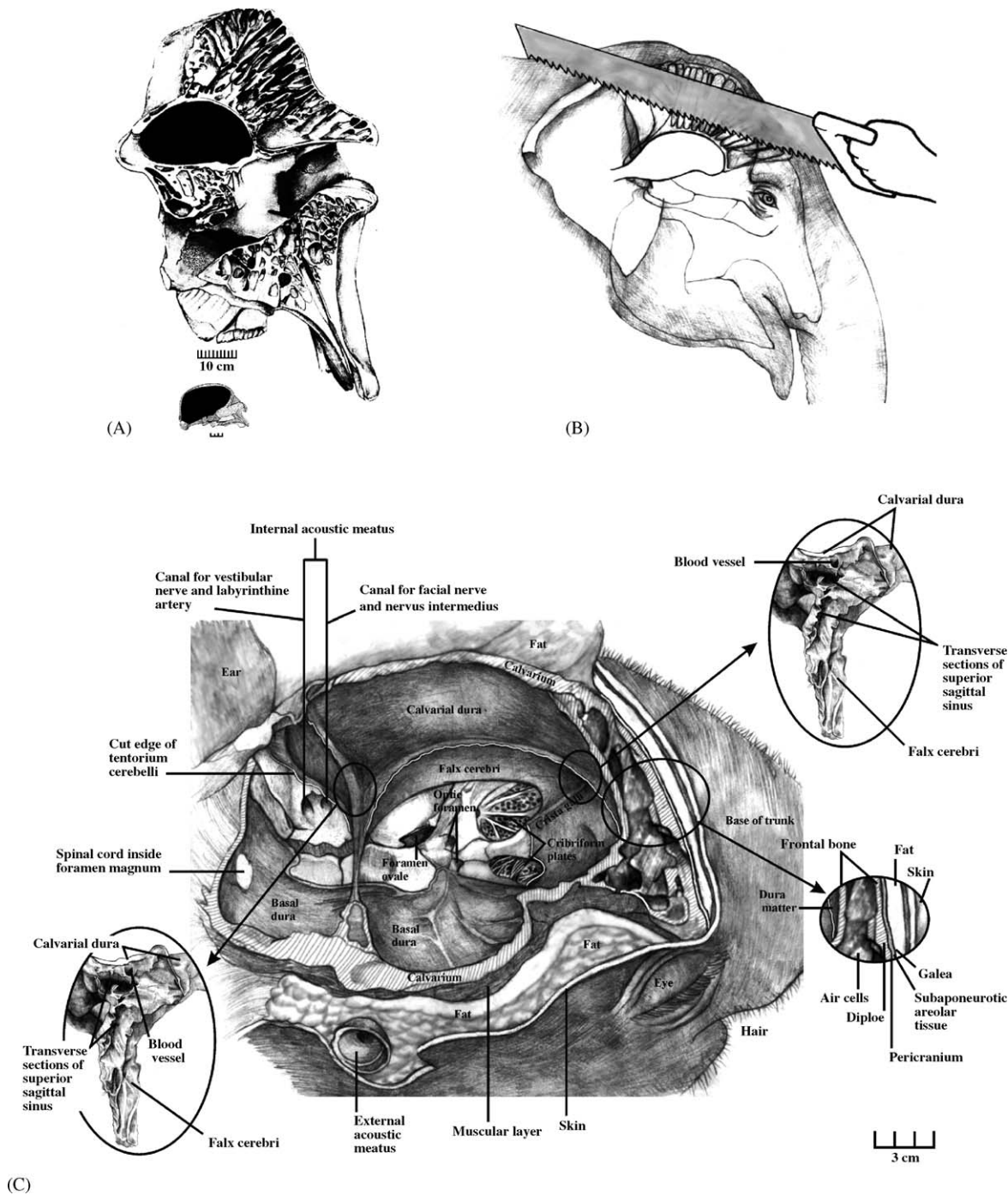


Fig. 1. Cranial (brain) cavity and structures inside elephant crania and heads. (A) Comparison of mid-sagittal plane of crania of a fetus and an adult elephant. (B) A simplified drawing of an adult Asian elephant, depicting location of cutting the calvarium in order to remove the brain intact. (C) Meninges and other structures of elephant brain in dorso-lateral view, depicted inside the braincase of a stillborn (specimen G in Table 1A). Sources: (A) adult *E. maximus* after AMNH 54261, fetus, *L. africana*, after ([36], plate VIII), (B) a generalized elephant, and (C) our dissection, and ([134], pp. 986–994) was consulted for terms (drawings by GHM).

phant brain he examined excluded the dura mater, whereas other investigators did not clarify how were the weights obtained. The extrapolated weight of the dura mater of a stillborn elephant fetus (specimen G) is 203 g, and that of an adult elephant weighs 630 g (Table 1A). Brains should, therefore, be weighed after removal of the dura.

The average brain weight of the five adult elephants we examined is 4648 g (average for human is 1400 g). Excluding the three highest adult brain weights (6500, 7475, and 9000 g), the weight of 17 adult elephant brains we studied and those reported in the literature range from 4000 to 6075 g (Table 1B), with an average of 4783 g. This average of 4783 g

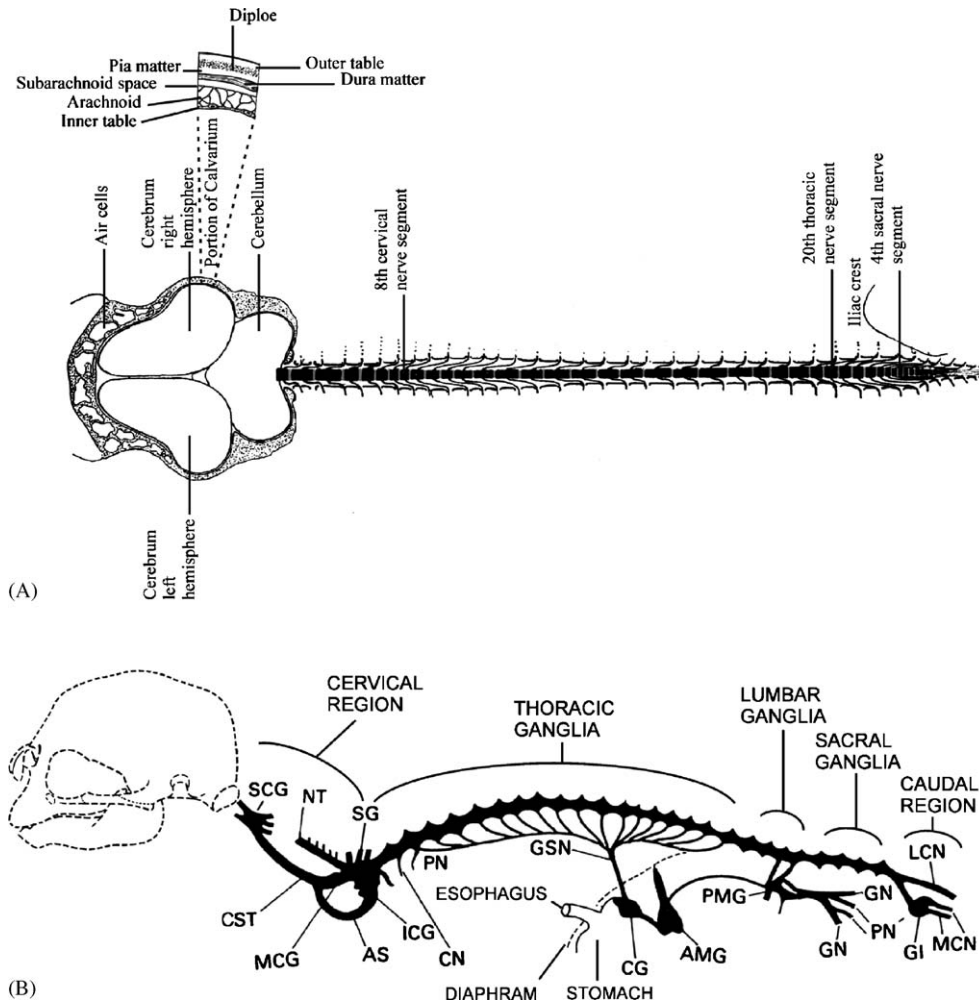


Fig. 2. Brain and spinal cord. (A) Dorsal view (modified after ([32], Fig. 6, p. 160). (B) Lateral view (modified after ([85], p. 163)). Key for letters in (B): AMG = anterior mesenteric ganglion, AS = ansa subclavia, CG = celiac ganglion, CN = cardiac nerves, CST = cervical sympathetic trunk, GI = ganglion impar, GN = genital nerves, GSN = great splanchnic nerve, ICG = inferior cervical ganglion, LCN = lateral coccygeal nerves, MCG = middle cervical ganglion, MCN = middle coccygeal nerves, NT = nervus transversarius, PMG = posterior mesenteric ganglion, PN = pulmonary nerves, PN' = parasacral nerves, SCG = superior cervical ganglion, SG = stellate ganglion.

is the largest brain weight among living and extinct terrestrial mammals [66,117]. Our data are limited for elephants with known gender; based on the available data, however (excluding the three out-of-range brain weights), the average for adult males ($n = 3$) is 5004 g, and for adult females ($n = 8$) is 4677 g (average for adult female human brains is 1350 g and for male is 1450 g [134]).

3.3. Meninges

Within the cranial cavity we identified these four folds of the dura mater (Fig. 1C): *falx cerebri* (between the two cerebral hemispheres), *tentorium cerebelli* (between the cerebrum and cerebellum), *falx cerebelli* (between the two lateral lobes of the cerebellum), and *diaphragma sellae* (covering the roof of the sella turcica with the pituitary body inside, leaving a small opening for the pituitary stalk). The dura mater in elephants measures about 10 mm in thickness; in humans, thickness reaches 3 mm.

We also identified the superior sagittal sinus, inferior sagittal sinus (Fig. 1C), and the straight sinus at the confluence of sinuses, also known as the torcular of Herophili [5,9,53]. These sinuses serve to collect blood from the cerebral veins and conduct it to the internal jugular veins. In the elephant, the thick dura at the posterior end of the falx and superior sagittal sinus and the large confluence of sinuses deeply indent the posterior cerebrum (parietal lobes), producing a prominent triangular defect and deeply grooving the posterior cingulate gyri on either side. In humans, a similar configuration can also be observed, with the torcular producing grooves in the occipital lobes on either side [134].

The arachnoid membrane, the subarachnoid space, and the pia mater appear similar to those of humans. In all the elephant brain specimens examined, we were not able to see arachnoid granulations with the naked eye [116]. Under the microscope, however, it was possible to discern arachnoid granulations. The pia mater is also relatively thick and closely follows the contours of the brain and the spinal cord. We hypothesize that functions

of all the meninges and associated structures in elephants are similar to that in humans.

3.4. Cranial arteries

Major arteries, including the arterial circle of the brain (Circle of Willis), have been identified (Fig. 3A and B). Like the human brain, the elephant brain is supplied by two pairs of arteries, the internal carotid and the vertebral arteries. The arterial circle of the brain is formed at the base of the brain by the joining of these arteries and their branches: paired posterior cerebral, posterior communicating, internal carotid, anterior cerebral (proximal segment) arteries, and a single anterior communicating artery [9,134].

We noted that the intracranial portions of the vertebral arteries (seen at the bottom of Fig. 3B) are relatively small. The middle cerebral arteries (labeled on both sides, close to the top of Fig. 3B) are the largest terminal branches of the internal carotid arteries. The internal carotid arteries are larger in diameter than those in humans and have thicker walls. The proximal intracranial internal carotid artery in specimen B measured 5.0 mm in diameter and 1.0 mm in wall thickness; in man it measured 4.5 and 0.8, respectively. In specimen B, the cavernous sinus, as observed in the dura mater on either side of the pituitary gland area, measured at least 30 mm in length, 15 mm in width, and 15 mm in depth. The internal carotid artery segment passing through this cavernous sinus is 7 mm in diameter and has 1.3 mm wall thickness. Venous channels were observed on either side,

juxtaposed to the internal carotid artery. In two elephant brain specimens (*E. maximus*, specimen B, and *L. africana*, specimen E) we noticed an abundance of large and small branches of the arterial circle of the brain, and secondary vessels associated with veins and cavernous sinuses that produce a vascular mat at the base of the brain.

3.5. Cranial nerves

The basic pattern and distribution of the 12 cranial nerves is similar in humans and elephants (Fig. 4). Minor differences (possibly size-related) are noted in Tables 2 and 3. Comparison of the emergence of cranial nerves in humans and elephants with regard to the blood vessels shows, with slight expected variations, that they have similar patterns (see Fig. 644 in Ref. [18]).

The intracranial portion of the facial nerve (VII) in an elephant is larger than observed in man, taking into account also the relative proportions of the respective brain sizes (see Fig. 644 in Ref. [18]; Figs. 4 and 5B; Table 2): an elephant brain is about 3.4 times larger than a human brain, but the measurement of the facial nerve of the elephants is 5.2 times larger than that of a human. In elephants, the most striking feature of the cranial nerves is the enormous size of the nerves supplying the proboscis. The maxillary division of the trigeminal sensory nerve (V) and the facial motor nerve (VII) that innervates the facial musculature unite extra-cranially anterior to the eye region to form the great proboscideal nerve [36].



Fig. 3. Intracranial arteries of specimen E, photographed on the brain in ventral view (A), and after removal intact, drawn, identified, and labeled (B). Source consulted: Ref. [134], pp. 937–638 (photograph and drawing by GHM).

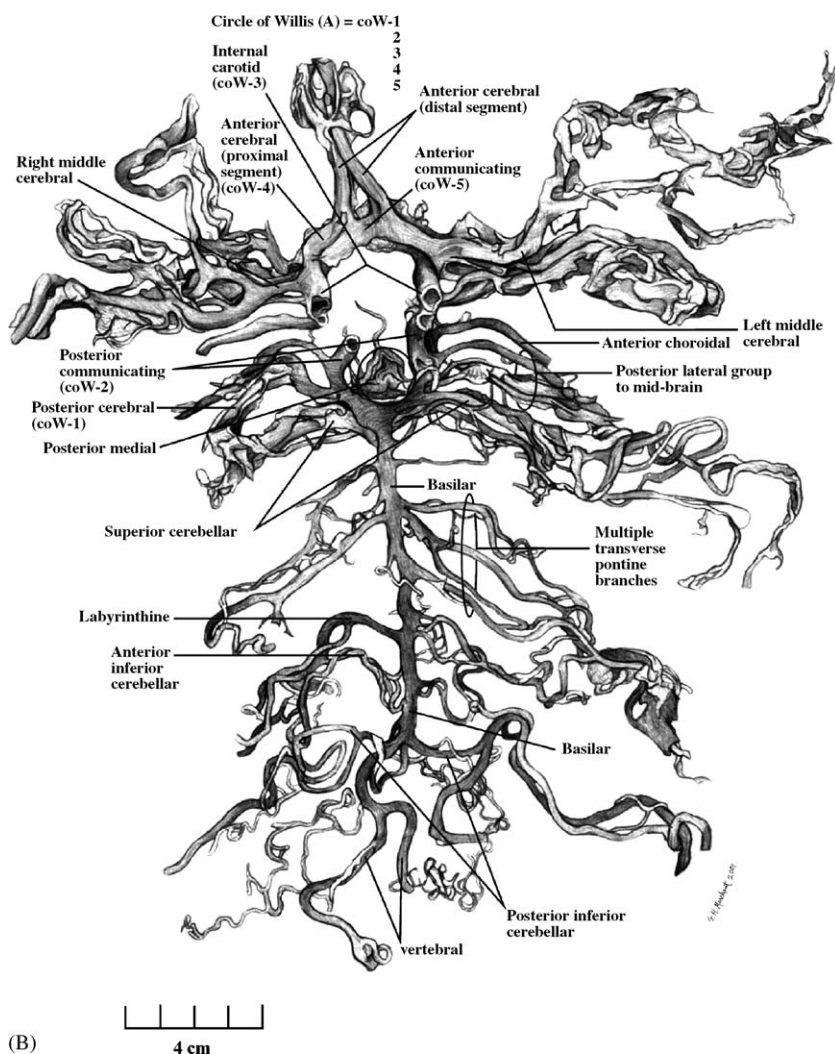


Fig. 3. (Continued).

Table 2

Cranial nerve (and associated structures) measurements and differences between elephant and human observed with a naked eye; all measurements are in mm

Cranial nerve	Difference between elephant and human (cf. Fig. 4)
I Olfactory	Length of the olfactory tract in specimen B is 10 and wide; in man it is 28 and narrow. Olfactory ventricle/bulb much larger and more bulbous; in specimen B it measured 65 long, 32 wide, 20 high, and its wall measured 1 thick. In human, there is no olfactory ventricle (the bulb is solid), its length is 10, width 4.5, and height 2.5
II Optic	5 × 4 (in specimens B and E); in man 5.5 × 3.3; in man the optic chiasm smaller, with long intracranial course
III Oculomotor	3 × 2 (in specimen C), 2.5 × 1.4 (in specimen B); in man 2.2 × 1.6. In specimen C it originates anterior to the posterior cerebral artery ([116], p. 51), in man between the posterior cerebral artery and the superior cerebral artery
IV Trochlear	1 × 1 (in specimen B); in man 0.7 × 0.7
V Trigeminal	19 × 8 (in specimen C), 15.1 × 7.6 (in specimen E); in man 3.6 × 2.4 ^a
VI Abducens	1.1 × 1.1 (in specimen B, as in man originates from the brain stem at posterior of the pons); in man 1.06 × 0.96 (average of three measurements)
VII Facial	6 × 4 (in specimen E), 8.4 × 3.3 (in specimen B); in man 1.9 × 0.7 ^a
VIII Vestibulocochlear	4 × 2 (in specimen E), 5.5 × 1.6 (in specimen B); in man 3.1 × 1.5. In elephants, the cochlear nerve ends in the temporal lobe
IX Glossopharyngeal	1.8 × 1.0 (in specimen B); in man 1.4 × 1.4
X Vagus	1.7 × 0.9 (in specimen B); in man 3.0 × 1.2. As in man nerve X is in close association with nerve IX
XI Accessory	As in man, it has multiple rootlets
XII Hypoglossal	As in man, it has multiple rootlets

See also Table 3.

^a In elephants the maxillary division of the trigeminal nerve (V) and the facial nerve (VII) that innervates the facial musculature unite to form the great proboscideal nerve ([36], personal observations).

Table 3
A summary of differences between elephant and human brains (additional information is given in parenthesis)

Structure	Observations and differences in elephants
General	
Brain size	1/600 of body size [134] or ~1/700, our data (1/50 in human)
Dura mater	Is thicker (1–5 mm) than that of human (0.5–2)
Torcular of Herophili	Deeply indents and grooves the posterior angles of the parietal lobes and the posterior cingulate gyri (in humans, a similar conditions sometimes develops, but the grooves are in the occipital lobes)
Arachnoid granulations	Are not visible with naked eye
Cerebrum and cerebellum	Convolutions of gyri are more numerous and appear more complex
Prosencephalon: telencephalon	
Neocortex	No apparent difference in thickness between pre- and post central cortex or between calcarine and adjacent cortex. No visible line of Gennari
Thalamus	Relatively large
Corpus callosum	Thick with prominent dorsal ridges of longitudinal striae and indusium griseum, genu and anterior body about as thick as the splenium. Number of commissural fibers in the corpus callosum is about twice as much in man (one specimen) than in elephant (one specimen)
Subcallosal gray matter in fornix	Substantially large (in human it is reduced or absent)
Hippocampus	Vertically oriented with relatively short fimbria, and ventral ridge of gray matter accompanying the fornix, broad subicular region, vertically oriented within the hippocampus
Parahippocampal gyrus (PG)	It is concealed medially by the large mass of the temporal lobe. In elephants the PG has transversely oriented subgyri (in human the PG is relatively smooth)
Amygdala	Located relatively posterior along ventral basal ganglia but still in proximity to pes hippocampi
Orbitofrontal surface	Is gyrated, yet it is not as developed laterally as in human (in human there is much enlargement of the frontal lobe laterally and anteriorly)
Olfactory (pyriform) lobe	Much developed, i.e., macrosmatic and exposed on the ventral surface (microsmatic, and not folded into limen insula in human)
Olfactory gyri and trigone	Very large and complex features unlike those on human and the striae are gyrated
Olfactory tract	Relatively foreshortened
Sulcus olfactorius	Not well defined, short and curved
Lateral olfactory stria	Gyrated
Temporal lobe	Disproportionately large and oriented vertically and projects laterally (in human it projects forward and slightly downward, and does not bulge laterally)
Occipital lobe	Relatively small and poorly defined, the parieto-occipital sulcus is not defined
Calcarine sulcus	Not so well defined as in human; apparent differences in thickness of calcarine sulcus
Lunate sulcus	Not found in elephants (in man, when present, it is associated with the calcarine sulcus)
Insula (Isle of Reil) lobe	Not as opercularized as in man
Lateral ventricles	Have broad flat frontal horn, inferior olfactory recess leading to olfactory ventricle, vertical inferior/temporal horn, short tapered posterior/occipital horn indented by white matter at bottom of calcarine sulcus; inferior horn indented by prominent collateral eminence
Prosencephalon: diencephalon	
Third ventricle	Interrupted by large massa intermedia thalami
Pineal gland	Small with prominent glial component relative to pineocytes
Mesencephalon	
Superior cerebellar peduncle	Diamond-shaped aqueduct, 4–5 mm
Cerebral peduncles	Broad with shallow interpeduncular fossa
Substantia nigra	With pale pigmentation
Nucleus ellipticus	Not reported in humans
Rhombencephalon: metencephalon	
Basis pontis	Relatively flattened and narrow compared to tegmentum
Locus ceruleus	Not visible grossly
Spinal trigeminal complex	Large
Rhombencephalon: myelencephalon	
Pyramids	Large, flattened
Olivary gray matter	Grossly less well-defined than human
Cerebellum	Have complex pattern of folia
Cerebellar weight	Averages 18.6% of brain (1.8 times larger than human)
Cerebellar recess	Lateral and lacking in midline
Nodulus and lingular lobules	In close proximity
Flocculus	Concealed in dorsal and ventral views
Superior medullary velum	Membrane, not thicker gliopendymal structure
Spinal cord	Larger number of segmental nerves (especially the thoracic region, after [32])

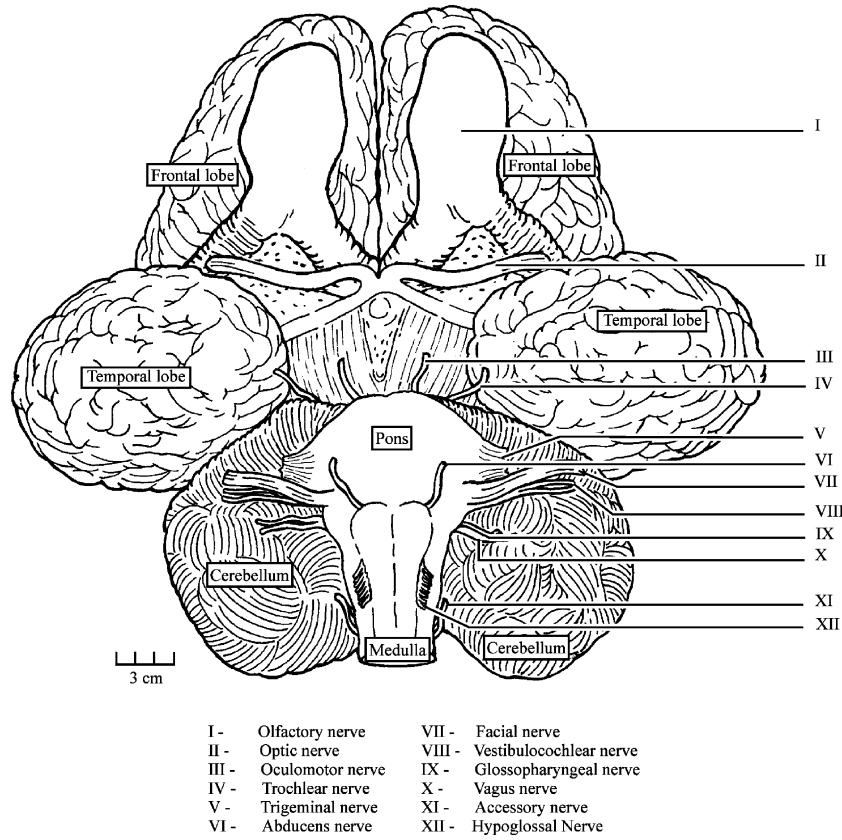


Fig. 4. Cranial nerves of specimen B, depicted in ventral view of brain. Source consulted: Ref. [134], p. 841 (drawing by GHM).

