

An examination of cetacean brain structure with a novel hypothesis correlating thermogenesis to the evolution of a big brain

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ABSTRACT

This review examines aspects of cetacean brain structure related to behaviour and evolution. Major considerations include cetacean brain-body allometry, structure of the cerebral cortex, the hippocampal formation, specialisations of the cetacean brain related to vocalisations and sleep phenomenology, paleoneurology, and brain-body allometry during cetacean evolution. These data are assimilated to demonstrate that there is no neural basis for the often-asserted high intellectual abilities of cetaceans. Despite this, the cetaceans do have volumetrically large brains. A novel hypothesis regarding the evolution of large brain size in cetaceans is put forward. It is shown that a combination of an unusually high number of glial cells and unihemispheric sleep phenomenology make the cetacean brain an efficient thermogenetic organ, which is needed to counteract heat loss to the water. It is demonstrated that water temperature is the major selection pressure driving an altered scaling of brain and body size and an increased actual brain size in cetaceans. A point in the evolutionary history of cetaceans is identified as the moment in which water temperature became a significant selection pressure in cetacean brain evolution. This occurred at the Archaeoceti – modern cetacean faunal transition. The size, structure and scaling of the cetacean brain continues to be shaped by water temperature in extant cetaceans. The alterations in cetacean brain structure, function and scaling, combined with the imperative of producing offspring that can withstand the rate of heat loss experienced in water, within the genetic confines of eutherian mammal reproductive constraints, provides an explanation for the evolution of the large size of the cetacean brain. These observations provide an alternative to the widely held belief of a correlation between brain size and intelligence in cetaceans.

Key words: intelligence, allometry, brain size, cerebral cortex, glia, marine mammals.

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I. INTRODUCTION

Many papers describing cetacean behaviour begin with a generalised statement to the effect of: ‘Dolphins are remarkably intelligent creatures ...’ (e.g. Tyack, 2000). Despite the high expectations placed upon the cetaceans as the only possible ‘alien’ species with which man may have a meaningful conversation of great intellectual depth (Lilly, 1962), scant evidence of this has been presented (Würsig, 2002). The compulsively anthropomorphic plurality of anecdotes provided in both the scientific and popular literature cannot be considered data (Budiansky, 1998; Forestell, 2002).

The belief in the apparently undeniable high level of intelligence is derived from two features of the cetaceans, one morphological and the other behavioural. The morphological rationale for exceptional intelligence is the large size and gyrencephalic nature of the brain (Fig. 1). Indeed, cetaceans have large brains, with some species having the largest brain of all animals, weighing in excess of 8 kg (Pilleri & Gahr, 1970). Humans also have large brains, which we recognise to be the basis of our intellectual capacities. One very influential view regarding the evolution of brain size is the relationship forwarded by Jerison (1973), that residual brain size (that remaining from a correction for body size) is a determinant of biological intelligence. Thus, the general conclusion is: large relative brain size equals great intelligence. This hypothesis has been attached to the cetaceans as proof of some form of extraordinary intelligence (Jerison, 1978). Perhaps unwittingly, Jerison has asserted that there can be only one reason for the brain to increase in relative size – an adaptive increase in its information-processing capacity, i.e. increased intelligence.

This assertion, which has been selectively examined in the case of cetaceans, and of which there is contradictory published data (e.g. the baleen whales have some of the lowest mammalian encephalisation quotients, so are they, despite having brains weighing several kilograms, therefore some of the most unintelligent mammals?), is the maxim for many studies of cetacean brain and behaviour. However, it is possible that increases in relative and actual brain size are not always adaptive responses to a need for greater information processing capacity but that brain size increases are a response to an alternative selection pressure. The present paper deals with this issue in regard to the evolution of brain size in cetaceans.

The second feature commonly construed to provide evidence of high intellectual capacities in the cetaceans is the vocal proclivity of this mammalian order. Language, dialects, conversations, grammatical competency, and several other human linguistic terms are often used to describe the vocalisations of cetaceans. All attempts to teach dolphins an imposed language are based upon stimulus-response behavioural paradigms (or operant conditioning) (Herman & Tavolga, 1980; Herman, 2002) – a basic form of learning (Thomas, 1996). At best, dolphins have been shown to be capable of learning approximately 40 symbolic associations (or ‘words’) (Herman & Tavolga, 1980; Herman, 2002). Other work has concentrated upon deciphering ‘dolphinsese’, i.e. the vocalisations themselves. However, studies of dolphin vocal repertoires have shown that they are limited to approximately seven (range 5–20) different characteristic sounds (Herman & Tavolga, 1980). The vocalisations are not a complex interwoven tapestry providing a basis for communication of thoughts and feelings, and they do not exhibit the higher order entropies typical of human language

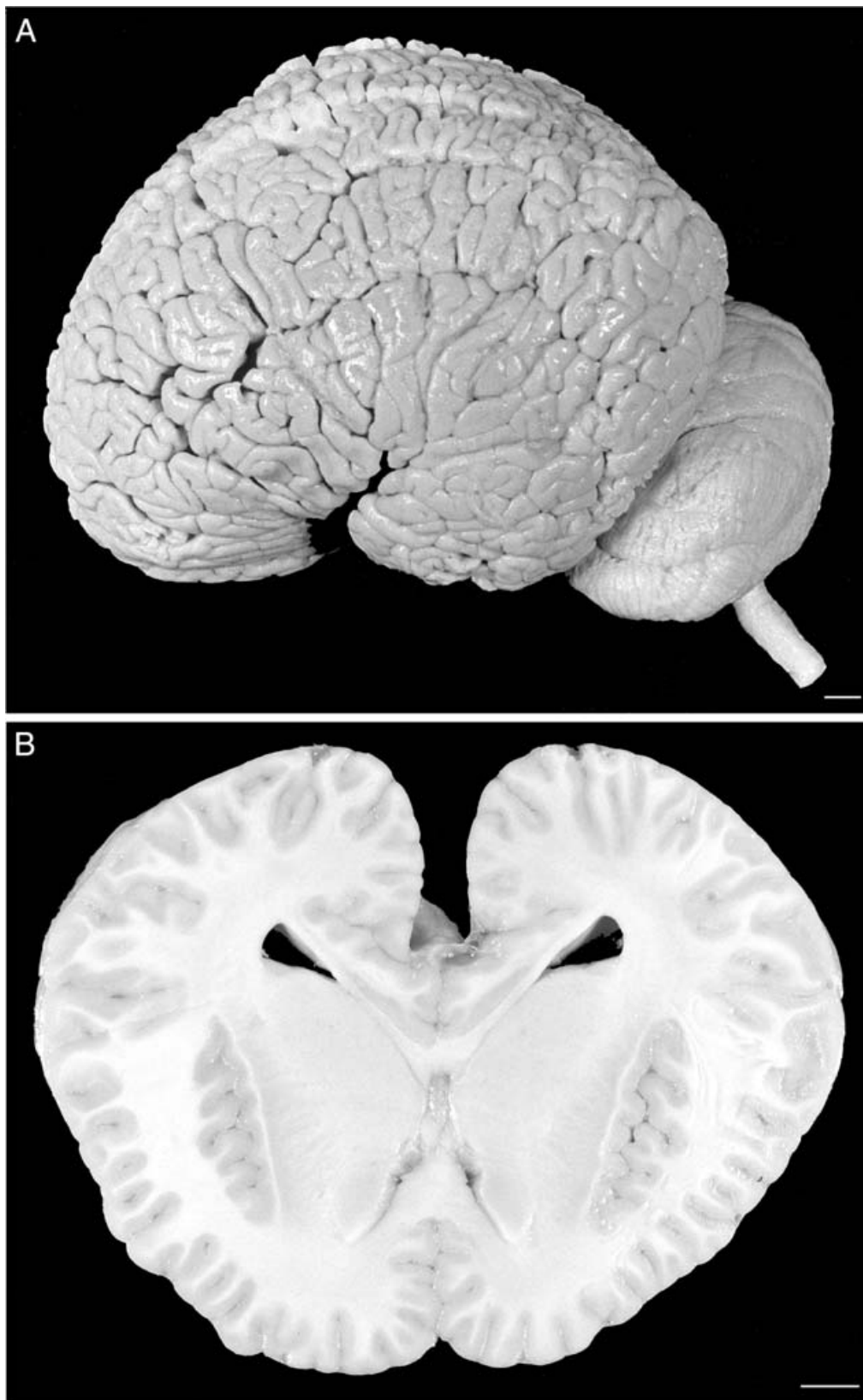


Fig. 1. (A) Photograph of the lateral surface of the killer whale (*Orcinus orca*) brain. Scale bar = 1 cm. (B) Photograph of a coronal slice through the brain of a piebald dolphin (*Cephalorhynchus commersonii*). Scale bar = 1 cm. The deep and convoluted sulci are characteristic of all cetacean brains. The sulci and gyri of the cetacean have the appearance of those found in human patients suffering from micropolygyria (Welker, 1990). The brains photographed here are from the collection of Dr Sam H. Ridgway.

Table 1. Brain mass, body mass, encephalisation quotients, and water temperatures used in the analyses included in the present study. Sources for brain and body masses are: (1) Gingerich (1998); (2) Schwerdtfeger *et al.* (1984); (3) Ridgway & Brownson (1984); (4) Ridgway (1990); (5) Marino (1998); (6) Pilleri & Gahr (1970); (7) von Bonin (1936); (8) Jacobs & Jensen (1964); (9) Jerison (1978); (10) Marino *et al.* (2004). Encephalisation quotients were calculated based on the general mammalian regression (see Fig. 2), and water temperatures were derived from the data compiled in Fig. 16.

