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Cetacean Brain Evolution: Dwarf Sperm Whale (Kogia sima) and Common Dolphin (Delphinus delphis) – An Investigation with High-Resolution 3D MRI

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Abstract

This study compares a whole brain of the dwarf sperm whale (Kogia sima) with that of a common dolphin (Delphinus delphis) using high-resolution magnetic resonance imaging (MRI). The Kogia brain was scanned with a Siemens Trio Magnetic Resonance scanner in the three main planes. As in the common dolphin and other marine odontocetes, the brain of the dwarf sperm whale is large, with the telencephalic hemispheres remarkably dominating the brain stem. The neocortex is voluminous and the cortical grey matter thin but expansive and densely convoluted. The corpus callosum is thin and the anterior commissure hard to detect whereas the posterior commissure is well-developed. There is consistency as to the lack of telencephalic structures (olfactory bulb and peduncle, olfactory ventricular recess) and neither an occipital lobe of the telencephalic hemisphere nor the posterior horn of the lateral ventricle are present. A pineal organ could not be detected in Kogia. Both species show a tiny hippocampus and thin fornix and the mammillary body is very small whereas other structures of the limbic system are well-developed. The brain stem is thick and underlies a large cerebellum, both of which, however, are smaller in Kogia. The vestibular system is markedly reduced with the exception of the lateral (Deiters') nucleus. The visual system, although well-developed in both species, is exceeded by the impressive absolute and relative size of the auditory system. The brainstem and cerebellum comprise a series of structures (elliptic nucleus, medial accessory inferior olive, paraflocculus and posterior interpositus nucleus) showing characteristic odontocete dimensions and size correlations. All these structures seem to serve the auditory system with respect to echolocation, communication, and navigation.

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Introduction

Toothed whales (odontocetes) are characterized by large and complicated brains (for definition of terms see Materials and Methods). This is an intriguing fact and needs some general explanation in order to facilitate the understanding of many details. In this respect it is of some interest that the toothed whales as well as the baleen whales (mysticetes) go back to common ancestors among the fossil hoofed animals (ungulates), from which they split off about 55 mya [Geisler and Luo, 1998; cf. Oel-

Abbreviations used in this paper			
I–IV	ventricles	IO	inferior olive
2	optic tract	IP	interpeduncular nucleus
5	trigeminal nerve	is	intercalate sulcus
5'	spinal tract and nucleus of trigeminal nerve	L	lateral (cerebellar) nucleus
7	facial nerve	LGN	lateral geniculate nucleus
7'	facial nucleus	ll	lateral lemniscus
8	cochlear nerve	LL	lateral lemniscus nuclei
A	nucleus ambiguus	M	medial accessory inferior olive
ac	anterior commissure	mcp	middle cerebellar peduncle
AC	amygdaloid complex	MGN	medial geniculate nucleus
aq	cerebral aqueduct	ml	medial lemniscus
bi	brachium colliculi inferioris	mt	medial tegmental tract
bs	brachium colliculi superioris	O	superior olivary complex
C	caudate nucleus	OL	oval lobule
cc	corpus callosum	OrL	orbital lobe
ce	crus cerebri	OT	olfactory tubercle/ olfactory lobe
Ce	cerebellum	P	pons
CG	central (periaqueductal) grey	Pa	globus pallidus
ci	commissure of the inferior colliculi	pc	posterior commissure
Cj	interstitial nucleus of Cajal	pci	posterior commissure, inferior part
Cl	claustrum	Pf	paraflocculus
CN	cerebellar nuclei	PIN	posterior interposed nucleus
cs	commissure of the superior colliculi	PL	parietal lobe
E	elliptic nucleus (nucleus of Darkschewitsch)	Pu	putamen
en	entolateral sulcus	Pul	pulvinar
Ent	regio entorhinalis	r	restiform body (inferior cerebellar peduncle)
es	ectosylvian sulcus	R	red nucleus
f	fornix	RF	reticular formation
FL	frontal lobe	s	sylvian sulcus
fm	forceps minor (cc)	SC	superior colliculus
FN	fastigial nucleus	scp	superior cerebellar peduncle
GC	gyrus cinguli	sl	lateral sulcus
GP	gyrus parahippocampalis	sp	suprasplenial sulcus (limbic cleft)
H	hypothalamus	SpC	spinal cord
He	cerebellar hemisphere	ss	suprasylvian sulcus
hi	habenulo-interpeduncular tract	T	thalamus
Hi	hippocampus	TB	trapezoid body and nucleus
I	insula	TL	temporal lobe
ic	internal capsule	v	central vestibular complex
IC	inferior colliculus	V	vermis
if	interpedundular fossa	VCN	ventral cochlear nucleus
im	intermediate mass		

Grey matter (cortex and nuclei) in capitals, cortical sulci and fiber systems in lower case, ventricles in Roman figures and lower case, cranial nerves in Arabic figures.

schläger et al., 2008]. From an evolutionary point of view it might therefore be advantageous to include remarks on the extant hoofed animals in order to elucidate the morphology and function of the cetacean brain (see below).

Among the smaller odontocetes, a similar increase in brain size might have happened during evolution as is known from primates [ascending primate series: Ste-phan, 1975; Schwerdtfeger et al., 1984; Matano et al., 1985; Stephan et al., 1988]. The highest encephalization is known from marine delphinid species [Schwerdtfeger et al., 1984; Ridgway and Tarpley, 1996; Manger, 2006; Oel-schläger et al., 2008, Oelschläger and Oelschläger, 2002, 2009], whereas pygmy and dwarf sperm whales of about the same body dimensions show distinctly smaller brains

per body mass. In adult male giant sperm whales *(Physeter macrocephalus)*, the average absolute brain mass, on the one hand, is the largest within the mammalia and only rivalled by those in the largest male killer whales [*Orcinus orca*; Osborne and Sundsten, 1981; Ridgway and Tarpley, 1996]. On the other hand, in the giant sperm whale, the ratio of brain mass as a percentage of total body mass is one of the smallest among mammalia [Oelschläger and Kemp, 1998] due to the negative allometry of the brain with increasing body size. This is obvious in the only mediosagittal section of an adult giant sperm whale skull in the literature showing the comparatively minute cranial vault [Flower, 1868–1869].

The two genera in the sperm whale (physeterid) family are rather different. Although the smaller species [pygmy sperm whale, *Kogia breviceps;* dwarf sperm whale, *K. sima;* Rice, 1998] are within the dimensions of smaller to medium-sized members of the delphinid family, the giant sperm whale was reported to attain almost 21 m in body length [Tomilin, 1967] and 57 metric tons [Rice, 1989] and exhibits the largest nose in the animal kingdom [Cranford et al., 1996; Cranford, 1999; Møhl et al., 2000; Huggenberger, 2004]. All sperm whales are deep-divers and mostly live on squids weighing 400–450 g; the giant sperm whale can dive down to 3,000 m depth and prey on giant squids of up to 18 m body length and 400 kg body mass. These squids can even be taken by blind whales and at considerable depths [Clarke et al., 1993; Gambell, 1995] presumably with the help of echolocation signals generated by their huge nose, the loudest sounds documented in the animal kingdom [Cranford, 1999; Møhl et al., 2000].

Among the Cetacea, sperm whales (Physeteroidea) represent an ancient evolutionary line; they go back to the late Oligocene period about 23 million years ago [Rice, 1998; Fordyce and De Muizon, 2001]. The beaked whales (Ziphioidea) are probably closely related. Beaked whales are deep-diving toothed whales which are intermediate in body size and brain morphology between the dwarf and pygmy sperm whales on the one hand and the giant sperm whale on the other (see below).

The scenario for such an impressive increase in brain size in smaller toothed whales seems to result from dramatic changes in life-style. The latter required profound adaptations in all organ systems and can be traced throughout the brain [Oelschläger and Oelschläger, 2002, 2009]. In mammals generally, the brain is responsible for processing external and internal input and the formulation of an adequate response for the survival of the individual.

Because sound is transmitted well in water and in view of the fact that other reliable sensory input is limited for these animals in their habitat [Oelschläger, 2008], the auditory system of odontocetes has attained an extreme in size, structural differentiation and physiological capacity among the mammalia [Zvorykin, 1963; De Graaf, 1967; Ridgway, 1983, 1986, 2000; Ridgway et al., 1981; Ridgway and Au, 1999, 2009]. In these animals, the hearing organ, which includes a highly modified middle and inner ear region [Wever et al., 1972; Oelschläger, 1990; Wartzok and Ketten, 1999; Nummela et al., 1999; Ketten, 2000; Kossatz, 2006], and the ascending auditory pathway are integrated into a powerful sonar system together with a unique ensemble of nasal structures [epicranial complex; Cranford et al., 1996; Cranford, 2000; Huggenberger, 2004; Comtesse-Weidner, 2007; Prahl, 2007; Prahl et al., 2009; Huggenberger et al., 2009]. This sonar system allows targeted locomotion by active orientation and echolocation as well as extensive communication independent from the time of day and water depth or quality. Therefore, it is not surprising that the auditory system has stamped its influence on the brain at any of its levels by the hypertrophy of the relevant structures involved in the processing of auditory information and acousticomotor (audiomotor) navigation [Ridgway, 1983, 1986, 2000; Ridgway and Au, 1999; Schulmeyer et al., 2000; Oelschläger et al., 2008; Oelschläger, 2008; Oelschläger and Oelschläger, 2002, 2009].

In contrast to the common dolphin, and even more the bottlenose dolphin [*Tursiops truncatus*; e.g., Morgane and Jacobs, 1972; Morgane et al., 1980], there is only a very little bit of information on the brain of sperm whales. Ontogenetic investigations [Oelschläger and Kemp, 1998] revealed that the giant sperm whale brain, in principle, develops as in other toothed whales [Buhl and Oelschläger, 1988; Wanke, 1990; Holzmann, 1991]. This is also shown in reduction tendencies: Thus the rostral part of the olfactory system (olfactory nerves and bulbs) is lost in the early stages of fetal odontocete development, whereas the adjacent nervus terminalis persists [Oelschläger et al., 1987; Ridgway et al., 1987]. Several components of the limbic system show early signs of regression (hippocampus, fornix, mammillary body). In contrast, some components of the auditory system (trapezoid body, inferior colliculus) are characterized by marked enlargement in the early fetal period, thereby anticipating their dominant position in the adult. Quantitative aspects of the subcortical auditory system in the odontocete brain were analyzed by Zvorykin [1963], Schulmeyer [1992], and Schulmeyer et al. [2000].

Table 1. List of the toothed whale brains investigated (MRI; serial sections, Nissl and fiber stain)

Species	ID number	Body length (cm)	Body mass (kg)	Brain mass (fresh; g)	Age	Sectional planes
Kogia sima	Ks9303B	194	–	577	adult?	MRI
Delphinus delphis	T375	153	37	788	subadult	coronal*
Delphinus delphis	T379	168	52	685	subadult	sagittal*
Delphinus delphis	Dd9347B	168	49	757	adult	MRI
Delphinus delphis	T377	190	61	830	adult	horizontal*

* Microslide series; sagittal, only sagittal and parasagittal sections were mounted on slides and stained.

In the giant sperm whale, the cerebellum and pons grow more slowly than in most smaller toothed whales and the pyramidal tract develops poorly whereas there is marked growth of the striatum and the inferior olivary complex [Oelschläger and Kemp, 1998]. In the early fetal period, the trigeminal, cochlear, and facial nerves are already the largest cranial nerves in diameter. In toothed whales generally, the facial and trigeminal nerves show high axon numbers [Morgane and Jacobs, 1972] and are probably responsible for the activity and control of nasal click generation for echolocation and communication. The cochlear nerve, which yields the auditory input via sound perception in the inner ear, is the thickest of all cranial nerves in most odontocetes; here, it might comprise several times more axons than in the human [cf. Oelschläger and Oelschläger, 2009].

Although the giant sperm whale *(Physeter macrocephalus)* has been investigated regarding the gross morphology of the adult brain by Ries and Langworthy [1937], Kojima [1951], and Jacobs and Jensen [1964], limited information is available on the structure of the brain in the pygmy sperm whale and the dwarf sperm whale [*Kogia breviceps, K. sima*: Haswell, 1884; Ogawa and Arifuku, 1948; Igarashi and Kamiya, 1972; Seki, 1984]. In older investigations, only one species *(Kogia greyi)* was listed [e.g., Kükenthal and Ziehen, 1893]. Their brains are distinctly smaller than those of delphinids in the same size range and are characterized by a lower number of neurons per cortical gray matter unit in their sensory cortices [Poth et al., 2005]. In a recent paper, Marino et al. [2003] presented an overview on the gross morphology of the dwarf sperm whale brain by means of MR scans but did not go into details regarding the detection of smaller structural details needed for a thorough functional interpretation of the brain systems.

In this paper, we present high-resolution MR scans in the standard planes and discuss the three-dimensional structural organization of the dwarf sperm whale brain with special emphasis on the characteristics of the odontocete bauplan including functional as well as evolutionary implications. To date, no adequate microslide series of *Kogia* brains have been reported in the literature which could serve as a correlative for MRI as shown for the common dolphin [Oelschläger et al., 2008]. A small number of histological sections through the brainstem of the pygmy sperm whale have been published by Ogawa and Arifuku [1948] and Igarashi and Kamiya [1972]. The little-known dwarf sperm whale is an oceanic species with a worldwide distribution in warm and temperate waters. In most reports, this species is characterized as rare or uncommon [Caldwell and Caldwell, 1989]. The animals live over or near the edge of the continental shelf and mostly feed on cephalopods for which they dive down to about 300 m [Duguy, 1995].

Materials and Methods

We compare our MRI dataset of one dwarf sperm whale brain with scans of the common dolphin brain which has been analyzed recently [Oelschläger et al., 2008] using microslide series of three more *Delphinus delphis* brains, each sectioned in one of the three major planes, from the Pilleri Collection (Natural History Museum and Research Institute Senckenberg in Frankfurt am Main, Germany; see table 1). Our *Kogia sima* brain comes from a female with a body length of 194 cm (body mass not available). This species reaches a standard length of about 270 cm and a body mass of 272 kg [Caldwell and Caldwell, 1989]. Sexual maturity in female and male dwarf sperm whales seems to occur in specimens between 210 and 218 cm, respectively [Caldwell and Caldwell, 1989]. The subadult (immature) animal investigated by Marino et al. [2003] was 166 cm in length, had a body mass of 107 kg, and a brain mass of 484.5 g; another specimen was cited as an adult with 168.5 cm body length and a brain mass of 622 g [Marino, 2002; Manger, 2006]. Therefore our *K. sima* brain specimen (length: 112.5 mm, width: 134.7 mm) with a mass of 577 g might be that of a young but not fully grown adult.

MRI

The formalin-fixed dwarf sperm whale brain (fresh total mass: 577 g) is distinctly smaller than the four common dolphin brains which serve as a reference for comparison. The dolphin brains in our series (total mass: 685–830 g; table 1) are considerably to slightly smaller than the average in adult animals of this species (835.6 ± 79.9 g) relating to an average body length of 193.1 ± 5.8 cm for both sexes and an average body weight of 67.6 ± 11.7 kg [Ridgway and Brownson, 1984; Oelschläger et al., 2008].