3.6. Brain

3.6.1. Telencephalon

3.6.1.1. Cerebral lobes. Major lobes, external and internal structures are depicted in Figs. 5–10 (Figs. 11–18 are related to brain internal structures after slicing, as discussed below). The brain is divided into two approximately symmetric hemispheres by a distinct interhemispheric fissure. The extremities or poles of each cerebral hemisphere include an anterior or frontal pole, a posterior or caudal pole, formed in the elephant by the posterior contour of the temporal lobe, and a temporal or inferior pole, formed by the temporal lobe. There is no definable occipital pole. On the medial aspect, the dorsocaudal angle represents the most posterior part of the medial “interhemispheric” surface [32]. The lateral cerebral surfaces include a large convex lateral surface formed by frontal, temporal, parietal lobes, and the insula. A flattened medial surface is formed by frontal and parietal lobes; a slightly convex posterior surface is formed chiefly by the temporal lobe; an orbitofrontal surface is formed on the inferior “orbital” aspect of the frontal lobe (Figs. 5 and 7).

The frontal lobe of the elephant includes the gyrated brain anterior to the lateral (Sylvian) sulcus and superior to the insula, and includes lateral, orbital, and medial surfaces. A presumptive identification of a central or Rolandic sulcus marking the caudal boundary of the frontal lobe is made on the basis of the presence of a relatively deep sulcus extending more or less continuously from the interhemispheric fissure to the lateral sulcus roughly at the midpoint of the brain when viewed from its lateral aspect.

Anterior to this, the lateral surface is marked by two or three larger vertically oriented sulci, denominated pre-Sylvian radial sulci [32] (Fig. 7A). No distinctive pattern of ectosylvian sulci is identified. The larger gyri are complexly folded. The medial surface includes the anterior part of the cingulate gyrus and many small gyri [53].

From the ventral view, the orbitofrontal surface is complexly folded, yet it is not as developed laterally as in a human brain (Fig. 10). In humans the frontal lobe expands laterally and anteriorly. Associated with this, lateral and anterior development of the human frontal lobe is the thin and elongated olfactory tract and the clearly demarcated gyrus rectus. In elephants, the olfactory tract is foreshortened relative to the size of the olfactory bulb, the lateral olfactory stria on the basal forebrain is gyrated, and a distinct gyrus rectus is not identifiable. The sulcus olfactorius (under the olfactory nerve) is not well defined. Two inter-related anatomical differences may account for the difference of sulcus olfactorius: (i) the olfactory bulb in an elephant is extremely large and expanded (Fig. 10B) and (ii) the human frontal lobe is much bigger relative to that of an elephant, and the olfactory tract is stretched along an elongated sulcus. In elephants, the sulcus olfactorius is shorter than in humans and it is curved (Fig. 10A). In humans, the lateral and medial olfactory striae merge in the olfactory tract (between these gyri the area is known as the ‘olfactory trigone’). In elephants, the striae and trigone are very large, and unlike those in humans, the striae are gyrated. In elephants, the olfactory bulb contains a ventricle (Figs. 6 and 10B).

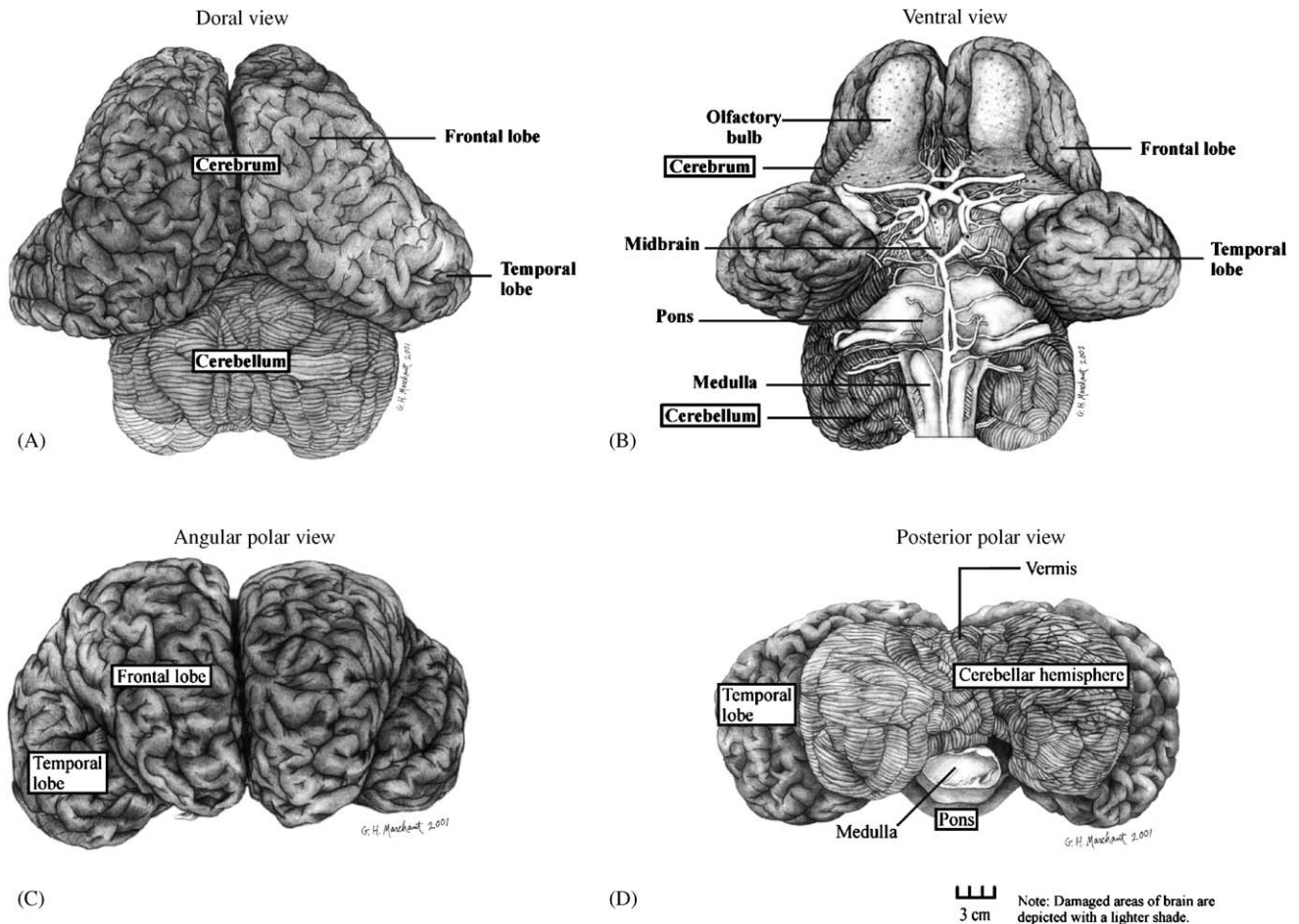


Fig. 5. Whole brains viewed from dorsal (A), ventral (B), anterior (C), and posterior (D) views, all drawings are based on specimen B brain (drawings by GHM).

Apart from the anterior boundary produced by the central sulcus (Fig. 7B), the parietal lobe boundaries are indistinct, and the parietal lobe is presumptively localized to the posterior superior aspect of the lateral cerebral surface and the posterior aspect of the medial surface, encompassing the dorsocaudal angle. The extent of the parietal lobe on the lateral and posterior surfaces merging with the large temporal lobe is uncertain.

The temporal lobe, defined by the lateral or Sylvian sulcus, includes lateral, postero-inferior, and medial surfaces and a distinct pole. It is marked by two distinct large and vertically oriented sulci on its lateral surface (Fig. 7A). These can be denominated anterior and posterior temporal sulci, respectively, and the gyri so defined can be denominated anterior, middle, and posterior gyri, bearing a topographic resemblance to the human superior, middle, and inferior gyri, respectively [134]. The large gyri, however, are subdivided by numerous small sulci into subgyri (based on four brains – specimens A, B, C, and E – each vertically folding temporal gyrus makes approximately 10–12 tertiary convolutions). The postero-inferior surface of the temporal lobe of the elephant is large and complexly gyrated and presumably corresponds to the occipito-temporal or fusiform gyri of the human brain.

The parahippocampal gyrus can be identified on the infero-medial aspect of the temporal lobe by a distinct parahippocampal or collateral sulcus in both elephant and human brains. In

humans, the parahippocampal gyrus is relatively smooth and visible on the ventral surface medial to the temporal lobe, whereas in the elephants it has transversely oriented subgyri and is largely hidden from view (Fig. 8C). Other differences between humans and elephants were observed in the shape and size of the temporal lobe. Viewed from the lateral side, in elephants, the anterior end of the temporal lobe extends ventrally and bulges laterally, forming a bulbous ‘inflated’ temporal lobe, whereas in humans the temporal lobe extends forward and slightly downward and does not bulge laterally (in the dorsal view there is a smooth contour line continuing from the frontal lobe along the temporal lobe and parieto-occipital lobe; in elephants there is a huge lateral expansion of the temporal lobe). This bulbous appearance is also evident when the brain is viewed ventrally (Figs. 5B and 10B).

At variance with the human brain, in which the occipital lobe is easily recognized and is separated from the parietal lobe on the medial surface of the cerebrum by the parieto-occipital sulcus and on the infero-lateral surface by the parieto-occipital notch, in elephants these structures are not distinct. The medially located calcarine sulcus of the human brain is also not well distinct in elephants (Table 3); the associated lunate sulcus in man was not found in elephants. A deep sulcus along the postero-medial aspect of the temporal lobe that extends nearly to the underlying posterior portion of the lateral ventricle presumably corresponds to the calcarine sulcus (Fig. 12).

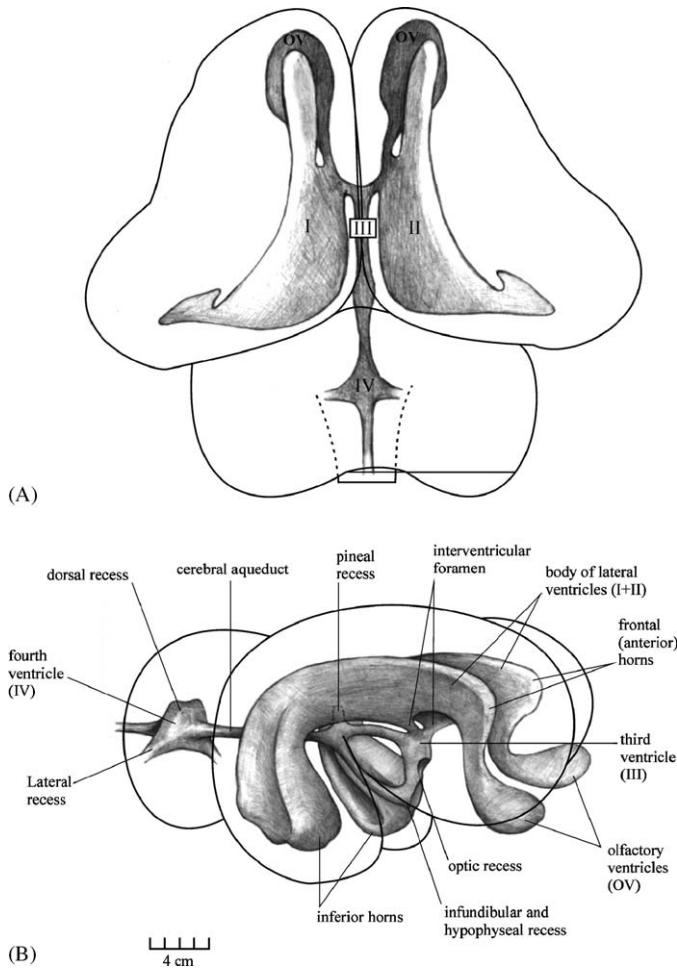


Fig. 6. Ventricles of elephant brains in dorsal (A) and lateral (B) views, composite restorations based on specimens A, B, C, E, and G. Sources consulted: Ref. [27], p. 220; Ref. [32], figs. 8, 14, 18, 30–31, 36–39; [62], pp. 31, 34; [134], pp. 878, 920, 968–9 (drawings by GHM).

The cingulate gyrus and parahippocampal gyrus are located along the medial surface of the cerebral hemisphere in proximity to the corpus callosum and best seen in mid-sagittal section (Fig. 8C). The cingulate gyrus is well delimited by a cingulate sulcus, narrows posteriorly into the isthmus and curves inferiorly to the splenium of the corpus callosum to blend with the posterior parahippocampal gyrus (Figs. 7B and 8C). The cingulate gyrus folds onto the superior surface of the corpus callosum in continuity with the gray matter ridge of the indusium griseum. In elephants the collateral sulcus (delimiting the parahippocampal gyrus from the rest of the inferior, ventral, lobe) and cingulate sulcus (separating the ventral cingulate gyrus from the superior gyri of the frontal lobe and parietal lobe) follow the human pattern. The infero-medial aspect of the parahippocampal gyrus is relatively narrow but broadens posteriorly; the supero-medial surface of this gyrus is extensive, especially posteriorly, and includes a broad expanse of the dentate gyrus.

3.6.1.2. The insula (Isle of Reil). In elephants, the insular lobe (Isle of Reil or central lobe), defined by the sulcus circularis insulae, is partially visible on the lateral surface (Fig. 7A). The

insula overlies the claustrum, a narrow layer of subcortical gray matter lateral to the putamen (Fig. 12A). The gyral pattern in the insula of the elephant is more complex than that observed in the brain of humans and non-human primates.

In the elephant, the insula is incompletely opercularized, i.e., not concealed by overlapping gyri from the surrounding frontal, temporal, and parietal lobes (referred to as opercula). There is a small frontal operculum overlapping the antero-superior portion of the insula. In humans, there are generally five insular gyri, grouped into long (two gyri) and short (three) gyri [93,134]. In one elephant (specimen B), we counted six insular gyri on the right side, but this is likely to be a character with an inter-individual variability. In the dolphin brain there are about 13 gyri in the insula (see Fig. 1 in Ref. [89]).

3.6.1.3. Corpus callosum. In elephantids, the corpus callosum is thick with well-formed genu, body, and splenium, as seen on midsagittal section (Fig. 7B).

In specimen E, the total length of the corpus callosum is 99 mm, the thickness (height) of the genu is 14 mm, the body 14 mm, and the splenium is 15 mm. In humans, the corpus callosum varies considerably in thickness from an individual to another. In one human brain, we obtained the following measurements: length 74 mm, thickness of genu 11 mm, body 5 mm, and splenium 12 mm. We calculated the areas of the corpora callosa of one elephant (specimen A, Fig. 8B) and of one human brain, and obtained 12.57 and 5.98 cm², respectively. The areas of the brains of these specimens in midsagittal sections (outlined in Fig. 8B), for the elephant is 271.05 cm² and for the human specimen is 170.67 cm².

3.6.2. Cerebral ventricles

All the ventricles in elephants appear structurally similar to those of the human brain, except for their larger volumes and different proportions (Fig. 6). In particular, in the elephant lateral ventricles, the frontal horns are relatively small; the olfactory ventricle communicates with the inferior recess of the frontal horn by a narrow aperture; there is no discrete occipital horn, but the calcarine sulcus can be identified as a deep sulcus indenting the posterior end of the inferior horn (temporal horn); in turn, the temporal horn is deeply indented by the parahippocampal (or collateral) sulcus producing a large collateral eminence.

In elephants, the olfactory ventricle is patent and large; in specimen B it measured 65 mm in length, 32 mm in width, 20 mm in height, and its wall was 1 mm thick. In humans, the olfactory ventricle is usually obliterated after the embryonic period. The third ventricle is traversed by a prominent massa intermedia thalami. The rostral portion of the roof of the fourth ventricle is attenuated to a thin membrane, representing a thin superior medullary velum. The ventricular surfaces are smooth and glistening.

Similar to humans, the choroid plexus was identified in the lateral, third, and fourth ventricles in elephants. The flow of cerebrospinal fluid from lateral ventricles to subarachnoid space is inferred to be analogous to that in humans. None of the specimens showed evidence of hydrocephalus (i.e., an enlargement of all or part of the ventricular system).

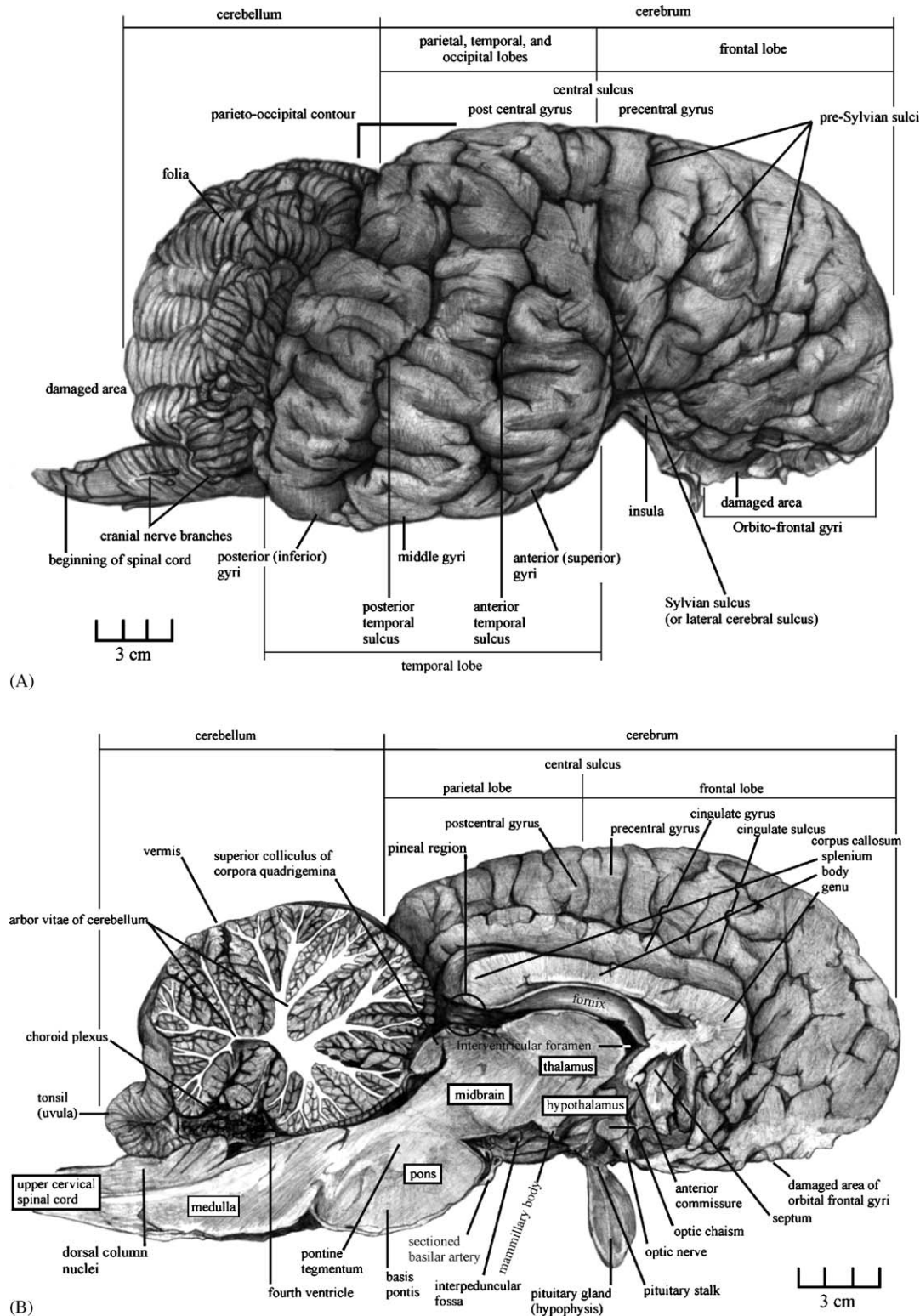


Fig. 7. Lateral (A) and close to midsagittal (B) views of elephant brain, based on brain of specimen A. Sources consulted: Ref. [32], p. 251; Ref. [70], p. 76. Note that in the lateral view (here it is reversed) the brain appears more flattened than other elephant brains; specifically the temporal lobe is not oriented vertically as depicted in (Ref. [62], p. 19). This appears to be a postmortem condition; cf. ([10], plate XXIII) where the temporal lobe has the same orientations as in our specimen (drawings by GHM).