Species	Brain mass (g)	Body mass (g)	Encephalisation quotient	Water temp. (°C)	Source
Eocene Archaeoceti					
<i>Saghacetus osiris</i>	388	350 000	0.66		1
<i>Dorudon atrox</i>	960	1 140 000	0.69		1
<i>Dorudon atrox</i>	1228.1	2 240 000	0.54		10
<i>Dorudon intermedius</i>	780	530 000	0.97		9
<i>Basilosaurus isis</i>	2520	6 480 000	0.51		1
<i>Basilosaurus cetooides</i>	2320.6	6 480 000	0.47		10
<i>Basilosaurus cetooides</i>	313.7	730 849	0.31		10
<i>Zygorhiza kochii</i>	829.6	2 040 000	0.39		10
<i>Rodhocetus kasrani</i>	290	590 000	0.34		1
<i>Rodhocetus kasrani</i>	301.5	290 000	0.58		10
<i>Dalanistes ahmedi</i>	400	750 000	0.39		1
Oligocene cetaceans					
indet. indet.	265.9	78 082	1.34		10
indet. indet.	525.8	54 811	3.44		10
<i>Agorophiidae</i> Genus Y n.sp.	1278.8	594 725	1.47		10
<i>Eosqualodontidae</i> n.gen. n.sp.	440.8	50 118	3.07		10
<i>Patriocetidae</i> n.gen. n.sp.	888	197 488	2.28		10
<i>Simocetus rayi</i>	549.7	94 268	2.42		10
<i>Xenorophus</i> n.sp.	892.4	96 849	3.85		10
Miocene cetaceans					
<i>Aulophyseter morricei</i>	2500	1 100 000	1.83		9
<i>Argyrocetus</i> sp.	650	72 000	3.48		9
indet. indet.	313.3	78 082	1.58		10
<i>Lagenorhynchus</i> n.sp. H	1169.9	98 674	4.98		10
<i>Lagenorhynchus</i> sp.	1392.4	112 805	5.37		10
<i>Kentriodon permix</i>	238.6	18 296	3.47		10
<i>Kentriodon permix</i>	285.9	17 037	4.38		10
<i>Kentriodon</i> sp.	661	41 653	5.28		10
<i>Kentriodon</i> n.sp. W	316.1	49 227	2.23		10
<i>Eurhinodelphis bossi</i>	983.5	123 019	3.56		10
<i>Eurhinodelphis bossi</i>	648.4	90 009	2.95		10
<i>Eurhinodelphis cristatus</i>	797.4	91 676	3.58		10
<i>Eurhinodelphis cristatus</i>	845.7	191 867	2.22		10
<i>Eurhinodelphis</i> n.sp. M	550.9	64 045	3.21		10
<i>Eurhinodelphis</i> sp.	447	57 772	2.81		10
<i>Eurhinodelphis</i> sp.	595.2	98 674	2.53		10
<i>Eurhinodelphis</i> n.sp. V	562.7	78 082	2.84		10
<i>Eurhinodelphis</i> n.sp. V	649.8	184 651	1.75		10
<i>Eurhinodelphis</i> sp.	674.2	57 772	4.24		10
<i>Schizodelphis</i> n.sp. B	358.6	74 379	1.88		10
<i>Schizodelphis</i> n.sp. B	496.1	64 904	2.87		10
<i>Schizodelphis</i> n.sp. H	665.8	57 030	4.23		10
<i>Schizodelphis</i> n.sp. H	354.4	62 426	2.11		10
<i>Schizodelphis</i> n.sp. H	494.1	85 894	2.33		10
<i>Schizodelphis longirostris</i>	402.1	94 819	1.76		10
<i>Schizodelphis longirostris</i>	512.9	89 984	2.33		10
<i>Schizodelphis longirostris</i>	617	84 253	2.95		10
<i>Schizodelphis longirostris</i>	374.2	90 009	1.70		10
<i>Schizodelphis</i> sp.	339.8	78 082	1.72		10
<i>Schizodelphis</i> sp.	431.2	67 363	2.42		10
<i>Orycterocetus crocodilimus</i>	2267.7	422 569	3.34		10
indet. indet.	635.6	57 470	4.01		10
<i>Allodelphis pratti</i>	885.6	170 823	2.53		10
indet. indet.	504	57 772	3.17		10

Table 1 (cont.)

Species	Brain mass (g)	Body mass (g)	Encephalisation quotient	Water temp. (°C)	Source
<i>Pomatodelphis</i> ? sp.	378.5	175 573	1.06		10
<i>Squalodon calvertensis</i>	653.4	151 534	2.03		10
<i>Squalodon calvertensis</i>	639.4	157 775	1.93		10
<i>Squaloziphius emlongi</i>	732.3	164 204	2.15		10
Extant cetaceans					
Suborder Odontocete					
Platanistidae					
<i>Platanista gangetica</i>	295	59 000	1.83		9
<i>Platanista minor</i>	164	18 300	2.38		2
Lipotidae					
<i>Lipotes vexillifer</i>	558	180 000	1.53	9–17	2
Pontoporiidae					
<i>Pontoporia blainvilliei</i>	220	34 900	1.99	15–25	2
Iniidae					
<i>Inia geoffrensis</i>	610	62 400	3.63	22–32	2
Monodontidae					
<i>Delphinapterus leucas</i>	2083	636 000	2.28	–1–9	3
<i>Monodon monoceros</i>	2997	1 578 330	1.69	–1–7	5
Phocoenidae					
<i>Phocoena phocoena</i>	477	52 300	3.23	2–19	2
<i>Neophocaena phocaenoides</i>	468	32 400	4.49	12–28	2
<i>Neophocaena asiaeorientalis</i>	422	34 000	3.91		2
<i>Phocoenoides dalli</i>	867	112 000	3.36	4–19	9
<i>Phocoenoides truei</i>	876	78 400	4.41		2
Delphinidae					
<i>Sotalia fluviatilis</i>	688	42 200	5.44	20–32	2
<i>Lagenorhynchus albirostris</i>	1126	67 500	6.32	2–17	2
<i>Lagenorhynchus acutus</i>	1200	120 000	4.43	3–21	2
<i>Lagenorhynchus obliquidens</i>	1140	90 000	5.19	4–14	2
<i>Grampus griseus</i>	2551	400 000	3.91	9–29	3
<i>Tursiops truncatus</i>	1530	165 000	4.47	13–29	4
<i>Stenella coeruleoalba</i>	820	56 300	5.25	15–29	2
<i>Delphinus delphis</i>	765	52 000	5.19	13–29	2
<i>Orcinus orca</i>	5617	2 049 000	2.62		3
<i>Globicephala melas</i>	2673	1 061 000	2.01	4–20	3
Ziphiidae					
<i>Ziphius cavirostris</i>	2004	2 273 000	0.87		3
<i>Mesoplodon mirus</i>	2355	929 000	1.95	8–18	5
<i>Mesoplodon europaeus</i>	2149	732 000	2.12	8–18	5
<i>Mesoplodon densirostris</i>	1463	767 000	1.39	18–29	5
Physeteridae					
<i>Kogia breviceps</i>	1012	305 000	1.89	13–23	5
<i>Kogia simus</i>	622	168 500	1.79	18–26	5
<i>Physeter catadon</i>	7818	37 093 000	0.44	15–23	3
Suborder Mysticete					
Eschrichtiidae					
<i>Eschrichtius robustus</i>	4316.67	30 000 000	0.28	–1–4	6
Balaenopteridae					
<i>Balaenoptera borealis</i>	4900	20 000 000	0.43	2–8	8
<i>Balaenoptera physalis</i>	7111.43	33 221 430	0.43		6
<i>Balaenoptera musculus</i>	3636	50 904 000	0.16	–1–5	9
Megaptera					
<i>Megaptera novaeangliae</i>	6439	39 311 330	0.35	–1–5	6

indet. = indetermined genus or species.

(McCowan, Hanser & Doyle, 1999). Rather, these seven typical vocalisations appear to be seven different species-specific calls, such as has been seen in many other animals, some of which have far more calls than the seven typically found for bottlenose dolphins. In summary, it appears that the evidence in favour of significant intellectual capacities of dolphins is tenuous, and based upon untested, unproven, unquestioned, and anthropomorphic assumptions.

The present paper provides a critical review of cetacean brain structure in comparison to the brain of other mammals. No invasive experiments of the cetacean brain have been undertaken in the modern era of neuroscience due to the Marine Mammal Protection Act; thus the only way to decipher cetacean brain function is from comparative information garnered from laboratory animal experimentation and compare this to post-mortem cetacean tissue. Observations on cetacean brain structure presented here are derived from sources in the literature and primary observations. Cetacean brain allometry is reanalysed and compared to both extant and extinct mammals, and to the environment of the various cetacean species. The allometry and structure of the cerebral cortex is reviewed in light of several recent and older studies demonstrating an atypical structure of the cerebral cortex in cetaceans. Two specialisations of the cetacean brain are described, which relate to the vocalisations and sleep physiology of the cetaceans. The evolution of the cetacean brain is traced by comparing fossil endocasts of extinct cetacean species with those of modern cetaceans. These data are assimilated to provide a neuro-anatomical basis indicating that cetaceans lack sophisticated cognitive abilities. Finally, a data-based hypothesis is forwarded suggesting that the evolution of large brain size in cetaceans is an adaptation to a thermally challenging environment.

II. ALLOMETRY OF THE CETACEAN BRAIN

(1) The brain-body mass relationship amongst mammals – interspecific and intraordinal comparisons

The allometric relationship between brain mass and body mass in vertebrates has been calculated, recalculated, and speculated upon for well over a century (reviewed in Jerison, 1973). It is clear that a significant, statistically reliable predictor of brain mass across the majority of vertebrate species is body mass, although the reasons for this are still speculative (Armstrong, 1990; Harvey & Krebs, 1990). Three types of allometric calculations are generally undertaken, those comparing species' averages from a range of orders (interspecific), those comparing species' averages from the same order (intraordinal), and those comparing data from individuals within the same species (intraspecific) (Armstrong, 1990). The first two of these comparisons are considered in this section, the latter in the next section.

Several studies have examined the brain mass *versus* body mass relationship of cetaceans (e.g. Pilleri & Gahr, 1970; Jerison, 1978), and a reanalysis of this relationship with additional data and a new perspective is undertaken here.

Brain mass and body mass data were taken from several published sources (see Table 1), and other mammals (Bininda-Emonds, Gittleman & Kelly, 2001; Crile & Quiring, 1940; Stephan, Frahm & Baron, 1981; Wood & Collard, 1999). Allometric equations using least-squares regression analysis were calculated for five groups: odontocete cetaceans, odontocete combined with mysticete cetaceans, hominids, primates, and the remaining mammals (Fig. 2). The division of the analysis into these five groups was done for the following reasons. Firstly, the majority of mammals show a similar brain-body scaling across species, thus, it is most efficient to deal with these data as an inter-specific comparison, to provide a baseline for comparison to the species of interest. An intraordinal analysis was used for primates (excluding the hominids), as it is clear from previously published material that this group, while scaling in a similar manner to other mammals, does have a substantially different brain mass: body mass ratio. An intrasubordinal analysis was appropriate for hominids because of the dramatic difference in scaling of this suborder in comparison to other primates. Finally, an intraordinal analysis of the cetaceans, and intrasubordinal analysis of the odontocetes were used, as in both cases the species within this order have a different brain mass: body mass scaling compared to that of other mammals.

In the present analysis, the plot of brain (M_{br}) *versus* body mass (M_b) for mammals in general (excluding cetaceans and primates) gave results similar to those previously published (e.g. Armstrong, 1990; Harvey & Krebs, 1990). The allometric equation calculated was:

$$M_{br} = 0.069M_b^{0.718} \quad (r^2 = 0.950; P = 2.4 \times 10^{-178}). \quad (1)$$

Note from equation (1) that the slope of the line (0.718) and the constant k (0.069) are in agreement with several previous studies (see references in Armstrong, 1990 and Harvey & Krebs, 1990). Also, the correlation coefficient is extremely high, thus, for most mammals 95 % of the variability in brain mass can be accounted for by the variability in body mass.

The equation calculated for primates (excluding hominids) is:

$$M_{br} = 0.100M_b^{0.756} \quad (r^2 = 0.939; P = 6.1 \times 10^{-50}). \quad (2)$$

The slope of this regression (0.756) reflects a similar pattern of scaling of primate brain mass *versus* body mass when compared with other mammals, but primates appear to have a greater brain mass relative to body mass than most mammals (as reflected in the higher constant, $k=0.100$). Again r^2 is high, with 94 % of the variability in brain size of primates being accounted for by changes in body size.