PD-weighted magnetic resonance (MR) images of the entire brain were acquired with a highfield MR scanner (3 Tesla; Siemens Magnetom Trio). A gradient echo imaging sequence (FLASH 3D) with the following protocol parameters was used: repetition time 11 ms, echo time 4.9 ms, flip angle 7°, slice thickness 0.5 mm, field of view 120 × 176 mm, matrix 240 × 352. Multiple repetitions of the imaging sequence were performed to improve the signal-to-noise ratio. Total scanning time was 16 h. The resulting MR dataset was isotropic with a voxel size of 0.125 mm^3 and can be reformatted in any direction without loss of resolution.

The pilot in figure 2 (sagittal scan) shows the levels given in figures 3 and 4 (coronal, horizontal scans); the levels in figure 4a indicate the position of the scans in figure 5 (mediosagittal, parasagittal scan).

Nomenclature and Labeling

Structures of the dolphin brain were labeled in the original scans following the nomenclature of Ogawa [1935a, b], Ries and Langworthy [1937], Ogawa and Arifuku [1948], Kojima [1951], Jacobs and Jensen [1964], Jansen and Jansen [1969], McFarland et al. [1969], Dailly [1972a, b], Igarashi and Kamiya [1972], Morgane and Jacobs [1972], Morgane et al. [1980], Pilleri et al. [1980], Schwerdtfeger et al. [1984], Oelschläger and Oelschläger [2002, 2009], Oelschläger et al. [2008], Oelschläger [2008] as well as Terminologia Anatomica [1998] and Schaller [1992]. Structures of gray substance are in capitals, white substance and cortical sulci in lower case, cranial nerves in Arabic numerals and ventricular spaces in lower case and Roman numerals.

Regarding the size of the whole brain and its constituents, the term 'well-developed' indicates that a brain structure or brain area is as large as would be expected for a hypothetical mammal with the same dimension in body and/or brain mass. The terms 'large' or 'small' mean that a structure is larger or smaller than would be expected hypothetically in the absence of exact quantitative data. The term 'reduced' is reserved for structures that are minimally sized with respect to the situation in other mammals.

The term 'complicated' for the cetacean brain means that here the degree of structural differentiation is as high as that seen in brains of terrestrial mammals with similar body and/or brain mass.

Results

General Aspects

In general, the brain of the dwarf sperm whale *(Kogia sima)* shows all the features known of adult dolphins (delphinids) and thus the common dolphin *(Delphinus delphis)* was used for comparison. Moreover, although in
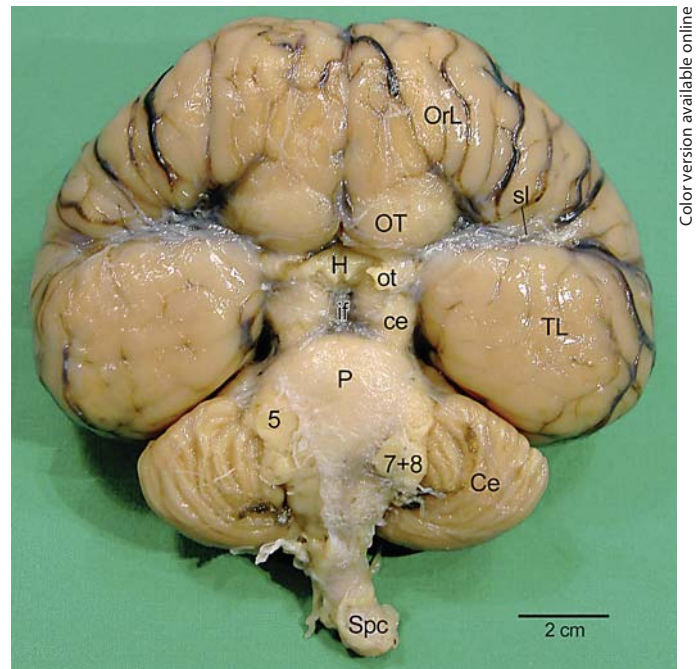
Fig. 1. Basal aspect of dwarf sperm whale brain (Ks9303B) with meninges largely removed. For abbreviations see list.

some absolute size parameters the *Kogia* brain approaches the situation known of the common dolphin (see below), its total mass is distinctly smaller (table 1). In correspondence with other adult odontocetes, the brain of *Kogia* is wider than long. This is seen in the basal aspect of the brain (fig. 1), in horizontal scans (fig. 4) as well as the quantitative data in table 2. As a whole, the *Kogia* brain seems to be much flatter than those of delphinid species [Oelschläger et al., 2008] and the brainstem (from mesencephalon to myelencephalon) is more straight and elongate. Thus, in midsagittal slices of the dwarf sperm whale, the pontine flexure is nearly absent [fig. 5; see also Ogawa and Arifuku, 1948]; here, the interpeduncular fossa (fig. 1, 3a, 4d, 5a: if) opens widely. As the external shape of our dwarf sperm whale brain is similar to the *Kogia* brains shown by Haswell [1884] and Marino et al. [2003], such differences with respect to the common dolphin and other delphinids seem to be authentic (see below). It cannot be discounted, however, that in our specimen the dorsoventral flattening of the brain might have been increased to some degree during fixation.

In adult cetaceans, the brain as a whole seems to be markedly shortened (telescoping) with respect to those of most other mammals; in part, however, this might also be due to the very strong development of the temporal
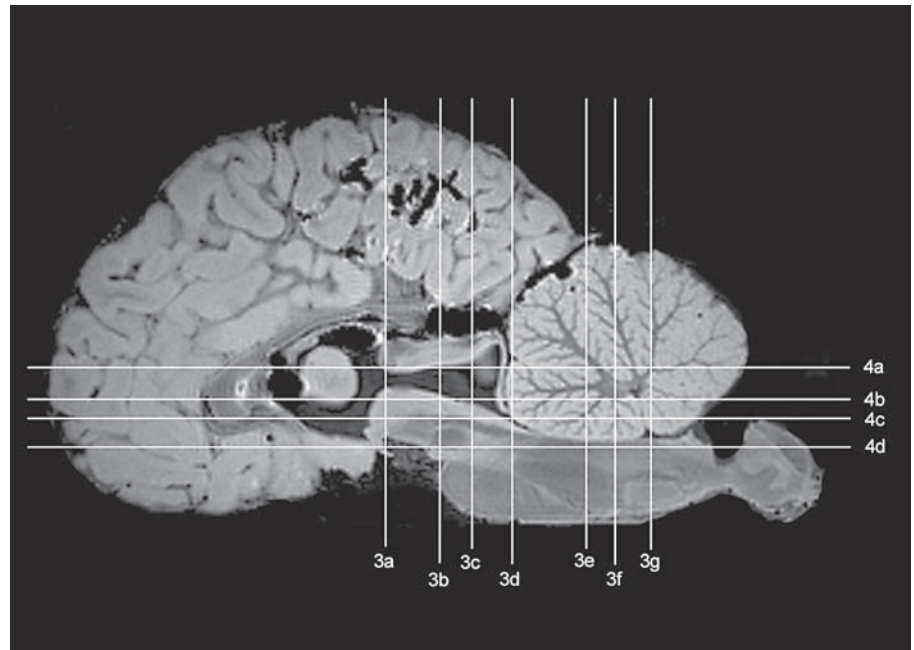
Fig. 2. Pilots for the following figures 3–5. Parallel vertical lines (3a–g) indicate the levels of the transverse (coronal) scans in figures 3a–g and the horizontal lines (4a–d) the levels of the horizontal (axial) scans in figure 4a–d.

lobes (fig. 1, 3c, 4d: TL). This telescoping is most obvious in marine dolphins and beaked whales [Kükenthal and Ziehen, 1893; Marino, 2007] and could be responsible for the towering of the forebrain hemispheres in these animals [Oelschläger et al., 2008]. Marked telescoping is not seen in the brainstem of the dwarf and pygmy sperm whales [*Kogia sima*, fig. 5; *K. breviceps,* Ogawa and Arifuku, 1948]. Also, although the delphinid medulla oblongata and cervical spinal cord might curve dorsocaudally around the cerebellum [cf. Oelschläger et al., 2008: common dolphin; Oelschläger and Oelschläger, 2002, 2009: bottlenose dolphin], this feature is not obvious in the dwarf and pygmy sperm whales. In the giant sperm whale [Ries and Langworthy, 1937; Kojima, 1951], the arching of the medulla and cervical spinal cord are extreme among the whales, in general. Because in early sperm whale fetuses [280 mm crown-rump length; Oelschläger and Kemp, 1998], the embryonic brain flexures have disappeared, the situation in the adult whale has to be taken as a 'secondary cervical flexure'. This phenomenon seems to be related to extreme allometric changes in the development and growth of the huge head in the adult giant sperm whale and the striking 'regression' of the brain within the cranium of this species [Flower, 1868–69; Ries and Langworthy, 1937].

As in dolphins, the telencephalic hemispheres in the dwarf sperm whale are large and the neocortex (including the underlying white matter) is voluminous, with the cor-

tical grey matter extremely expanded and folded into deep and complicated gyri and sulci (fig. 1–5). The limbic and paralimbic clefts [Jacobs et al., 1979; Morgane et al., 1980; synonyms in mammalian tetrapods: suprasplenial (cingulate) sulcus and entolateral sulcus (fig. 3a, b: sp, en), respectively] divide the neocortex into three main tiers: the limbic and paralimbic lobes that arise above the corpus callosum (cc), and the supralimbic lobe that extends on the lateral surface of the brain [cf. Morgane et al., 1980; Oelschläger and Oelschläger, 2002, 2009]. In addition, an orbital/frontal, parietal, and a large temporal lobe can be distinguished (fig. 1, 3c, 4d, 5: FL, OrL, PL, TL). In more detail, the surface of the supralimbic lobe is subdivided by three lateral major sulci which are also known from other mammals: the ectosylvian (es), suprasylvian (ss), and lateral (ls) sulcus (fig. 3a). They delimit gyri which are denominated accordingly [cf. Oelschläger and Oelschläger, 2002]. As in whales generally, the hemisphere of *Kogia sima* does not exhibit an occipital lobe and the insular region is covered by so-called 'opercula' from the neighboring frontal, parietal, and temporal neocortical areas known from other large-brained mammals [cf. Oelschläger and Oelschläger, 2002]. The cortical surface in the dorsal medial wall of the paralimbic lobe shows a characteristic folding pattern which led to the term 'oval lobule' (fig. 5a, b: OL). This pattern, not shown in baleen whales (mysticetes) and the Amazon river-dolphin *(Inia geoffrensis)*, is also found in delphinid species but is most
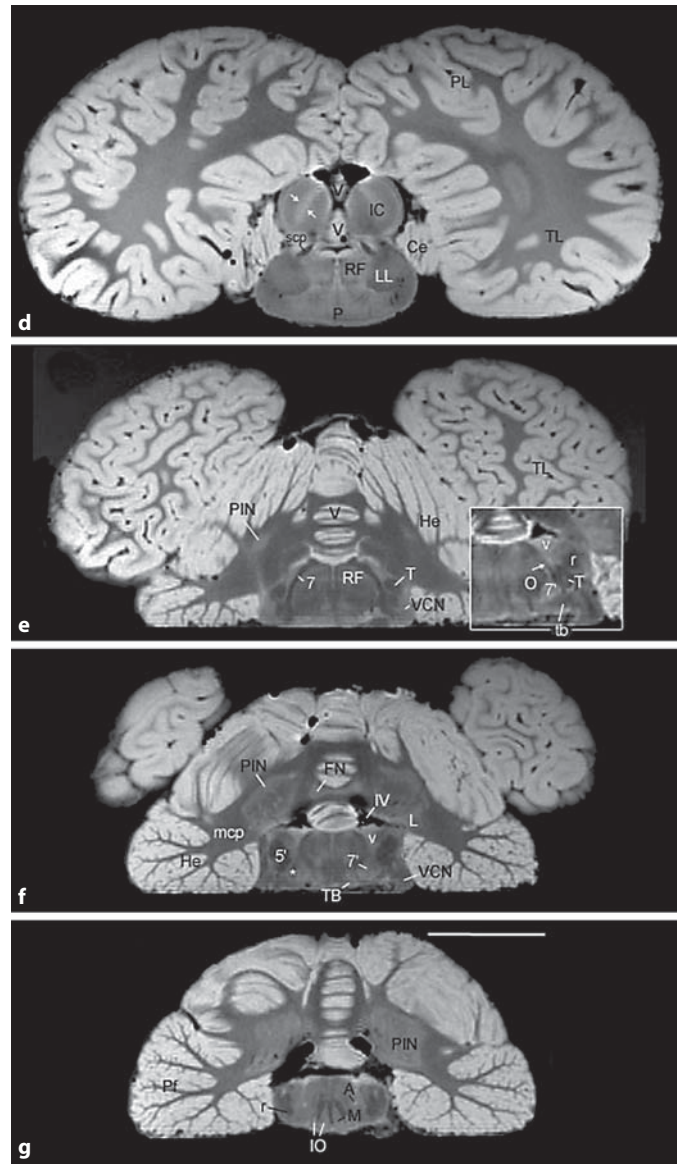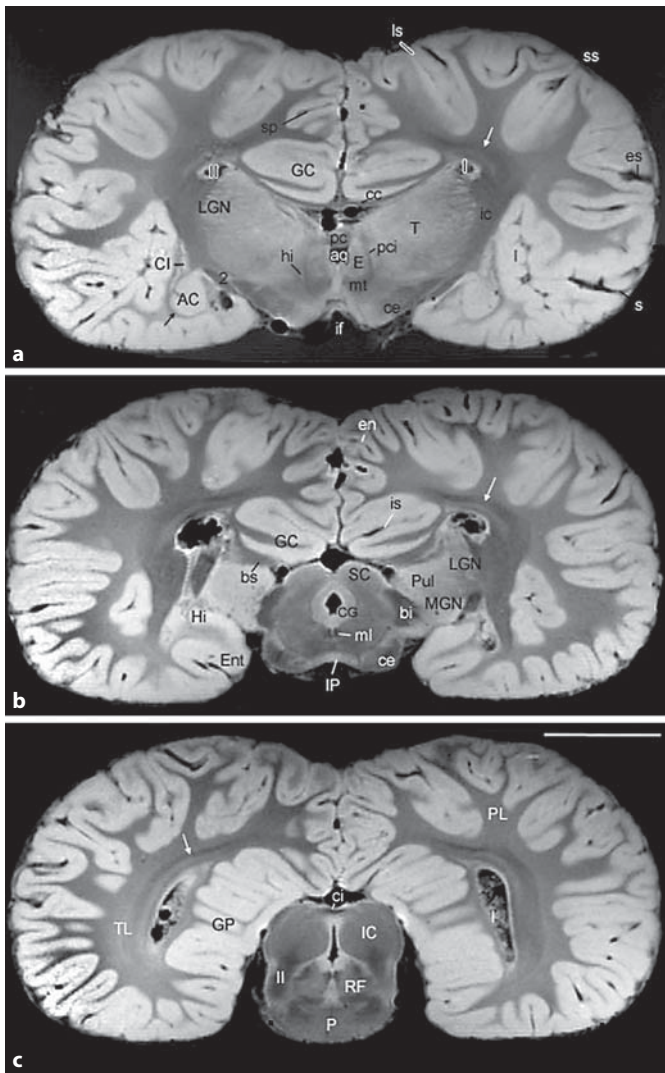
Fig. 3. Coronal scans through specimen Ks9303B. **a** At the transition of the posterior diencephalon into the rostralmost part of the mesencephalon with the posterior commissure (pc, pci), elliptic nucleus (E), lateral geniculate nucleus (LGN) and amygdaloid complex AC); **b** at an anterior midbrain level with superior colliculus (SC), medial geniculate nucleus (MGN), hippocampus (Hi), and crus cerebri (ce); **c** at the transition from midbrain to the pons (P) with the central part of the inferior colliculus (IC) as well as the lateral lemniscus (ll); **d** with the pons region, the caudalmost part of the inferior colliculus, and the rostralmost parts of the cerebellum (Ce, V). White arrows mark the hyperintense zone in the inferior colliculus; **e** through the anterior medulla oblongata showing the facial nerve (7), the spinal tract of the trigeminal