3.6.3. Cerebral cortex and white matter

In the elephant, despite the complexity of the sulcal pattern, the sulci are generally shallow with relatively few “buried gyri”, as compared other complexly gyrated brains, such as those of

cetaceans [135]. The cortical thickness is relatively uniform. No definite difference is apparent in the cortical thickness to demarcate precentral from postcentral cortex in the central region. In the temporal lobe, the collateral sulcus is deep and associated

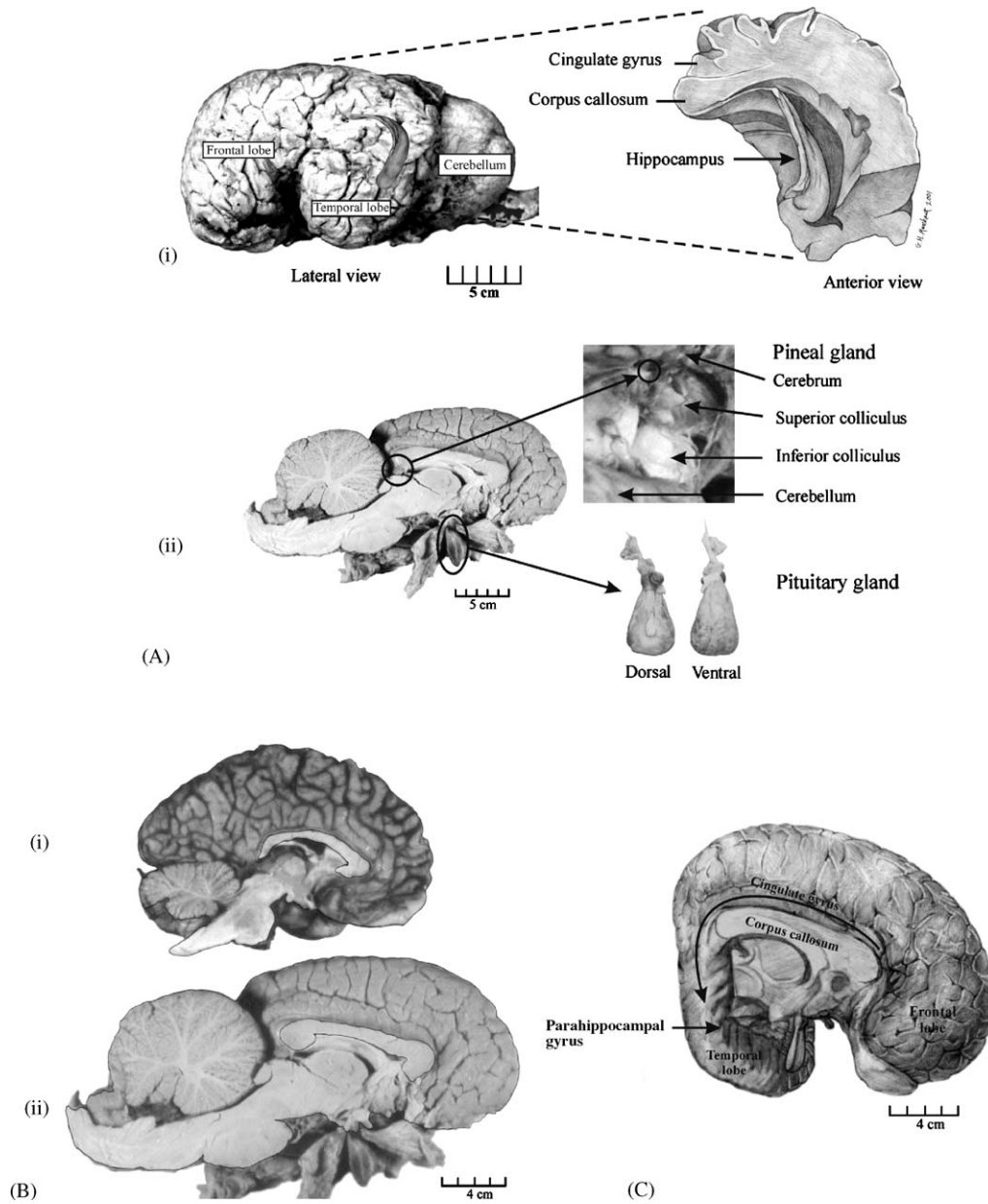


Fig. 8. A(i) Location of the hippocampus inside elephant brain in lateral view, and enlargement of the hippocampus in anterior view. A(ii) Locations and enlargements of the pineal and pituitary glands in a mid-sagittal section of specimen A. B(i and ii) Midsagittal views of brains of human (i) and an elephant (ii, specimen A), depicting in outline whole brains and corpora callosa for which surface areas were calculated. (C) Midsagittal section of specimen B cerebrum representing portions of limbic lobe (cingulate gyrus and parahippocampal gyrus); arrows depict relationships of cingulate gyrus to parahippocampal gyrus. Sources: A(i) after Ref. [77], A(ii) our dissections, mid-sagittal section, and pituitary glands are of specimen A, but the pineal gland is of specimen E; B(i and ii) our dissections; C our dissection. Photographs in A(ii) and B(i and ii) by Ben True (BT), drawing in (C) by Brian Cressman (BC).

with a prominent bulge of white matter (collateral eminence) on the ventricular surface of the temporal horn. Posteriorly, the calcarine sulcus (Fig. 14, IV, no. 3) produces a ventricular white matter bulge. No band of myelinated fibers comparable to the stria of Gennari seen in human calcarine cortex is noted.

Data for cortical thickness in two adult elephants (specimens A and E) and a middle-aged adult human were collected. Measurements were taken at six sections for a human and seven sections for two elephants. These data provide ranges and a

general average of the cortex thickness for human and elephants. For comparison, in the human, a minimum thickness (2.0 mm) and a maximum (3.5 mm) over the crest of convolutions were obtained. Comparable data for the elephants were 2.3 and 4.1 mm, respectively (Fig. 18, I–IV). Similarly, in the human, a minimum thickness (2.0 mm) and a maximum (2.5 mm) at cortex at bottom of sulcus were obtained, and for elephants these data were 2.0 and 2.5 mm. The average of cortical thickness in humans at the crest of the convolution is 2.8 mm ($n = 10$) and for elephants it is 3.0 mm ($n = 12$). The average of

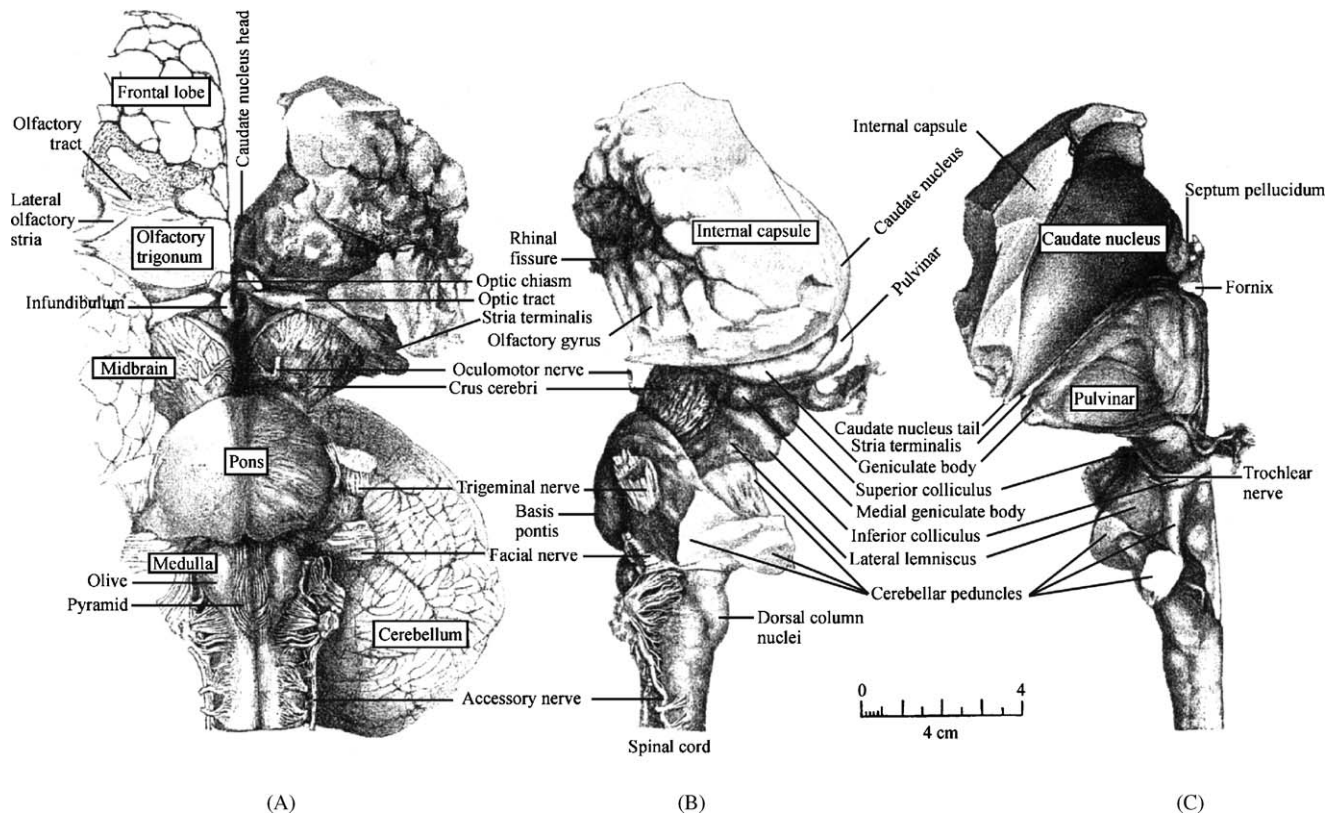


Fig. 9. Ventral (A), lateral (B), and dorsal (C) views of the brain of an Asian elephant ([32], figs 20, 21; and [18], pp. 216, 223, and 229, respectively) depicting structures deep in the brain. These structures were identified on the brains we studied.

cortical thickness at deeper areas of convolution is 2.1 mm in humans ($n = 12$) and 2.3 mm in elephants ($n = 10$).

3.6.3.1. Hippocampal formation (HC), parahippocampus, and cingulate gyrus. The elephant HC [32,62,74,77] is identified along the medial surface of the temporal lobe, oriented along a ventral–dorsal axis parallel to the similarly oriented temporal lobe, and arches posteriorly and medially towards the splenium of the corpus callosum along the medial aspect of the parietal lobe (Fig. 8Ai).

The hippocampus measures about 8 cm from anterior-most HC, known as the pes hippocampi, to the splenium of the corpus callosum. The hippocampal eminence, produced by the mass of HC indenting the ventricular surface of the temporal horn, measures 1 cm in width at the widest point of the pes hippocampi and tapers to 0.2 cm under the splenium of the corpus callosum. The margo denticulatus represents a portion of the fascia dentata of the HC visible on the medial surface of the temporal lobe, bounded by the fissura hippocampi and by the sulcus fimbriodentatus, measures 0.5 cm in width anteriorly, and narrows to 0.4 cm at the splenium of the corpus callosum. The surface of the margo denticulatus is smooth and gray anteriorly, unlike the human's, which frequently shows shallow bulges resembling blunt teeth. Posteriorly, shallow undulations corresponding to the gyrus fasciolaris are noted. The gyrus fasciolaris tapers to a thin indusium griseum along the caudal contour of the splenium and passes onto the dorsal surface of the splenium. Prominent dorsal ridges of longitudinal striae and indusium griseum were

identified on the superior surface of the corpus callosum. There was also a prominent ridge of gray matter associated with the fornix ventral to the corpus callosum; in human this subcallosal gray matter, possibly representing the bed nucleus of the fornix or related structure, is not grossly visible.

The elephant HC is approximately of the same size as the human HC, but is small relative to the overall size of the elephant cerebrum. The configuration is similar in both species with the HC drawn forward into the temporal lobe, but the long axis of the HC is more vertical in the elephant, reflecting the nearly vertical axis of the temporal lobe. Minor configurational differences include relatively indistinct digitationes hippocampi (indentations along the ventricular surface of the anterior end of hippocampus), a relatively broad and flat gyrus dentatus, and a relatively broad and thin fimbria fornix.

The parahippocampal gyrus lies between the fissura hippocampi and a deep sulcus on the inferomedial aspect of the temporal lobe known as the parahippocampal or collateral sulcus, which separates it from the irregular gyri on the posteroinferior surface of the temporal lobe (known as the fusiform or occipitotemporal gyrus in the human brain). The parahippocampal gyrus runs obliquely from the anterior temporal lobe to the splenium of the corpus callosum, forms the caudal and ventromedial surfaces of the medial temporal lobe, and tapers from anterior to posterior. The medial contour of the anterior parahippocampal gyrus, known as the uncus, is flattened. The superomedial surface of the parahippocampal gyrus is bounded by the fissura hippocampi, which is deep anteriorly and shallow posteriorly.

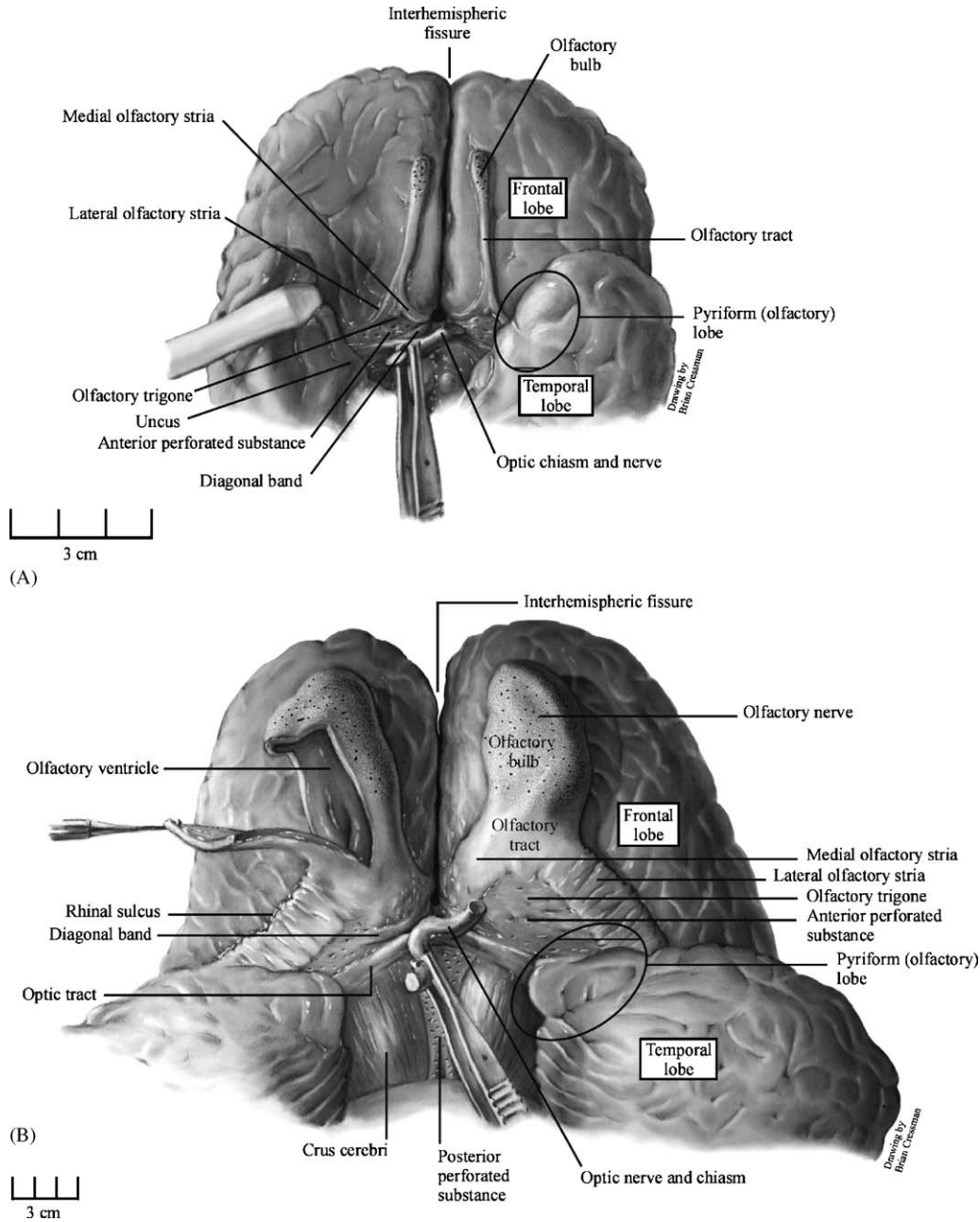


Fig. 10. Comparing frontal lobe regions of human (A) and elephant (B, of specimen B). Olfactory bulb and associated structures are depicted (drawings by BC).

The posterior parahippocampal gyrus passes along the contour of the splenium to become continuous with the cingulate gyrus (Fig. 8C). The fundus of the parahippocampal cortex at the bottom of the collateral sulcus and its subjacent white matter form a prominent bulge (collateral eminence) on the floor of the temporal horn, creating a deep ventricular sulcus medially between the parahippocampal white matter and the hippocampal eminence. The collateral sulcus is deep with shallow branches delineating three smaller gyri buried within the sulcus.

3.6.4. Basal ganglia

Structures visible with the naked eye in this region of the elephant brain include major divisions of the basal ganglia (cau-

date nucleus, putamen, and globus pallidus), nucleus accumbens [73], claustrum, amygdala, diagonal band of Broca, and the substantia innominata (Figs. 7–10, 12–16). The elephant brain shows a large well developed caudate nucleus and putamen, commensurate with the overall cerebral size.

3.6.5. Pituitary gland (hypophysis) and pineal gland (epiphysis)

In specimen A, an Asian elephant, the pituitary gland is large and weighed 6.16 g. This pear-shaped structure (Fig. 8Aii) measured 32 mm in length, 2.2 mm at its widest point, and 13 mm in thickness. The proximal “infundibular” part of the pituitary is narrow and hollowed inside (the infundibular recess of the third

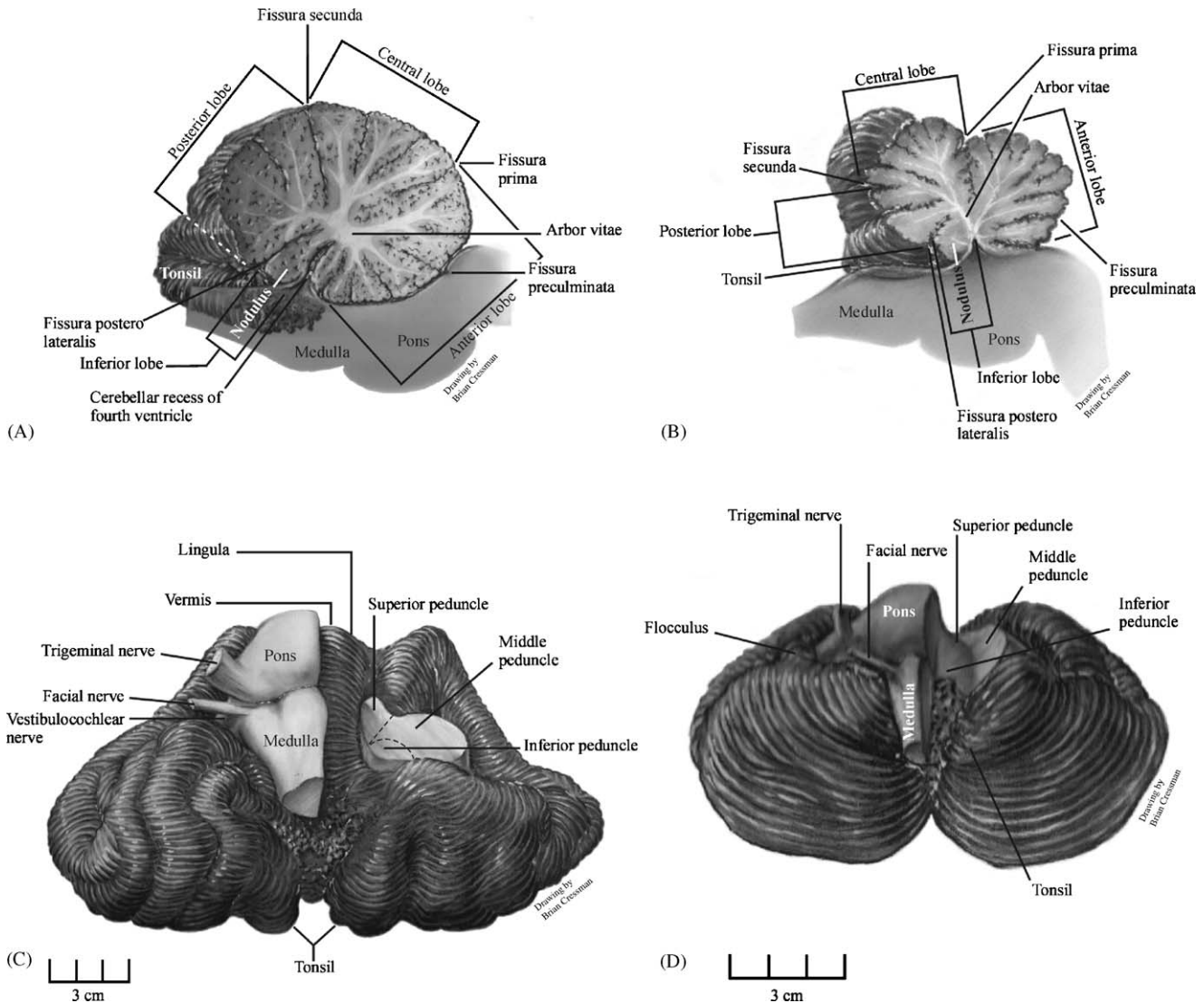


Fig. 11. Comparing cerebella of an Asian elephant (A and C) and human (B and D). (A) Is from specimen B and (C) from specimen A. (A and B) Midsagittal views and (C and D) ventral views (drawings by BC).

ventricle). The infundibular portion of the gland is constricted as it passes through the small opening of the diaphragma sellae (the fold of dura that covers the roof of the shallow sella turcica). The large bulbous adenohypophysis lies nearly horizontally on the cranium base between the floor of the sella and the diaphragma sellae. Other structures are similar to those in human brains.