The scaling of brain mass and body mass in hominid species, both extinct and extant is given by:

$$M_{br} = 0.000003M_b^{1.793} \quad (r^2 = 0.867; P = 0.00016). \quad (3)$$

The slope of the line (1.793) appears steeper than that seen for mammals (equation 1) and primates (equation 2) (although $P=0.059$ using the mean squares between and within slopes, indicating that while the slopes calculated by the regression analysis are not statistically different, the P value is close to significance, possibly as a result of the

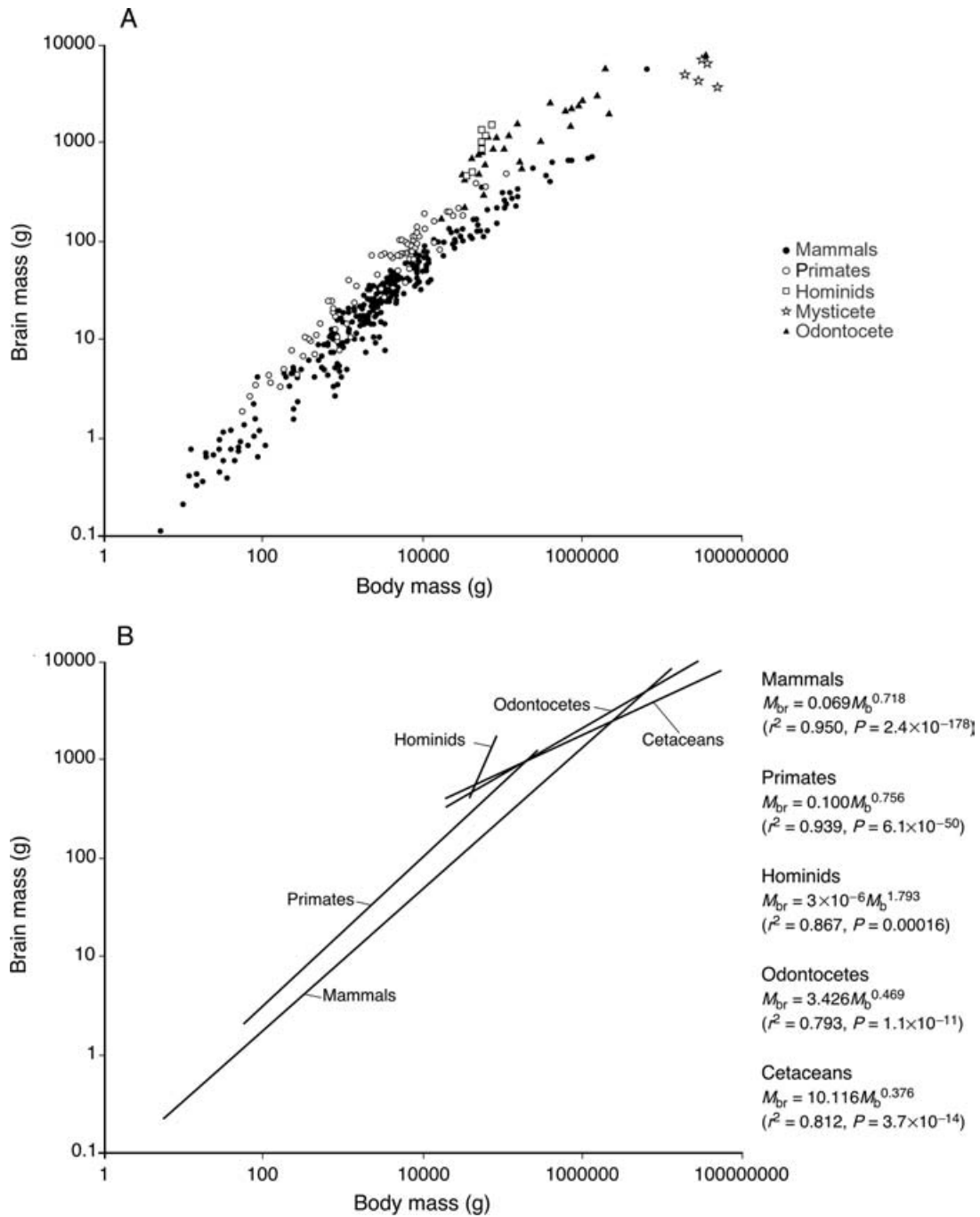


Fig. 2. (A) Plots of the raw data of brain (M_{br}) and body mass (M_b) of a variety of mammalian species. The present analysis examined four groups, mammals in general (black circles), primates (open circles), hominids (open squares), and cetaceans (odontocetes – triangles, mysticetes – stars). (B) Regression lines and allometric equations of the various groups examined in the present analysis. Note the altered scaling for both hominids and cetacean species from that seen for mammals and primates. The data used in this plot are derived mainly from Crile & Quiring (1940), and other sources listed in Table 1.

small sample size for hominids compared to mammals); r^2 is lower so that for hominids, only 87 % of the variability in brain mass can be accounted for by body mass variation.

For the odontocetes the regression equation is:

$$M_{br} = 3.426M_b^{0.469} \quad (r^2 = 0.793; P = 1.1 \times 10^{-11}), \quad (4)$$

and for all cetacean species (odontocetes + mysticetes):

$$M_{br} = 10.116M_b^{0.376} \quad (r^2 = 0.812; P = 3.7 \times 10^{-14}). \quad (5)$$

For odontocetes, the slope of the line, at 0.469, is significantly less steep than that of the other mammalian groups examined ($P = 1.6 \times 10^{-8}$, using the mean squares between

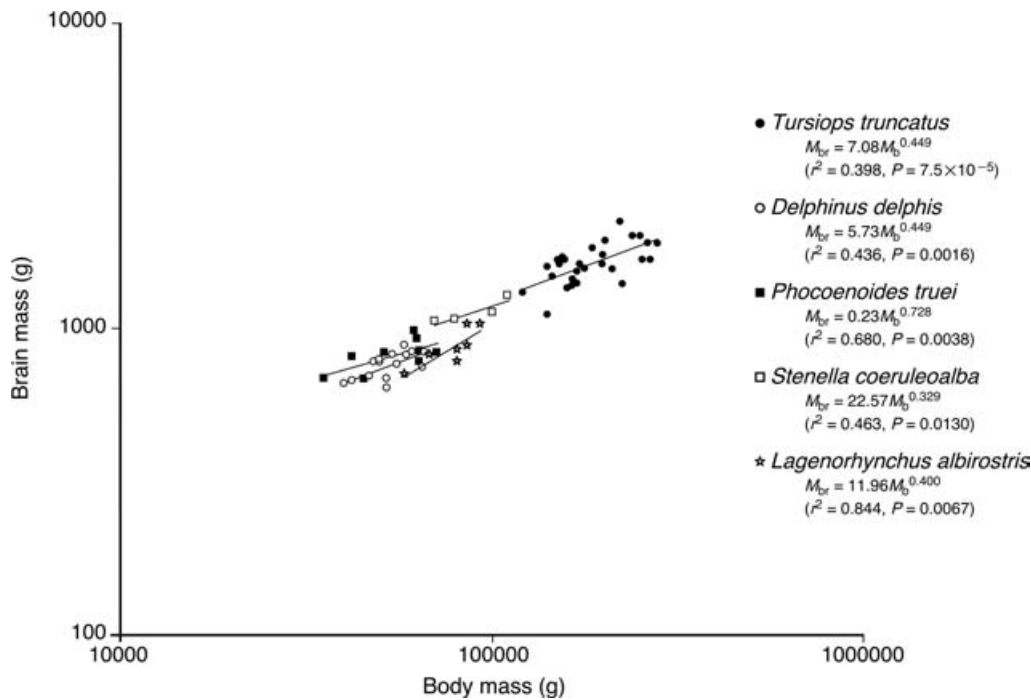


Fig. 3. Intraspecific scaling of brain mass (M_{br}) versus body mass (M_b) for five cetacean species. Data are derived from Pilleri & Gihir (1970), and Ridgway (1990).

and within slopes). For all cetaceans (equation 5), the slope flattens even more, at 0.376 (comparison with the other four groups using the mean squares between and within slopes $P=9.1 \times 10^{-26}$). Note that cetaceans vary from the general mammalian, or primate brain-body mass scaling in the opposite direction to the trend shown by hominids. For the odontocete cetaceans and all cetaceans, only 80% or 81%, respectively, of the variability in brain mass can be accounted for by variability in body mass.

These calculations indicate that the brain mass versus body mass relationship in cetaceans differs significantly from that for other mammals while the hominid data also suggest a different trend (see above). Analyses of individual orders of mammals give slopes in the range of 0.55–0.66 (see the evolutionary analysis of ungulates in Section VI and Fig. 12; and the results of the studies referenced in Armstrong, 1990). We can conclude that while there is a trend for increasing brain size with increasing body size in cetaceans and hominids, in accordance with the general trend in mammals (and indeed in other vertebrates), there must be additional factors causing the observed differences in scaling. The altered scaling of cetaceans is in the opposite direction to the trend seen in hominids, and while cetaceans are fully aquatic, hominids have remained terrestrial, thus, it seems likely that different selection pressures acted upon cetaceans and hominids leading to the observed scaling in these groups.

(2) The brain-body mass relationship within a single species – intraspecific comparisons

Intraspecific comparisons have shown that the brain-body mass scaling within a single species is quite different to

that of intraordinal and interspecific scaling with a mean slope of 0.22 (see Armstrong, 1990, and references listed therein). Thus, an individual twice the body mass of a conspecific is likely to have a brain $2^{0.22}$, or 116.47%, larger. This scaling has been found in a range of mammalian species, including humans, various primates, moles, dogs, sheep, pigs, raccoons and ferrets (see references in Armstrong, 1990). The curious exception to this general consensus is the domestic cat, where the slope was 0.67, closer to the intraordinal or interspecific scaling values (Bronson, 1979).

While intraspecific analyses of cetacean species are available (Pilleri & Gihir, 1970), a reanalysis of these data with additional data from other publications (e.g. Ridgway, 1990) is undertaken here. Only data judged to be reliable are used, thus, individual data points that lie grossly out of the normal range of the adult, presumably indicating either a juvenile or sick animal, were excluded. Moreover, data where body mass was estimated rather than measured, such as for the larger cetaceans, were also excluded. Intraspecific analyses were undertaken on *Lagenorhynchus albirostris*, *Stenella coeruleoalba* (formerly *Stenella styx*), *Phocoenoides truei*, *Delphinus delphis*, and *Tursiops truncatus* [data from Pilleri & Gihir (1970) except *Tursiops truncatus* which were from Ridgway (1990)]. Allometric equations, as described above, were calculated for each of these species (Fig. 3).

These allometric equations have slopes ranging between 0.329 and 0.728, which appear to differ from the slope of 0.22 found for the majority of mammalian species previously studied (Armstrong, 1990). In the above intraordinal analyses of the odontocetes (eq. 4) and all cetaceans (eq. 5), the slopes were 0.469 and 0.376. The intraspecific allometric

slopes are very close to these values, with one exception, that of *Phocoenoides truei*, where the slope was 0.728. The range of slopes, and lower correlation coefficients, found in the intraspecific analysis may be due to the small data sets. However, to a first approximation the general trend for intraspecific scaling of brain and body mass in cetacean species is similar to that found for the intraordinal allometric scaling (in all cases the calculated regression slopes for individual cetacean species are not significantly different to that of the slope calculated for odontocetes using the mean squares between and within slopes: *T. truncatus* vs odontocetes, $P=1$; *D. delphis* vs odontocetes, $P=1$; *P. truei* vs odontocetes, $P=1$; *S. coeruleoalba* vs odontocetes, $P=1$; *L. albirostris* vs odontocetes, $P=1$).