nerve (T), and the ventral cochlear nucleus (VCN). Inset: Right detail of coronal slice 4.4 mm further caudally showing the superior olivary complex (O), area of the vestibular nuclei (v), rootlet of the glossopharyngeal nerve (white arrow), nucleus of the facial nerve (7'), inferior cerebellar peduncle (r) as well as the trapezoid body (tb); **f** showing the maximal sectional area of the middle cerebellar peduncle (mcp), the cerebellar nuclei (PIN, FN, L), nucleus of trapezoid body (TB), and the caudal end of the superior olivary complex (asterisk); **g** a slice through the posterior medulla oblongata with the paraflocculus (Pf), nucleus ambiguus (A) and inferior olive (IO, M). White arrows in **a–c**, hypointense fiber tracts. For other abbreviations see list. Scales in **a–g**: 2 cm.
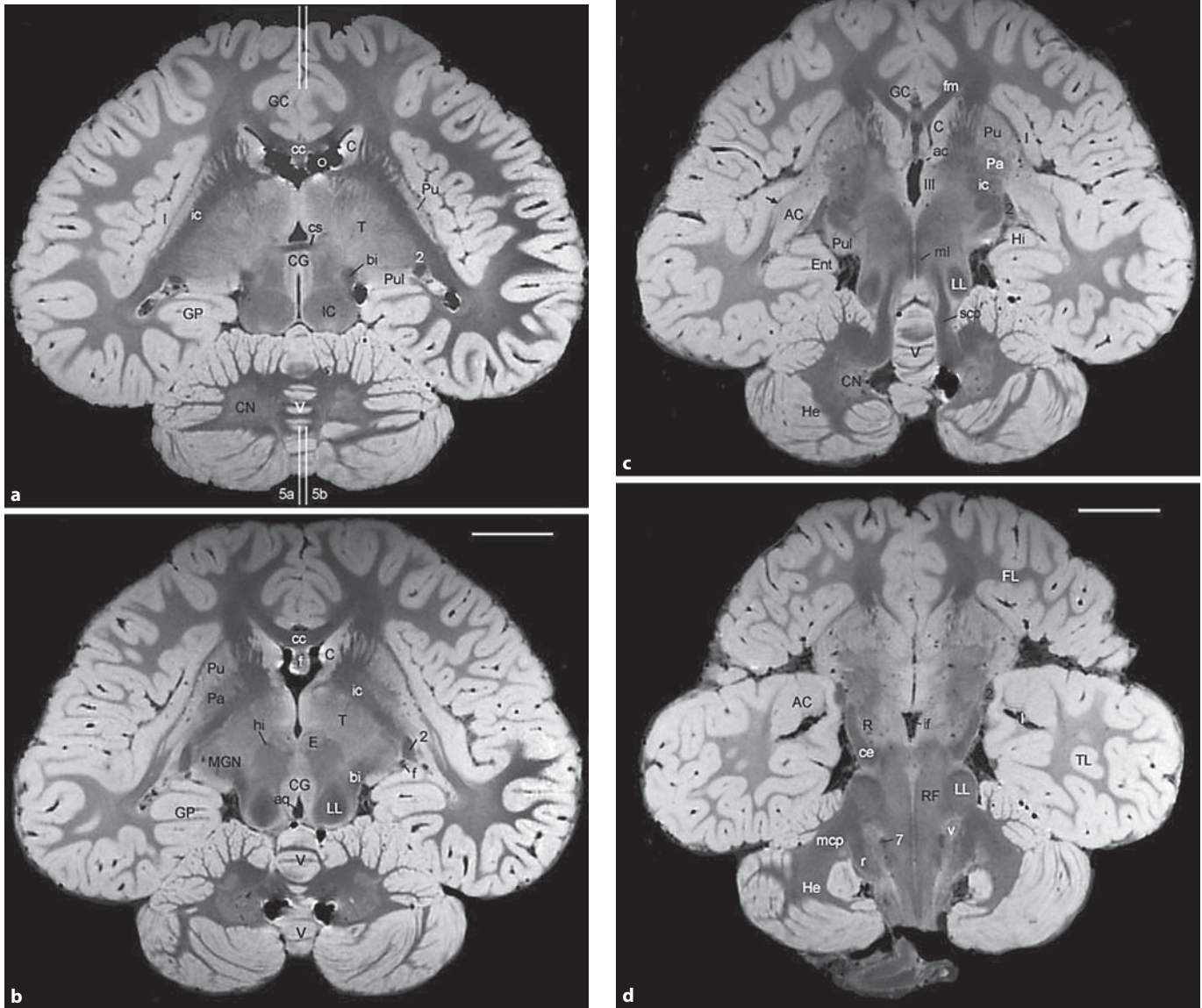
Fig. 4. Horizontal (axial) scans. **a** Dorsalmost level with the commissure of the superior colliculi (cs) and the inferior colliculi (IC). **b** Level of the elliptic nucleus (E), medial geniculate nucleus (MGN). **c** Basal ganglia (AC, C, Pa, Pu), Hippocampus (Hi), superior cerebellar peduncle (scp). **d** Ventralmost level with basal brainstem structures: crus cerebri (ce) with red nucleus (R), re-ticular formation (RF), vestibular nuclear complex (v), facial nerve (7), decussation of the superior cerebellar peduncles (not labeled), and inferior cerebellar peduncle (r). o, artifact. Scale for **a–d**: 2 cm. Vertical lines in **a** (5a, b) indicate the levels of the sagittal and parasagittal slices in figure 5a, b.

obvious in the bottlenose dolphin [*Tursiops truncatus*; Morgane et al., 1980]. In sagittal/parasagittal scans of our *Kogia* brain, the oval lobule is found dorsal to the posterior third of the cc although blurred a little by some artificial air bubbles in our specimen (fig. 5a, b: black). The sulci of this cortex are comparatively superficial and less dense compared with the deep and complex folding pattern of the limbic cortex (Gyrus cinguli; fig. 3a, b, 4a, c, 5: GC). The cingulate gyrus narrows beyond the splenium corporis callosi and above the tectal area of the midbrain and blends with the parahippocampal gyrus (fig. 3c, 4a, b: GP) to form the limbic lobe [Morgane et al., 1980]. In supracallosal horizontal scans (not shown), the deep cingulate gyri comprise the center of the brain.

In the two odontocetes investigated with MRI (table 2), brain length is a little higher in *Kogia* (Ks9303B) than in *Delphinus* (Dd9347B). The *Kogia* brain is somewhat narrower and distinctly flatter, however, resulting in a markedly lower brain mass (our data: dwarf sperm whale 577 g, common dolphin 757 g). The width of the diencephalon is almost identical in both specimens, whereas the width of the mesencephalon at the inferior colliculi is again smaller in *Kogia* and the height of the inferior colliculi is equal (table 2). The cerebellum of *Kogia* (fig. 1, 3d–g, 4a–d, 5: Ce, CN, He, Pf, V) is impressive in size although its dimensions are smaller than in *Delphinus* (table 2). In giant sperm whales *(Physeter)*, the volume ratio of the cerebellum in the total brain approximates the minimum found within the cetaceans [6.5–7.5%; Ganges river dolphin *(Platanista gangetica)*; Pilleri, 1972; Ridgway and Tarpley, 1996]. In dolphins the cerebellum consists of large hemispheres (fig. 3e, f, 4c, d: He) and a comparatively narrow vermis (fig. 3d, e, 4a–c, 5a, b: V). With respect to total cerebellar width, the vermis is again broader in *Delphinus* than in *Kogia*. In addition, the vermis is markedly wound in the common dolphin as was reported in bovid hoofed animals [Yoshikawa, 1968; Brauer and Schober, 1970; Schober and Brauer, 1975; Nickel et al., 1984]. The caudal brainstem (medulla oblongata) is well-developed in both species, its maximal diameter between the lateralmost surfaces of the ventral cochlear nuclei appearing almost identical in *Kogia* and *Delphinus*. In the caudal direction, the brainstem narrows quickly in both species and merges in the cervical spinal cord.

As to the external morphology of the brainstem in *Kogia sima*, there is good correspondence with the evidence in the pygmy sperm whale [Igarashi and Kamiya, 1972]. Details will be given in the framework of functional systems (see below).

Ventricles

The ventricular system of the dwarf sperm whale corresponds well with that in the common dolphin (fig. 3a, c: I, II, aq; fig. 4b: aq; fig. 4c, 5: III, aq) and other toothed whales [e.g., bottlenose dolphin; McFarland et al., 1969]. The lateral ventricles are semicircular in lateral view, an olfactory recess is lacking, and a posterior horn is absent as is an occipital lobe of the telencephalic hemisphere. The third ventricle (fig. 4c: III) is largely displaced by the extended fusion of the two thalami (intermediate mass, fig. 5a: im). There is no pineal recess and the pineal organ is also lacking (see below). The cerebral aqueduct (fig. 3a, 4b, 5a: aq) is tubular beneath the superior colliculi but
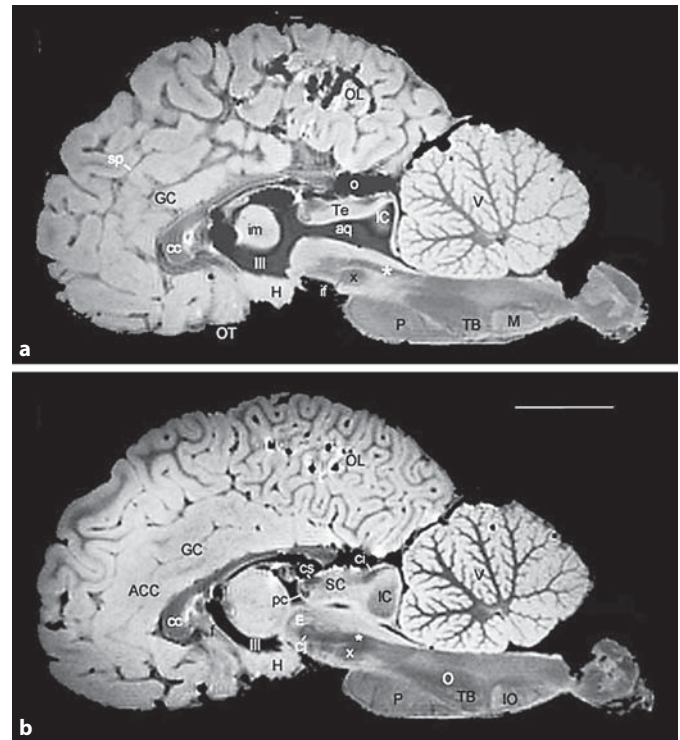
Fig. 5. Sagittal scans. **a** Median plane with tectum and ventricular system (III, aq), largely intact surface configurations of the telencephalic hemisphere and vertical extension of the cerebral aqueduct. Inferior colliculus (IC) not sectioned. Medial lemniscus and medial tegmental tract (*) running dorsal to the decussation of the superior cerebellar peduncles (x). **b** Parasagittal scan with both collicular nuclei in section, separate posterior commissure (pc) as well as the commissures of the superior and inferior colliculi (cs, ci). The medial lemniscus and medial tegmental tract (*) in continuity with the elliptic nucleus (E) and Cajal's nucleus (Cj). Scale for **a** and **b**: 2 cm.

nearly collapsed (fig. 3c, 4a; not labeled) in the area of the very large inferior colliculi (IC) which are located more laterocaudally. Caudally, the aqueduct opens for the rostral convexity of the vermis (fig. 4a: V) which displaces the aqueduct except for a narrow cone-like residue. As in *Delphinus,* the fourth ventricle of *Kogia* (fig. 3f: IV) does not show any conspicuous specializations.

Telencephalon

Cortex. In the dwarf sperm whale and the common dolphin, the primary neocortical areas are located in the same regions as in other odontocetes (bottlenose dolphin, harbor porpoise, La Plata dolphin) [Morgane et al., 1980; Fung et al., 2005; Oelschläger and Oelschläger, 2002, 2009]. In our specimens, the very large auditory

Table 2. Size parameters of the brains of the dwarf sperm whale *(Kogia sima)* and the common dolphin *(Delphinus delphis)* investigated, taken from MR scans

Parameter	*Kogia sima* Ks9303B [X]	*Delphinus delphis* T379 [Y]	Ratio X/BrW *(Kogia)* (134.7 mm)	Ratio Y/BrW *(Delphinus)* (141.0 mm)	Ratio X/BrL *(Kogia)* (109.6 mm)	Ratio Y/BrL *(Delphinus)* (105.2 mm)	Ratio X/BrH *(Kogia)* (67.08 mm)	Ratio Y/BrH *(Delphinus)* (92.22 mm)
Brain width (BrW)	134.7[1]	141.0[1]						
Brain length (BrL)	109.6[2]	105.2[2]	0.81	0.75				
Brain height (BrH)	67.08[3]	92.22[3]	0.50	0.65				
Width of diencephalon	59.3	62.2						
Inferior collicular width	29.0[4]	35.8[4]	0.22	0.25				
Inferior collicular height	13.0	13.0						
Cerebellar width	84.64	92.83	0.63	0.66				
Cerebellar hemisphere length	43.11	59.19			0.39	0.56		
Cerebellar hemisphere height	44.39[5]	59.31[5]					0.66	0.64
Vermis width (max)	12.17	20.46	0.09	0.15				
Vermis length	36.38	38.86			0.33	0.37		
Vermis height	29.34	32.56					0.44	0.35

All figures in mm.
[1] Distance between lateralmost parts of temporal lobes; [2] maximal distance between frontal pole of telencephalic hemisphere and posterior extremity of vermis and cerebellar hemisphere (average); [3] height of telencephalic hemisphere perpendicular to basal contour of ventral pons (average); [4] line connecting the lateralmost parts of both inferior colliculi; [5] perpendicular to brain base (average).

and the smaller visual projection field comprise most of the vertex of each hemisphere, i.e., in the ectosylvian, suprasylvian and lateral gyri between the posterior ectosylvian sulcus and the entolateral sulcus (fig. 3a, b: es, en). The somatosensory field is found in the anteriormost part of the short frontal lobe (fig. 4d: FL) and the motor field is found medially adjacent near the frontal pole of the telencephalic hemisphere (cortices not labeled). Both areas are separated from each other more or less strictly by the cruciate sulcus (not labeled), possibly a homolog of the central sulcus in primates. For detailed analysis of the surface configurations of the dolphin brain we refer to Morgane et al. [1980].