Contrary to one author who did not find the pineal gland in the elephant [32], we could identify this gland, although it is not really distinct (see specimen E, Fig. 8Ai). On the other hand, we could not find the pineal gland or any pineal tissue in specimen B. In the brain of specimen E, the pineal gland weighed 0.08 g. A sample was taken for histological confirmation and showed a prominent component of cells showing the features of pinealocytes. Macro- and microscopic observations of the pineal gland of an African elephant were provided by Haug [63]. The occurrence of the pineal gland was also reported for the Asian elephant [87].

3.6.6. Diencephalon: general observations

Structures visible with the naked eye found in the diencephalon include the thalamus, with medial and lateral geniculate nuclei, and the hypothalamus [33], with the tuber cinereum of hypothalamus (sometimes with infundibulum), bordered by the internal capsule, optic nerve (cranial nerve II), optic chiasm and tracts, pituitary stalk and gland, pineal organ (gland), and containing the third ventricle, with the choroid plexus on the roof of this ventricle (Figs. 7B, 9, 10, 12). Similarities and differences between the elephant and human brains include the following observations: in the elephant, the thalamus is relatively large (see also Ref. [1]), and subnuclei and anatomic divisions, such as the internal medullary lamina are indistinct. The massa intermedia thalami is large. The mammillary bodies are relatively small and flattened. The optic nerve is of about the same size in elephants and man despite brain size differences (Table 2).

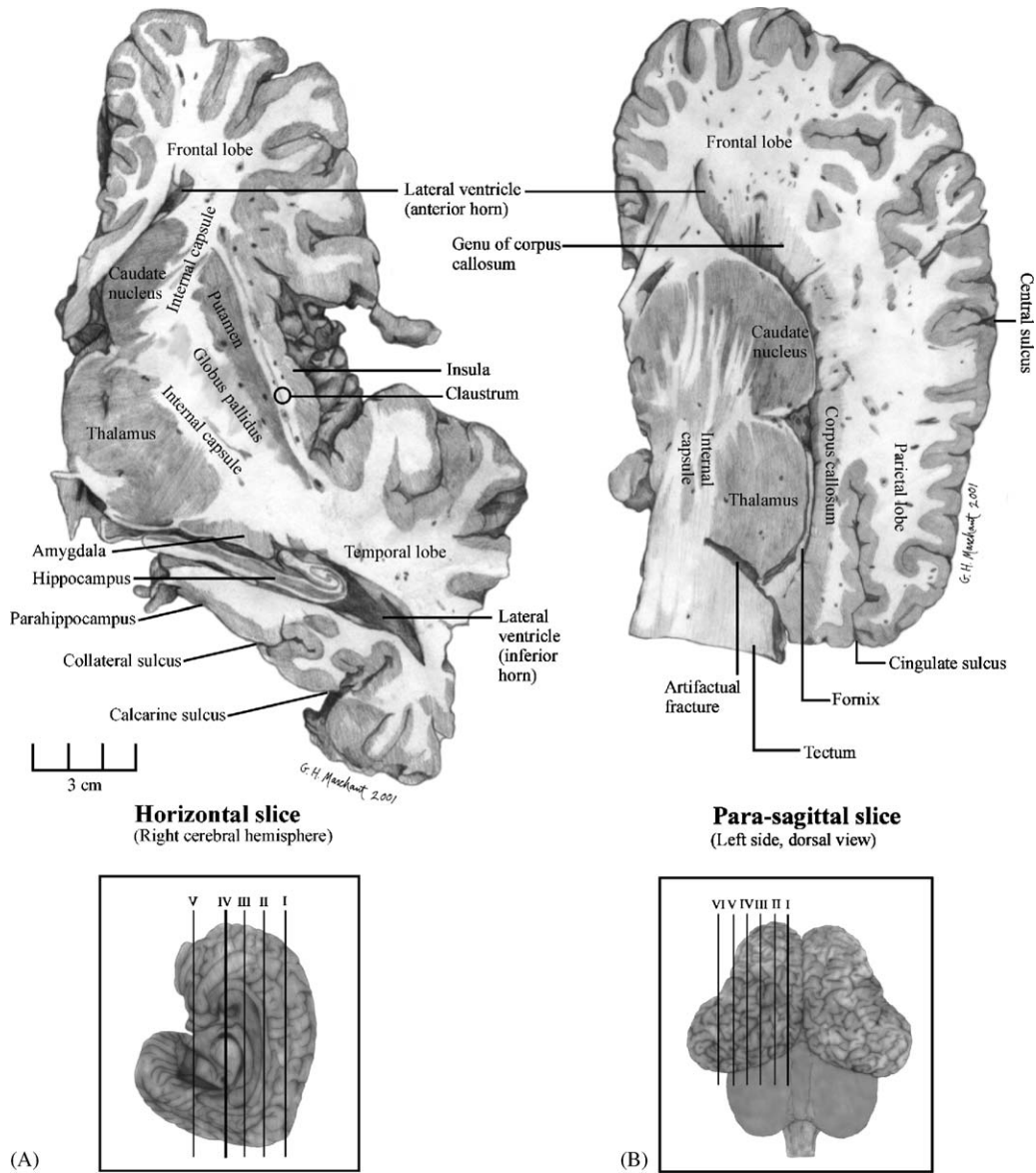


Fig. 12. Horizontal (A) and parasagittal (B) sections of right and left cerebral hemispheres, respectively. Simplified drawings in boxes indicate locations of sections, the darkest line represents the sections shown above. Depicted in section A are deep structures in African elephant brain (photographs by BT, drawings by GHM). Section B is the same as section in Fig. 13, I, right (denoted by an asterisk), and section A is the same as section in Fig. 14, IV, all from the same brain, specimen E in Table 1A (denoted by an asterisk).

3.6.7. Brain stem

Sections of the brainstem and cerebellum of specimens A, B, and E are depicted in Figs. 11 and 17.

3.6.7.1. *Mesencephalon.* Structures visible with the naked eye in the elephant midbrain are the superior and inferior colliculi, the cerebral aqueduct, the periaqueductal gray matter, the paired red nuclei, the substantia nigra, the cerebral peduncles (crura), and the cranial nerves III (oculomotor) and IV (trochlear) (Figs. 5,7B,9). The superior and inferior colliculi are not visible in a dorsal view, but they can be seen in the sagittal plane (Fig. 7B). The nucleus ellipticus is noted in Fig. 16. Differences between elephants and humans include the large diamond-shaped aqueduct (4–5 mm), the broad cerebral peduncles with shallow interpeduncular fossa, and the relatively pale

pigmentation of the substantia nigra. Melanin pigmentation could, however, be identified in neurons of the substantia nigra of the elephant at the microscopic examination.

3.6.7.2. *Pons.* Compared to the human brain, the basis pontis appears relatively small, flattened, and narrow compared to the pontine tegmentum. The locus coeruleus, another pigmented nucleus, a paired structure located in the rostral pontine tegmentum, is not grossly identifiable, but no other differences are noted (Figs. 7, 9, 11, 17).

3.6.7.3. *Medulla oblongata.* The medulla gives rise to cranial nerves IX, X, XII, and, with contributions from the upper cervical spinal cord, XI (Figs. 4 and 5). Surface landmarks include the pyramids, olives, caudal part of the fourth ventricle with

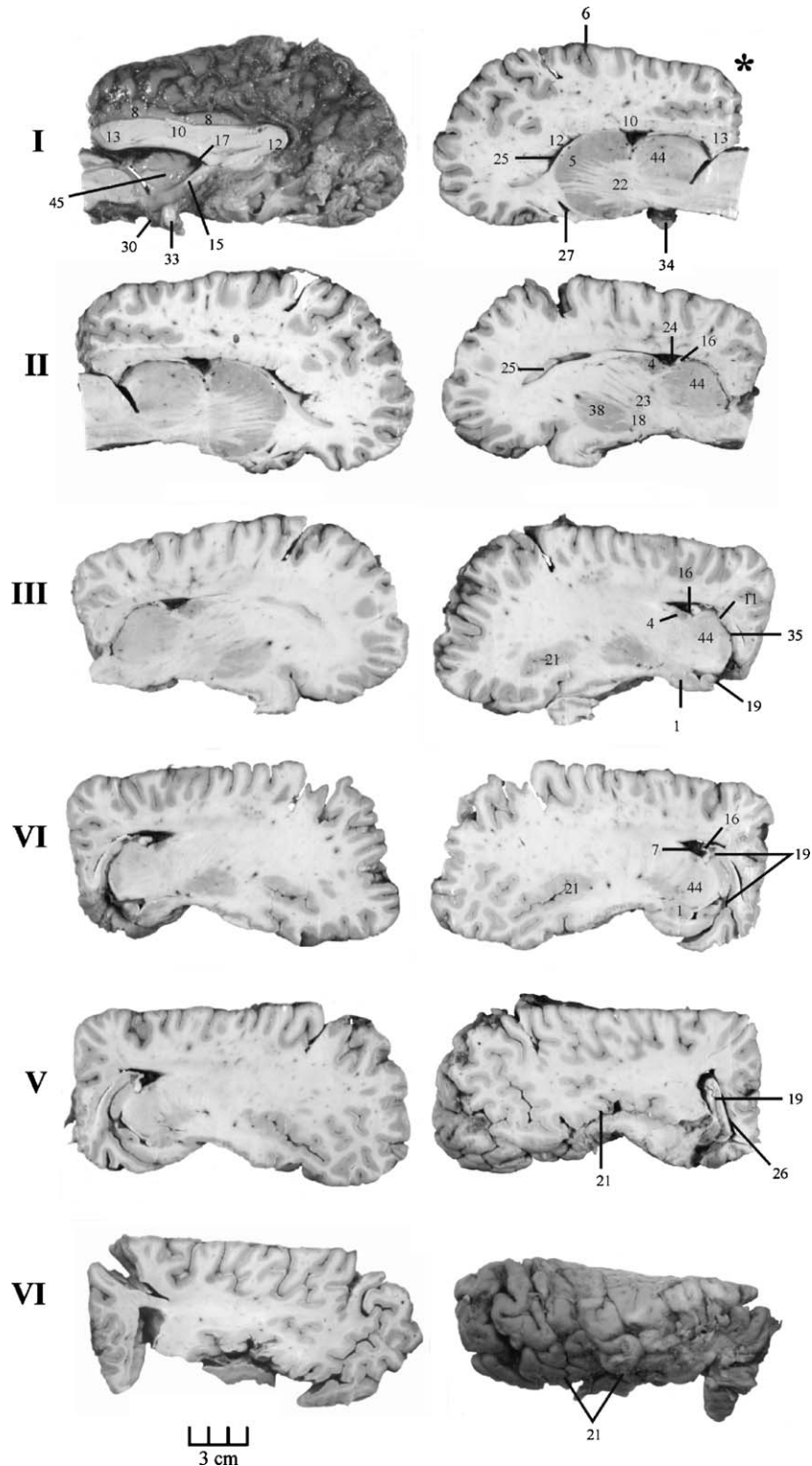


Fig. 13. Twelve (12) parasagittal sections of left cerebral hemisphere of specimen E brain. The photographed section on top right (denoted by an asterisk) was drawn by GHM and labeled in Fig. 12B (photographs by BT). Key to brain structures for Figs. 13–16: 1, amygdala; 2, anterior commissure; 3, calcarine sulcus; 4, caudate nucleus (body); 5, caudate nucleus (head); 6, central sulcus; 7, choroid plexus; 8, cingulate gyrus; 9, claustrum; 10, corpus callosum (body); 11, corpus callosum (forceps); 12, corpus callosum (genu); 13, corpus callosum (splenium); 14, fornix (body); 15, fornix (column); 16, fornix (fimbria); 17, interventricular foramen (of Monro); 18, globus pallidus; 19, hippocampus; 20, hypothalamus; 20a, hypothalamic sulcus; 21, insula; 22, internal capsule (anterior limb); 23, internal capsule (posterior limb); 24, lateral ventricle (body); 25, lateral ventricle (anterior/frontal horn); 26, lateral ventricle (inferior/temporal horn); 27, lateral ventricle (olfactory recess); 28, lateral ventricle (posterior horn); 29, longitudinal striae/indusium griseum; 30, mammillary body; 31, nucleus accumbens; 32, olfactory nerve; 33, optic chiasm; 34, optic nerve; 35, parahippocampal gyrus; 36, pituitary; 37, pituitary stalk; 38, putamen; 39, septum; 40, septum pellucidum; 41, stria medullaris thalami; 42, stria terminalis; 43, substantia innominata; 44, thalamus; 45, third ventricle; 46, nucleus ellipticus.

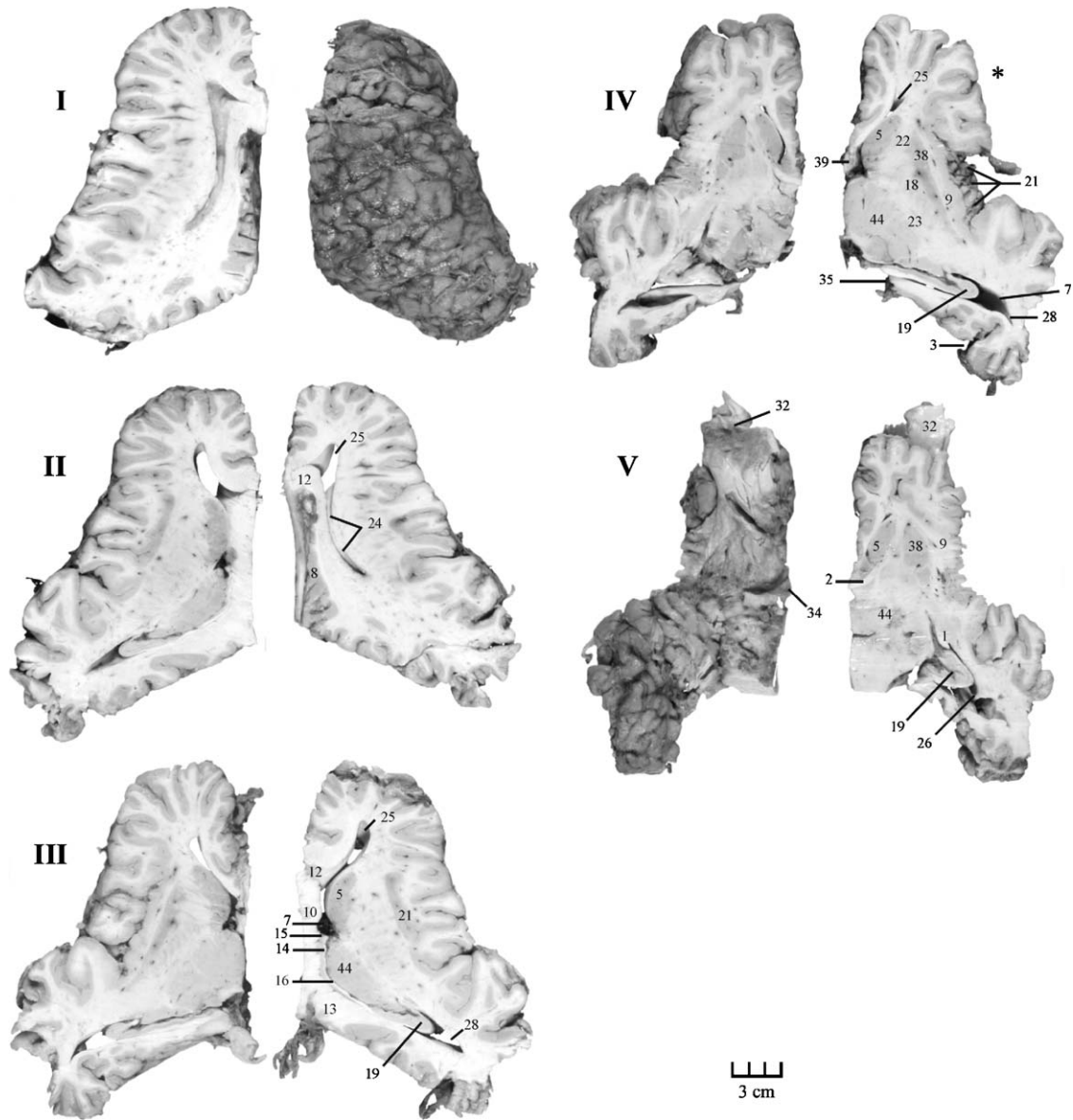


Fig. 14. Ten (10) horizontal sections of right cerebral hemisphere of specimen E. The photographed section on top right (denoted by an asterisk) was drawn by GHM and labeled in Fig. 12A (photographs by BT). Key as for Fig. 13.

attached choroid plexus, the inferior cerebellar peduncle, and the dorsal column nuclei (gracilis and cuneatus).

Landmarks on the ventricular floor include the median sulcus and the eminences produced by the underlying nuclei of the hypoglossal and vagal nerves and the area postrema. On brain slices, with the naked eye, one can see the pyramids, inferior olivary nuclear complex, medial brain stem core (the reticular formation), and outlines of cranial nerve nuclei. Of particular note are the large spinal trigeminal complex, the mass of olivary gray matter that lacks the serrated outline of human inferior olive, and the large flattened pyramids (Figs. 4, 5, 7B, 9, 17; see also Refs. [15,129–131]).

3.6.8. Cerebellum

Nomenclature of cerebellar fissures, lobes, and lobules varies among different authors. Major fissures demarcate the chief

anatomical subdivisions, known as lobes. Smaller subdivisions are known as lobules and sublobules. In specimens A and B, the cerebella of Asian elephants, it can be seen that the vermis contains 12–13 branches of arbor vitae, corresponding to lobules (Figs. 7B, 11A).

The cerebellum has been classically divided into three lobes: anterior, posterior, and flocculonodular [96]. Based on comparative anatomy, the cerebellum is divided into four lobes: anterior, central, posterior, and inferior (flocculonodular lobe) [3]. The flocculonodular lobe is composed of two parts: the nodulus at the midline and the flocculus at the lateral ends. As can be observed in Figs. 11 and 17, in elephants this flocculus is not visible in dorsal or ventral views.