It has been proposed that: 'If species-specific differences arose through natural selection, one obvious hypothesis is that individual differences within a species would have the same slope, so that selection for a bigger body (or brain) would scale the correlated feature to the appropriate size.' (Armstrong, 1990). This clearly is not the case for most mammals (Armstrong, 1990); however, the scaling of intraspecific differences in brain and body mass in cetaceans is similar to the intraordinal scaling of these species. It is therefore likely that natural selection, *via* a specific selection pressure, initiated the altered scaling of brain and body in cetaceans, and that this selection pressure continues to influence brain-body scaling in extant cetacean species. Thus, identification of a selection pressure influencing the scaling seen in extant cetaceans could also explain the evolution of the difference in scaling of the entire order.

(3) The encephalisation quotient

Jerison (1973) suggested that the encephalisation quotient (EQ), i.e. the relative amount of brain per unit body size, can be used as a direct estimate of the intelligence of a species. This use of the EQ is encapsulated by Gibson (2001, p. 3): 'In Jerison's framework, mammals were the most intelligent vertebrates, and those mammals whose brain size exceeded the predicted brain size of other mammals of similar body size were the most intelligent mammals.' While a superficial examination of the data seems to fit intuitive reasoning concerning the intellectual abilities of certain species, this proposal has not stood up to scrutiny as a measure of biological intelligence (Harvey & Krebs, 1990). Despite this, the modern literature on cetacean brain-body allometry still uses the EQ as cause for speculation on the intellectual capacities of cetaceans (e.g. Marino, 1998).

I have recalculated the EQs of all cetaceans using the allometric equation obtained for most mammals (eq. 1). The choice of a reference group is a much-debated issue in the study of allometry (Bauchot & Stephan, 1966; Jerison, 1973; Stephan *et al.*, 1981), however, as we are investigating differences between cetaceans and other mammals, the use of equation (1) is appropriate. The EQs of cetaceans (Fig. 4) show that some species have large EQs (second only to humans) while some have very low values (lower than the average mammalian EQ of 1). The range of values seen is not surprising, as the slope of the allometric equation for

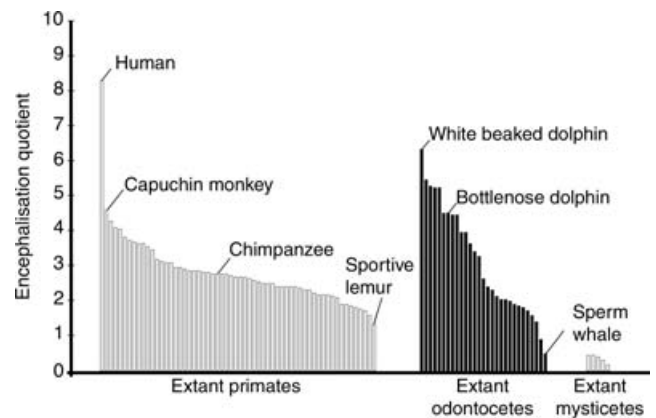


Fig. 4. Bar graph of the encephalisation quotients (EQs) of extant primates and cetaceans.

brain mass: body mass for cetaceans (Fig. 2B) is quite shallow, intersecting the regression lines derived for most mammals and for primates. The raw data plot (Fig. 2A), shows that some cetaceans fall well above the regression lines for most mammals and primates, while some are well below.

The calculation of the EQ is a relatively simple matter and, to an extent, the conclusions drawn are dependent on the species included in the data set. For example, Marino (1998) calculated the EQ of odontocete cetaceans, however, did not include published data for several key odontocete species. The exclusion of such species as *Physeter catadon*, which has both a large brain and body mass is likely to alter the outcome of this analysis: the slope calculated for the brain: body mass scaling of odontocetes by Marino (1998) is 0.53, which is statistically similar to that found in the present study: 0.469, equation (4) [comparison of the regression slopes calculated for the data of Marino (1998) compared with that used in the present study for odontocetes only revealed no significant difference ($P=0.275$) using the mean squares between and within slopes]. The inclusion of the mysticetes into the regression analysis leads to a significant shallowing of the slope of the regression: 0.38, equation (5) [comparison of the regression slopes calculated for the data of Marino (1998) compared with that used in the present study for all cetaceans revealed a significant difference ($P=0.029$) using the mean squares between and within slopes]. Conclusions regarding ordinal encephalisation levels should aim to include as many data points as possible. Marino (1998) only included odontocetes with similar brain mass: body mass ratios to the anthropoid primates (see Fig. 1 in Marino, 1998). Not surprisingly therefore Marino (1998) concludes: '... the gap between human and non-human levels of encephalisation (and, in a general way, intelligence) is substantially narrowed by a nonprimate group ...'. Marino (1998) goes on to assert that cetaceans, especially the highly encephalised Delphinidae, are second only to humans in intelligence. While the EQ is a useful allometric measure (see Section VIII), it is difficult to resolve this as a measure of biological intelligence as proposed by

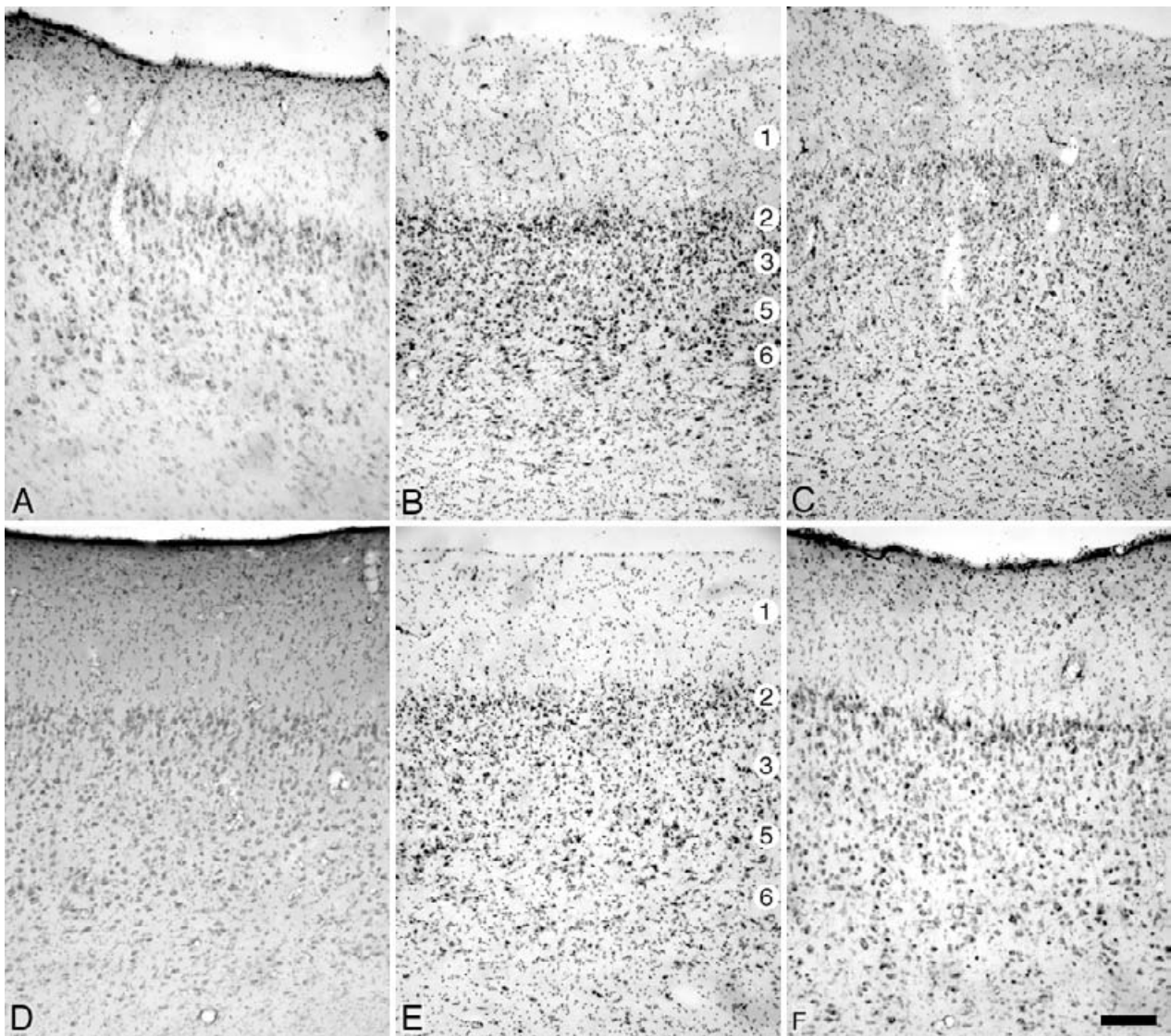


Fig. 5. Nissl-stained sections of the cerebral cortex in three cetacean species from different families. Cortical layers 1–3, 5 and 6 are identified in B and E. A–C are from putative primary visual cortex (V1); D–F are from putative primary auditory cortex (A1). A and D are from a beluga whale (*Delphinapterus leucas*, brain mass 2083 g), B and E from a pilot whale (*Globicephala melas*, brain mass 2673 g), and C and F from a goose-beaked whale (*Ziphius cavirostris*, brain mass 2004 g). Features of the cetacean cortex, such as a lack of the granular layer 4, poor columnar organisation, thick layer 1, unclear lamination of layers 3 to 6, low cellular density, and high glia density, among others, are evident in these sections of primary sensory cortex. Scale bar = 500 μm , applies to all panels. The photomicrographs used in this figure were generously supplied by Patrick Hof from the Morgane-Jacobs-Glezer marine mammal brain collection.

Jerison (1973). The high EQ values found in some cetaceans may simply be due to the altered allometric scaling of brain and body masses.

III. THE CETACEAN CEREBRAL CORTEX

The cerebral cortex is the most complex information-processing station in the brain of all mammals. It is thought to be central to many major processes, such as intra- and inter-sensorial perceptual binding, and long-term memory,

and is believed by many to be essential for complex cognitive behaviours.

(1) Lamination of the cetacean cerebral cortex

Several previous studies have described the cytoarchitectural features and lamination of the cerebral cortex of cetaceans. The majority of these reach conclusions that do not differ from much earlier examinations (Major, 1879). A brief overview of the cytoarchitecture of the cetacean cerebral cortex is provided here with representative examples shown in Fig. 5.