Several allocortical areas in the *Kogia and Delphinus* brains differ considerably from those in non-cetacean mammals (fig. 2–5). Characteristic for toothed whales, the paleocortex as a whole seems to be relatively small; during ontogenesis, the olfactory bulbs are totally reduced and olfactory peduncles are only rarely seen in adult giant sperm whales and bottlenosed whales [*Hyperoodon*; Kükenthal and Ziehen, 1893]. The large hourglass-shaped area called 'olfactory tubercle' in odontocetes (or olfactory lobe; fig. 2, 5: OT) for the most part results from a ventral protrusion of the large basal ganglia in this area (fundus striati). In *Delphinus,* no cortical plate was found at the surface of the olfactory tubercle whereas in *Kogia* the latter perhaps could not be identi-

fied because of too little resolution in the MR slices. The archicortex comprises the hippocampus and other cortical regions and borders on several areas that represent transitional zones to the neocortex [limbic lobe; Morgane et al., 1980; Oelschläger and Oelschläger, 2009]. From our MR scans (fig. 3b, 4c: Hi) it can be concluded that the hippocampus of *Kogia sima* is about as small in absolute and relative terms as in *Delphinus* and other odontocete species. This is enigmatic because in most mammals the hippocampus is a major center within the limbic system, responsible for orientation, learning and memory as well as for vegetative and emotional processes [Trepel, 2008]. With our MR resolution, the substructures of the cornu ammonis [hippocampus proper, fascia dentata (dentate gyrus), subiculum] cannot be discriminated. In correlation with the smallness of the hippocampus, the fornix is very thin in *Kogia* (fig. 4b, 5b: f) but slightly thicker in *Delphinus*. The mammillary bodies are small (not labeled in fig. 5). The amygdaloid complex of *Kogia* is well-developed as in *Delphinus* (fig. 3a, 4d: AC) and the areas of the periarchicortical limbic lobe [Morgane et al., 1982], which comprise the cingular and parahippocampal gyri of other mammals, are also large (fig. 3a–c, 4a–c, 5b: GC, GP, ACC). Located at the medial surface of the telencephalic hemisphere, these areas extend between the cc and the suprasplenial sulcus or limbic cleft (fig. 3a, 5a: cc, sp) and continue along the medial surface of the temporal lobe

(parahippocampal gyrus including the entorhinal cortex, fig. 3b, 4c: Ent). Interestingly, the anterior supracallosal part of the limbic lobe is wide in *Kogia* as in other toothed whales and shows an intrinsic so-called intercalate sulcus (fig. 3b: is; see Discussion).

Commissures. The anterior (rostral) commissure of *Kogia sima* is so thin and inconspicuous that it is difficult to identify in the MR scans (fig. 4c: ac). As in the bottlenose dolphin and the common dolphin [Morgane et al., 1980; Oelschläger et al., 2008] there seems to exist only a modest exchange of hypointense fiber bundles between the two hemispheres in this area. A similar situation is seen in histological sections of *Kogia breviceps* [Igarashi and Kamiya, 1972], where thin transverse fiber bundles are found on both sides lateral to the columna fornicis. This phenomenon might parallel the weak development of the cc (see below) and is in part due to a highly reduced state of the olfactory system which in odontocetes completely lacks its anterior part [olfactory bulb and tract; for more information cf. Oelschläger and Buhl, 1985; Oelschläger and Oelschläger, 2002, 2009; Oelschläger et al., 2008; Oelschläger, 2008]. The fornix (fig. 5: f) which passes immediately caudal to the anterior commissure (fig. 4c: ac) is also very thin but can be followed from the hypothalamus (mammillary body inconspicuous) to the hippocampal area (fig. 3b, 4c: Hi). In other toothed whales (Amazon river-dolphin, bottlenose dolphin, white whale, bottlenosed whale) [Kükenthal and Ziehen, 1893; Morgane et al., 1980], however, both the anterior commissure and fornix are obviously better developed and easy to identify at the macroscopic scale. The hippocampal commissure in *Kogia* is so weak that, in coronal scans, it is hardly visible as a thin line at the lower contour of the cc (not labeled in fig. 3a, 5). In ungulates this size relationship is inverse; thus for example, in pig the thickness of the hippocampal commissure is about double that of the cc [Yoshikawa, 1968].

In *Kogia sima*, the cc (fig. 3a, 4a, b, 5: cc), which links the two large telencephalic hemispheres, is remarkably thin as in the common dolphin and the harbour porpoise. In *Delphinus* and even more in *Kogia*, the genu is by far the thickest area (mediosagittal plane, maximal thickness 3.3 vs. 4.1 mm in the two species), whereas the splenium is moderately developed and the intermediate part (truncus) is minimal in thickness (see Discussion).

Basal Ganglia. Concerning the morphology and topography of the basal ganglia (corpus striatum, nucleus accumbens septi, globus pallidus, amygdaloid complex), there is good correspondence between the dwarf sperm whale and other toothed whales. Thus, the corpus stria-

tum (fundus striati; nucleus caudatus and putamen; fig. 4a–c: C, Pu) of the dwarf sperm whale protrudes at the base of the telencephalic hemisphere as the 'olfactory tubercle' or olfactory lobe [fig. 1, 5: OT; for definition cf. Morgane et al., 1980]. Although these authors found paleocortex covering the striatum on the surface of the olfactory lobe in the bottlenose dolphin, we were not able to verify this in the common dolphin under the microscope [Oelschläger et al., 2008; but cf. Morgane et al., 1971, 1980; our discussion] but cannot exclude a paleocortical covering of the fundus striati for *Kogia*. MR scans of the dwarf sperm whale show an indistinct claustrum and extreme capsule (not shown). The amygdaloid complex is well-developed (fig. 3a, 4c, d: AC); its lateral and basal nuclei are clearly visible in the MR scans [cf. Jansen and Jansen, 1953; on the fin whale *(Balaenoptera physalus)*; not labeled in our figures]. The authors suggested that the remarkable size of these nuclei could be correlated to the considerable development of the temporal lobe in cetaceans and to audition. This assumption, originally put forward by Freeman and Williams [1952], is supported by several experimental studies in other mammals [cf. Stephan and Andy, 1977]. In figures 3a, 4c, d, the amygdaloid complex is shown in near-maximum cross-section between the optic tract (2) and a layer of white matter (arrow) adjacent to the cortex of the temporal lobe (TL) and continuous with the external capsule [cf. Yoshikawa, 1968].

Diencephalon

As in the common dolphin, the diencephalon of the dwarf sperm whale is voluminous and short but broad and high. As a whole, the thalamus (fig. 3a, 4a, b, 5a: T, im) is very large in comparison with the epithalamus (not shown) and hypothalamus (H). The anterior, medial and lateral thalamic nuclei (not labeled) as well as the lateral geniculate nuclei (fig. 3a, b: LGN) are located immediately below the cc. Although in many terrestrial mammals [e.g., ungulates, carnivores; Yoshikawa, 1968; Igarashi and Kamiya, 1972; Schober and Brauer, 1975] the hippocampus is large and situated between the cc and the diencephalon, this part of the archicortex has become relatively very small and was shifted onto the temporal lobe during the rotation of the hemisphere. The anterior thalamic group (not labeled in fig. 4a) was reported to be well-developed in toothed whales [Kruger, 1966: bottlenose dolphin] but is difficult to discriminate in the *Kogia* scans. In terrestrial mammals they belong to the limbic system and receive projections from the mammillary body and (pre-)subiculum, and they project to the cingu-

late, the anterior limbic cortex, the (pre-)subiculum as well as to the retrosplenial cortex [Van Dongen and Nieuwenhuys, 1998].

Structures of particular interest are the lateral and medial geniculate nuclei, important centers of the visual and auditory systems, respectively. In figures 3a, b and 4a–d the optic tract (2; optic nerves and chiasm lacking in our dwarf sperm whale brain) circles around the diencephalon between the temporal lobe and the thalamus and enters the lateral geniculate nucleus which is characterized by a diffuse texture of fiber bundles (fig. 3a, b: LGN). At the dorsal tip of the LGN (dorsalmost and lateralmost part of the diencephalon), a single fiber bundle of the optic tract (brachium of the superior colliculus: fig. 3b: bs, SC) runs in the direction of the mesencephalic tectum between the caudal part of the cc and the pulvinar and at the level of the posterior commissure. As in the common dolphin, it terminates in the superior colliculus immediately caudal to the commissural complex (continuity not shown in our figures). As a type of 'counterpart', the brachium of the inferior colliculus (fig. 3b, 4b: bi) assembles at the lateral surface of the inferior colliculus (IC) and the lateral lemniscus (fig. 4b: LL). In two thick bundles, the auditory axons turn to the medial geniculate body (fig. 3b, 4b: MGN) which is located medial and ventral to the LGN. In our scans, the MGN is homogeneous compared to the LGN and appears a little brighter (more hyperintense). The pulvinar thalami do not show any fibers; in horizontal scans, it is located between the optic tract laterally and the brachium colliculi inferioris medially and almost as hyperintense as the cortical grey matter of the adjacent parahippocampal gyrus (fig. 4a–c: 2, Pul, GP, Ent). In correspondence with the thickness of the optic tract, the LGN is well-developed although not as much as the MGN, a fact which correlates well with the very strong development of the auditory system (e.g., inferior colliculus and brachium, lateral lemniscus and nucleus: fig. 3b–d, 4a–d: IC, bi, ll, LL). In all these features, the dwarf sperm whale corresponds well with the common dolphin and other toothed whales [e.g., bottlenose dolphin; Morgane and Jacobs, 1972].

As in the common dolphin, there were no traces of a pineal organ in *Kogia* but here, in contrast to the situation in *Delphinus* [Oelschläger et al., 2008], the condition of the area caudal to the splenium corporis callosi (fig. 5a: o) does not allow an unambiguous statement. In the bottlenose dolphin, a pineal organ has been reported by Lyamin et al. [2008] from a single pregnant dolphin. The giant sperm whale exhibited a pineal organ in a single adult specimen and in an early fetus [Ries and Langworthy, 1937; Oelschläger and Kemp, 1998].

The commissural complex [cf. Oelschläger and Kemp, 1998; Oelschläger et al., 2008] includes the posterior or epithalamic commissure (fig. 3a, 5: pc) as well as the habenular commissure which is thin and situated slightly dorsorostral to the pc (not shown). The posterior commissure seems to consist of two parts, a ventral and weaker fiber bundle and a stronger dorsal part. In a few scans more caudally, the distinct commissure of the superior colliculi (fig. 4a: cs) adjoins the commissural complex. Thus, although the latter stands vertically like a narrow plate (mediosagittal plane) and is clearly visible in fiber stained sections [common dolphin; Oelschläger et al., 2008], the complex is not easy to delimit from the commissure of the superior colliculi in macroscopical preparations [Morgane et al., 1980] or in MR scans. The weaker inferior part of the posterior commissure on both sides turns ventrally (fig. 3a: pci), symmetrically arching around the central grey and the elliptic nucleus/interstitial nucleus of Cajal (fig. 3a, 4b, 5b: E), whereas the superior part can be followed laterally into the pretectum and pulvinar (not shown). Whereas in the common dolphin the superior part of the pc seems to be thicker, the inferior part of the pc is obviously weaker than that in the dwarf sperm whale. The habenulo-interpeduncular tracts (fig. 3a, 4b: hi) run from the habenular nuclei ventrally, circle laterally around the elliptic nuclei/central grey and the medial lemnisci, more or less in parallel to the inferior part of the pc, before they converge and terminate in the interpeduncular nucleus (fig. 3b: IP).

Auditory System

As reported for the telencephalon and diencephalon, the auditory system is also very well-developed throughout the mesencephalon as well as the pons and medulla oblongata, (fig. 3b–f, 4a–d, 5). The central auditory pathway starts caudally with the thick cochlear nerve (not shown), the very large ventral cochlear nucleus (fig. 3f: VCN) as well as the trapezoid body and nucleus (fig. 3e, f, 5b: tb, TB) that bulge at the basal surface of the brainstem between the pons and the inferior olivary complex (fig. 3d–g, 5a: P, IO, M). The auditory input ascends via the large superior olivary complex (fig. 3e, f: O, asterisk) and the thick lateral lemniscus which blends in the voluminous inferior colliculus (fig. 3c, d, 4a–d: ll, LL, IC). From here, the auditory pathway proceeds to the well developed medial geniculate body (fig. 3b, 4b: MGN) via the brachium colliculi inferioris (bi) and through the internal capsule (fig. 3a, 4a–c: ic) to the extended neocortical auditory projection field in the ectosylvian and suprasyl-

vian gyri between the ectosylvian and lateral sulci [fig. 3a: es, ls; cf. Oelschläger and Oelschläger, 2002, 2009].

In more detail, the ventral cochlear nucleus, located in the medulla oblongata near the transition to the pons area (cerebellopontine angle), is well-developed in *Kogia* and was reported to be as large as in the Pacific white-sided dolphin [*Lagenorhynchus obliquidens*; Ogawa and Arifuku, 1948]. As is the case for many toothed whales, Ogawa and Arifuku [1948] did not find a dorsal cochlear nucleus (DCN) in their species with conventional methods. Our histological investigations [*Pontoporia, Phocoena, Delphinus*; Schulmeyer, 1992; Schulmeyer et al., 2000; Malkemper et al., unpublished], however, showed rudiments of this nucleus more or less 'in place'. In our present MR investigation of *Kogia*, a DCN could not be detected presumably due to insufficient resolution in the scans. When compared to the Pacific whitesided dolphin, the trapezoid body is less extended dorsoventrally in the pygmy and dwarf sperm whales [Ogawa and Arifuku, 1948], but this might result from the generally flat shape of the brain due to a lesser telescoping of the brainstem in these physeterid species and possibly because of fixation artifacts.

Within the ascending auditory system of the medulla oblongata, the area of the hypointense superior olivary complex (fig. 3e, f: asterisk, O) is of particular interest. In this scan the complex is located between the facial nucleus (7') laterally [cf. Jansen and Jansen, 1969] which is hyperintense, the trapezoid body (tb) ventrally, the nucleus of the tb (TB) medially and ventrally and the dorsal parolivary nucleus medially [not labeled; cf. bottlenosed whale, *Hyperoodon ampullatus*; De Graaf, 1967]. In fig. 3e (inset), the superior olivary complex is sectioned in its caudalmost part and the facial nucleus in its anteriormost part; both nuclei showing their half-maximal cross-sectional area and similar topographical relations as in the fetal narwhal [*Monodon monoceros;* cf. Holzmann, 1991; Oelschläger and Oelschläger, 2002]. Dorsally and medially, the SOC is bordered by reticular formation [Nucleus reticularis pontis caudalis; cf. Brodal, 1957; Birkmayer and Pilleri, 1966; Nieuwenhuys et al., 1991]. Other characteristic details in this coronal sectional plane are the central vestibular complex which is largely represented by the well-developed Deiters' lateral vestibular nucleus [v; hyperintense; cf. Kern et al., 2009] and the restiform body (inferior cerebellar peduncle; r) as well as the spinal tract of the trigeminal nerve and its nucleus (fig. 3f: 5') together with a rootlet of the glossopharyngeal nerve (arrow).