Surface landmarks observed with the naked eye include the vermis, hemispheres, major lobes and fissures, nodulus and flocculus, tonsils (paired eminences on the caudal cerebellar surface

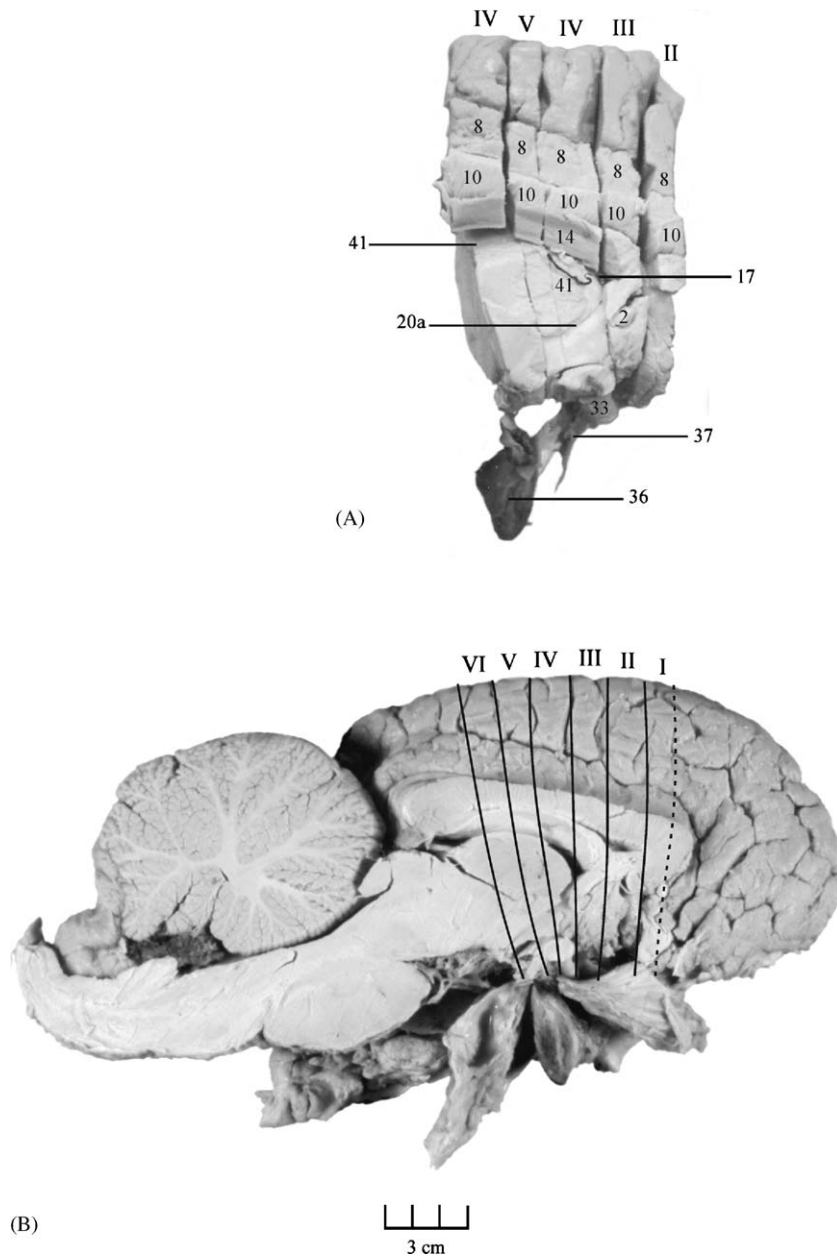


Fig. 15. Coronal slices II–VI (A) taken from a mid-sagittal section of specimen A. (B) Depicting location of these coronal slices. Dotted line in B indicates the position of slice I in Fig. 16 (photographs by BT, artwork by GHM). Key as for Fig. 13.

produced by the uvular lobules, part of the posterior lobe), and the cerebellar peduncles (superior, middle, and inferior). Brain slices also show the individual folia of the cortex, one of the deep nuclei (dentate nucleus), and the white matter. The cerebellar recess of fourth ventricle deeply indents the cerebellum (Figs. 7, 8, 11 and 17).

3.6.8.1. Differences between elephant and human cerebellum.

In humans, the cerebellum is relatively small compared to the cerebrum and is hidden beneath the cerebrum when viewed dorsally. In elephants, the cerebellum is massive and can be viewed dorsally. Comparative to other mammals, the ability to view the cerebellum dorsally (as in elephants) is primitive, and the concealment of the cerebellum in dorsal view is a derived character

associated with bipedal locomotion. Although our data are limited, it appears that the elephant cerebellum (average 18.6% of total brain weight; in humans the cerebellum is 10.3% of brain weight) is proportionally larger than that of other mammals. Elephant's cerebellum is 1.8 times larger than that of human and 1.9 times larger than that of sheep (Table 1). Gyri and sulci on the cerebellar hemispheres have complicated patterns with many subconvolutions, and the transverse orientation of sulci is consequently obscured, relative to human cerebellum (Fig. 11). The cerebellar recess is deeper laterally and lacking at the midline, with the result that the nodulus and lingular lobules are in close proximity and the superior medullary velum is membranous, not a thick gliopendymal structure. The cerebellum to cerebrum ratio of the elephant brain is larger than the human

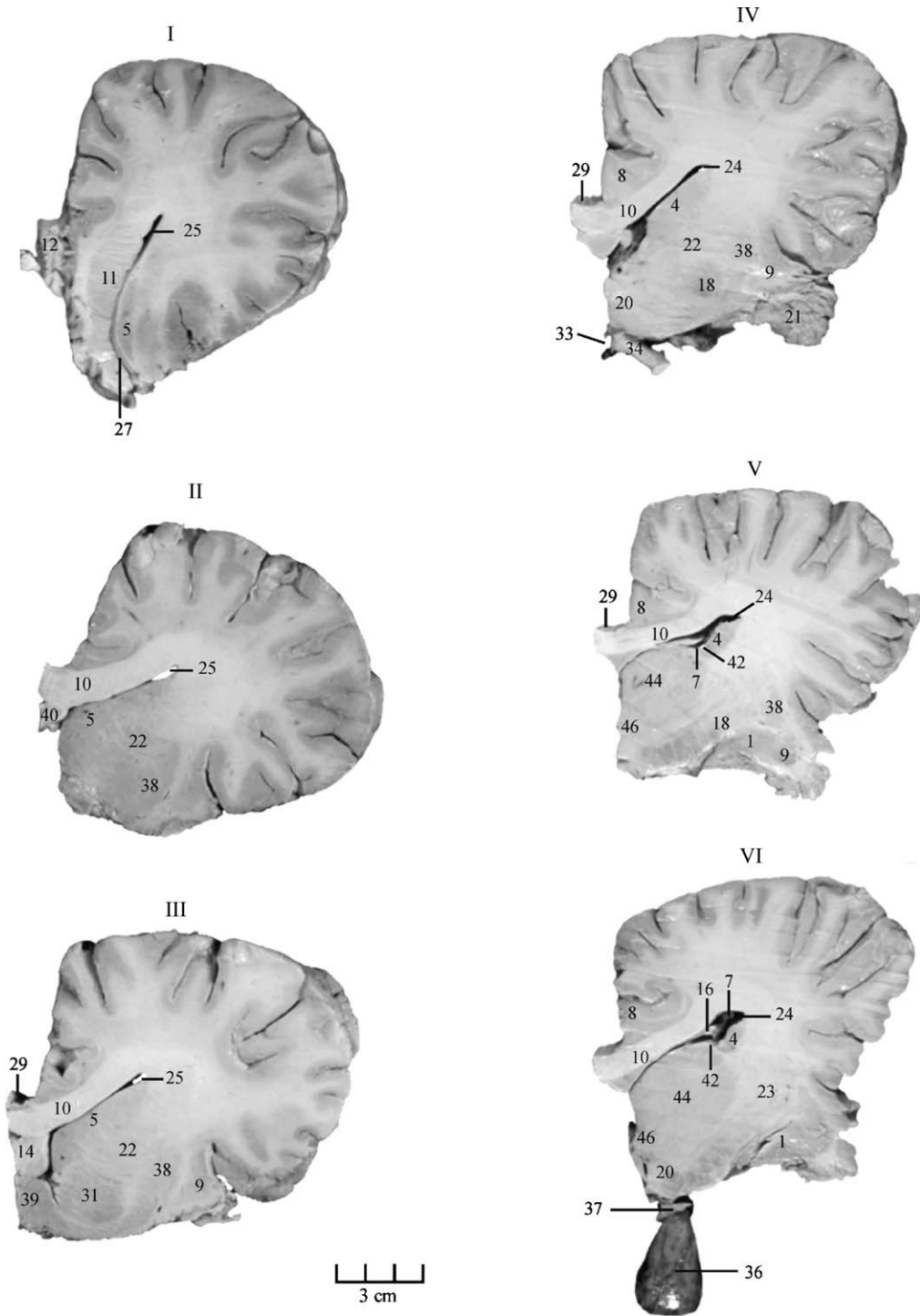


Fig. 16. Coronal slices I–VI taken from specimen A, shown in Fig. 15 (photographs by BT, artwork by GHM). Key as for Fig. 13.

and chimpanzee ratios. The lingula and uvular lobules are relatively large, the former contributing to the shape of the cerebellar recess of the fourth ventricle noted above. The inferior or flocculonodular lobe lies between the posterolateral fissure and the inferior medullary velum and choroid plexus, which serve as the caudal roof of the fourth ventricle (Fig. 7B, see also Ref. [3]). The flocculus is largely concealed in ventral view by the large uvular lobule (Figs. 11 and 17). These and other differences are summarized in Table 3.

3.6.9. Spinal cord

The only segment of the spinal cord we have examined is the uppermost cervical spinal cord in continuity with the medulla and close to the foramen magnum of specimen E. This is ovoid in shape, measuring 35 mm × 18 mm. Structures of gray and white matter in this spinal cord section (Fig. 17, III) are similar to those in humans. The first and second cervical nerves originate here.

The spinal cord of an elephant was investigated at the beginning of the 20th century [59], and the drawing of this study

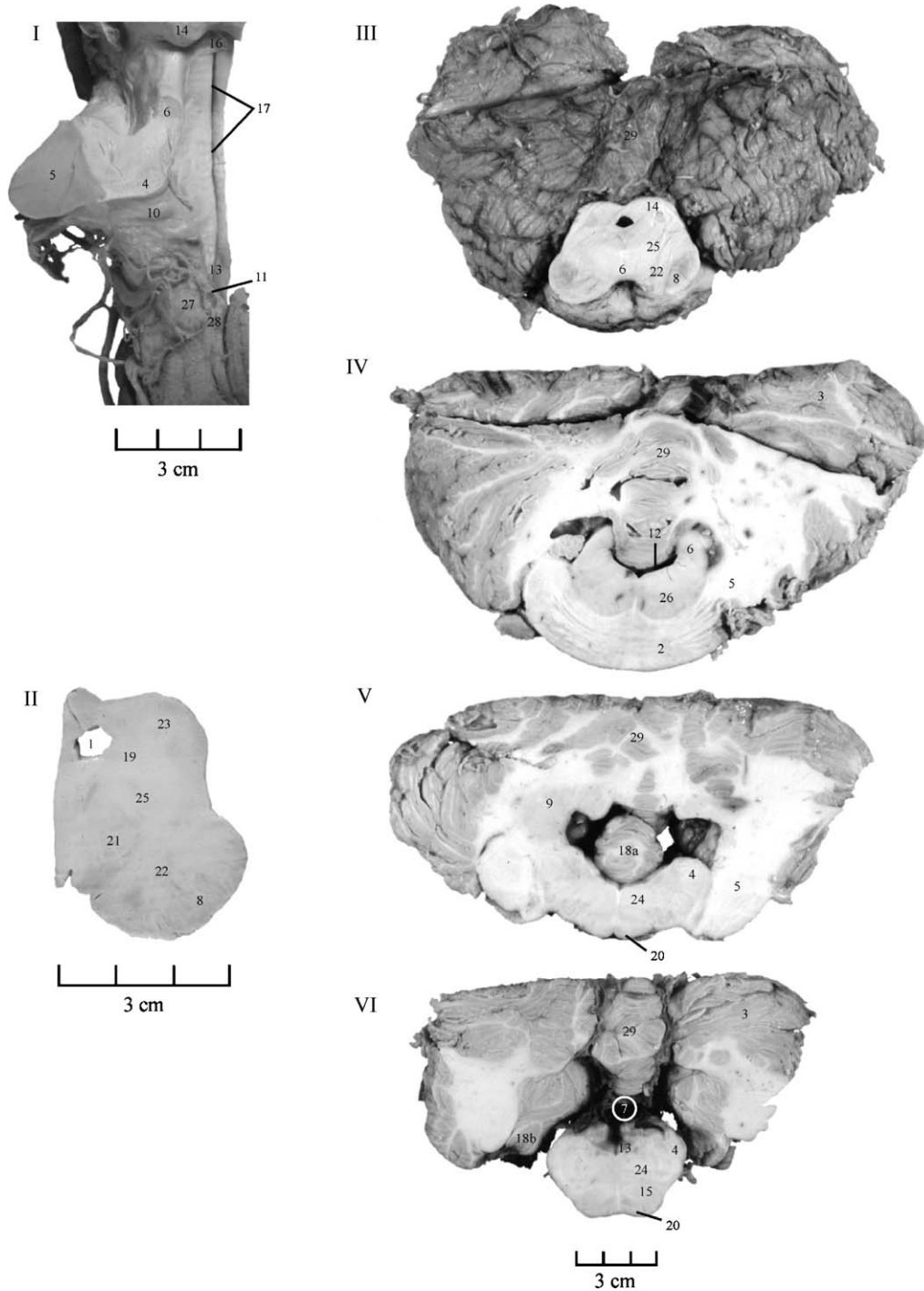


Fig. 17. Sections of elephants cerebellum and brainstem of specimen A (sections I and II) and specimen E (sections III–VI). Section I is a dorsal view of brain stem with cerebellum removed, revealing the fourth ventricle. Sections II–VI are progressive posterior views from anterior to the posterior end: hemisection II is the same view of section III, lower area; section III is at mid brain; section IV is at mid pons; section V is at ponto-medullary junction; and section VI is at mid medulla—see Fig. 7B for orientation (photographs by BT, artwork by GHM). Key to sections for Fig. 17: 1, cerebral aqueduct (of Sylvius); 2, basis pontis; 3, cerebellar cortex; 4, cerebellar peduncle-inferior; 5, cerebellar peduncle-middle; 6, cerebellar peduncle-superior; 7, choroid plexus of fourth ventricle; 8, crus cerebri; 9, dentate nucleus; 10, lateral foramen of the fourth ventricle (foramen of Luschka); 11, median foramen of the fourth ventricle (foramen of Magendie); 12, fourth ventricle; 13, hypoglossal trigone; 14, inferior colliculus; 15, inferior olivary nucleus; 16, lingula; 17, median sulcus of fourth ventricle; 18a, nodulus; 18b, flocculus; 19, periaqueductal gray matter; 20, pyramid; 21, red nucleus; 22, substantia nigra; 23, superior colliculus; 24, tegmentum-medulla; 25, tegmentum-midbrain; 26, tegmentum-pons; 27, tuberculum of nucleus cuneatus; 28, tuberculum of nucleus gracilis; 29, vermis.

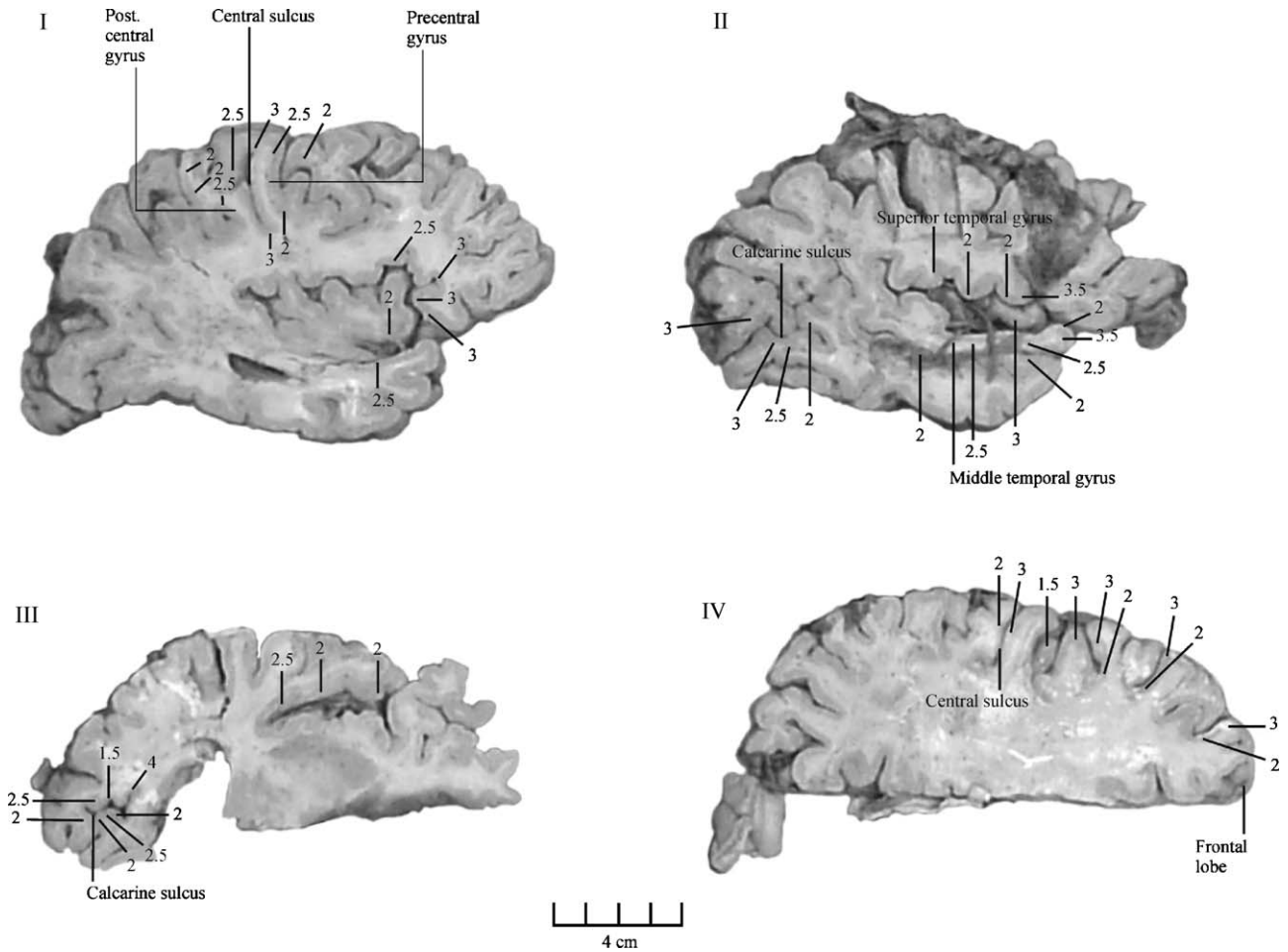


Fig. 18. Parasagittal (I and II) and horizontal (III and IV) sections of cerebral hemispheres, with thickness measurements of cerebral cortex indicated (on specimen E). Section I is through cerebrum lateral to basal ganglia, section II is through cerebrum lateral to section I lateral sulcus, section III is through cerebrum at mid basal ganglia, and section IV through cerebrum superior to section III, at centrum semiovale (photographs by BT, drawings by GHM).

was reproduced also later [22]. Based on these publications, structures in the elephant spinal cord appear to be similar to those in humans [96,134]. Yet, additional spinal cord sections from various segments of the spinal column would be useful to study in detail similarities and differences between elephants and humans.

4. Discussion

4.1. Historical and current perspectives

Anatomical studies of elephant brains were conducted by various investigators [1,10,19,32,44–46,55,61–63,72–74,77,79–81,87,99,109,119,122,129–131]. Each of these investigators focused on certain areas, or made general observations; the study of Dexler [32] was the most comprehensive. The recent review by Cozzi et al. [22] brought to light the paucity of basic detailed research on elephant brains. The present study is an attempt to investigate elephant brains systematically, providing illustrations for clarifications and attempting to fill in missing, incorrect, or misunderstood information in a holistic approach to gain knowledge of the largest living terrestrial mammal.

In absolute terms, an elephant brain is about 3.4 times larger than a human brain. Compared to body size, however, that of a human is 1/50, while that of an elephant is 1/600 of the body [134], ~1/700, based on our data. For the largest mammal in the world, the blue whale (*Baleaenoptera musculus*), the ratio of brain (6800 g) to body size is 1/850; in dolphins, however, the ratio is 1/40. In small mammals, e.g., a mouse, the ratio may be 1/35, while in a small primate (squirrel monkey) the ratio is reported as low as 1/12 [134].

On the whole, the elephant brain follows the basic brain plan of higher placental mammals with a well-developed telencephalon, corpus callosum, and a prominent development of cerebral gyri and sulci, showing a degree of gyral complexity intermediate between the primate (human) and cetacean patterns. An elephant brain, however, depicts a number of differences in proportion and configuration with respect to the human brain (Table 3).

4.2. Differences between the elephant brain and the human brain or the brain of other mammals

Major differences between elephant and human brains in the telencephalon, diencephalon, and mesencephalon include: rel-

ative proportions of the cerebral lobes, differences in size, and configuration of the ventricular system, differences in the cerebral gyral pattern and complexity, the relatively large size of the olfactory nerve with its persistent ventricle, the large size of the pituitary gland, and the small size of the pineal gland. Compared to the human brain, elephants have relatively smaller frontal lobes, relatively larger temporal lobes, ill-defined occipital and parietal lobes, and incompletely opercularized insula. In the rhombencephalon, the differences include the relatively large size and greater degree of gyral complexity of the cerebellum, and the complexity of the vascular network at the base of the brain.

Elephants are considered to have a macrosomatic brain, since their olfactory lobe or rhinencephalon, is very large. Of particular prominence are the large size of the olfactory bulb, the persistence of an olfactory ventricle, the large olfactory trigone region, and the prominent gyration of both the medial and lateral olfactory striae. Other reported evidence includes the larger number of the ethmoturbinals (ethm.) in the nasal cavity (five in elephants). This parallels the findings in other mammals with macrosomatic brains, such as the spiny anteater (*Echidna*, seven ethm.), ungulates (average of six ethm.), edentates (eight ethm.), and armadillo (nine ethm.). The armadillo has the “highest number among mammals (extreme macrosomatism)”; macrosomatism is directly associated with very large rhinencephalon, implying a good sense of smell [54]. Duckbill platypus (*Ornithorhynchus*, three ethm.), anthropoid primates (four ethm.) including humans (three ethm.), and cetaceans (three) are all mammals with microsomatic brains, reduced rhinencephalon, and low number of ethmoturbinals [54].