Several authors comment upon the thickness of layer 1 across the entire cetacean cerebral cortex (e.g. Haug, 1987; Hof *et al.*, 2000; Kesarev, Malofeyeva & Trykova, 1977; Kojima, 1951; Revishchin & Garey, 1991). Layer 2 is generally acknowledged to be the most cell-dense, thinnest, and distinct layer in the cetacean cerebral cortex. Moreover, it is regularly reported that the majority of neurons in layer 2 are pyramidal in nature, with a scarcity of granular neurons, i.e. a 'pyramidalisation' of layer 2 has occurred (e.g. Kojima, 1951; Manger *et al.*, 1998; Pilleri & Gühr, 1970). Layer 3 is a relatively thick cortical layer in cetaceans, and is composed of a moderate density of large pyramidal cells. The size of the pyramidal cells increases with depth in this layer (Kojima, 1951), and some authors have described sublamina on this basis (Morgane, Glezer & Jacobs, 1988). Almost all authors agree that layer 4 is either absent or extremely underdeveloped (e.g. Breathnach, 1960; Glezer, Hof & Morgane, 1998; Hof *et al.*, 1994, 2000; Kesarev *et al.*, 1977; Kojima, 1951; Morgane *et al.*, 1988). Glezer, Jacobs & Morgane (1988) describe layer 4 as 'incipient'. Layer 5 appears to show little regional differences in thickness. It is especially prominent in the motor region of the cortex, due to the giant cells of Betz. However, the border between layers 3 and 5 is often described as indistinct (e.g. Breathnach, 1960; Kesarev *et al.*, 1977; Kojima, 1951). Layer 6 is also found in all regions of the cortex and is made up of several neuronal types including scattered large pyramidal, round and stellate neurons (e.g. Breathnach, 1960; Kesarev *et al.*, 1977; Kojima, 1951).

Three points of interest emerge from the above: the lamination of the cetacean cerebral cortex is not distinct; layer 2 exhibits 'pyramidalisation'; and layer 4 appears to be largely absent. Various names have been given to the type of cerebral cortex exhibited by the cetaceans; however, Brodmann's (1909) terminology appears most appropriate. On the basis of the lack of layer 4, cetacean cerebral cortex is a 'heterotypical formation' resulting from a reduction in the number of cortical layers. This is supported by the observation of a thin layer 4 in the visual cortex of the bottlenose dolphin during development (Garey & Leuba, 1986). Brodmann (1909) also noted the pyramidalisation (Pilleri & Gühr, 1970), or the 'secondary transformation', of the neuronal elements of layer 2 in various species of mammals. The laminar organisation of the cetacean cerebral cortex should thus be considered a heterotypical formation in which layer 2 has undergone a secondary transformation specific to the Cetacea.

(2) Parcellation of the cerebral cortex

An increase in the number of cortical areas is commonly thought to reflect an increase in behavioural complexity. Kaas (1995) stated that: '... the functioning of large brains may be enhanced by having more subdivisions'. The number and organisation of cortical areas in several species of mammals has been studied, however, few attempts have been made to subdivide the cortex of the cetaceans. Subdivision of the cortex can be assessed using several techniques; however, those used on the cetacean cortex are

limited to cytoarchitectural analysis and a small amount of electrophysiological mapping.

The large surface area of the cerebral cortex of the cetaceans makes parcellation a daunting task, especially under the generally accepted paradigm that larger brains are composed of more sensory subdivisions (Kaas, 1995). However, several studies have localised regions of bottlenose dolphin neocortex using cytoarchitectural techniques (Garey & Leuba, 1986; Kesarev *et al.*, 1977; Kojima, 1951; Manger *et al.*, 1998; Morgane *et al.*, 1988) and electrophysiological recording (Bullock & Gurevich, 1979; Ladygina, Mass & Supin, 1978; Lende & Akdikmen, 1968; Lende & Welker, 1972; Sokolov, Ladygina & Supin, 1972). These provide a reasonable degree of detail regarding localisation of areas within the bottlenose dolphin cortex (Fig. 6).

Kesarev *et al.* (1977) describe six major cytoarchitectonic regions within the dolphin neocortex (Fig. 6A–D). These regions are in turn subdivided into one or more cytoarchitectonic fields. Physiological observations have provided details of the locations of sensory projection areas in the neocortex, these being visual and auditory (Ladygina *et al.*, 1978; Sokolov *et al.*, 1972) and somatosensory and motor areas (Lende & Akdikmen, 1968; Lende & Welker, 1972) (Fig. 6E–H). There appears to be good correlation between the cytoarchitectural and electrophysiological observations.

Kesarev *et al.* (1977) describe a region of cortex that they term occipital (O), located on the occipital and posterior midline cortex. This region corresponds to regions of cortex responsive to visual stimulation (Ladygina *et al.*, 1978; Sokolov *et al.*, 1972). Kesarev *et al.* (1977), Morgane *et al.* (1988) and Sokolov *et al.* (1972) describe three cytoarchitectonic fields within this region, one of which probably corresponds to primary visual cortex (described as medial occipital area, Om; heterolaminar; and short latency, respectively in these three publications). Photomicrographs of sections through this region suggest that layer 4 may be present although cells that are granular in appearance are interspersed within lower layer 3 and upper layer 5 (Kesarev *et al.*, 1977). The second cytoarchitectonic field (described as superior occipital, Os; homolaminar; and long latency, respectively) may correspond to extrastriate visual cortex; however, this region has not been subdivided into multiple areas as in other mammalian species, as no further studies have examined this region of the cetacean cortex. The third cytoarchitectonic field, the borderline medial occipital area (Olm), lies in a position postero-medial to the Om, and exhibits an architecture that indicates that it might correspond to the splenial visual area of other mammals (assuming that Om is primary visual cortex) (Rosa, 1999).

Lateral to the occipital cortex, Kesarev *et al.* (1977) describe a large region of dorsal surface cortex, which they term parietal cortex (P). This region corresponds with the region known to be responsive to auditory stimulation (Ladygina *et al.*, 1978; Sokolov *et al.*, 1972). This P region has been subdivided into four cytoarchitectonic fields (superior parietal Ps, medial parietal Pm, inferior parietal Pi, and transitional parietal Pli), each of which is likely to represent an auditory cortical area. It is unclear which cytoarchitectonic field represents primary auditory cortex and which are secondary or tertiary auditory areas.

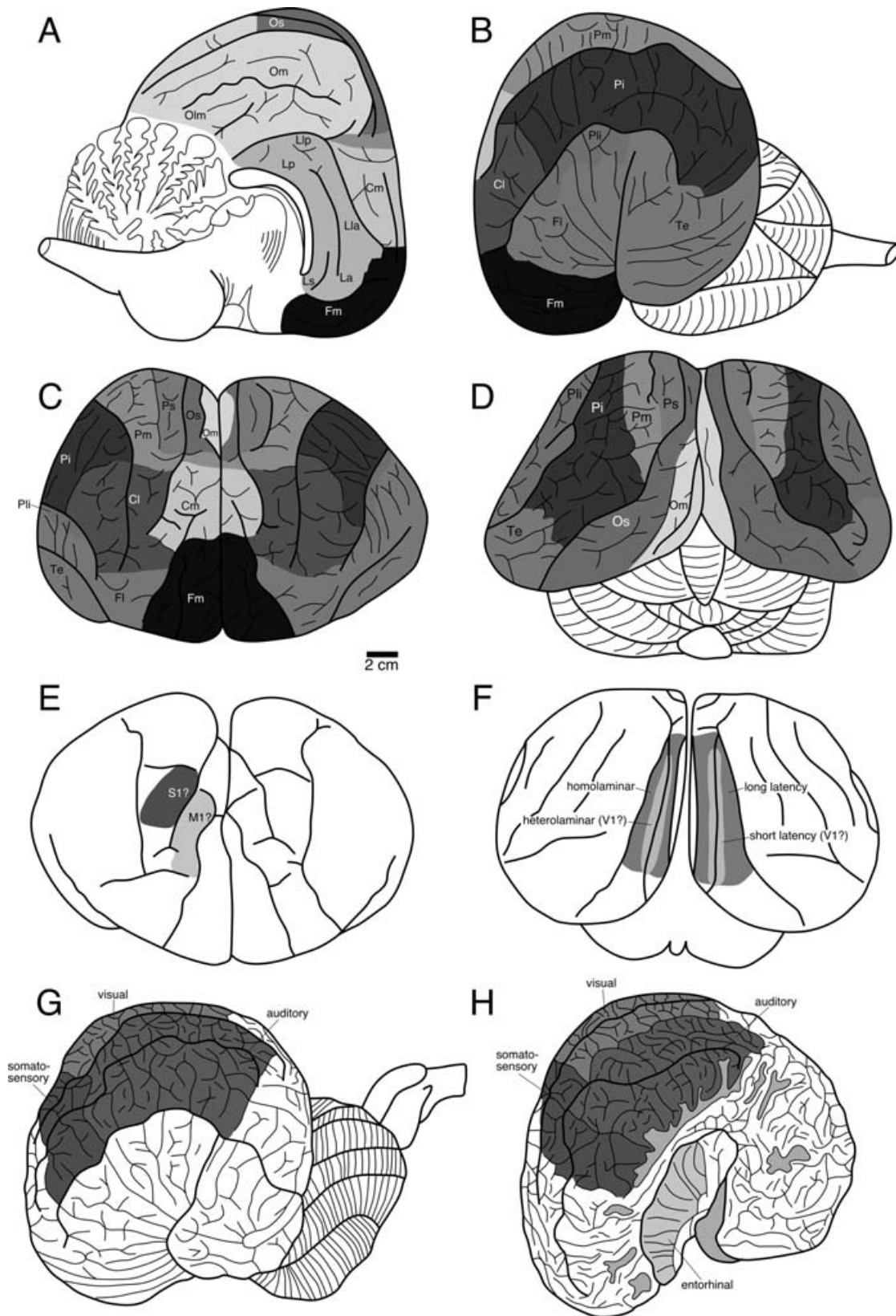


Fig. 6. Parcellation of the cetacean cerebral cortex demonstrating the architectonic and physiological subdivisions of the cerebral cortex of the bottlenose dolphin. A–D are redrawn from the architectonic subdivisions of Kesarev *et al.* (1977). The regions are labelled according to the original publication as follows: Cl, central lateral area; Cm, central medial area; Fi, frontal lateral area;

Lateral and posterior to both the occipital and parietal regions of cortex is an underdeveloped wedge-shaped piece of cortex termed temporal cortex (T) by Kesarev *et al.* (1977). This is likely to correspond to the temporal cortex of other mammalian species, an assumption based on its location relative to the visual and auditory regions. It is composed of two cytoarchitectonic fields, the internal temporal area (Ti) and the external temporal area (Te). Anterior to both the occipital (visual) and parietal (auditory) regions of cortex lies a region designated as central (C) by Kesarev *et al.* (1977). This region corresponds to the regions responsive to somatosensory stimulation (Ladygina *et al.*, 1978; Lende & Welker, 1972; Sokolov *et al.*, 1972) and that producing motor actions upon electrical stimulation (Lende & Akdikmen, 1968). Kesarev *et al.* (1977) described central lateral (Cl) and central medial (Cm) cytoarchitectonic fields; Cl appears to correspond to somatosensory cortex and Cm to primary motor cortex. The Cm region appears to correspond to the region designated primary motor cortex in the sperm whale by Kojima (1951) (Fig. 7), due to the presence of Betz cells (Kesarev *et al.*, 1977).