From our scans it is not possible to determine whether in *Kogia* the superior olivary complex comprises a lateral and a medial subnucleus. In figure 3e this nucleus (O) shows only part of its maximal cross-sectional area. Ogawa and Arifuku [1948] reported that the SOC is relatively larger in *Kogia breviceps* than in dolphins. In coronal histological sections of the brainstem they depicted both superior olivary subnuclei for the pygmy sperm whale, with the size of the lateral nucleus by far exceeding that of the medial one. In other toothed whales (La Plata dolphin, Amazon river-dolphin, common dolphin, harbor porpoise, narwhal), only one SO nucleus has been found in morphological and embryological studies [Dailly, 1972a, b; Holzmann, 1991; Schulmeyer, 1992] and the division into a lateral and a medial subnucleus is hardly recognizable in the Pacific white-sided dolphin *(Lagenorhynchus obliquidens)* nor in the bottlenose dolphin [*Tursiops truncatus*; Ogawa and Arifuku, 1948]. In baleen whales (mysticetes: fin whale, *Balaenoptera physalus*; minke whale, *B. acutorostrata*; Northern Right whale, *Balaena glacialis*) as well as in large toothed whales (bottlenosed whale, *H. ampullatus*), both a medial and lateral subnucleus have been reported by De Graaf [1967]. As a whole, the superior olives are smaller in baleen whales than in toothed whales of the same body dimensions '...but still in a slightly more advanced state of development than in the human'. Consistently however, the medial subnucleus seems to be the larger component in baleen whales in parallel with the situation in larger toothed whales. It might be that, at least in part, size differences in the SOC subnuclei in whales are correlated with differences in body dimensions, ecological niche, feeding mode and thus in the auditory spectrum of these animals.

Another important correspondence between the sperm whales *(Kogia, Physeter)* and delphinids concerns the large size of the lateral lemniscus. Ogawa and Arifuku [1948] report that the lemniscus is even 'colossal' in the sperm whales, and they also use this term for the nucleus of the lateral lemniscus and the brachium colliculi inferioris, although no quantitative data were given in that paper. Taken together, the authors state that *Kogia* and *Physeter* surpass dolphins in the massive development of the superior olive, lateral lemniscus, and the inferior colliculus (IC). The latter was reported to be extremely large in physeterids even for toothed whales [Ogawa and Arifuku, 1948]. In our scans, the nucleus of the lateral lemniscus is a little smaller (thinner) in *Kogia* than in *Delphinus*. The IC is ovoid in *Delphinus* and more wedge-shaped in *Kogia*; in parasagittal aspect, the lemnisco-collicular complex is reminiscent of a thick club or distorted barbell in *Delphinus* but rather of a mushroom in *Kogia*, with the inferior colliculus representing the asymmetrical cap

(not shown). The collicular width (between the lateral surfaces of the ICs) is somewhat smaller in our *Kogia* than in *Delphinus* both in absolute numbers (29 vs. 36 mm) and with respect to brain width (table 2: ratios 0.22 vs. 0.25) whereas the height of the colliculi is identical in both species (13 mm). In figure 3c, the inferior colliculus of *Kogia* shows a submaximal cross-sectional area. Within the caudal half of the ICs (fig. 3d), a dorsolateral part is delimited from a medioventral part by a hyperintense zone (double arrow); in the dorsalmedial direction, both zones converge, standing at about 60° to the horizontal plane. In the rostral direction, each of the hyperintense zones exhibits a thin hypointense line obviously representing a sheet of white matter (not shown), both of them slightly arching medially. In the rostral part of the ICs, the hyperintense zones fade and the two sheets of fibers converge in the direction of the commissure of the inferior colliculi (fig. 3c: ci). At the transition from the inferior to the superior colliculi, the organization of the IC in *Kogia* seems to correspond well with that of the cat [Oliver and Huerta, 1992]. Here, the central nucleus of the IC and its relation to the nucleus of the lateral lemniscus are obvious as are the dorsomedial nucleus of the IC bulging into the central grey as well as the lateral nucleus underlying the brachium of the IC (not shown).

As reported for the common dolphin recently [Oelschläger et al., 2008], coronal scans of our *Kogia* brain reveal a dorsoventral lamination pattern of the superior colliculus (SC) as a series of fine parallel lines which presumably correspond to thin sheets of fibers and grey matter (not shown). This pattern seems to comply with the situation found in terrestrial mammals [cat; cf. Voogd, 1998d], but so far has not been analyzed for toothed whales. In *Kogia*, the inner layers adjacent to the central grey are more distinct than the outer layers. As far as can be concluded from our MR scans, the relative size and topography of the intermediate grey layer in the dwarf sperm whale does not show conspicuous differences when compared to the common dolphin and the cat.

Premotor and Motor Systems
Selected Brain Stem Nuclei. At the rostral end of the mesencephalon, between the interthalamic adhesion and the habenulo-interpeduncular tract, i.e., at the beginning of the central grey, the elliptic nucleus stands out as a general characteristic structure of the whales and dolphins (fig. 3a, b, 4a, b, 5b: CG, E). The nucleus is large in the pygmy sperm whale [length/width/height: 7.0/ 4.0/ 3.5 mm; Ogawa, 1935b] and situated rostral and dorsal to the oculomotor nuclear complex [Oelschläger and Oel-

schläger, 2002]. In this area, the nucleus of Darkschewitsch and the interstitial nucleus of Cajal lie closely together. Regarding their shape and size relations, these nuclei are reminiscent of the situation found in the fetal narwhal [*Monodon monoceros*; Holzmann, 1991]. In our MR scans of the dwarf sperm whale and the common dolphin, the two nuclei can be clearly distinguished. Whereas the nucleus of Darkschewitsch (fig. 3a, 4b, 5b: E) is large, situated more rostrally and dorsally, nearly as hyperintense as the central grey and surrounded by a thin sheet of fibers, Cajal's nucleus (fig. 5b: Cj) is much smaller, situated more caudally and ventrally, hypointense and enclosed in a distinct capsule of fibers which includes terminations of axons from the cerebellar interposed nucleus (fig. 3e–g: PIN). Both the nuclei of Darkschewitsch and Cajal project in the direction of the inferior olive as the medial tegmental tract [mt; De Graaf, 1967; Jansen and Jansen, 1969; Verhaart, 1970; Zuleger and Staubesand, 1976; von Hagens et al.,1990; fig. 5: asterisk] which was reported to occur also in primates and the human [Nieuwenhuys, 1998]. The mt forms immediately ventral to the medial longitudinal fascicle (mlf) and is conspicuous throughout its course from the rostral mesencephalon to the medial accessory inferior olive [Verhaart, 1970]. In the bottlenosed whale [De Graaf, 1967] the mt proceeds dorsal to the decussation of the brachia conjunctiva (superior cerebellar peduncles) at rostral pontine levels as seen in our *Kogia* scans (fig. 5a, b: x). At the level of the superior olivary complex and the facial nerve and nucleus, the mt approaches the medial lemniscus (ml) and finally arrives at the dorsomedial surface of the medial accessory inferior olive (fig. 3g, 5a: M). In the cat, the mt descends along the midline close to the medial longitudinal fascicle. Although the medial tegmental tract was reported to be well-developed in toothed whales [Verhaart, 1970] and can be detected easily in histological sections by means of its fiber pattern [De Graaf, 1967], the tract is difficult to identify in our MR scans. Here, it seems to join the medial longitudinal fascicle, including fibers of the interstitial nucleus of Cajal and of the elliptic nucleus (Darkschewitsch; fig. 5a, b: E, Cj, asterisk). In *Kogia*, all these fibers form a hypointense gutter (fig. 3a: mt) ventral to the nuclei (E, Cj) and the topography and pattern of the single components in this area to some degree deviate from the situation in *Delphinus*. Caudal to the rostral third of the medial accessory inferior olive, the mt cannot be recognized any more in the dwarf sperm whale. Ogawa [1935b, 1939] reported that in cat this tract as well as the central tegmental tract are composed of fine fibers and both have the same origin and termination. In

whales, however, the fibers are characterized as relatively thick. In mammals, Darkschewitsch's nucleus was reported to receive important input from the cerebral cortex and to project to the inferior olive [cf. Voogd, 1998c]. Apart from this, the elliptic nucleus (E) receives afferents from the spinal cord and the dorsal column nuclei that bypass the cerebellum and thalamus [Voogd, 1998c].

The facial nerve and nucleus (fig. 1, 3e, f, 4d: 7, 7') are very large in cetaceans and easy to detect in MR scans of the dwarf sperm whale. In these scans the nucleus is located immediately medial and caudal to the descending facial nerve and extends in the caudal direction for about 15 scans (6.0 mm; scan thickness: 0.4 mm) to border the inferior olivary complex laterally (fig. 3g and inset: IO). Along its course, the facial motor nucleus changes its shape but no individual neuron populations could be detected in the scans. In mammals, generally, this nucleus is not only responsible for the motor innervation of the superficial facial musculature involved in mastication and vocalization but also in hearing and mimetic expressions of the face. In toothed whales, this musculature has been profoundly reorganized and integrated into a new (nasal) sound/ultrasound generator (cf. Discussion).

The ambiguus nucleus (fig. 3g: A), reported to be large in cetaceans, begins in *Kogia* a few scans caudal to the end of the facial nucleus. It is located exactly in the center of its half brainstem and extends over about 10 scans (4 mm) further caudally with a diameter of a little less than 1 mm. Interestingly, in the minke whale *(Balaenoptera acutorostrata)*, a baleen whale species, the ambiguus nucleus is much larger than in toothed whales of about the same body dimensions as the bottlenosed whale *(Hyperoodon rostratus)* and the killer whale [*Orcinus orca*; cf. De Graaf, 1967; see Discussion]. In mammals generally, the ambiguus nucleus innervates the striated muscles of the pharynx, larynx, and esophagus via the vagus group of cranial nerves (glossopharyngeus, vagus, accessorius).

The central vestibular complex is characteristic in whales and dolphins. Here the 'genuine' vestibular nuclei, which receive direct input from the semicircular canals, are much reduced in size in parallel to the latter [Spoor et al., 2002]. In contrast, the lateral vestibular (Deiters') nucleus (fig. 3f: v) is at least as large or larger than in the human [Voogd, 1998c; Kern et al., 2009]; with respect to body mass it is 2.4 times larger in *Delphinus* than in humans and with respect to brain mass 3.1 times. Zvorykin reported Deiters' nucleus to be even 9 to 16 times larger in *Delphinus* than in the human [Zvorykin, 1975].

Although the genuine vestibular nuclei of mammals are mainly involved in the vestibuloocular reflex and nystagmus, horizontal gaze holding, and smooth pursuit and are much reduced in size in toothed whales, the lateral vestibular nucleus (LVA; Deiters' nucleus) is closely correlated with the cerebellum ('precerebellar' nucleus). This nucleus receives projections from the anterior vermis as well as from the interstitial nucleus of Cajal and spinovestibular afferents [cat, monkey; Voogd, 1998c]. The LVA sends multiple diffuse projections into the reticular formation as well as efferents into the anterior motor horn of the spinal cord, thus providing a major source for spinal activation and control in acousticomotor navigation [Büttner-Ennever, 1992; Voogd, 1998a, b; Kugler, 2004; Neuhuber, 2004; Oelschläger, 2008].

The inferior olives (fig. 3g, 5: M, IO) are well-developed, particularly the medial accessory subnuclei (M), which are in contact with each other at the midline. In comparison with evidence in ungulate species [Yoshikawa, 1968] they seem to have approached each other during cetacean evolution. Here, a rotation of the inferior olivary complex in a ventral and medial direction may have brought the subhorizontal more or less laminar components into a vertical orientation. In rat the caudal part of the medial accessory inferior olive (M) receives somatosensory input from the spinal cord, dorsal column nuclei, spinal nucleus of the trigeminal nerve as well as from the posterior interposed nucleus in the cerebellum (see below). In cat, direct afferents from motor and premotor cortical areas (4, 6, including the frontal eye field) have been reported [cf. Voogd, 1998b]. An interesting source of indirect input is the anterior cingulate cortex [cf. Oelschläger, 2008]. The medial accessory olive also receives afferents from nuclei at the mesencephalic-diencephalic border. A continuum of neurons surrounding the fasciculus retroflexus, encompassing the rostral part of the elliptic nucleus (Darkschewitsch) and the rostral interstitial nucleus (Cajal) of the medial longitudinal fascicle projects to M; specific afferents come from the sensorimotor and parietal association cortices [Paxinos, 2004]. The medial subnucleus (M) as a whole receives input via the medial tegmental tract including the central grey and input from a variety of nuclei in the auditory system.

Compared to other mammals, the anterior part of M is very much enlarged in cetaceans. It heavily projects to the cerebellar cortex (paraflocculus) and via the posterior interposed nucleus back to the elliptic nucleus. In terrestrial mammals, the latter nucleus receives auditory input and is involved in mass movements of the body. Moreover, as IO afferents are reported to transmit a variety of sensory modalities that are integrated at different levels

with cerebral input, its function might be that of a detector of events and errors resulting from a variety of physiological processes [Paxinos, 2004]. In toothed whales, which are very much focused on the input of the ascending auditory pathway, the thick inferior olives are probably important for acoustico (audio-) motor navigation [Oelschläger et al., 2008; Oelschläger, 2008; Oelschläger and Oelschläger, 2002, 2009; see below].

Cerebellum. The cerebellum of *Kogia* shows all the features known of odontocetes investigated so far (fig. 1, 3–5). Based on its dimensions, however, its absolute volume seems to be distinctly smaller (table 2). Moreover, with respect to the total brain, most dimensions of the cerebellum are also slightly to distinctly smaller. This is particularly obvious in cerebellar hemisphere length (ratio 0.39 vs. 0.56) or vermis width. The ratio/percentage of cerebellar width in interhemispheric brain width is only slightly smaller in *Kogia* (63%) than in *Delphinus* (66%). In the giant sperm whale, for comparison, this ratio is distinctly less [51%; after Ries and Langworthy, 1937; Kojima, 1951; Jacobs and Jensen, 1964] and the cerebellar volume fraction of the total brain was estimated to be about 7.5% [after Ries and Langworthy, 1937]. This latter value comes close to the minimal cerebellum/brain volume percentage among cetaceans which was found in the plesiomorphic Ganges river-dolphin [*Platanista gangetica*: 6.7%; Pilleri and Gihr, 1970]. In this respect, beaked whales (ziphiidae), which are closely related to the sperm whales (physeteridae), seem to hold an intermediate position between the two small physeterid species and the giant sperm whale [Kükenthal and Ziehen, 1893; Marino, 2007]. For comparison, the cerebellar volume attains about 15% of the brain volume in delphinids [common dolphin, bottlenose dolphin; after Marino et al., 2000]. In double-logarithmic regressions [Ridgway and Tarpley, 1996] baleen whales range a little higher than sperm whales, beaked whales, and river dolphins but distinctly below the delphinid cetaceans. In other words, in a group of delphinid species, indices of total brain and cerebellum mass relative to body mass exceeded other groups (river dolphins, sperm whales, baleen whales) by up to three times. A similar trend seems to exist for the ratio of vermis width/cerebellar width: this ratio accounts for 14.4 versus 16.8–22% in our *Kogia* and *Delphinus*, respectively (not shown). In larger physeterids such as the bottlenosed whale [*Hyperoodon rostratus*; Kükenthal and Ziehen, 1893], sperm whale [Ries and Langworthy, 1937] as well as the fin whale [Jansen, 1950], the relative vermis width appears even smaller but no exact data are available. Concerning the shape of the vermis, the arrangement of the vermal lobuli in *Kogia* is exactly in the sagittal plane whereas in *Delphinus* the caudal lobuli are displaced laterally as has been reported for the bottlenosed whale [Jansen, 1950] with respect to the folium/tuber and pyramis region. In *Kogia*, the rostralmost and caudalmost lobules (i.e., the ventral lobules) are the narrowest, whereas the top region of the vermis is distinctly wider (culmen, declive and folium) as found in the cat [Schaller, 1992].