Comparing the position of the olfactory bulb in elephants to other mammals we examined and from the literature, we note that in a fetus (Fig. 1C and plate VIII in Ref. [36]) and adult elephants, this bulb is not visible in dorsal view (it is hidden beneath the frontal lobe). In monotremes and marsupials the olfactory bulb extends anterior to the cerebrum [67,142]. Similarly, the olfactory bulb is visible in the dorsal view of the brain in insectivores (e.g., *Gymnura* and *Erinaceus* [67,142], armadillo and edentates [118], rodents, e.g., *Rattus* (see plate III in Ref. [81]), *Cavia* (our observation), and lagomorphs (*Oryctolagus*) [133]. In domestic animals (horse, cow, pig, dog, and cat [28–31]) the olfactory bulb is also exposed dorsally; the position of this bulb in the zebra brain we examined was similar to that of a horse. In the sheep, however, the olfactory bulb is almost even with the frontal lobe ([29] and our observations). Among primates, in prosimians [26,142] the olfactory bulb is visible in dorsal view, but in man it is invisible [134]. In cetaceans (e.g., *Tursiops* [62]), the olfactory bulb is also concealed in the dorsal view. From these observations, it is evident that the primitive condition for the class Mammalia occurs when the olfactory bulb is visible in the dorsal view of the brain. Thus, the elephant, dolphin, and man exhibit the derived condition.

Both human and elephant brains are marked by prominent sulci and gyri. Compared to the human brain, the elephant brain shows a more complex pattern of gyri and sulci (Figs. 5 and 7). The normal patterns of gyri and sulci of Elephantidae (order Proboscidea) and other non-human mammalian orders with com-

plex gyral patterns (e.g., cetaceans, such as a porpoise) have not been well defined. Without close correlation between function and structure, it is risky to infer homology based solely on topographic features. In addition, as in humans, apart from major divisions, there may be considerable variation in fine gyral and sulcal patterns among individual elephants. The shape and orientation of gyri and sulci differ among different species as observed on brains of non-proboscideans and non-primates listed in Table 1. In general, larger brains tend to be more convoluted than smaller brains, and more convoluted brains tend to exhibit greater cytoarchitectonic diversity within the cortex, though there are exceptions [135].

Comparing the degree of gyrations on the cerebral hemispheres among the 13 mammalian taxa we studied (listed in Table 1A–E), we note the following general observations, made by naked eye. Elephants and humans have the highest degree of convolutions, followed by chimpanzee, sheep, and zebra that have approximately comparable degrees of convolutions, followed by the maned wolf and cat, the talapoin monkey and rock hyrax, and then by the chinchilla and guinea pig. Chinchilla and guinea pig have the least degree of convolution on their cerebral hemispheres among the mammals compared. We note that these general observations with the naked eye do not necessarily imply evolutionary trends of cerebral gyrations.

Based on our observations of the cerebral and the temporal lobes, an elephant appears to have a larger ratio of weight and surface area to the cerebral cortex surface area than that of humans and of other mammals studied. In humans, the temporal lobe is associated with hearing, learning, memory, and emotion. Although the configuration of the limbic lobe (cingulate gyrus, parahippocampus and hippocampus) is similar, the elephant hippocampus is oriented more posteriorly and vertically, reflecting the orientation of the temporal lobe.

Comparing the hippocampus of humans and elephants, we note that they are of approximately the same size; that of the elephant, however, is smaller relative to its cerebrum. A different and somewhat contradicting result was reported recently [57]. These authors noted that “. . . the elephant has an unusually large and convoluted hippocampus compared to primates and especially to cetaceans. This may be related to the extremely long social and chemical memory of elephants” [57]. As for the orientation of the temporal lobe, in humans the hippocampus is oriented almost horizontally, whereas the elephant’s is oriented more posteriorly and vertically. In humans, functions attributed to the hippocampus/hippocampal formation include formation of recent memories of facts and events as well as the control of emotional behaviors and neuroendocrine functions [38,93,127]. We presume that similar functions could be assigned to the hippocampus in elephants.

In elephants, the degree of development of senses changes with age. Compared to other mammals, they have an excellent sense of hearing, an acute sense of smell, very good sense of touch, unknown sensitivity to taste (seems to be selective), and poor sense of vision, though it is good in dull light.

It is noted that a human has a well-developed occipital lobe composed of primary visual cortex and association cortex, associated with a well-developed sense of vision. In elephants, on

the other hand, vision is one of the least developed senses, and corollary to that is the small and ill-defined occipital lobe. This observation also holds for size and development of other lobes associated with other senses. For example, the elephant has well-developed temporal lobes, including the anterior temporal gyrus which may be analogous to the superior temporal gyrus of the human brain, and with the large olfactory structures. Although elephants are known to have a very good sense of touch, the size of the parietal lobe, which in humans is the lobe associated with cortical somatosensory representation, is relatively small. Electrophysiological mapping of the elephant somatosensory cortex is, however, lacking. It is noted, on the other hand, that evidence for pain sensation in elephants was recently discussed in detail [115]. An elephant's sensitivity to taste is unknown; it seems to be selective. In humans, taste nerve fibers reach the nucleus ventralis posterior medialis in the thalamus and project to the sensorimotor cortex and the limen insulae [75,134]. In elephants, the thalamus is relatively large and one investigation has focused on it at the microscopic level [1]. The large size appears commensurate with the large degree of development of the cerebral cortex and reinforces the similarity of overall structure between elephant and human brains.

The recent behavioral observations on vision in elephants presented by Nissani et al. [92] provide support to anatomical observations. Vision and short-term memory tests on a total of 20 Burmese working elephants of both genders with varying ages and different histories at three logging camps in the forests of Myanmar (Burma) were conducted [92]. Experiments included control and experimental groups. Their results, although tentative, provide a glimpse into the Asian elephant's visual acuity and short-term memory. Their data from both the black and white and the large and small discriminations showed a surprising age effect, and suggest that elephants beyond the age of 20–30 years either may be unable to acquire these visual discriminations or may require an inordinate number of trials to do so [92]. These observations corroborate the anatomical data presented in the present study that elephants have ill-defined occipital lobes. The elephant's temporal lobes, on the other hand, are extremely well developed [64].

Variations in cortical thickness might have resulted from the angle in which brain slices were cut. In humans, "the thickness of the cortex varies from 4.5 mm in the precentral gyrus to about 1.5 mm in the depth of the calcarine sulcus" [96]. The cortex is always thickest over the crest of a convolution and thinnest in the depth of a sulcus. Our data confirm these observations. The variation in cortical thickness reflects differences in cortical regions: in general, the primary sensory cortex is thinner and more compact than the motor cortex. The association cortex is intermediate. The differences between gyral crest and depth of sulcus also probably reflect differences in function [135]. The comparable thickness, despite the larger brain weight, probably reflects a basic similarity in organization, and optimal thickness over many higher mammals.

Calculation of callosal area in midsagittal section may reflect more accurately the fiber content than simple descriptive data as given above. Values in humans were reported at $6.2 \pm 0.2 \text{ cm}^2$ in males and $6.3 \pm 0.2 \text{ cm}^2$ in females, and suggest a relatively

larger commissural system in females than in males [143,144]. It has been reported that, in humans, the splenial portions of the female corpus callosum are larger than those of males [25], yet Bleier et al. [12] found no such sex-related differences. In addition, correlation between handedness and callosal size has also been reported [97]. Possible sex-related differences in the function of the left versus right cerebral hemispheres have also been reported [132,137]. Our data for the areas of the corpora callosa of brains of one elephant (12.57 cm^2) and one human (5.98 cm^2) were compared to the areas of the brains in midsagittal section of the elephant (271.05 cm^2) and human (170.67 cm^2). Calculation of the ratio of the corpus callosum surface area to the midsagittal section area in the elephant gives 4.6% and for human the ratio is 3.5% (Fig. 8B). There is a reported correlation between corpus callosum area and brain size [143]. For this reason, we calculated the ratio of the corpora callosa to the weight of the entire brain and also to the approximate weight of the cerebrum (by subtracting 10% of the total weight [96,134], noting that the cerebellum weighs about 10% of the total brain volume/weight). Our results show that the ratio of corpus callosum surface area to the weight of brain of an elephant is $0.0024 \text{ cm}^2/\text{g}$, and the ratio to the cerebrum is $0.0027 \text{ cm}^2/\text{g}$. For humans, these values are 0.0043 and $0.0047 \text{ cm}^2/\text{g}$, respectively. Based on these limited data, we can assume, as a crude estimate, that the number of commissural fibers in the corpus callosum is about twice as much in man compared to the elephant. Much more data ought to be collected to confirm these differences in the relative size of the corpus callosum. Hakeem et al. [57] noted that the ratio of neocortical gray matter volume to corpus callosum cross-sectional area are similar in the elephant and human brains (108 and 93.7, respectively), compared to cetaceans, with a ratio of 181–287.

As noted above, the pituitary gland is large, yet, unlike the condition in humans, it fits into a shallow sella turcica (which is deep in humans). The pituitary gland of the African elephant (*L. africana*) [58,117] and of the Asian elephant (*E. maximus*) [70,140,141] was investigated previously. Macro- and microscopic photographs of this gland were provided [70]. A summary of these studies, with sketches of the glands of both elephant species, was given [43]. We learn that the average weight for three elephants for this gland is 5.31 g [70,117], and measurement (length, width, and thickness) for two elephants was $32 \text{ mm} \times 21.5 \text{ mm} \times 11 \text{ mm}$ and $37 \text{ mm} \times 22 \text{ mm} \times 11 \text{ mm}$ [70]. A weight of 1.9 g for a pituitary of a female 7–8 years old Asian elephant was given [108]. The pituitary weight (6.16 g) of specimen A is 1.34 g less than the weight of 7.5 g [70], and the dimensions of this pituitary gland fall within the range of other elephants.

The pineal body has been thought to be an involuted or hypoplastic organ, and its presence in the elephant has even been disputed [32,63]. This organ has been inadequately studied, possibly because its identification has been hampered by its small size and diffuse structure. In addition, the pineal body is located in an area of the brain that is easily disrupted when the brain is removed. It is possible that the pineal organ is developed in younger elephants, and then it becomes involuted in an adult. Resolution of this question requires examination of more

brains from younger elephants. Keeping these considerations in mind, the function of the pineal gland may change during ontogeny.

The basal ganglia are considered to be derivatives of the telencephalon and are often divided into two major components: the corpus striatum (comprising the caudate nucleus, putamen, and globus pallidus), concerned primarily with somatic motor functions, and the amygdaloid nuclear complex (comprising two main nuclear masses, the corticomедial nuclear group and the basolateral nuclear group), functionally related to the hypothalamus and limbic system as well as to the corpus striatum and cerebral cortex [96], and possibly the claustrum. The caudate nucleus and putamen of the corpus striatum develop in close association with the cerebral cortex and receive input from both neocortical and limbic areas, the latter projecting to the nucleus accumbens and other parts of the basal forebrain, referred to collectively as the ventral striatum. Histological details of the elephant nucleus accumbens and other paralimbic structures have been reported [74]. The configuration of these structures maintains the same relative relationships as in the human brain, with the exception of the amygdala, which appears located relatively posteriorly. Functions attributed to the amygdala include recognizing, displaying and experiencing fear [78]. The claustral gray matter is present in the elephant brain, but its temporal portions are ill-defined to the naked eye.

The nucleus ellipticus, a specialization of the peri-aqueductal gray matter, was reported in the mesencephalon of cetaceans and elephants [84,99,129], but not in humans [22]. The elephant brainstem macroscopically differs from the human brainstem chiefly in proportion (Table 3). Additional differences include a visible nucleus ellipticus, the large size of the trigeminal nuclear complex, probably reflecting the large size of the area of innervation represented by the elephant head and trunk, and the absence of visible pigmentation in the substantia nigra and locus ceruleus. Given the large size of the cerebellum, the proportionally small size of the basis pontis may reflect a relatively small volume of corticopontine input to the cerebellum.

In elephants, the cerebellum is larger than that of humans in absolute and relative terms (elephant cerebellum averages 18.6% of total brain weight; comparable value for humans is 10.3%). In addition, compared to humans, gyri and sulci on the cerebellar hemispheres of elephants have complicated folia patterns with many subconvolutions (Fig. 11; Table 3). Elephant cerebellum can be viewed dorsally; that of a human is concealed under the cerebrum (Fig. 8B). In humans, the cerebellum appears to be involved in coordinating movements and locomotion and maintaining posture. Other functions attributed to the cerebellum include the cognitive roles of acquisition and discrimination of sensory information [37,47,68,93,134].

The large size of the cerebellum and basal ganglia appears to be correlated with the ability of elephants to perform complex and coordinated motor functions, ranging from acting as working elephants to performing in circuses. A photograph of a young Asian elephant walking on wooden bottles is a testimony to “extraordinarily sure-footedness and delicate sense of balance” [112]. In the wild, elephants have been observed standing on their hind legs while reaching with their stretched trunks for

foliage high on trees [42], an example of their well-developed sense of balance.

4.3. Possible carotid rete and other cranial arteries

The vascular mat observed at the base of the brain of two specimens could be interpreted as a counter-current system or carotid rete. This rete could allow cool venous blood arriving from the nasal area (via the ophthalmic vein after evaporative cooling) to get in contact with warmer arterial blood (the internal carotid artery) before it enters the cranial cavity to supply the brain. A similar mechanism to cool the brain has been observed in carnivores and bovids [7,8,124,128].

Our observations in elephants, thus far, indicate that the labyrinthine and anterior inferior cerebellar arteries arise independently from the basilar artery (Fig. 3B). Variations in the branching pattern of cranial arteries and the arterial circle of the brain in humans are usual. For example, a previous study (see Fig. 644 in Ref. [18]) depicted the labyrinthine and anterior inferior cerebellar arteries to emerge separately from the basilar artery, whereas another study [90] showed these two arteries to have a common trunk. The basilar artery of the African elephant depicted in Fig. 3B is not bifid. On the other hand, we observed a bifid basilar artery in an Asian elephant (specimen C). A bifid or plexiform basilar artery has been observed in humans [24,35,88,95].

4.4. Neonate and adult brain sizes

It has been reported that the brain of an elephant calf at birth is only 35% of its adult brain weight [34]. Our data (Table 1) and that of other sources [32,106,117,120] indicate that elephant brain weight at birth averages 2551 g, that is, about 50% (53%) of 4783 g average brain weight of 17 adult elephants. For human, the corresponding ratio of brain weight at birth is 25% of adult brain weight [106,134] and for mammals ($n = 100$) this ratio is 34% [106]. Although the data are meager, it appears that compared to human brain which grows 75% post-natally, that of the elephant develops about 50% after birth for approximately the same lifespan. In both species, long periods of brain development post parturition provide much time for learning. Furthermore, during the first year of extra uterine life, the human brain doubles its weight, by the sixth year it reaches 90% of its adult weight, and by the 16th or 17th year it reaches adult weight [134]. Comparable data for elephant brain weights are not available for the first, sixth and 17th years, yet based on the little data available in the literature [117], elephant brain appears to reach its adult size at an earlier age, between the fifth and the 15 year. These differences are possibly related to the neotenic human brain [51,97] as well as the altricial versus precocial state at birth of human and elephant, respectively [86,117,134].

Brain size is directly related to body size [66], yet there also appears to be correlation between brain size and ecology. For example, arboreal species tend to have relatively bigger brains than grassland species [40,82]. Further, nocturnal species have larger brains than diurnal, and insectivores, frugivores, and granivores have larger brains than folivores [82]. Elephants are

large, grassland dwelling, crepuscular, and they feed on grass, leaves and fruits. These factors in tandem with the facts that elephants are highly social and have a long life span (ca. 80 years) may contribute to large brain size in elephants [39,112,123].

4.5. Brain size, encephalization quotient, and memory

Intelligence is very difficult to measure in humans, let alone in animals. The encephalization quotient (EQ [66]) has been employed as a measure of the ability of an animal to cope with newly developed challenges and obstacles in its environment. EQ, as defined by Ref. [66] and further elaborated by Ref. [39], is the ratio between observed and expected brain size for a given body weight (“The expected brain size is a kind of ‘average’ for living mammals that takes body size into account” [66]). In this system, a mammal with a brain/body ratio with an EQ value equal to 1.0 is considered to have average EQ. A value of EQ less than 1.0 may be associated with a less than average level of attributes that might be interpreted as “intelligence”. Conversely, an EQ value higher than 1.0 may be associated with more than average intelligence. For example, the pig has an EQ of 0.27, and the sheep has an EQ of 0.541, the rat 0.835, the fox squirrel 1.426, the European cat 1.14, and the ring-tailed lemur has an EQ of 1.449. The gorilla has an EQ range of 1.402–1.68, the chimpanzee 2.18–2.449, and humans have an EQ range of 7.33–7.69 (EQ values derived from Ref. [39]).

Of the 16 brains from adult elephants for which we calculated the EQ, 9 were African (4 females, 3 males, 2 unknown), and 7 were Asian (4 females, 3 unknown). The EQ for all 16 elephants ranges from 1.13 to 2.36. The total EQ average is 1.88, with an average of 2.14 for Asian elephants, and 1.67 for African; 2.1 for females, $n=4$, and 1.3 for males, $n=3$. Higher EQ values for female than male elephants were also reported in the literature [39,111]. Sources for the brains are given in Table 1. One aspect of relative brain size cannot be overlooked “Species with larger average brains, in relation to average body size (related to EQ), show greater ability to process and utilize complex information” [65].

Elephants have proverbially been known to have a long-lasting memory. We hypothesize that brain size seems to be associated with memory storage. Memory and intelligence seem to be interrelated [20,101–103]. Of living mammals, those with an EQ value of near and above 2 have been observed to make and use tools; these include primates (humans and chimpanzees) and elephants [49]. Examples of tool use among elephants include the use of a stick to scratch their backs and to place twigs and branches under their feet to prevent sinking in soft ground [112]. Elephants have also been reported to plug, with mud, wooden bells they wear on their necks so that the clappers cannot ring while they enter a grove of cultivated bananas at night [138]. The question arises whether elephants perform these behaviors through associative learning (that is, by trial and error) or by causal reasoning. Discussions for [17,60] and against [91] this question have been reported in the literature. Observed behaviors have been interpreted differently [91], and thus the question of whether or not elephants perform these behaviors causally cannot be answered satisfactorily.

In one report [49], elephants were observed to chew the bark of a tree to make a “cork” to plug a waterhole they dug. Later, these same elephants were observed to return to that waterhole, unplug the cork and have a drink. These observations, in our opinion, illustrate a higher degree of tool-making ability, as well as body and neural coordination, and the elephant can also be viewed as a toolmaker.

An incident in which an elephant appeared to be able to think was recalled when the elephant, Chandrasekharan, was given a command to lower a wooden pillar into a pre-excavated hole; it did not execute the command until a dog that was sleeping in the hole was chased away [98]. One author reported a case where an elephant carefully planned the timing of an attack to kill [107]. Another author subtitled his paper “Should elephants be moved to near the top of the animal-intelligence list?” This article recalls unique behaviors exhibited by elephants that “points towards a higher consciousness. “For example, elephants have been observed to spend time next to carcasses of elephants, but not next to carcasses of other animals, e.g., a buffalo. This author believes that “. . . elephants grieve and therefore have a concept of life and an idea of missing another elephant” [14].

4.6. Development and evolution

Ontogenetic stages inferred from brain weights of the material at our disposal and from the literature show an expected increase in brain size from a fetus to a fully mature individual. Brain lengths, widths, and heights (in cm) for adult versus near term fetus are: 35 versus 17, 30 versus 15, and 20 versus 8, respectively [85,117]. Brain weights, in kilograms, were provided for eight elephants in the wild, as follows: 18 months (M= male), 2.7; calf (F= female), 3.0; juvenile (M), 4.5; teens (F), 4.1; teens (M), 4.3; prime adult (F), 4.1; prime adult (M), 5.3; and senile adult (F), 4.0 [117]. The following developmental changes were observed in brains of elephants: increase in size, increase in proportion, particularly increased relative size of the temporal and frontal lobe areas, increase of air-cell development (pneumatization) in the cranium, and a change from low flat to tall cranium. These changes have also been observed as phylogenetic trends among the order Proboscidea [114]; such a trend of increase in body size and correlated increase in brain is known as Cope’s Law or Rule [2]. Brain size increases at a much slower rate than body size. Among adult mammals, the brain increases at about two-thirds the rate of the body [50].