Anterior to central cortex (somato-motor cortex) is a small region designated frontal (F) by Kesarev *et al.* (1977). This region is composed of frontal lateral (Fl) and frontal medial (Fm) cytoarchitectonic fields, and is located on the most anterior pole of the cerebral cortex. On topological grounds, one might be tempted to designate this region prefrontal cortex; however, several observations indicate that this is probably not the case. The exact definition of prefrontal cortex across mammals is a complex and much debated issue (e.g. Divac & Öberg, 1990; Preuss, 1995); however, this debate may be avoided by a closer examination of the cytoarchitecture of this region. The feature of most interest is the presence of numerous giant pyramidal cells in this region of cortex (dolphin – Langworthy, 1932; Kesarev *et al.*, 1977; sperm whale – Kojima, 1951) (Fig. 7). These cells exist in primary motor cortex and premotor cortex of other species of mammals (Brodal, 1968, 1978, 1980) (Fig. 7), and give rise to the cortico-pontine projection. They are not found in prefrontal cortex. This observation suggests that this region of cortex is premotor cortex, and stimulation of this region does produce motor movements (Lilly, 1962). One must note that this cytoarchitectonically distinct region of cortex extends to the most anterior portion of the cerebral cortex, thus, *if* there is a region of cortex that may be defined as prefrontal in the cetaceans, it is very small.

On the medial surface of the hemisphere, located between the corpus callosum and the cingulate sulcus, is the region of cortex defined as limbic cortex (L) by Kesarev *et al.* (1977) (Fig. 6). Compared to other mammals, this region of cortex is rather reduced in size, and probably corresponds to cingulate cortex. Kesarev *et al.* (1977) describe five cytoarchitectonic fields in this region but also note the rather homogeneous nature of this cortex. Finally, on the medial bank of the insular cortex, entorhinal cortex has been located, in a topological position that is consistent with its location in other mammals (Manger *et al.*, 1998).

The assignments of the cortical regions given above are consistent with studies of thalamocortical connectivity in cetaceans (Revischin & Garey, 1990). Within the realms of interspecies comparisons, it therefore appears that the overall topology of the areal subdivision of cerebral cortex in cetaceans does not differ dramatically from that seen in other mammals. However, four points of importance emerge: there does not appear to be a prefrontal cortical region; the number of subdivisions of the cortex appears to be low compared with other mammals with similarly sized brains or even mammals with far smaller brains; the temporal cortical region is small and undeveloped; and the limbic region of cortex, or cingulate cortex, is small, especially in its anterior aspect.

(3) Columnar organisation of the cerebral cortex

Vertically oriented columnar structures within the sensory cerebral cortex have been identified in a range of mammalian species. These include several distinct types, from the physiological columns first described by Mountcastle (see review by Mountcastle, 1997), that often correspond to anatomically identifiable modules (e.g. Manger *et al.*, 1998), to the microcolumns (or minicolumns) that make up the larger cortical columns (Jones, 2000). These radially organised columns cross layer boundaries and are thought to represent the fundamental processing units of the sensory cerebral cortex. In cetaceans, visually identifiable cortical columnar organisation has only been reported in the entorhinal cortex of the bottlenose dolphin (Manger *et al.*, 1998). It is difficult to identify columnar and microcolumnar organisation in the photomicrographs of architectonically defined regions of dolphin brain provided by Kesarev *et al.* (1977), whereas these features are readily identifiable in the cortex of other mammals (Jones, 2000; Manger *et al.*, 1998;

Fm, frontal medial area; La, anterior limbic area; Lla, anterior borderline area; Llp, posterior transitional, or borderline, limbic area; Lp, posterior limbic area; Ls, anterior subgenual area; Olm, borderline medial occipital area; Om, medial occipital area; Os, superior occipital area; Pi, inferior parietal area; Pli, transitional parietal area; Pm, medial parietal area; Ps, superior parietal area; Te, external temporal area. (E) The approximate locations of primary somatosensory (S1) and primary motor (M1) cortex from the mapping studies of Lende & Akdikmen (1968) and Lende & Welker (1972). Note the correspondence of the partial maps to the areas termed Cl and Cm by Kesarev *et al.* (1977). (F) Architectonic and physiological locations of visual cortex from the studies of Morgane *et al.* (1988) and Sokolov *et al.* (1972). It appears that the heterolaminar and short latency regions correspond to V1 of other mammals. Note the correspondence between these regions and the regions termed Os and Om by Kesarev *et al.* (1977). (G, H) Physiological subdivisions of dolphin cerebral cortex from Ladygina *et al.* (1978). Note the correspondence of the visually responsive cortex to regions Os, Om and Olm, auditory to regions Pi, Pli, Pm and Ps, and somatosensory to Cl, in the scheme of Kesarev *et al.* (1977). The location of entorhinal cortex is from Manger *et al.* (1998). Scale bar in C applies to all panels.

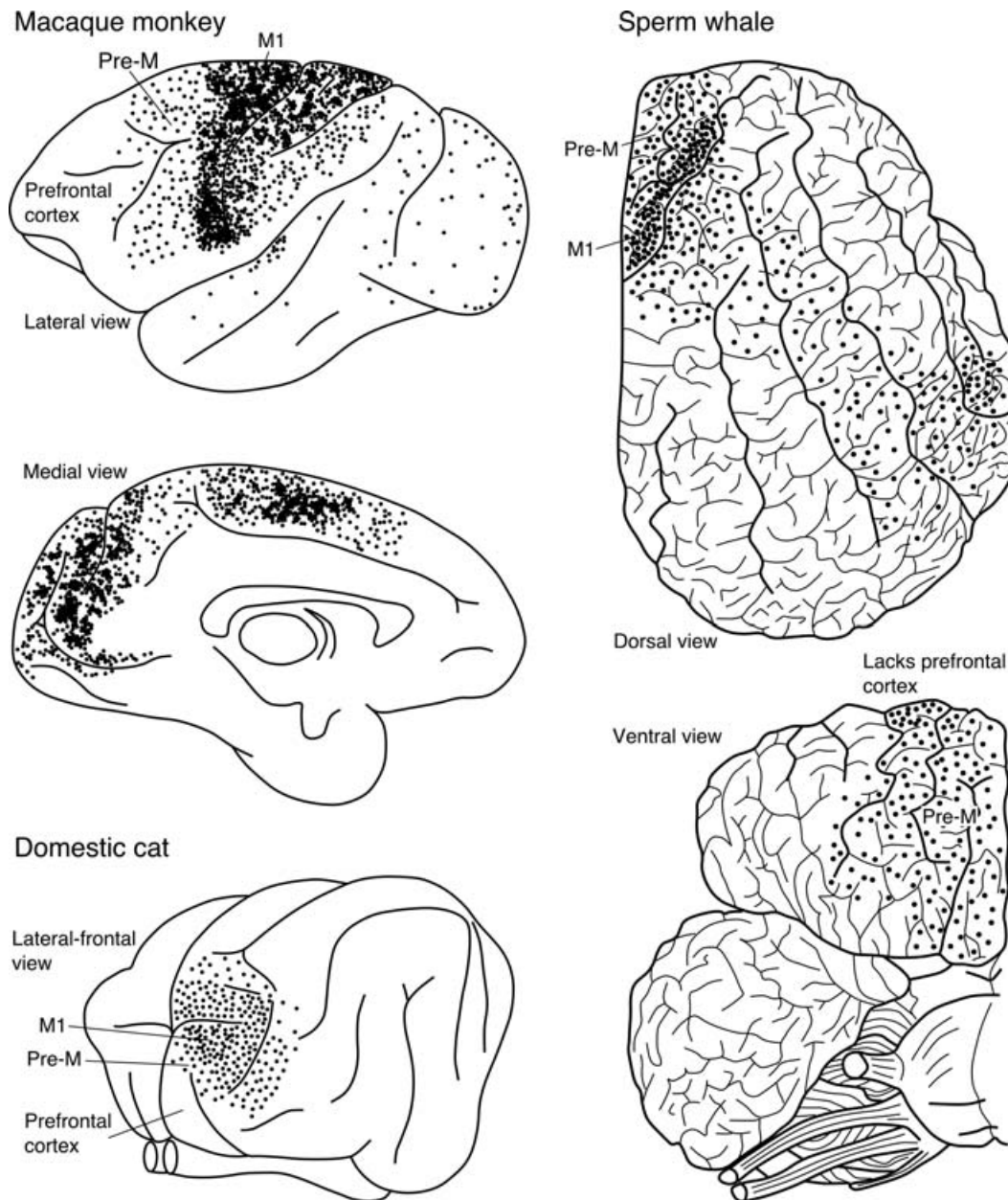


Fig. 7. The location of the giganto-pyramidal cells that indicate the origin of the cortico-pontine tract in the macaque monkey (Brodal, 1978, 1980), domestic cat (Brodal, 1968), and sperm whale (Kojima, 1951). Note the high density of these cells in primary motor cortex (M1) and the moderate density in premotor cortex (Pre-M). None of these cells are seen in prefrontal cortex of the macaque monkey or domestic cat. However, there appears to be no region anterior to the origin of the corticopontine tract in the sperm whale that would indicate the presence of a prefrontal cortical region.

Mountcastle, 1997). Despite this Morgane *et al.* (1988) identified two radially oriented columnar structures in dolphin visual cortex using computer-assisted methods: minor columns with diameters of around $20\ \mu\text{m}$, significantly smaller than the mean of $56\ \mu\text{m}$ found in other mammals (Mountcastle, 1997); and major columns, approximately $168\ \mu\text{m}$ diameter, which are again smaller than the cortical columns or modules (range $250\text{--}1000\ \mu\text{m}$) found in the cortex of other mammals (Manger *et al.*, 1998). Morgane

et al. (1988) note that these columns are often discontinuous across the cortical layers.

(4) Neuronal morphotypes within the cerebral cortex

One major feature of the mammalian cerebral cortex is the diversity and complexity of the neuronal morphology. Several studies have found a low diversity of neuronal types

in the cerebral cortex of odontocete cetaceans. These studies confirm that the majority of cortical neurons are pyramidal in nature, they have a few simple shapes, and there is sparse ramification of the dendrites (Kesarev, 1971; Kesarev *et al.*, 1977; Glezer *et al.*, 1988; Morgane, Jacobs & Galaburda, 1985; Morgane *et al.*, 1988; Morgane, Glezer & Jacobs, 1990). An interesting feature to emerge from these studies is the presence of extraverted pyramidal neurons in layer 2. These neurons exhibit a dendritic ramification into layer 1 and, by comparison with other pyramidal neurons of cetacean cerebral cortex, are quite spinous. These neurons are not a common feature of the cerebral cortex of other mammals. The majority of pyramidal neurons in the cetacean cerebral cortex exhibit triangular, club-shaped or clavate-type soma, which are thought to indicate a poor degree of differentiation of neuronal morphologies (Morgane *et al.*, 1990).

Non-pyramidal, or stellate, cells make up around 12% of the neuronal population in odontocete cetacean cortex (Morgane *et al.*, 1985). The majority of these neurons are of the long-radiator type, which is thought to represent an undifferentiated neuronal morphology (Morgane *et al.*, 1990). Stellate neurons of the short-radiator type have been reported only occasionally (Morgane *et al.*, 1985, 1990).

In a series of studies Hof *et al.* (1999, 2000) and Glezer *et al.* (1998) used calcium-binding protein immunohistochemistry to examine the inhibitory component of the cetacean cortical network. Many neurons immunoreactive for the calcium-binding proteins, calbindin, calretinin and parvalbumin are also immunoreactive for γ -aminobutyric acid (GABA) and are thus considered to be inhibitory. Cetaceans have a high proportion of calbindin- and calretinin-immunoreactive neurons compared to those showing parvalbumin immunoreactivity (approximately 4:1), whereas the ratio is closer to 1:1 in primates and rodents (Hof *et al.*, 1999, 2000; Glezer *et al.*, 1988). However, cetaceans have almost twice as many of these neurons as primates and rodents when they are expressed as a proportion of total neuronal number (Hof *et al.*, 2000). In cetaceans, calbindin- and calretinin-immunoreactive cells are found mostly in the upper cortical layers, while parvalbumin-immunoreactive cells are located in the lower cortical layers. The diversity in neuronal morphologies of these inhibitory neurons is low in cetaceans compared to many other mammals (Hof *et al.*, 1999).