In correspondence with the situation in other cetaceans, the anterior lobe of the cerebellar hemisphere is comparatively small in *Kogia*, a fact that might be correlated with the loss and strong modification of the posterior and anterior limbs, respectively [Jansen and Jansen, 1953; Manni and Petrosini, 2004]. In contrast, the posterior lobe is very large in dolphins in both absolute and relative terms, particularly the ventral paraflocculus which in situ might heavily protrude on both sides of the brainstem. In cetaceans, the paraflocculus was reported to comprise three fourths of the cerebellar surface [Jansen and Jansen, 1969] and the ventral paraflocculus to contain half of the surface of the cerebellar hemisphere. In the ontogenesis of the giant sperm whale, the paraflocculus attains its dominant position already in early fetal stages [280 mm crown-rump length; Kemp, 1991; Oelschläger and Kemp, 1998]. In correlation with the outstanding size of the ventral paraflocculus, Wilson [1933] estimated that in the blue whale *(Balaenoptera musculus)* this part of the cerebellar hemisphere might receive three fifths of the pontocerebellar fibers. In *Kogia* the paraflocculus seems to have about the same very large volume within the cerebellum as in the common dolphin and presumably other (delphinid) toothed whales as well as *Hyperoodon* [Jansen, 1950], the adult giant sperm whale [Ries and Langworthy, 1937] and in baleen whales [fin whale; Jansen and Jansen, 1953]. For comparison, the paraflocculus in ungulates [pig, goat, sheep, cattle, horse; Yoshikawa, 1968] is only as large as other cerebellar lobuli and protrudes laterally but not ventrally. In contrast, the flocculus of the cetaceans is always very small, particularly in toothed whales [Jansen and Jansen, 1953, 1969; Oelschläger and Kemp, 1998]. In our scans of the dwarf sperm whale, the flocculonodular lobe seems to be developed as in the common dolphin and even somewhat smaller than in baleen whales [Jansen and Jansen, 1953; Oelschläger and Oelschläger, 2002]. In the bottlenosed whale [Jansen, 1950] the flocculonodular lobe was described as rudimentary.

In principle, the shape and topography of the cerebellar nuclei in the dwarf sperm whale correspond well with

the situation found in the bottlenose dolphin [Ogawa, 1935a; Morgane and Jacobs, 1972; Voogd, 1998b]; however, although the nuclei are obviously as large with respect to the cerebellum as a whole, they are less distinct in *Kogia* compared to *Tursiops* [Ogawa, 1935a; Morgane and Jacobs, 1972; Voogd, 1998b] and *Delphinus* (our scans). In the dwarf sperm whale, the nuclei seem to be much more interspersed with axon fiber bundles and thus are less hyperintense than in the two delphinids. In the rostrocaudal sequence of the coronal scans, the first encounter is with the posterior interposed nucleus (fig. 3e: PIN), a homolog of the globose nucleus in primates [Voogd, 1998b], at the level of the facial nerve and genu (7) and the ventral cochlear nucleus (VCN). A little further caudally (fig. 3f), the whole set of cerebellar nuclei can be identified in the scans: the fastigial nucleus (FN) within the vermis, the large posterior interposed nucleus (PIN) lies laterally, the anterior interposed nucleus (homolog: emboliform nucleus; not labeled) lateroventrally, and the lateral (dentate) nucleus ventral to the PIN and lateral to Deiters' lateral vestibular nucleus [fig. 3f: L, v; cf. Voogd, 1998b]. A few scans more caudally (fig. 3g), only the PIN is left. As far as toothed whales have been investigated, the latter nucleus is by far the largest and most massive cerebellar nucleus. Further caudally the PIN divides, enters the white matter of the arbor vitae, and extends as far as the level of the inferior olive. In hoofed animals [Yoshikawa, 1968: pig, goat, sheep, cattle, horse] the cerebellar nuclei are in the same locations but arranged more or less horizontally. Their size is more uniform in these animals but the anterior interposed nucleus obviously could not be detected. There is evidence that in dolphins, apart from corticopontocerebellar projections, the posterior interposed nucleus gets massive input from the elliptic nucleus via the medial tegmental tract, inferior olive and the paraflocculus; all these nuclear structures show an unusual size progression when compared to other mammals [cf. Oelschläger, 2008].

Although the cerebellum is distinctly smaller in *Kogia*, the pons is almost as extended rostrocaudally as in *Delphinus* (maximal length: 24.29 vs. 26.17 mm). Nevertheless, in the dolphin, the brainstem appears to be much thicker and, at the same time, markedly protrudes rostroventrally in the pons area [cf. Oelschläger et al., 2008], probably because of a stronger development of the accessory brainstem nuclei and fiber tracts in this area and a marked telescoping of the brain in *Delphinus*. In the dolphin, the brain as a whole is distinctly more voluminous although it is a little shorter than in *Kogia* (length in common dolphin 105.2 mm vs. 109.6 mm in the dwarf sperm

whale, table 2), but somewhat wider (141.0 vs. 134.7 mm) and higher (92.22 vs. 67.08 mm).

MR Imaging of the Dwarf Sperm Whale Brain
The brain morphology of *Kogia sima* was documented with high-resolution MR scans and even small details could be shown as, for example, the fornix, anterior commissure, habenulointerpeduncular tract, the commissures of the superior and inferior colliculi and the composition/layering of the latter, the medial lemniscus, medial longitudinal tract, the rootlets of cranial nerves as well as the small hippocampus.

As in the body dimensions of other odontocetes, the neocortical gray matter is relatively thin but extremely extended and convoluted. In MR slices of both species, the deepest parts of the narrow sulci do not show because of a lack of resolution. In general, the size, shape, and topography of individual brain structures are rather similar in *Kogia* and *Delphinus*.

In most cases, the MR images (fig. 2–5) acquired with the specified MR sequence show gray matter (cortex, nuclei) as hyperintense (brighter) areas and white matter (nerve fiber material, fiber tracts) as hypointense (darker) areas [cf. Oelschläger et al., 2008]. As in *Delphinus*, the optic tract as well as the facial nerve are particularly hypointense in *K. sima*. The same is true for rootlets of other cranial nerves (e.g., glossopharyngeal rootlet; fig. 3e: white arrow) and fiber masses of the internal capsule which run lateral and dorsal to the lateral ventricles in the direction of the dorsomedial wall (neocortex) of the telencephalic hemisphere (fig. 3a–c: white arrows). In contrast, motor nuclei as well as Deiters' nucleus are rather hyperintense, presumably because of the considerable size of their perikarya.

Discussion

Shape of the Brain
In an older description, Haswell [1884] reported on a *Kogia* brain without being able to identify the species. In dorsal aspect, the specimen shows telencephalic hemispheres, the lateral contours of which distinctly converge rostrally and give the impression of a triangular forebrain (fig. 2). In the neonate giant sperm whale, this 'triangular' shape of the anterior telencephalic hemispheres is also obvious [Ridgway, unpublished photograph]. This is in contrast to the situation in *Delphinus* and most other toothed whales where the rostral brain is more rectangular in dorsal aspect [Kükenthal and Ziehen, 1893; Igarashi

and Kamiya, 1972; Morgane et al., 1980; Oelschläger and Oelschläger, 2002, 2009]; here, the orbitofrontal areas of the telencephalic hemispheres are obviously much better developed. In the sagittal plane, the telescoping of the brain seems to be little pronounced in the *Kogia* brain described by Haswell [1884]; in principle, this corresponds with our *Kogia sima* brain (fig. 5a, b) and with the specimen depicted by Marino et al. [2003]. In addition, the rotation of the telencephalic hemisphere, typical for highly encephalized mammals and particularly strong in cetaceans, humans, and elephants, is less advanced in *Kogia*. The interpeduncular fossa (former mesencephalic flexure) is wide, in contrast to delphinid cetaceans where the hypothalamus and the rostral pons approach each other [*Delphinus*; Oelschläger et al., 2008] or might even come so close to each other that only a narrow transverse cleft persists [*Tursiops*; Morgane et al., 1980; Oelschläger and Oelschläger, 2002, 2009]. Another interesting point concerning the length/width ratio in the odontocete brain includes the development of the parietotemporal part of the telencephalic hemispheres in *Kogia* in which a comparatively moderate transverse size progression of these areas might have led to a weaker broadening of the brain and thus (indirectly) to a lower degree of telescoping.

A typical pontine flexure does not seem to exist in the *K. sima* specimen presented here and is also not obvious in the specimen of Marino et al. [2000]. Therefore, the inconspicuous flexure depicted in the dwarf sperm whale of Haswell [1884] behind the pons area could be interpreted as a first sign of the 'secondary cervical flexure' seen in adult specimens of the giant sperm whale and the bottlenose dolphin [Ries and Langworthy, 1937; Oelschläger and Kemp, 1998; Oelschläger and Oelschläger, 2002, 2009]. Several other brain characteristics given by Haswell nicely correspond to those in our dwarf sperm whale (shape and thickness of cc, shape and width of the limbic lobe, surface configurations of the neocortex, etc.). There is, however, in Haswell's paper neither a description of the brainstem and cerebellum nor any presentation of histological details. Ogawa and Arifuku [1948], in their investigation of the auditory system in cetaceans, published several coronal microslides from the pygmy sperm whale *(K. breviceps)* through different levels of the brainstem that correspond rather well with our MR scans. The authors wrote that … 'no telescoping of the brainstem was observed on *Kogia, Physeter, and Balaenoptera'*. In the ontogenesis of the giant sperm whale [Oelschläger and Kemp, 1998], the flexures of the brainstem are markedly pronounced in early fetal stages [as in

the harbor porpoise, *Phocoena phocoena*; Buhl and Oelschläger, 1988 and the spotted dolphin, *Stenella attenuata;* Wanke, 1990]. In later ontogenetic stages of the sperm whale, the flexures are smoothed out and the brainstem and cervical spinal cord secondarily circle dorsally around the cerebellum [Oelschläger and Kemp, 1998].

Progression of Brain Size

Although the close relationship of all sperm whales is obvious from non-neural characters [Cranford et al., 1996; Rice, 1998; Mchedlidze, 2002] their brains at first sight are rather different. Although the brains of *Kogia (K. sima, K. breviceps)* are somewhat smaller for the body size of these species [lower encephalization; Ridgway and Tarpley, 1996] in comparison with marine odontocetes (e.g., delphinids) of the same dimensions, the organization of the giant sperm whale *(Physeter macrocephalus)* exhibits an extreme extrapolation of the cetacean bauplan with respect to several growth phenomena. For instance, in smaller marine toothed whales, the brain mass/body mass ratio is very high and only second to that in the human (trend 1: encephalization effect). In the case of the giant sperm whale, however, the body is so large that the fundamental effect of negative allometric growth (regression) of the total brain has subdued the encephalization effect and reached an end-point within the mammalia. Thus, although *Physeter* has the largest brain in absolute terms, the latter is dwarfed in relative terms by the stunning oversize of the body [trend 2: regression effect; Manger, 2006]. This is most obvious in Flower's lithograph of an adult sperm whale skull which had been sectioned mediosagittally through the huge rostrum and amphitheater, the basis for the gigantic epicranial (nasal) sonar generator and transmitter [Flower, 1868–1869; Cranford, 1999; Huggenberger, 2004; Huggenberger et al., 2009]. In adult male giant sperm whales the skull is up to six meters long and the spherical braincase, although exhibiting a volume approximating 10 L, is comparatively minute [see Kojima, 1951]. Furthermore, the maximal absolute growth rate in the giant sperm whale brain as a whole is combined with other developmental phenomena which seem to come to their endpoints here, too: the size increase of the telencephalon (trend 3: telencephalization effect), that is, a maximal dominance of the telencephalon over the rest of the brain. Finally, the size increase of the neocortex (trend 4: neocorticalization effect), which is the utmost expansion of the neocortex with respect to brain mass and its ultimate dominance over the other telencephalic cortex formations (paleocortex,

archicortex). An intermediate situation for trends 2–4, (i.e., regression, telencephalization, neocorticalization effects), is seen in beaked whales, close relatives of the sperm whales [North Atlantic bottlenosed whale, *Hyperoodon ampullatus*; Kükenthal and Ziehen, 1893; Blainville's beaked whale, *Mesoplodon densirostris*; Marino, 2007]. In the largest delphinid species (killer whale; *Orcinus orca*), the biggest males might have a brain equal in size to that of the largest males of *Physeter*, a fact supported by measurements of cranial capacity in *Orcinus* by Osborne and Sundsten [1981]. Even adult female killer whales might have larger brains than adult female sperm whales of three-fold higher body mass; only in the average absolute adult brain mass, male sperm whales are still on top [Ridgway and Tarpley, 1996]. But all the delphinids do not show one phenomenon characteristic of sperm whales: in the latter, the size increase of the total brain does not imply a similar size increase of the cerebellum. Thus, although *Kogia* brains are distinctly smaller than those of delphinids, their cerebellum is even less in proportion to the total brain size. Beaked whales, in this respect, seem to be about halfway in the increased negative allometry of the cerebellum, whereas the giant sperm whale exhibits the minimum proportion of the cerebellum in total brain volume, with a similar percentage as shown by the small and plesiomorphic Ganges river-dolphin *(Platanista gangetica)* which shows a series of conserved features [minimal adult brain size, low encephalization, long rostrum, archaic ear region; cf. Pilleri, 1972; Ridgway and Tarpley, 1996; Marino et al., 2000; Kossatz, 2006; Huggenberger and Oelschläger, in press]. In contrast, killer whales, as the largest delphinids, show a very large cerebellum in the same proportion to the total brain as known from smaller dolphin species. Delphinid cerebellum mass relative to body mass might thus exceed other groups (among them sperm whales and beaked whales) by up to three times. Moreover, the maximal development of the neocortex in the giant sperm whale is not correlated with a maximal size increase in the cerebellum (neocerebellum) as seen in delphinids, a quantitative relationship also known from the ascending primate series [Schwerdtfeger et al., 1984]. At the same time the cc, connecting the telencephalic hemispheres midsagittally, seems to be comparatively small in *Physeter* [Tarpley and Ridgway, 1994]. The extreme size of the giant sperm whale telencephalic hemisphere and the concomitant minimal relative volume of the cerebellum imply that, here, the neocortex could have attained a maximal 'independence' within the brain among the physeterids as seen in the Ganges river-dolphin, but on another quantitative

level which represents the opposite end of the size spectrum in cetaceans. Whether these characteristics are correlated with or favor the phenomenon of 'unihemispheral sleep' [Mukhametov, 1984; Lyamin et al., 2008] is an open question (see below). Sleep alternating between the two hemispheres could ... 'ensure a high muscular tonus and reflectory activity which is necessary for normal and safe respiration' ... mediated by the awake hemisphere and the brainstem in the locomotory apparatus of animals which have to come to the surface to breathe.