We compared the ontogenetic development of African elephants (*L. africana*; Fig. 19A) to a series of proboscidean skulls that exhibit from low to high domed skull, where the center of gravity shifts posteriorly (Fig. 19B). It is noted that, with age, the position of the nuchal fossa at the back of the head and the nuchal eminence (point c) are shifted higher on the cranium. This ontogenetic change is similar to the gradual change that occurs during evolution, a change that is associated with the shift of the center of gravity towards the back of the skull. On the whole, we note that Haeckel’s Biogenetic Law [56] may apply to these features but is an oversimplification (the Biogenetic Law – “Ontogeny recapitulates phylogeny” – states briefly that an organism passes through developmental stages resembling vari-

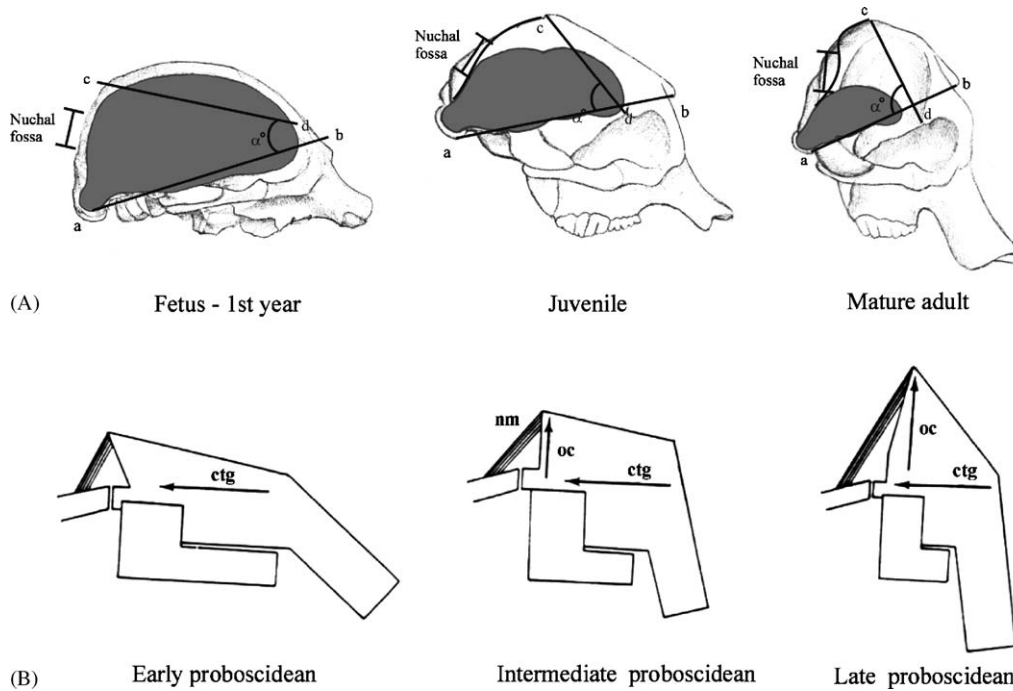


Fig. 19. (A) Ontogenetic development of crania and brains (not to scale) from fetus to mature adult African elephant, *L. africana*. (B) Simplified representation of evolutionary changes in proboscidean skulls (ctg = center of gravity, nm = nuchal musculature, oc = occipital region). Note that during ontogeny (A), the base of the brain remains relatively constant in relation to the line drawn between points a and b (point a is the ventral margin of the occipital condyle, point b is the ventral side of the nasal process at the dorsal margin of the external naris, point c is the nuchal eminence, the suture of the occipital and parietal bones, and point d is the superior postorbital process). As an elephant grows, angle alpha becomes larger and larger. Sources: (A) ontogenetic stages are modified after ([69], p. 29)—Fetus cranium, after AMNH 119620, and ([36], plate VIII); juvenile after ([126], p. 254); mature adult after ([36], plate XI; [126], p. 256); (B) adapted after ([83], p. 105, reversed).

ous levels in the phylogeny of its group; see, however Ref. [51]). In the fetus of elephants, for example, the position of the cribiform plate is the same as in the adult, unlike the condition in extinct proboscideans (Fig. 20). We find a similar intra-ordinal primitive-derived character trend within Primates where in early primates (e.g., a prosimian [26]) the olfactory bulb is visible in dorsal view, but in man is invisible [134].

With reference to the position of the superior and inferior colliculi (corpora quadrigemina), when viewed in dorsal view,

either one pair of these colliculi or both of them are visible between the cerebrum and cerebellum in mammals. This character was observed in monotremes and marsupials [67,142], insectivores [67,142], rodents, and lagomorphs ([133], our own observations). The colliculi are concealed under the cerebrum in domestic animals (horse, cow, sheep, pig, dog, and cat [28–31]; our own observations for zebra, sheep, cat, and wolf), primates [26], and in cetaceans [62]. It is apparent from these observations that the primitive condition for Mammalia is when one or

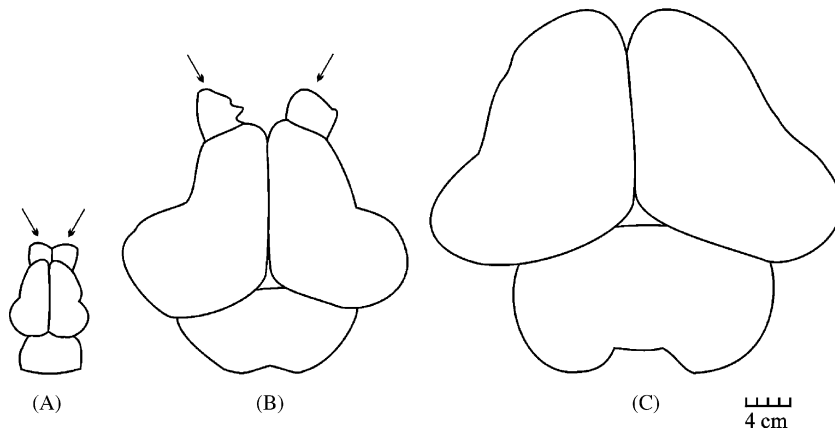


Fig. 20. Simplified drawings of proboscidean brains in dorsal views drawn to scale: *Moeritherium lyonsi* (A, extinct), *Mammuth americanum*, the American mastodon (B, extinct), and *Elephas maximus* (C, extant). In A and B the olfactory bulbs (arrows) protrude anterior to the frontal lobe. The olfactory bulbs are not visible in dorsal view in living elephants (see text for the significance of this character). Encephalization quotient (EQ) value of *Moeritherium* as calculated by [66] is 0.2 and a high value for *Elephas* (calculated by Shoshani) is 2.36. EQ can be viewed as a character subjected to natural selection during a phylogeny of a lineage, e.g., within Primates and Proboscidea (brains of A and B after Ref. [66], C after specimen B; drawings by GHM).

both pairs of colliculi are visible in dorsal view of the brain; the elephant is among mammals that exhibit the derived condition.

In its primitive condition, the flocculus of cerebellum is visible dorsal view, e.g., in *Echinosorex*, an insectivore [52,67], and edentates [118]. Of the 11 non-elephant mammalian brains we examined, only those of chinchilla, guinea pig, and rabbit exhibited the primitive character [6]. One of the synapomorphic (derived) characters for Ferungulata is “flocculus of cerebellum vestigial or not visible in dorsal view” [113]; these ferungulate taxa – listed as they appear on the cladogram – exhibit this derived character state: Carnivora, Pholidota, Tubulidentata, Artiodactyla, Cetacea, Perissodactyla, Hyracoidea, Proboscidea, and Sirenia.

A number of brain features can be considered in evolutionary perspective when comparing living elephants to other members of the class Mammalia on a cladogram [113]. The corpus callosum is present (absent in non-eutherians). The optic nerve passes through a separate opening, the optic foramen (confluent with the orbital fissure; Placentalia). The EQ is greater than 0.21 (clade Preprotheria). The superior and inferior colliculi are not visible in the dorsal view (Ferungulata). The flocculus of cerebellum is vestigial or not visible in dorsal view (Ferungulata). The rhinencephalon is very large with the olfactory bulb concealed under the cerebral frontal lobe in dorsal view (intra-ordinal derived character). The cerebrum is highly convoluted (intra-ordinal and inter-ordinal derived character). The cerebral temporal lobes are highly enlarged and bulbous (intra-ordinal derived character). The cerebellum is extremely convoluted (intra-ordinal derived character). The occipital lobe is not developed. The hippocampus has been drawn into the temporal lobe (temporalization). Insula is incompletely opercularized in elephants. In the most basic mammalian plan, the cerebrum and the cerebellum lie on a relatively horizontal plane so that both are visible dorsally.

From an evolutionary perspective, the elephant brain incorporates a well-developed neopallium (neocortex), but on the other hand, it retains and develops phylogenetically primitive components of the brain, viz., the large olfactory bulb and the relatively large paleopallium [105]. The olfactory bulb retains its original function (olfaction), and the well-developed paleopallium, or palaeocortex (pyriform lobe), appears to be associated with their excellent olfactory sense [64]. In elephants the olfactory region of the brain includes complex functions, such as flehmen that involves sensing chemicals important in social or reproductive behavior [100] and activity associated with the Jacobson’s (vomeronasal) organ at the roof of the mouth.

Clues for inferring evolutionary trends were made based on our examination of one elephant fetus brain (specimen G), from endocasts [4,66,71,94], and from structures preserved in cranial cavities of extinct proboscideans. Data and photographs of endocasts of elephantid taxa (“*E. indicus*”, “*L. africana*”, and “*Hesperoloxodon antiquus italicus*”) were provided by Osborn [94], and those of *Moeritherium lyonsi* and *Mammuth americanum* were provided by Jerison [66]. An endocast of *M. americanum* (MCZ 11106) that is housed at the Museum of Comparative Zoology at Harvard University was also examined by the senior author. From these data and illustrations, one can draw the general conclusion that advanced or derived proboscideans had very

large brains (in absolute terms) along with huge and bulbous temporal lobes and relatively large cerebellum. *M. lyonsi* (one of the earliest proboscideans) also had a relatively large temporal lobe. On some of these endocasts, it is possible to observe surface grooving marking the site of major fissures (e.g., inter-hemispheric and Sylvian fissures). Osborn [94] also provided a formula to estimate the weight of the brain from an endocast, i.e., volume in cubic cm minus 20% equals brain weight in grams.

Fig. 20 includes a comparison of simplified drawings of two endocasts from extinct species and brain outline from one extant species. In all three proboscideans, the temporal lobe is relatively large (a possible derived inter-ordinal character). In *Moeritherium* and *Mammuth* the olfactory bulbs protrude anterior to the frontal lobe, whereas they are concealed under the frontal lobe in *Elephas* (a derived intra-ordinal character). Two other observations can be made on these endocasts. The cerebellum and the olfactory bulb are relatively large, implying a good sense of balance and a good sense of smell in early and late proboscideans. In living elephants, the frontal lobe grew forward over the olfactory bulb. In a human fetus, the olfactory bulb is relatively large but is dwarfed by the developing telencephalon from the embryonic period towards adult stages. Calculations of EQ of *Moeritherium* and *Mammuth* show that the value increased by 10 fold – from 0.2 for *Moeritherium* and up to 2.2 for *Mammuth* – during the evolution of Proboscidea [66]. The EQ can be viewed as a character subjected to natural selection during phylogeny of a lineage.

4.7. Concluding remarks

4.7.1. General summary

In the present investigation we have documented gross morphological observations on the elephant brain, including details, which were not hitherto reported. Many of our observations are also accompanied by illustrations. Our data indicate that, for many of the behavioral repertoires of elephants, there are correlations with the gross anatomy of the brain.

New material and observations concerning the nervous system of elephants included in this paper are summarized below. This roster is intended to provide an overview of our new findings in drawings and photographs:

- Illustrations depicting differences between adult and fetus crania, structures inside the cranial cavity and how to remove elephant brain undamaged (Fig. 1).
- Photographs and illustrations of labeled cranial arteries including a postulated counter-current system, or carotid rete (Fig. 3A and B).
- Illustrations of anterior and posterior views of the brain (Fig. 5).
- Illustrations of the ventricles in dorsal and lateral views of the brain (Fig. 6).
- Illustrations depicting locations of hippocampus, pineal and pituitary glands, and limbic system (Fig. 8).
- Illustration depicting a close-up of the olfactory region (Fig. 10).

- Illustrations depicting the cerebellum whole and in sections (Fig. 11).
- Illustrations depicting horizontal and parasagittal sections with detailed labeling of internal structures (Fig. 12).
- Photographs depicting various sections in successive layers depicting internal structures (Figs. 13–18).
- Illustrations comparing ontogenetic to phylogenetic changes in proboscidean skulls (Fig. 19).
- Comparison among brains of three proboscideans, two extinct and one extant (Fig. 20).

We suggest that similarities between human and elephant brains are due to convergent evolution. Among mammals, the humans, chimpanzees and elephants are known to make and use tools [49], observations that have been associated with high EQ, near or above 2. Like morphological characters, EQ may be subjected to natural selection. As the largest land mammal and a keystone species [110,136], the elephant is a key illustration of adaptive biology. Understanding the form and function of the most complex organ in the elephant body, the brain, will help us better understand the natural history of these endangered species and help us as we make every effort to protect them.

4.7.2. Future research trends

In our study, a relatively small sample size of brains was studied ($n = 7$); more brains would need to be examined to reach firm conclusions. Ideally, the sampling should include ontogenetic stages, as well as specimens of adult and elderly individuals of both sexes, and from all three species of elephants, to learn about variations. One of the secondary goals of this long-term study is to search for evidence of aging changes and for the occurrence of age-related neurodegenerative diseases that occur in humans, e.g., Alzheimer's disease.

Obtaining an elephant for a dissection is not a common event; once a carcass is available, every effort should be made to retrieve as much data as possible. Nervous tissue (especially that of a fetus) decomposes more easily than other tissues, and should be preserved as soon as possible. Special efforts should be made to obtain well-preserved brains of fetuses and juvenile elephants. Because of individual variation (e.g., of tertiary gyration), it would help to obtain as many specimens as possible of adult individuals of both sexes and from all three living species of elephants. A large sample size may help answer some unanswered questions (e.g., boundary between parietal and occipital lobes, structure and function of pineal body), and it may help predict sizes of brain components from absolute brain size [41]. Suggestions for specific future research include counting the number of axons in cross-sections of cranial nerves, especially in nerves where there are discrepancies in the quality of functions, such as the optic, trigeminal, and facial nerves. Sections through the spinal cord from all segments should be collected for comparison with corresponding structures in humans. In addition, more inter-ordinal comparative brain studies would help us better understand which features are primitive and which are derived. Detailed research with phylogenetic aim in mind would be useful. In this context, brains of members of Sirenia (manatees and dugongs), Hyracoidea (hyraxes), Perissodactyla

(horses, tapirs, rhinos), Cetacea (dolphins, whales), and Tubulidentata (aardvark) are of particular interest since they are all ungulate mammals; Sirenia is the most closely related to Proboscidea and Tubulidentata is the least related in this roster [113].

Acknowledgements

Credits for the brains (or parts of them) of specimens A–G are given in Table 1. These individuals deserve special acknowledgments: veterinarians Dalen Agnew, Ann Duncan, and Cindy Stadler (all from the Detroit Zoological Institute), veterinarians Richard J. Montali (National Zoological Park) and Wynona Schallenberger (Toledo Zoo), and Bucky Steele (Seagoville, Texas)—for providing brain specimens. Charles R. Chaff (Museum of Comparative Zoology, MCZ, at Harvard University, Cambridge, MA, USA) permitted study of the endocast of the American mastodon. Staff of the American Museum of Natural History (New York, NY, USA) allowed us to study skeletal specimens in their collection. We extend heartfelt thanks to Brian Cressman (of Ann Arbor—for drawing Figs. 8C,10,11) and to Ben True (Department of Medical photography, Children's Hospital of Michigan—for Figs. 8A(ii) and B(i and ii), 12–18). Nicholas J. Mizeres and Jose Rafols (Wayne State University, School of Medicine) helped in the initial stages of this study. We also acknowledge Robert Kakos, Roger Kakos, and Robert D. Berman (of Wayne State University) for the use of image analysis to calculate the surface areas of sections of the corpus callosum and whole brains of human and elephant. For help with various aspects of this study, we thank Richard Chiger, Kim Cook, Estelle Davidson, Iain Douglas-Hamilton, Saba Francis, Joann M. Holden, M. Phil Kahl, Anne Krawchuk, Nancy (Zumwalde) Mannisto, Mahmood Mokhayesh, Moti Nissani, Mary D. Rigby, Bree D. (Schultz) Guirey, Sandra Shoshani, Raman Sukumar, and Jean Vorkamp. Craig Watson (Department of Neurology, School of Medicine, Wayne State University) and anonymous reviewers made useful comments to improve an earlier version of this paper.

References

- [1] Y. Abe, Zur Cytoarchitectonik des Thalamus beim Elefanten, *Folia Psychiatr. Neurol. Jpn.* 5 (1952) 213–239.
- [2] J. Alroy, Cope's rule and the dynamics of body mass evolution in North American fossil mammals, *Science* 280 (1998) 731–734.
- [3] J. Altman, S.A. Bayer, Development of the Cerebellar System in Relation to its Evolution, Structure, and Functions, CRC Press, Boca Raton, 1997.
- [4] C.W. Andrews, A Descriptive Catalogue of the Tertiary Vertebrata of the Fayûm, Egypt, British Museum (Natural History), London, 1906.
- [5] J. Anthony, Soulèvements corticaux d'origine vasculaire sur le cerveau de l'éléphant, *C. R. Acad. Sci. III* (1947) 1179–1181.
- [6] J. Anthony, Le névraxe de mammifères, in: P.-P. Grassé (Ed.), *Traité de zoologie: anatomie, systématique, biologie (mammifères, système nerveux, organes des sens, appareil circulatoire, sang et lymphé)*, vol. 16, no. 4, Masson et Cie Éditeurs, Paris, 1972, pp. 1–275.
- [7] M.A. Baker, A brain-cooling system in mammals, *Sci. Am.* 240 (1979) 130–137, 139, 184.
- [8] M.A. Baker, Brain cooling in endotherms in heat and exercise, *Ann. Rev. Physiol.* 44 (1982) 85–96.