Calbindin- and calretinin-immunoreactive neurons have been implicated in the flow of inhibitory influences in the vertical dimension in cerebral cortex, i.e. within a cortical column, and parvalbumin-immunoreactive cells function in horizontal inhibitory flow, i.e. between cortical columns. The high proportion of calbindin- and calretinin-immunoreactive cells in cetacean cerebral cortex suggests marked vertical inhibitory influences. This, combined with a low diversity in neuronal morphology, might indicate a high degree of monotonous specificity in vertical information processing, which might be seen as indicative of detailed perceptual abilities. By contrast, the relative paucity of parvalbumin-immunoreactive cells indicates a lack of horizontal inhibitory influences, potentially characterizing inefficient horizontal processing between cortical columns, and suggesting poor integrative abilities.

(5) Allometry of the cerebral cortex: the corticalisation index (CI)

Glezer *et al.* (1988) used the percentage of the total brain volume that is cerebral cortex [the corticalisation index (CI)] to assess the relative size of the cerebral cortex in cetaceans. They compared the CI of bottlenose dolphin against two species of insectivores and six primates and found that the CI of the bottlenose dolphin was significantly smaller than that of these other mammals.

I have repeated this analysis with the addition of further species (see Table 2), and calculated the CI using two different methods. First, the CI was calculated as the total combined volume of the grey and white matter of the cerebral cortex expressed as a percentage of brain volume. Fig. 8A shows the CI calculated using this method plotted against brain volume. Using this method, we see that the cetaceans show similar CIs to those of the simian primates. The average CI for simian primates was 70.22% (range 66.09–84.02%), and for odontocete cetaceans 72.14% (range 70.39–73.40%). Both these groups cluster above the average and range found for other mammals (average 45.81%, range 22.18–63.96%), prosimian primates (average 49.57%, range 33.87–59.55%), and insectivores (average 23.67%, range 11.84–57.31%). This analysis indicates that the amount of the odontocete brain devoted to grey and white matter of the cerebral cortex is comparable to that in simian primates, but greater on average than that seen in prosimians, other mammals and insectivores.

In the second method CI was calculated as the volume of the grey matter of the cerebral cortex expressed as a percentage of brain volume (see Table 2 and Fig. 8B). Using this method, a slightly different picture emerges. The simian primates have an average CI of 52.69% (range 49.17–56.07%), while the odontocete cetaceans have an average CI of 40.56% (range 36.14–42.44%). Thus, this second method separates the odontocete cetaceans from the simian primates. Moreover, they average less than the other mammals (average 47.29%, range 40.13–56.73%) included in this analysis, and the one prosimian used (CI = 49.08%), but higher than the insectivores (average 28.49%, range 26.31–30.03%). The single mysticete for which data was available had a CI of 20.53%.

These two analyses offer somewhat contradictory views. Using the first method, the odontocete cetaceans group with the simian primates, indicating that in these two groups, similar amounts of the total brain volume is devoted to the grey and white matter of the cerebral cortex. But when only the grey matter of the cerebral cortex is used (method 2), the odontocetes have a smaller CI than the simians and other mammals used in this analysis. This indicates that while much of the odontocete brain is occupied by the cerebral cortex, as in simians, the amount of grey matter in odontocete (and mysticete) cetaceans is less than that of simians and other mammals of similar brain sizes. This indicates that a greater proportion of the cerebral cortex of cetaceans is occupied by white matter, which connects the various regions of the brain, rather than by grey matter where neuronal computation occurs. This

Table 2. Calculation of the corticalisation index (CI) (see Fig. 8). The brain volume was calculated as brain mass divided by the specific gravity of brain tissue (1.036; Stephan *et al.*, 1981) where not directly provided in the source. The CI was calculated using two methods: (1) total volume of grey and white matter of cerebral cortex (neocortex plus schizocortex as defined by Stephan *et al.*, 1981), expressed as a percentage of brain volume, or as otherwise described in the text; (2) volume of grey matter only, expressed as a percentage of brain volume. Where it was not given in the original reference, the cortical volume was calculated by multiplying the cortical surface area by 0.175, which is the maximum cortical thickness reported for *Tursiops truncatus* (range 1.3–1.75 mm; Ridgway & Brownson, 1984). Data sources: (1) Hofman (1985, 1988); (2) Ridgway & Brownson (1984); (3) Kesarev *et al.* (1977); (4) Stephan *et al.* (1981); (5) Pirlot & Nelson (1978); (6) Reep & O'Shea (1990); (7) Schwerdtfeger *et al.* (1984).

Species	Brain volume (cm ³)	Cortical surface area (cm ²)	Cortical volume (grey and white, cm ³)	CI (method 1)	Cortical volume (grey only, cm ³)	CI (method 2)	Source
Cetaceans							
<i>Phocaena phocaena</i>	483	—	340	70.39	205	42.44	1
<i>Tursiops truncatus</i>	1118	—	815	72.89	463	41.41	1
<i>Grampus griseus</i>	1588	—	1127	70.97	624	39.29	1
<i>Globiocephala macrorhyncha</i>	2786	—	2045	73.40	1177	42.24	1
<i>Stenella styx</i>	623	1474	455	73.03	258	41.41	1
<i>Delphinus delphis</i>	722	1717	—	—	300	41.55	1
<i>Ziphius cavirostris</i>	1934	3996	—	—	699	36.14	2
<i>Orcinus orca</i>	5962	13 629	—	—	2385	40.00	2
<i>Balaenoptera borealis</i>	4730	4854	—	—	971	20.53	3
<i>Pontoporia blainvillei</i>	212	—	—	63.00	—	—	7
<i>Platanista gangetica</i>	285	—	—	68.00	—	—	7
Insectivores							
<i>Solenodon paradoxus</i>	4.28	—	0.82	19.16	—	—	4
<i>Tenrec ecaudatus</i>	2.32	—	0.34	14.66	—	—	4
<i>Setifer setosus</i>	1.39	—	0.18	12.94	0.41	29.50	1,4
<i>Hemicentetes semispinosus</i>	0.76	—	0.09	11.84	—	—	4
<i>Echinops telfairi</i>	0.57	—	0.07	12.28	—	—	4
<i>Oryzorictes talpoides</i>	0.54	—	0.09	16.66	—	—	4
<i>Microgale cowani</i>	0.39	—	0.07	17.94	—	—	4
<i>Limnogale mergulus</i>	1.05	—	0.23	21.91	—	—	4
<i>Nesogale dobsoni</i>	0.51	—	0.08	15.68	—	—	4
<i>Nesogale talazaci</i>	0.74	—	0.12	16.21	—	—	4
<i>Micropotamogale lamottei</i>	0.74	—	0.18	24.32	—	—	4
<i>Patamogale velox</i>	3.88	—	1.20	30.93	—	—	4
<i>Chlorotalpa stuhlmanni</i>	0.69	—	0.15	21.73	—	—	4
<i>Chrysochloris asiatica</i>	0.66	—	0.13	19.70	—	—	4
<i>Aethechinus algirus</i>	2.86	—	0.61	21.32	—	—	4
<i>Erinaceus europaeus</i>	3.23	—	1.06	32.81	0.97	30.03	1
<i>Hemiechinus auritus</i>	1.71	—	0.98	57.31	—	—	4
<i>Elephantulus fuscipes</i>	1.23	—	0.28	22.76	—	—	4
<i>Rhynchocyon stuhlmanni</i>	5.68	—	1.33	23.42	—	—	4
<i>Sorex minutus</i>	0.11	—	0.03	27.27	0.03	27.27	1
<i>Sorex araneus</i>	0.19	—	0.06	31.57	0.05	26.31	1
<i>Neomys fodiens</i>	0.31	—	0.1	32.25	0.09	29.03	1
<i>Crocidura occidentalis</i>	0.41	—	0.07	17.07	—	—	4
<i>Crocidura russula</i>	0.17	—	0.06	35.29	0.05	29.41	1
<i>Crocidura flavescens</i>	0.43	—	—	—	0.12	27.91	1
<i>Suncus murinus</i>	0.35	—	0.07	20.00	—	—	4
<i>Talpa europaea</i>	0.95	—	0.22	23.16	—	—	4
<i>Desmana moschata</i>	3.62	—	1.15	31.76	—	—	4
<i>Galemys pyrenaicus</i>	1.23	—	0.38	30.89	—	—	4
Prosimian primates							
<i>Urogale everetti</i>	4.28	—	1.45	33.87	—	—	4
<i>Cheirogaleus major</i>	6.8	—	3.09	45.44	—	—	4
<i>Cheirogaleus medius</i>	3.14	—	1.87	59.55	—	—	4
<i>Microcebus murinus</i>	1.78	—	0.78	43.82	—	—	4
<i>Lepilemur ruficaudatus</i>	7.6	—	3.48	45.78	—	—	4
<i>Lemur fulvus</i>	23.3	—	12.63	54.21	—	—	4
<i>Lemur variegatus</i>	31.5	—	15.89	50.44	—	—	4
<i>Avahi laniger</i>	10.49	—	5.05	48.14	—	—	4

Table 2 (cont.)