Commissures

Part of the commissural fiber systems seem to be less developed in toothed whales than in other mammals. This is seen in the anterior commissure (ac), hippocampal commissure (commissura fornicis), and the cc [Tarpley and Ridgway, 1994; Keogh and Ridgway, 2008], whereas the posterior (epithalamic) commissure is well-developed [Morgane and Jacobs, 1972; Oelschläger and Oelschläger, 2002; Oelschläger et al., 2008; Oelschläger, 2008]. In primates [rhesus monkey; Schmahmann and Pandya, 2006], the ac is comparatively well-developed and contains interhemispheric axons traversing between the prefrontal (orbitofrontal), superior temporal and inferior temporal regions [including the parahippocampal gyrus and amygdaloid complex; Asan and Nitsch, 2004]; the genuine olfactory component in the ac is only moderately developed in primates. In baleen whales, this commissure interconnects the olfactory bulb, olfactory tubercle, and areas near the temporal pole (piriform lobe) of both telencephalic hemispheres as seen in terrestrial mammals [Schaller, 1992], but on a rather low developmental level and in correlation with the reduced state of the olfactory system in mysticetes.

Whereas in toothed whales the delicateness of the ac can be correlated with the extreme reduction of the olfactory system and thus interhemispheric olfactory connections, the situation is more complicated in the cc. The latter is thin in the harbor porpoise *(Phocoena phocoena)* as well as in the striped dolphin *(Stenella coeruleoalba)*, *Delphinus* and *Kogia,* and somewhat thicker in the Amazon river-dolphin and bottlenose dolphin, white whale, bottlenosed whale and sperm whale [Ries and Langworthy, 1937; Igarashi and Kamiya, 1972; Morgane et al., 1980; Pilleri et al., 1980; Oelschläger and Kemp, 1998]. Tarpley and Ridgway [1994] have shown that in odontocetes there might be a general inverse relationship between the size of cc midsectional area and brain mass, so that one of the smallest species (Ganges river-dolphin) has the highest ratio and the large-brained killer whale

the lowest known ratio. Seen in a wider context this means that with larger brain size and increasingly larger telencephalic hemispheres the amount of the neocortical interhemispheric connections becomes smaller. In primates, however, such a strong negative allometric trend is not obvious for the cc. Thus, humans exhibit the same midsagittal callosal area as the adult killer whale with a brain approximately five times heavier [Ridgway, 1986; Tarpley and Ridgway, 1994].

This phenomenon of a small cc in toothed whales and its relative size decrease with increasing brain mass calls for explanations. Interestingly, there are at least two possibilities for allometric trends which can be related to cc size in toothed whales: (1) Allometric analyses of mammalian brains have revealed that cerebral cortex volume (gray and white matter) increases disproportionately with brain size but that the ratio of cortical gray matter to total cortical volume decreases in larger brains [disproportionate increase of white matter; Hofman, 1989]. Glezer et al. [1988] and Manger [2006] calculated a corticalization index 1 (CI 1; cortical grey and white matter vs. brain mass) for odontocetes (average 72.14) similar to that in simian primates (average 70.22%) and much higher in comparison with those of other mammals, which can be taken as a clear sign for increased telencephalization. Instead, the corticalization index 2 (CI 2; cortical grey matter vs. brain) shows the primates on top (average 52.69%), followed by ungulates (average 47.69%) and odontocetes (average 40.56%). So the progression of the odontocete neocortex proportion as a whole, which is about as strong as that in simian primates, seems to be due more to an increase in white matter than grey matter. In other words, there are two types of increased corticalization, one leading to a maximal development of neocortical white matter (odontocetes) and another extreme leading to maximal growth of the grey matter (simian primates). (2) This brings us to an additional trend concerning cell density in the grey matter. Whereas within one animal group larger brains only show a gradual and moderate increase in the thickness of the cortical gray, the latter seems to get more expanded tangentially and more intensively folded. As the absolute number of neurons in a brain increases, the volume devoted to the neuropil required to maintain a given level of interconnectivity increases faster than that of the neurons [Ringo, 1991; Doty, 2007; three-dimensional white matter vs. two-dimensional grey-matter growth]. Thus, the distance that the axons must traverse contralaterally through the cc necessarily increases with brain growth [Ringo et al., 1994]. This effect, as it were, favors changes to less numerous but larger projection

neurons [Deacon, 1990]. Because the volumetric synapse density obviously remains invariant as a function of brain size [Abeles, 1991; Changizi, 2001, 2007], such larger neurons should show a compensatory increase in the individual number of their synapses. In toothed whales this was shown for the striped dolphin (*Stenella coeruleoalba*) and the human [Glezer and Morgane, 1990] where the total numbers of cortical synapses were given as 0.87×10^{14} in the dolphin versus 1.3×10^{14} in the human. In addition, the increasing temporal delay for interhemispheric transmission in larger brains might favor intrahemispheric instead of bihemispheric computation. An increase in the diameter of the commissural axons in order to accelerate conduction velocity might not solve the problem because this would by itself enlarge the brain and increase the distance for communication. All this seems to result in increasing hemispheric specialization, i.e., brain 'lateralization' [Doty, 2007; see below]. Possibly as a compromise, large-brained animals have a few exceptionally large and heavily myelinated cc fibers which are absent in smaller brains [Olivares et al., 2001; Aboitiz et al., 2003]. In *Tursiops and Orcinus*, Keogh and Ridgway [2008] found only a small percentage of cc fibers larger than 5 μm. Existing data [Tarpley and Ridgway, 1994; Poth et al., 2005; Manger, 2006] indicate that in odontocetes the trends concerning the growth of grey matter, the increase in total neuron numbers, and the decrease of neuron density per cortical volume unit take place on a lower quantitative level compared with other mammals of the same body dimension (primates). In this regard, the pygmy sperm whale [Poth et al., 2005] exhibits even lower cortical neuron counts than other odontocetes, a fact which might apply to sperm whales in general, but which cannot be explained satisfactorily at the moment. Concomitantly, lower neuron numbers in odontocete cortices do not seem to be compensated by a thickening of the grey matter [Striedter, 2005]. Instead, the opposite seems to be true: toothed whales tend to have thin cortical plates comparable to those in domestic ungulates [cattle, sheep, goat: 1.30–1.70 mm; Hummel, 1975; bottlenose dolphin: 1.30–1.85 mm; Ridgway and Brownson, 1984, Morgane et al., 1988; Furutani, 2008], and the neocortices of odontocetes, in general, are thinner than those of primates and humans [Blinkov and Glezer, 1968; Striedter, 2005]. Theoretically, such a thickening of the grey matter would interfere with the 'gyral window' hypothesis [Prothero and Sundsten, 1984; Poth et al., 2005] which means that gyral width cannot fall below a certain value without a loss of connectivity and that the degree of cortical folding thus cannot surpass a certain limit in large brains,

which seems to exists at a brain mass of about 10 kg (killer whale, sperm whale). In other words, an increase in the significance of a functional system (auditory system) might be associated with the expansion of the corresponding cortical areas rather than their thickening.

The phenomena accompanying the increase in brain mass of large odontocetes (telencephalization, neocorticalization) and correlated allometric trends (weaker relative growth of grey matter, stronger relative growth of white matter, generally lower neuron counts in the cortical grey matter, reduced midsagittal callosal sectional area) might imply a decline in 'relative connectedness' of each hemisphere with its counterpart and with the brainstem. This is most obvious in the adult giant sperm and killer whales which have brains of the same maximal size dimension. Concomitantly, the brainstem has decreased in size, particularly in the giant sperm whale. In contrast to humans, where the crura cerebri are thick and compact trunks of fiber masses, odontocete crura form rather a superficial 'shell' of projection fiber tracts around the mesencephalic tegmental nuclei [ruber and niger; cf. Dailly, 1972b; von Hagens et al., 1990]. All this seems to indicate that in a global view more information is processed in the telencephalon of odontocete brains within each single hemisphere, and particularly in larger species. Moreover, this suggests that in the brain of larger toothed whales, less of the cetacean cerebral cortex is devoted to computation and more is occupied by wiring, which might impact negatively on the computational power of the brain as a whole [Manger, 2006]. The computational power of the cetacean brain, however, is a matter of debate [Marino et al., 2007, 2008].

It seems possible that a certain independence of one telencephalic hemisphere from the other can be correlated with the phenomenon of unihemispheric (monocular) sleep in toothed whales [Ridgway, 1990; Tarpley and Ridgway, 1994; Manger, 2006; for review see Lyamin et al., 2008]. Here unilateral slow-wave sleep episodes are characterized by marked asymmetries in simultaneous electroencephalograms (EEG) from right and left hemispheres of bottlenose dolphins and were also detected in a series of other odontocetes [Butler and Hodos, 2005; Ribeiro and Nicolelis, 2007; Lyamin et al., 2008]. The sleep episodes can last for more than two hours and obviously include not only the hemispheral cortex but also subcortical structures [thalamus; Mukhametov, 1984]. This could also indicate a type of periodic functional 'lateralization' in toothed whales compared to the situation in primates (human), as both odontocete hemispheres are believed to play the same role although alternating in intervals during periods of rest.

The midsagittal cross-sectional area of the odontocete cc (apart from some individual variability possibly related to age) seems to be rather species-specific. Thus for example in the bottlenose dolphin, a middle-sized toothed whale with a maximally wide frequency spectrum [Ketten, 2000], all parts of the cc are relatively thick, with a moderate accentuation of the genu and a little more pronounced splenium whereas the trunk is distinctly thinner, particularly in its posterior part. In general, the proportions of the cc midsection in *Tursiops* to some degree are reminiscent of the situation in humans; however, its overall thickness is only about two thirds that in the latter species. The shape of the cc cross-section in *Delphinus* is similar to that in *Tursiops* but with a somewhat less pronounced genu and splenium and is only about half as thick throughout its length [Morgane et al., 1980; Pilleri et al., 1980; our scans]. In comparison, the cc in *Kogia* is rather different in mid-section: whereas the genu is more pronounced, the splenium is much weaker and the trunk extremely thin. The fact that the genu in *Kogia* is by far the thickest part within the moderately developed cc does not seem to be consistent with the situation in the accessory cortical areas. In primates (rhesus monkey), the term genu stands for the medial part of the forceps minor (fig. 4c: fm), a strong fiber system interconnecting the frontal lobes in mammals [including the prefrontal, anterior cingulate, premotor and part of the motor cortices; cf. Schmahmann and Pandya, 2006]. In odontocetes and particularly in *Kogia*, however, the anterior extremity of the telencephalic hemisphere rostral to the motor cortex and above the orbita (orbital lobe) is moderately developed. This does not hold for the anterior cingulate cortex (ACC), however, which seems to be well-developed in toothed whales. In humans, both ACCs are interconnected via the genu corporis callosi and considered 'executive regions' that comprise areas for vocalization as well as attention to action and seem to be sensitive to the mental operations of visual target detection and cingulate emotion processing [Posner, 1995; Vogt, 2005]. In odontocetes, these areas are presumably involved in the initiation and maintenance of audiomotor navigation via the elliptic nucleus/interstitial nucleus of Cajal and a circuit involving the inferior olivary complex, paraflocculus, and the posterior interposed nucleus [Oelschläger, 2008]. The fact that in the cc the posterior part of the trunk and the splenium are thin is puzzling at first glance: In primates, the posterior part of the cc connects the superior temporal cortex as well as the posterior parietal, inferior temporal, posterior cingulate, and occipital

cortices of both hemispheres [Schmahmann and Pandya, 2006]. Nieuwenhuys et al. [1991] summarize that homotopic commissural fibers from the auditory cortex cross the midplane in the caudal trunk of the cc, together with commissural fibers of the parietal lobes. Presumably as in other mammals, the bilateral auditory cortical representation in odontocetes does not depend much on the cc because the ascending auditory pathway from the cochlear nuclei to the thalamus might cross contralaterally or run ipsilaterally [uncrossed; Nieuwenhuys et al., 1991]. Thus, although much of the auditory computation is done subcortically, the awake hemisphere of the resting whale can react rapidly to auditory arousal by activating the efferent acousticomotor pathway [Oelschläger, 2008]. This could be a mechanism critical for the ability of *Tursiops* to maintain auditory vigilance for five continuous days [Ridgway et al., 2006, 2009].

Currently, it is not clear whether there is a general mammalian bauplan with respect to a sequential pattern of the different fiber systems crossing within the cc and whether the shift of cortical fields across the surface of the hemispheres in several groups during evolution has influenced this pattern. Interestingly, however, the general sequence of the primary cortical projection fields [irrespective of the different topography of multisensory association areas; Nieuwenhuys, 1998] is the same in cetacea, ungulata and carnivora. Given that the arrangement of fiber systems in the cc is similar to that in other mammals (including primates), the weak development of the caudal cc in *Kogia* could be explained by the reduction or lack of occipital lobes, i.e., the fact that in toothed whales the visual cortices are located in the dorsalmost part of the parietal lobes, and perhaps a lesser development of the temporal lobes in this species. The low neuron density in *Kogia*, which is even lower than that in other toothed whales of the same body dimensions [Poth et al., 2005], might also be a limiting factor for the development of the cc in this sperm whale.

Functional Aspects of Brainstem Structures

A few nuclei in the brainstem indicate specific adaptations of odontocetes to their environment. A comparison with other highly encephalized groups of mammals provides the background for a better understanding of the evolutionary implications.

Elliptic Nucleus. The elliptic nucleus so far has only been found in cetaceans [and probably the elephant; Precechtel, 1925; Kruger, 1966; Dailly, 1972b; Voogd, 1998c] and is considered to represent the hypertrophied nucleus of Darkschewitsch [cf. Oelschläger et al., 2008]. In terres-

trial mammals, this nucleus is also called nucleus of the posterior commissure and was reported (among other implications) to be involved in visuomotor behavior. Most remarkably, both in odontocetes and the elephant, the elliptic nucleus (and potential elliptic nucleus, respectively) and the inferior olivary complex are very well-developed. In toothed whales, as in other mammals, these nuclei seem to be integrated in important premotor circuitry [Voogd, 1998c; Oelschläger, 2008] together with the cerebellum.

Facial Motor System (VII). In mammals, neurons within the facial motor nucleus (fig. 3e, f: 7') innervate the superficial facial musculature via the facial nerve (7) and hence comprise the final common output of circuits related to various behaviors including respiration, ingestion, protective reflexes, emotional expression, vocal communication, echolocation and sensory exploration of the environment [Sherwood, 2005]. Although in principle all these functional implications of the facial motor system have to be assumed for cetacean ancestors, extant cetaceans are highly adapted to their aquatic lifestyle. Interestingly, however, the facial nerve and nucleus are much larger in odontocetes than in mysticetes of the same body dimensions [De Graaf, 1967; see below]. In all the cetaceans investigated so far, the facial nerve has only a reduced responsibility for the ear region because the pinnae were lost during evolution. Concomitantly, vocalization in toothed whales is achieved by the epicranial complex [Cranford et al., 1996]: here, the 'blowhole part' of the facialis musculature is very well-developed and arranged in several sheets with changing texture around the upper respiratory tract and its secondary airsacs which are specific for odontocetes and unique among the mammalia. All these structures are involved in the pneumatic generation of echolocation (ultrasound) and communication (sound) signals. Thus the facial nerve runs as a strong trunk along the side of the head from the stylomastoid foramen via the zygomatic arch, and through the antorbital notch in the skull roof to the blowhole musculature [Huggenberger, 2004; Rauschmann et al., 2006; Comtesse-Weidner, 2007; Oelschläger et al., 2008; Huggenberger et al., 2009; Mead and Fordyce, 2009; Huggenberger and Oelschläger, in press]. Baleen whales, in contrast, do not exhibit such a highly specialized epicranial complex and might produce sounds in the larynx or laryngeal sacs. The epicranial musculature of toothed whales presumably was derived from perioral and perinasal portions of the facialis (maxillonasolabial) musculature and highly modified into a more or less cone-shaped complex of potentially semi-independent layers.