- [9] R. Barone, Appareil circulatoire, in: P.-P. Grassé (Ed.), *Traité de zoologie: anatomie, systématique, biologie (mammifères, système nerveux, organes des sens, appareil circulatoire, sang et lymphe)*, vol. 16, no. 4, Masson et Cie Éditeurs, Paris, 1972, pp. 703–921.
- [10] F.E. Beddard, On the brain of the African elephant, *Proc. Zool. Soc. Lond.* (1893) 311–315, +2 pls.
- [11] F.G. Benedict, *The Physiology of the Elephant*, Carnegie Institution of Washington (Publication No. 474), Washington, DC, 1936.
- [12] R. Bleier, L. Houston, W. Byne, Can the corpus callosum predict gender, age, handedness, or cognitive differences? *Trends Neurosci.* 9 (1986) 391–394.
- [13] J.E.V. Boas, S. Paulli, *The Elephant's Head: Studies in the Comparative Anatomy of the Organs of the Head of the Indian Elephant and Other Mammals. Part II*, Gustav Fischer, Jena, 1925.
- [14] C. Braden, Not so dumb: should elephants be moved to near the top of the animal-intelligence list? *BBC Wildl.* 21 (2003) 32–38.
- [15] L.E. Bregmann, Neue Untersuchungen zur Kenntnis der Pyramidenbahn. 2. Die Oblongatapyramide des Elephanten, *Anat. Anz.* 48 (1915) 235–240.
- [16] R. Brummelkamp, Das Wachstum der Gehirnmasse mit kleinen cephalisierungssprüngen (sog. $\sqrt{2}$ -Sprüngen) bei den Ungulaten, *Acta Neerlandica Morph. Norm. et Path.* 2 (1939) 260–267.
- [17] S. Chevalier-Skolnikoff, J. Liska, Tool use by wild and captive elephants, *Anim. Behav.* 46 (1993) 209–219.
- [18] C.D. Clemente, *Anatomy: A Regional Atlas of the Human Body*, Urban & Schwarzenberg, Baltimore, 1987.
- [19] G. Cole, J.W. Neal, The brain in aged elephants, *J. Neuropathol. Exp. Neurol.* 49 (1990) 190–192.
- [20] P. Cottureau, Elephant memory, *Bulletin de l'Academie Veterinaire de France* 42 (1969) 897–899.
- [21] E.W. Count, Brain and body weight in man: their antecedents in growth and evolution, *Ann. N. Y. Acad. Sci.* 46 (1947) 993–1122.
- [22] B. Cozzi, S. Spagnoli, L. Bruno, An overview of the central nervous system of the elephant through a critical appraisal of the literature published in the XIX and XX centuries, *Brain Res. Bull.* 54 (2001) 219–227.
- [23] G. Crile, D.P. Quiring, A record of the body weight and certain organ and gland weights of 3690 animals, *Ohio J. Sci.* 40 (1940) 219–259.
- [24] E.C. Crosby, T. Humphrey, E.W. Lauer, J.A. Kappers, B.L. Baker, C.A. Fox, L.A. Gillian, K. Scharensberg, *Correlative Anatomy of the Nervous System*, The MacMillan Company, New York, 1962.
- [25] C. de Lacoste-Utamsing, R.L. Holloway, Sexual dimorphism in the human corpus callosum, *Science* 216 (1982) 1431–1432.
- [26] T.W. Deacon, Primate brains and senses, in: S. Jones, R. Martin, D. Pilbeam (Eds.), *The Cambridge Encyclopedia of Human Evolution*, Cambridge University Press, Cambridge, 1992, pp. 109–123.
- [27] H.-D. Dellmann, R.C. McClure, Central nervous system, in: R. Getty (Ed.), *Sisson and Grossman's The Anatomy of the Domestic Animals*, vol. 1, fifth ed., W.B. Saunders Company, Philadelphia, 1975, pp. 202–225.
- [28] H.-D. Dellmann, R.C. McClure, Equine nervous system, in: R. Getty (Ed.), *Sisson and Grossman's The Anatomy of the Domestic Animals*, vol. 1, fifth ed., W.B. Saunders Company, Philadelphia, 1975, pp. 633–702.
- [29] H.-D. Dellmann, R.C. McClure, Ruminant nervous system, in: R. Getty (Ed.), *Sisson and Grossman's The Anatomy of the Domestic Animals*, vol. 2, fifth ed., W.B. Saunders Company, Philadelphia, 1975, pp. 1065–1080.
- [30] H.-D. Dellmann, R.C. McClure, Porcine nervous system, in: R. Getty (Ed.), *Sisson and Grossman's The Anatomy of the Domestic Animals*, vol. 2, fifth ed., W.B. Saunders Company, Philadelphia, 1975, pp. 1360–1369.
- [31] H.-D. Dellmann, R.C. McClure, Carnivore neurology, in: R. Getty (Ed.), *Sisson and Grossman's The Anatomy of the Domestic Animals*, vol. 2, fifth ed., W.B. Saunders Company, Philadelphia, 1975, pp. 1371–1699.
- [32] H. Dexler, Zur Anatomie des Zentralnervensystems von *Elephas indicus*, *Arb. Neurol. Inst. Wein* 15 (1907) 137–281, +2 pls.
- [33] R. Diepen, P. Janssen, F. Engelhardt, H. Spatz, Recherches sur le cerveau de l'éléphant d'Afrique (*Loxodonta africana* Blum) II—Données sur l'hypothalamus, *Acta Neurol. Psychiatr. Belg.* 56 (1956) 759–789.
- [34] I. Douglas-Hamilton, O. Douglas-Hamilton, *Among the Elephants*, Viking Press, New York, 1975.
- [35] L. DuBreuil-Chambardel, Deux cas de duplicité du tronc basilaire, *Bull. Soc. Anat. Paris* 93 (1923) 62.
- [36] N.B. Eales, The anatomy of the head of a foetal African elephant, *Elephas africanus (Loxodonta africana)*, *Trans. R. Soc. Edinburgh* 54 (1926) 491–551, with 12 plates.
- [37] R. Eckert, D. Randall, G. Augustine, *Animal Physiology: Mechanisms and Adaptations*, third ed., W.H. Freeman and Company, New York, 1988.
- [38] H. Eichenbaum, How does the brain organize memories? *Science* 277 (1997) 330–332.
- [39] J.F. Eisenberg, *The Mammalian Radiation*, University of Press, Chicago, 1981.
- [40] J.F. Eisenberg, D.E. Wilson, Relative brain size and demographic strategies in didelphid marsupials, *Am. Natur.* 118 (1981) 1–15.
- [41] B.L. Finlay, R.B. Darlington, Linked regularities in the development and evolution of mammalian brains, *Science* 268 (1995) 1578–1584.
- [42] R. Fléaux, Histoire d'une merveille d'ingénierie mécanique: Genèse de la trompe, *Sci. Avenir* 611 (1998) 42–46.
- [43] F. Frade, Ordre des proboscidiens (Proboscidea Illiger, 1811), in: P.-P. Grassé (Ed.), *Traité de Zoologie*, vol. 17, no. 1, Masson et Cie Éditeurs, Paris, 1955, pp. 715–875.
- [44] M. Friant, Le premier stade de l'évolution ontogénique du cerveau chez l'éléphant, *Rev. Zool. Bot. Afr.* 38 (1944) 75–78.
- [45] M. Friant, Deux stades de l'évolution du cerveau (télencéphale) de l'éléphant (*Loxodonta africana* Blum.), *Acta Univ. Lund N. F. Adv.* 2 (47) (1951) 3–10.
- [46] M. Friant, Développement et morphologie du cerveau d'un proboscidien, l'éléphant d'Afrique (*Loxodonta africana* Blum.), *Acta Neurol. Psychiatr. Belg.* 69 (1969) 20–32.
- [47] J.-H. Gao, L.M. Parsons, J.M. Bower, J. Xiong, J. Li, P.T. Fox, Cerebellum implicated in sensory acquisition and discrimination rather than motor control, *Science* 272 (1996) 545–547.
- [48] W. Gilchrist, *A Practical Treatise on the Treatment of the Diseases of the Elephant, Camel, and the Horned Cattle with Instructions for Preserving their Efficiency*, Government Press, Calcutta, 1851.
- [49] J.A. Gordon, Elephants do think, *Afr. Wildl.* 20 (1966) 75–79.
- [50] S.J. Gould, *Ever Since Darwin*, W.W. Norton & Company, New York, 1977.
- [51] S.J. Gould, *Ontogeny and Phylogeny*, The Belknap Press of Harvard University Press, Cambridge (Massachusetts), 1977.
- [52] P.-P. Grassé, Ordre des édentés, in: P.-P. Grassé (Ed.), *Traité de Zoologie*, vol. 17, no. 2, Masson et Cie Éditeurs, Paris, 1955, pp. 1182–1246, 2295.
- [53] H. Gray, in: T.P. Pick, R. Howden (Eds.), *Anatomy Descriptive and Surgical* (1974 printing), Running Press, Philadelphia, 1901.
- [54] W.K. Gregory, The orders of mammals, *Bull. Am. Mus. Nat. Hist.* 27 (1910) 1–524.
- [55] G. Haas, Verhaltensstörungen durch Knochenauflagerungen um den Nervus intermediofacialis und statoacusticus bei einer indischen Elefantentkuh (*Elephas maximus bengalensis*), *Zool. Garten* 48 (1978) 297–298.
- [56] E. Haeckel, *Generelle Morphologie de Organismen: Allgemeine Grundzüge der organischen Formen-Wissenschaften, mechanisch begründet durch die von Charles Darwin reformierte Descendenz-Theorie*, vol. 2, Georg Reimer, Berlin, 1866.
- [57] A.Y. Hakeem, H.P. Hof, C.C. Sherwood, R.C. Switzer III, L.E.L. Rasmussen, J.M. Allman, Brain of the African elephant (*Loxodonta africana*): neuroanatomy from magnetic resonance images, *Anat. Record Part A: Discoveries Mol., Cell. Evol. Biol.* 287 (1) (2005) 1117–1127.
- [58] B. Hanström, The hypophysis in a tiger and an Indian elephant (*Elephas maximus*), *Acta Univ. Lund. N. F. Adv.* 42 (1946) 1–24.

- [59] I. Hardesty, Observations on the medulla spinalis of the elephant with some comparative studies of the intumescencia cervicalis and the neurones of the columna anterior, *J. Comp. Neurol.* 12 (1902) 125–182.
- [60] B.L. Hart, L. Hart, M. McCoy, C.R. Sarath, Cognitive behaviour in Asian elephants: use and modification of branches for fly switching, *Anim. Behav.* 62 (2001) 839–847.
- [61] H. Haug, Comparative studies of the brains of men, elephants and toothed whales, *Verh. Anat. Ges.* 64 (1970) 191–195.
- [62] H. Haug, Der makroskopische Aufbau des Grosshirns; Qualitative und quantitative Untersuchungen an den Gehirnen des Menschen, der Delphinoidea und des Elefanten, *Ergeb. Anat. Entwicklungsgesch.* 43 (1970) 3–70.
- [63] H. Haug, Die Epiphyse und die circumventrikulären Strukturen des Epithalamus im Gehirn des Elefanten (*Loxodonta africana*), *Z. Zellforsch. Mikrosk. Anat.* 129 (1972) 533–547.
- [64] P. Janssen, H. Stephan, Recherches sur le cerveau de l'éléphant d'Afrique (*Loxodonta africana* Blum). I. Introductions et considérations macroscopiques, *Acta Neurol. Belg.* 56 (1956) 731–757.
- [65] C. Jensen, M.E. Hahn, B.C. Dudek, Introduction: toward understanding the brain behavior relationship, in: M.E. Hahn, C. Jensen, B.C. Dudek (Eds.), *Development and Evolution of Brain Size: Behavioral Implications*, Academic Press, New York, 1979, pp. 1–7.
- [66] H.J. Jerison, *Evolution of the Brain and Intelligence*, Academic Press, New York, 1973.
- [67] K.V. Kardong, *Vertebrates: Comparative Anatomy, Function, Evolution*, Wm. C. Brown Publishers, Dubuque (Iowa), 1995.
- [68] S.-G. Kim, K. Ugurbil, P.L. Strick, Activation of a cerebellar output nucleus during cognitive processing, *Science* 265 (1994) 949–951.
- [69] J. Kingdon, *East African Mammals: an Atlas of Evolution in Africa*, vol. III. Part B (Large mammals), Academic Press, London, 1979.
- [70] J. Kladetzky, Von. Mitteilung, über die Hypophyse eines weiblichen indischen Elefanten, *Anat. Anz.* 19–52 (1952) 75–79.
- [71] V.I. Kochetkova, *Paleoneurology*, John Wiley & Sons (Halsted Press), New York, 1978.
- [72] H. Koikegami, S. Kido, Y. Mayeda, Zum Riechhirn des indischen Elefanten, *Gegenbaurs Morphol. Jahrb.* 85 (1941) 512–524.
- [73] H. Koikegami, N. Ozaki, Studies on the paralimbic brain structures. III. On the nucleus accumbens and on the olfacto-tegmental tract in the Indian elephant, *Acta Med. Biol. (Niigata)* 15 (1967) 131–140.
- [74] H. Koikegami, Y. Hirata, J. Oguma, Studies on the paralimbic brain structures. I. Definition and delimitation of the paralimbic brain structures and some experiments on the nucleus accumbens, *Folia Psychiat. Neurol. Jpn.* 21 (1967) 151–180.
- [75] R. Kotulak, *Inside the Brain: Revolutionary Discoveries of How the Mind Works*, Andrews McMeel Publishing, Kansas City (Missouri), 1997.
- [76] J. Krueg, Ueber die Furchen auf der Grosshirnrinde der zoonoplacentalen Säugethiere, *Z. Wiss. Zool.* 33 (1880) 595–672, +XXXIV–XXXVIII tables.
- [77] W.J. Kupsky, G.H. Marchant, K. Cook, J. Shoshani, Morphologic analysis of the hippocampal formation in *Elephas maximus* and *Loxodonta africana* with comparison to that of human, in: G. Cavarretta, P. Gioia, M. Mussi, M.R. Palombo (Eds.), *Proceedings of the 1st International Congress of "La Terra degli Elefanti"*, The World of Elephants, Consiglio Nazionale delle Ricerche, Roma, 2001, pp. 643–647.
- [78] J. LeDoux, *The Emotional Brain: the Mysterious Underpinnings of Emotional Life*, Simon & Schuster, New York, 1996.
- [79] F.R. Leuret, P. Gratiolet, *Anatomie Comparée du Système Nerveux, considérée dans ses rapports avec l'intelligence*, Tome Premier, J.-B. Baillièrre et Fils, Paris, 1839–1857.
- [80] F.R. Leuret, P. Gratiolet, *Anatomie Comparée du Système Nerveux, considérée dans ses rapports avec l'intelligence*, Tome Second, J.-B. Baillièrre et Fils, Paris, 1839–1857.
- [81] F.R. Leuret, P. Gratiolet, *Anatomie Comparée du Système Nerveux, considérée dans ses rapports avec l'intelligence*, Atlas de 32 planches dessinées d'après nature et gravées, J.-B. Baillièrre et Fils, Paris, 1839–1857.
- [82] G.M. Mace, P.H. Harvey, T.H. Clutton-Brock, Brain size and ecology in small mammals, *J. Zool. Lond.* 193 (1981) 333–354.
- [83] V.J. Maglio, Origin and evolution of the elephantidae, *Trans. Am. Philos. Soc. Philadelphia, New Series* 63 (1973) 1–149.
- [84] P.R. Manger, K. Fuxe, S.H. Ridgway, J.M. Siegel, The distribution and morphological characteristics of catecholaminergic cells in the dien-cephalon and midbrain of the bottlenose dolphin (*Tursiops truncatus*), *Brain Behav. Evol.* 64 (2004) 42–60.
- [85] D. Mariappa, *Anatomy and Histology of the Indian Elephant*, Indira Publishing House, Oak Park (Michigan), 1986.
- [86] R.D. Martin, Relative brain size and basal metabolic rate in terrestrial vertebrates, *Nature* 293 (1981) 57–60.
- [87] A.F.J.C. Mayer, Beiträge zur Anatomie der Elefanten und der übrigen Pachydermen, *Nova Acta Acad. Leop., Phys.-Med.* 22 (1845–1847) 1–88, +ix tables.
- [88] R.M.H. McMinn, A case of non-union of the vertebral arteries, *Anat. Rec.* 116 (1953) 283–286.
- [89] M.-M. Mesulam, E.J. Mufson, The insula of Reil in man and monkey: architectonics, connectivity and function, in: A. Peters, E.G. Jones (Eds.), *Cerebral Cortex*, vol. 4: Association and Auditory Cortices, Plenum Press, New York, 1985, pp. 179–226.
- [90] N.J. Mizeres, *Human Anatomy: a Synoptic Approach*, Elsevier, New York, 1981.
- [91] M. Nissani, Do Asian elephants apply causal reasoning to tool use tasks? *J. Exp. Psych.: Anim. Behav. Processes.* 32 (1) (2006) 91–96.
- [92] M. Nissani, D. Hoefler-Nissani, U.T. Lay, U.W. Htun, Simultaneous visual discrimination in Asian elephants, *J. Exp. Anal. Behav.* 83 (2005) 15–29.
- [93] J. Nolte, J.B. Angevine Jr., *The Human Brain in Photographs and Diagrams*, second ed., Mosby Publishers, St. Louis (Missouri), 2000.
- [94] H.F. Osborn, *Proboscidea*, vol. II: Stegodontoidea, Elephantoida, The American Museum Press, New York, 1942.
- [95] D.H. Padgett, Designation of the embryonic intersegmental arteries in reference to the vertebral artery and subclavian stem, *Anat. Rec.* 119 (1954) 349–356.
- [96] A. Parent, *Carpenter's Human Neuroanatomy*, ninth ed., Williams & Wilkins, Baltimore, 1996.
- [97] G. Paxinos (Ed.), *The Human Nervous System*, Academic Press, Inc., San Diego, 1990.
- [98] N.G. Pillai, On the height and age of an elephant, *J. Bombay Nat. Hist. Soc.* 42 (1941) 927–928.
- [99] A. Precechtel, Some notes upon the finer anatomy of the brain stem and the basal ganglia of *Elephas indicus*, *Proc. R. Acad. Sci., Amsterdam* 28 (1925) 82–92.
- [100] L.E.L. Rasmussen, M.J. Schmidt, R. Henneous, D. Groves, G.D. Daves Jr., Asian bull elephants: flehmen-like responses to extractable components in female elephant estrous urine, *Science* 217 (1982) 159–162.
- [101] B. Rensch, Increase of learning capability with increase of brain size, *Am. Nat.* 90 (1956) 81–95.
- [102] B. Rensch, The intelligence of elephants, *Sci. Am.* 196 (1957) 44–49.
- [103] B. Rensch, R. Altevoigt, Visuelles Lernvermögen eines indischen Elefanten, *Z. Tierpsychol.* 10 (1953) 119–134.
- [104] W. Robertson-Bullock, The weight of the African elephant, *Loxodonta africana*, *Proc. Zool. Soc. Lond.* 138 (1962) 133–135.
- [105] A.S. Romer, T.S. Parsons, *The Vertebrate Body*, sixth ed., Harcourt Brace Jovanovich College Publishers, Fort Worth (Texas), 1986.
- [106] G.A. Sacher, E.F. Staffeldt, Relation of gestation time to brain weight for placental mammals: implications for the theory of vertebrate growth, *Am. Nat.* 108 (963) (1974) 593–615.
- [107] M.J. Schmidt, The elephant beneath the mask, in: J. Shoshani (Ed.), *Elephants: Majestic Creatures of the Wild*, Checkmark Books, New York, 2000, pp. 92–97.
- [108] Y. Shimizu, T. Fujita, T. Kamiya, S. Isokawa, Anatomy of a female Indian elephant with special references to its visceral organs, *Acta Anat. Nippon* 35 (1960) 261–301 (In Japanese, with English figures captions, tables, and summary).
- [109] J. Shoshani, Elephants have a large neocortex too, *Behav. Brain Sci.* 11 (1988) 100.

- [110] J. Shoshani, Elephants: the super keystone species, *Swara* 16 (1993) 25–29.
- [111] J. Shoshani, Understanding proboscidean evolution: a formidable task, *Trends Ecol. Evol.* 13 (1998) 480–487.
- [112] J. Shoshani, J.E. Eisenberg, Intelligence and survival, in: J. Shoshani (Ed.), *Elephants: Majestic Creatures of the Wild*, Checkmark Books, New York, 2000, pp. 134–137.
- [113] J. Shoshani, M.C. McKenna, Higher taxonomic relationships among extant mammals based on morphology, with selected comparison of results from molecular data, *Mol. Phylogenet. Evol.* 9 (Special Issue) (1998) 572–584 (plus seven appendices on the website <http://www.idealibrary.com>).
- [114] J. Shoshani, P. Tassy, in: J. Shoshani, P. Tassy (Eds.), *The Proboscidea: Evolution and Palaeoecology of Elephants and their Relatives*, Oxford University Press, Oxford (England), 1996.
- [115] J. Shoshani, L.E.L. Rasmussen, W.J. Kupsky, D.W. Agnew, G.S. Borszcz, Do elephants feel pain and if so, how do we know this? *Elephant* 2 (2000) 48–52.
- [116] J. Shoshani, et al., On the dissection of a female Asian elephant (*Elephas maximus maximus* Linnaeus, 1758) and data from other elephants, *Elephant* 2 (1) (1982) 3–93.
- [117] S.K. Sikes, *The Natural History of the African Elephant*, Weidenfeld and Nicolson, London, 1971.
- [118] G.E. Smith, The brain in the Edentata, *Trans. Linnean Soc. Lond., Sec. Ser., Zool.* 7 (1899) 277–394.
- [119] G.E. Smith, *Descriptive and Illustrated Catalogue of the Physiological Series of Comparative Anatomy Contained in the Museum of the Royal College of Surgeons of England*, vol. II, second ed., Printed for the College; and sold by Taylor and Francis, London, 1902.
- [120] C.A. Spinage, *Elephants*, T. & A. D. Poyser, London, 1994.
- [121] D. Starck, Le crâne des mammifères, in: P.-P. Grassé (Ed.), *Traité de Zoologie*, vol. 16, no. 1, Masson et Cie Éditeurs, Paris, 1967, pp. 405–549, 1095–1102.
- [122] H. Stephan, P. Janssen, Recherches sur le cerveau de l'éléphant d'Afrique (*Loxodonta africana* Blum.) III. L'organe subfornical, *Acta Neurol. Psychiatr. Belg.* 56 (1956) 789–812.
- [123] R. Sukumar, *The Living Elephants: Evolutionary Ecology, Behavior, and Conservation*, Oxford University Press, Oxford, 2003.
- [124] C.R. Taylor, The eland and the oryx, *Sci. Am.* 220 (1969) 88–95.
- [125] D.B. Tower, Structural and functional organization of mammalian cerebral cortex: the correlation of neurone density with brain size. Cortical neurone density in the fin whale (*Baleonoptera physalus* L.) with a note on the cortical neurone density in the Indian elephant, *J. Comp. Neurol.* 101 (1954) 19–51.
- [126] N.J. Van der Merwe, A.J. Bezuidenhout, C.D. Seegers, The skull and mandible of the African elephant (*Loxodonta africana*), *Onderstepoort J. Vet. Res.* 62 (1995) 245–260.
- [127] F. Vargha-Khadem, D.G. Gadian, K.E. Watkins, A. Connelly, W. Van Paesschen, M. Mishkin, Differential effects of early hippocampal pathology on episodic and semantic memory, *Science* 277 (1997) 376–380.
- [128] T.A. Vaughan, J.M. Ryan, N.J. Czaplewski, *Mammalogy*, fourth ed., Saunders College Publishing, Fort Worth (Texas), 2000.
- [129] W.J.C. Verhaart, The pyramid in the medulla and the cord of the elephant, *Acta Morphol. Neerlando-Scandinavica* 2 (1958) 174–181.
- [130] W.J.C. Verhaart, Anatomy of the brain stem of the elephant, *J. Hirnforschung Hirnforschung* 5 (1962) 455–525.
- [131] W.J.C. Verhaart, Pyramidal tract in the cord of the elephant, *J. Comp. Neurol.* 121 (1963) 45–49.
- [132] C. Wade, C. Tavis, *Psychology*, third ed., HarperCollins College Publishers, New York, 1993.
- [133] W.F. Walker, K.F. Liem, *Functional Anatomy of the Vertebrates: An Evolutionary Perspective*, second ed., Saunders College Publishing, Fort Worth, 1994.
- [134] R. Warwick, P.L. Williams (Eds.), *Gray's Anatomy*, 35th British ed., W.B. Saunders Company, Philadelphia, 1973.
- [135] W. Welker, Why does cerebral cortex fissure and fold? A review of determinants of gyri and sulci, in: E.G. Jones, A. Peters (Eds.), *Cerebral Cortex*, vol. 8B, Plenum Press, New York, 1990, pp. 3–136.
- [136] D. Western, The ecological value of elephants: a keystone role in African ecosystems, in: S. Cobb (Ed.), *The Ivory Trade and the Future of the African Elephant*, vol. 2, section 5.2, The Ivory Trade Review Group, Oxford, 1989.
- [137] M.C. Whitrock, J. Beatty, J.E. Bogan, M.S. Gazzaniga, H.J. Jerison, S.D. Krashen, R.D. Nebes, T.J. Teylor, *The Human Brain*, Prentice-Hall Inc., Englewood Cliffs (New Jersey), 1977.
- [138] J.H. Williams, *Elephant Bill*, Rupert Hart-Davis, London, 1950.
- [139] K. Wirz, Zur quantitativen Bestimmung der Rangordnung bei Säugetieren, *Acta Anat.* 9 (1950) 134–196.
- [140] G.B. Wislocki, Note on the hypophysis of an adult Indian elephant, *Anat. Rec.* 74 (1939) 321–329.
- [141] G.B. Wislocki, The topography of the hypophysis in the elephant, manatee and hyrax, *Anat. Rec.* 77 (1940) 427–445.
- [142] J.Z. Young, *The Life of Vertebrates*, third ed., Clarendon Press, Oxford, 1981.
- [143] K. Zilles, Biometrische Analyse der Frischvolumina verschiedener prosencephaler Hirnregionen von 78 menschlichen adulten Gehirnen, *Gegenbaurs Morphol. Jahrb.* 118 (1972) 234–273.
- [144] K. Zilles, Cortex, in: G. Paxinos (Ed.), *The Human Nervous System*, Academic Press, Inc., San Diego, 1990, pp. 757–802.