Versatile and precise contractions of individual muscle portions [Ridgway et al., 1980] allow the generation of a broad spectrum of sound and ultrasound signals. In the bottlenosed whale *(Hyperoodon ampullatus)*, a member of the beaked whales (ziphiids), which are closely related to the sperm whales [Physeteroidea; Fordyce and De Muizon, 2001], the dorsomedial group of neurons in the facial nucleus was found to be very large [De Graaf, 1967] and many times more voluminous than in the little piked whale *(Balaenoptera acutorostrata)*, a small baleen whale (mysticete) species of about the same body dimensions. In the latter species, the dorsomedial group of neurons was again the largest component of the facial nucleus, but on a much lower quantitative level.

Although in the literature [cf. Sherwood, 2005] there is some agreement on a potential basic pattern of musculotopic innervation of the facialis neurons for the mammalia as a whole, differences seem to exist between mammalian groups regarding the subdivision of the facial motor neurons [Voogd, 1998c]. Extirpation experiments in the cat and other terrestrial mammals [dog, rat, guinea pig; Papez, 1927], revealed that the labial, zygomatico-orbital, and nasal parts of the facialis muscles are innervated by dorsolateral, lateral, and ventrolateral groups of neurons; in this case, the dorsomedial neurons might innervate external auricular muscles. In a recent study, Sherwood [2005] supported older evidence on the functional implications of the medial facialis subnucleus: in the cat it is significantly larger than the other facialis subdivisions and its neurons innervate the auricular muscles. In bats, several apparent specializations were found which point to enhanced mobility of the ears with respect to sound localization [Friauf and Herbert, 1985]: the medial subnucleus (mostly motoneurons of the pinna) contains 49% of the total number of neurons in the VII. Whales generally do not have external ears (pinnae) and there are only rudiments of external (superficial) auricular muscles. Hoofed animals [sheep and goat; Störmer et al., 1990] exhibit a small dorsal cell group (zygomatico-orbital formation) in correlation with the moderate facial expression in this region in both species. The intermediary and lateral cell groups, however, are large and can be correlated with enhanced lip movements in these animals. In primates, motoneurons of the perioral muscles and those operating the vibrissae are located laterally, neurons of the pinna muscles are in the medial part of the nucleus.

Currently it is difficult to explain why the musculotopic innervation given by De Graaf [1967] for whales (odontocetes) differs so much from the situation found in other mammals. Taking into consideration all the information regarding the targets of the medial subnucleus of the facial nucleus in terrestrial mammals, the latter does not seem to be equivalent to the 'dorsomedial' subnucleus in cetaceans. This aberrant odontocete type of facialis nuclear composition and the topography of its subnuclei might rather be the result of (a) reduction phenomena (outer ear, its muscular equipment as well as the innervating neuron population) and (b) the concomitant establishment of the sonar system including the relevant parts of the facial musculature and the associated facial neurons innervating the blowhole area. Thus, particularly in toothed whales, there seems to be a quantitative correlation between the considerable size of the dorsomedial group of facial neurons and the morphogenetic change in the topography and arrangement of their muscular periphery. In odontocetes, generally, the labial and nasal parts of the mammalian maxillonasolabialis muscle are extremely modified and seem to be shifted against the vertex of the head along with the blowhole, as the motor center of a powerful sound- and ultrasound-generating epicranial complex. Therefore, the dorsomedial group of the facial nucleus in odontocetes, presumed to innervate the muscular component of the epicranial complex, is extremely large in both absolute and relative terms. In this respect, baleen whales are plesiomorphic: they do not possess a sonar system and their nasal tract is much less derived and seems to be responsible for respiration and chemoreception only [a miniaturized but complete olfactory system is present; Oelschläger, 1989]. In consequence, the diameter of the facial nerve is distinctly smaller and the number of axons is less in baleen whales than in toothed whales of the same body size dimensions [Morgane and Jacobs, 1972]. Therefore it seems plausible that in baleen whales [and in contrast to the situation in toothed whales; De Graaf, 1967], the dorsomedial neuron population is comparatively small [*Balaenoptera sulfurea*, Wilson, 1933; minke whale, *Balaenoptera acutorostrata,* De Graaf, 1967]. The fact that in baleen whales the small dorsomedial cell group is again the largest subnucleus within VII might reflect moderate adaptations of the blowhole area to surfacing, respiration, and diving.

Recent investigations [cf. Sherwood, 2005] have revealed that in catarrhine primates as well as in humans the size of the individual facial subnucleus corresponds to the size of the related peripheral muscle fiber population. In this respect it is of some importance that in toothed whales not only the facial nucleus (our 'dorsomedial' subnucleus) is very large, but that the number of axons in the facial nerve is extraordinarily high (21,000–

173,000). Thus even the smallest dolphins probably have higher axon counts in the facial nerve than other mammalian species [cat and dog: approx. 10,000 axons; human 12,500; Blinkov and Glezer, 1968]. Also, among species of about the same body dimensions, most marine dolphins show axon counts several times higher than those in humans [Morgane and Jacobs, 1972]. Although in toothed whales the volume of the musculature in the epicranial complex is not known (and the same is true for the number of muscle fibers innervated by one axon) the large number of axons in the facial nerve reflects small numbers of muscle fibers in the respective motor units. This, in turn, is an interesting hint for the generation of precision movements within the epicranial musculature related to nasal echolocation and communication ['fine adjustment of nasolabial activity'; Ridgway et al., 1980; Hinrichsen and Watson, 1983, 1984] mediated by input from the cerebellum, central grey, and superior colliculus [cf. Sherwood, 2005]. Moreover, as a possible parallel with the situation in primates [cf. Sherwood, 2005], it can be expected that the odontocete VII receives direct cortico-motoneuronal innervation (as a completion of indirect input via the reticular formation) for the enhancement of diversity, flexibility, precision, and velocity of motor behaviors [Sherwood, 2005] particularly in the sense of 'acoustic facial expressions' [Oelschläger, 2008]. Thus, within the facial motor subsystem of odontocetes, the generally large size of the VII as well as the high number of axons in the motor part of the facial nerve appear to represent the 'standard equipment' for predatory aquatic life and communication on the basis of complex sound/ultrasound generation and processing.

Nucleus Ambiguus. In comparison with the facial nerve nucleus, which is much larger in odontocete than in mysticete whales, the situation is directly opposite for the ambiguus nucleus. Although it was reported to be large in both cetacean suborders with respect to brain mass when compared to the evidence in humans and elephants [De Graaf 1967], the ambiguus nucleus is much larger in baleen whales than in toothed whales. This is obvious in the comparison of the odontocete bottlenosed whale *(Hyperoodon ampullatus)* with the mysticete minke whale *(Balaenoptera acutorostrata)*, which are of about the same body dimensions. These size differences in the nuclei of the two species might be correlated with different mechanisms of ultrasound/sound production for echolocation and communication, respectively. In odontocetes, both acoustic processes obviously take place in the epicranial nasal tract [Cranford et al., 1996, Huggenberger, 2004; Huggenberger et al., 2009], whereas baleen whales do not show the features of a sonar system and are believed to communicate via low-frequency sound produced in their large larynx or laryngeal sacs.

Inferior Olivary Nuclear Complex and Paraflocculus. Although there is good correspondence among species regarding the identity of its components [cf. Kooy, 1917; Korneliussen and Jansen, 1964; Voogd, 1998b], the quantitative composition of the inferior olivary nuclear complex in mammalian taxa can only be understood via functional considerations. In primates, the principal nucleus is the dominant component within the inferior olivary complex; it receives important input from the red nucleus via the central tegmental tract and forms a loop with the D-zone of the cerebellar cortex and the dentate nucleus which projects back to the red nucleus. Cetaceans (toothed whales), however, exhibit a parallel situation: the nuclei involved all show an exceptionally large size, with the medial accessory inferior olive (M) receiving important input from the elliptic nucleus (nucleus of Darkschewitsch) and the interstitial nucleus of Cajal via the medial tegmental tract and forming a loop with the C2- (intermediate lateral) zone in the cerebellar cortex (paraflocculus) and the posterior interposed nucleus which projects back to the nuclei of Darkschewitsch and Cajal [Oelschläger, 2008; Oelschläger et al., 2008; Oelschläger and Oelschläger, 2009]. The medial accessory inferior olivary subnucleus also receives afferents from the trigeminal system and spinal cord [cat: Boesten and Voogd, 1975; Molinari, 1985; Voogd, 1998b] and is involved in directional hearing [Oelschläger and Oelschläger, 2002]. In terrestrial mammals (rat), the paraflocculus integrates afferents from the (elliptic) nucleus of Darkschewitsch (via the anterior half of the medial accessory inferior olive) with input from the spinal cord [spino-olivary tract; Voogd, 1998b] and receives the major part of the auditory ponto-cerebellar projection (rat). In the blue whale *(Balaenoptera musculus)*, the paraflocculus was estimated to receive three fifths of the pontocerebellar fibers [Wilson, 1933; Jansen, 1950]. Generally in cetaceans the paraflocculus has been related to the propulsion by the trunk and tail and acoustico- (audio-) motor navigation [Jansen, 1950; Jacobs and Jensen, 1964; Leonhardt and Lange, 1987; Oelschläger et al., 2008; Oelschläger, 2008].

Concerning the inferior olivary nuclear complex, the relative size of its subnuclei might provide evidence regarding possible motor specializations of the respective group of mammals. Whereas in toothed whales the medial accessory subnucleus is strongly hypertrophied, elephants and primates (humans) have very large principal subnuclei [Voogd, 1998b; Glickstein et al., 2007]. In hu-

mans [Trepel, 2008], the principal inferior olive is involved in precision movements of the limb (hand) and the larynx musculature, respectively, and the accessory olives are involved in the coordination of mass movements of the body and limbs [Leonhardt and Lange, 1987]. These different qualities of motor activity are obviously conveyed by separate projections to individual areas of the cerebellar cortex with appropriate head and body representations [Manni and Petrosini, 2004]. From this it is plausible that, while in humans the large principal inferior olivary nucleus is engaged in manipulation, elephants perhaps use it in a somehow analogous way for 'precision movements' of the trunk (proboscis), whereas the large anterior medial accessory subnucleus in cetaceans communicates mass movements of the body stem (spinal locomotory apparatus). Thus, apart from eye movements in all the mammalian groups considered and the corticospinal system in the human (plexus brachialis: hand), additional precision movements in the human and in toothed whales as well as in elephants are effected (1) by the facial nucleus and nerve via superficial facial muscles for visually relevant mimics (human) and vocally relevant mimics (sound production in the epicranial complex of toothed whales; sonar) as well as motor activity of the proboscis (elephants) and (2) by the nucleus ambiguus (vagus nerve: larynx) for speech and other low-frequency communication (human, elephants). In contrast to humans, however, where (again excluding eye movements) altogether three kinds of precision movements are obvious (manipulatory movements of the hand, facial expression, vocalization), elephants seem to have two types of more or less equivalent motor behaviors, i.e. 'manipulatory' movements/'facial expression' of the trunk and the activity of the larynx (vocalization). Toothed whales presumably have only one type of precision movements, i.e. the activity of the blowhole musculature during echolocation/vocalization. In odontocetes, the larynx is believed to be responsible for respiration, protection against choking and for the transport and pressurization of air with respect to nasal sound and ultrasound generation [Huggenberger, 2004; Huggenberger et al., 2009; Huggenberger and Oelschläger, in press].

Conclusions

This paper gives an overview of the shape of the dwarf sperm whale brain and the three-dimensional topography of internal key structures with their appearance in high-resolution MR scans. As far as is known from limited information in the few relevant papers in the literature, the morphology of the dwarf sperm whale *(Kogia sima)* brain corresponds well to the evidence found in the pygmy sperm whale *(K. breviceps)* and delphinid cetaceans [*Delphinus delphis, Tursiops truncatus*; cf. Langworthy, 1932; Jansen and Jansen, 1969; Breathnach, 1960; McFarland et al., 1969; Igarashi and Kamiya, 1972; Morgane and Jacobs, 1972; Morgane et al., 1980; Pilleri et al.,1980; Ridgway, 1990, 2000; Oelschläger et al., 2008; Oelschläger, 2008; Oelschläger and Oelschläger, 2002, 2009].

In detail, the dwarf sperm whale brain investigated shows the following major macroscopical characteristics known of other smaller toothed whales: (1) Brain wider than long; (2) considerable encephalization, telencephalization and neocorticalization; (3) thin but extremely expanded cortical grey matter; (4) thin cc; (5) the typical odontocete neocortical gyrification pattern; (6) olfactory bulb and tract lacking; (7) very small hippocampus and archicortex, in general, but well-developed cingulate and parahippocampal cortices; (8) very large basal ganglia, including the amygdaloid complex; (9) large to maximal size of many components of the auditory system; (10) very large size of brainstem nuclei involved in audiomotor navigation [Darkschewitsch (elliptic) nucleus, pontine nuclei, inferior olivary complex (particularly: medial accessory nucleus)]; (11) large cerebellum (particularly paraflocculus, posterior interposed nucleus).

Features characteristic of the genus *Kogia* are, e.g., the size and shape of the brain which is somewhat smaller and flatter than other toothed whale brains of similar body dimensions (delphinids), the shape of the telencephalic hemispheres which converge rostrally, and the straight brain stem (tegmentum) which does not show a pontine flexure. With respect to the common dolphin, the midbrain (inferior collicular width) is narrower and the cerebellum smaller. A comparison of brain size in dolphins, dwarf and giant sperm whales reveals some allometric trends. Thus, in absolute numbers, the increase of brain mass in *Physeter* has attained a maximum, whereas its size proportion in the head and body, respectively, has shrunk to a minimum. The volume proportion of the telencephalic hemisphere in the total brain of *Physeter* is maximal among toothed whales, that is the brain stem and the cerebellum are at a minimum. The brains of beaked whales show a maximal shortening (telescoping) and seem to be intermediate in the size relations of the cerebellum [Kükenthal and Ziehen, 1893; Igarashi and Kamiya, 1972]. The cc, which is very thin and peculiar in *Kogia*, seems to be more compact in beaked whales and giant sperm whales.

Concluding from the existing data, it is difficult to interpret sperm whale brains with respect to potential eco-physiological adaptations. Interestingly, there is no strict size correlation between the neocortex and pons and the neocerebellum as seen in primates [cf. Schwerdtfeger et al., 1984; Matano et al., 1985; Stephan et al., 1988]. In the giant sperm whale, the neocortex seems to have a growth rate of its own, obviously showing a maximum of intracortical wiring among the mammalia. Whether this phenomenon implies a larger relative independence of the hemispheres from each other and from the brainstem, respectively, or even a lateralization of the hemispheres, is unclear at the moment. Obviously in sperm whales, and particularly in the giant sperm whale, audiomotor navigation and communication can be performed with a comparatively smaller brainstem and cerebellum. At the same time, and in comparison to delphinids, the number of different sound types produced by sperm whales seems to be reduced [Madsen et al., 2003, 2005].

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