Species	Brain volume (cm ³)	Cortical surface area (cm ²)	Cortical volume (grey and white, cm ³)	CI (method 1)	Cortical volume (grey only, cm ³)	CI (method 2)	Source
<i>Avahi occidentalis</i>	9.67	—	4.67	48.29	—	—	4
<i>Propithecus verreauxi</i>	26.7	—	13.61	50.97	—	—	4
<i>Indri indri</i>	38.3	—	20.96	54.73	—	—	4
<i>Daubentonia madagascariensis</i>	45.15	—	23.17	51.31	—	—	4
<i>Loris tardigradus</i>	6.6	—	3.62	54.84	—	—	4
<i>Nycticebus coucang</i>	12.5	—	6.41	51.28	—	—	4
<i>Perodicticus potto</i>	14	—	7.01	50.07	—	—	4
<i>Galago crassicaudatus</i>	10.3	—	4.91	47.67	—	—	4
<i>Galagoides demidoff</i>	3.26	—	1.75	53.68	1.6	49.08	1
<i>Galago senegalensis</i>	4.8	—	2.25	46.88	—	—	4
<i>Tarsius</i> sp.	3.6	—	1.83	50.83	—	—	4
Simian primates							
<i>Callithrix</i> sp.	11.5	—	7.6	66.09	6.1	53.04	1
<i>Cebuella pygmaea</i>	4.3	—	3.41	79.30	—	—	4
<i>Saguinus oedipus</i>	9.54	—	5.90	61.84	—	—	4
<i>Saguinus tamarin</i>	9.57	—	6.01	62.80	—	—	4
<i>Callimico goeldii</i>	10.51	—	6.61	62.89	—	—	4
<i>Aotus trivirgatus</i>	15	—	9.42	62.80	7.5	50.00	1
<i>Callicebus moloch</i>	17.94	—	11.39	63.48	—	—	4
<i>Pithecia monacha</i>	32.87	—	21.31	64.83	—	—	4
<i>Alouatta</i> sp.	49.01	—	32.17	65.63	—	—	4
<i>Ateles geoffroyi</i>	101.03	—	71.59	70.86	—	—	4
<i>Lagothrix lagotricha</i>	95.54	—	66.55	69.66	—	—	4
<i>Cebus</i> sp.	66.94	—	46.82	69.94	—	—	4
<i>Saimiri sciureus</i>	25.2	—	17.3	68.65	13.3	52.78	1
<i>Macaca mulatta</i>	100	—	76.2	76.20	55.1	55.10	1
<i>Cercocebus albigena</i>	97.6	—	69.36	71.07	—	—	4
<i>Papio anubis</i>	190.96	—	141.45	74.07	—	—	4
<i>Cercopithecus ascanius</i>	70.56	—	50.55	71.64	—	—	4
<i>Miopithecus talapoin</i>	37.78	—	26.67	70.59	—	—	4
<i>Chlorocebus aethiops</i>	64.2	—	50.7	78.97	36	56.07	1
<i>Erythrocebus patas</i>	103.17	—	77.83	75.44	—	—	4
<i>Pygathrix nemaeus</i>	72.53	—	49.59	68.23	—	—	4
<i>Nasalis larvatus</i>	92.8	—	63.54	68.47	—	—	4
<i>Colobus badius</i>	73.82	—	51.72	70.06	—	—	4
<i>Hylobates lar</i>	97.51	—	66.94	68.65	—	—	4
<i>Pan troglodytes</i>	382.1	—	293.61	76.84	—	—	4
<i>Gorilla gorilla</i>	470.36	—	344.17	73.17	—	—	4
<i>Homo sapiens</i>	1389	—	1167	84.02	683	49.17	1
Other mammals							
<i>Ornithorhynchus anatinus</i>	8.57	—	4.09	47.83	—	—	5
<i>Tachyglossus aculeatus</i>	26.58	—	11.37	42.35	—	—	5
<i>Didelphis marsupialis</i>	6.49	—	1.44	22.18	—	—	5
<i>Tupaia glis</i>	3.04	—	1.13	37.17	1.22	40.13	1, 4
<i>Tupaia minor</i>	2.43	—	0.87	35.80	—	—	4
<i>Dolichotus spec.</i>	30.8	—	13.1	42.53	13.1	42.53	1, 4
<i>Felis catus</i>	31.8	—	15.3	48.11	15.3	48.11	1
<i>Vulpes vulpes</i>	48.3	—	27.4	56.73	27.4	56.73	1
<i>Ovis aries</i>	105	—	51.8	49.33	51.8	49.33	1
<i>Sus scrofa</i>	162	—	78.8	48.64	78.8	48.64	1
<i>Bos taurus</i>	486	—	226	46.50	226	46.50	1
<i>Equus caballus</i>	609	—	282	46.31	282	46.31	1
<i>Trichechus manatus</i>	351	—	—	63.96	—	—	6

suggests that less of the cetacean cerebral cortex is devoted to computation, and more is occupied by wiring, which may impact negatively on the computational power of the cetacean brain.

(6) Neuronal density, the glia:neuron index, and the composition of the neuropil

Previous authors have noted that there is a very low neuronal density in the cetacean brain, ranging between 34 000 and 50 000 neurons mm^{-3} in *Tursiops truncatus* (Morgane *et al.*, 1988), 65 444 mm^{-3} in *Globiocephala melaena* (Pilleri & Gahr, 1970), and 13 112 mm^{-3} in *Balaenoptera physalus* (Pilleri & Gahr, 1970). This low neuronal density has been stated to be a correlate of brain size (Haug, 1987; Prothero, 1997). However, neuronal density from homologous cortical areas in different cetaceans has not been examined systematically even though it is well known that neuronal density differs in different areas of the cortex. The neuronal density even differs among different studies in the same species, which is a cause for concern [for example compare values in Haug (1987), and Prothero (1997)]. In other mammals, the neuronal density in primary motor cortex (area 4) has been quantified: *Mus musculus* – 950 000 mm^{-3} ; *Cavia cobaya* – 538 000 mm^{-3} ; *Rattus rattus* – 502 000 mm^{-3} ; *Lepus cuniculus* 302 000 mm^{-3} ; *Felis domesticus* – 242 000 mm^{-3} ; *Canis familiaris* – 204 000 mm^{-3} ; *Bos taurus* – 174 000 mm^{-3} ; *Capra hircus* – 172 000 mm^{-3} ; *Ovis aries* – 170 000 mm^{-3} ; *Sus scrofa* 115 000 mm^{-3} ; *Equus caballus* – 115 000 mm^{-3} ; *Homo sapiens* – 163 000 mm^{-3} (Chow, Blum & Blum, 1950).

Reichenbach (1989) showed that the glia:neuron index increases with increasing thickness of the cerebral cortex (see his Fig. 3); however, his analysis did not include cetaceans. The glia:neuron index from the cerebral cortex of two species of cetaceans, the bottlenose dolphin (values ranging from 2:1 to 3:1; Garey & Leuba, 1986) and the fin whale (4.5:1 to 5.9:1; Hawkins & Olszewski, 1957), are available to compare with the allometric relationship derived by Reichenbach (1989). The cetacean cerebral cortex ranges between 1 and 2 mm in thickness (e.g. Ridgway, 1990) and from the allometric relationship determined by Reichenbach (1989), the predicted glia:neuron index for cetaceans would be 0.2:1–0.7:1. Thus it appears that the cetacean cerebral cortex has a substantially higher proportion of glia than is found in other mammals.

One of the most important features of the neocortex in terms of computational abilities is thought to be the composition and amount of neuropil. Here, the term neuropil refers to that part of the cerebral cortex that is not occupied by neuronal and glial cell bodies and blood vessels. Thus, the neuropil is that fraction of the cerebral cortex made up of axons, dendrites, boutons, spines, glial processes, myelin sheaths, and extracellular space. Chklovskii, Schikorski & Stevens (2002) found that the cerebral cortex of rats is organised in a manner that balances the proportion of these constituents to ‘optimize the wiring’ of the cerebral cortex, such that axons and dendrites occupy around 60% of the neuropil volume. Several features indicate that this differs in cetacean cerebral cortex.

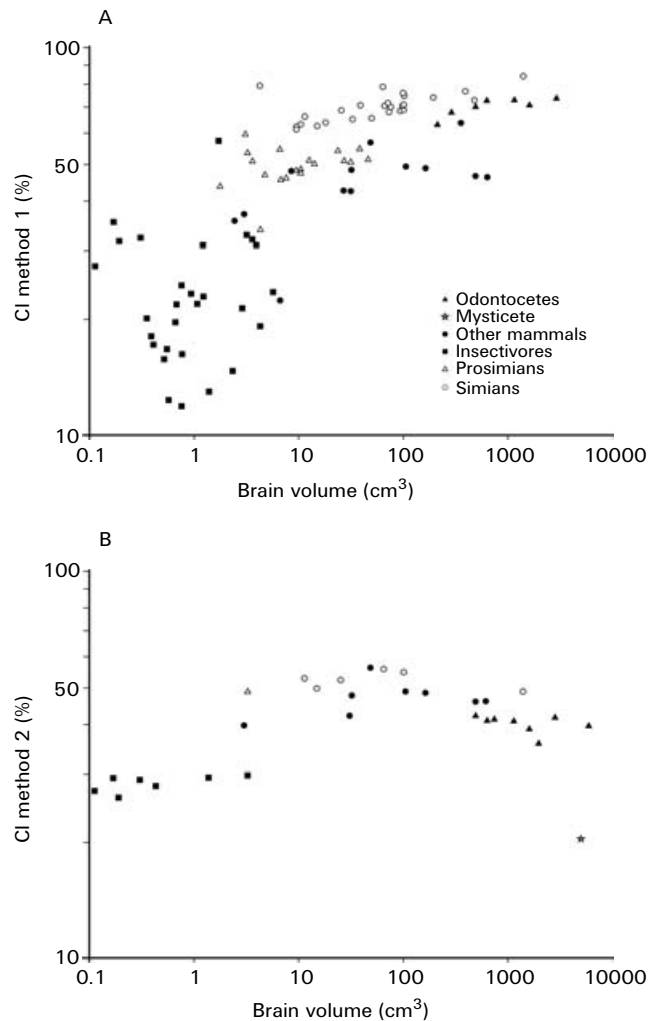


Fig. 8. Plots of the corticalisation index (CI) against brain volume (A, CI calculated using method 1 with cortical volume = total combined volume of grey and white matter; B, CI calculated using method 2 with cortical volume = volume of grey matter only) in a variety of mammal species. The data in this plot are derived from Table 2.

As discussed above, there appears to be a high proportion of glial cells in the cetacean cerebral cortex. It is therefore reasonable to assume that glial processes occupy a greater proportion of the neuropil in cetaceans than in other mammals. The cerebral cortex of cetaceans stains heavily for myelin (e.g. Manger *et al.*, 1998). Glezer *et al.* (1988) have shown that myelinated thalamocortical axons pass through the cetacean cerebral cortex reaching layer 1 before turning to branch into the cellular layers. A high density of myelinated axons indicates that a higher proportion of the neuropil is occupied by myelin sheaths. Moreover, the passage of thalamocortical axons through the cortex will lower the potential computational volume of the neuropil. Golgi studies of cetacean cortical neurons indicate a poor degree of dendritic arborization, as well as a low number of spines (Kruger, 1966). A smaller percentage of the cetacean

neuropil is therefore likely to be occupied by dendrites and spines in comparison with other mammals.

These features indicate that the relative proportions of the constituents of the cetacean cerebral cortex neuropil are likely to differ from other mammals. This suggests that the cetacean cerebral cortex may not be optimally wired (Chklovskii *et al.*, 2002), presumably impacting negatively on processing efficacy and power of the cetacean cerebral cortex.

IV. THE CETACEAN HIPPOCAMPAL FORMATION

The hippocampal formation of mammals is composed of four subregions: the dentate gyrus, the hippocampus, subiculum, and entorhinal cortex (Amaral & Soltesz, 1997). This formation is involved in the assimilation of sensory and other neural information, interacting with storage areas to consolidate this information into long-term, or enduring, memories (e.g. Amaral & Soltesz, 1997). Thus, it has an indirect, but essential role for cognitive behaviours. Breathnach & Goldby (1954) and Jacobs, McFarland & Morgane (1979) give detailed descriptions of the cetacean hippocampal formation. All four components of the hippocampal formation can be found in cetaceans; however, the hippocampal formation is of relatively small size. Moreover, other regions of the brain generally associated with the hippocampal formation, such as the mammillary region, anterior thalamic nuclei (Breathnach & Goldby, 1954), anterior cingulate cortex (Morgane, McFarland & Jacobs, 1982), and prefrontal cortex (see Section III.2), are all also greatly reduced.

A quantitative assessment of the hippocampal formation of cetaceans is difficult due to a lack of data; however, three values are available: for the harbour porpoise (*Phocaena phocaena*) (Breathnach & Goldby, 1954) hippocampal formation volume can be calculated to be 10% [hippocampal index (HI)=0.22%] that found in humans and for two species of river dolphin, the franciscana (*Pontoporia blainvillei*) (HI=0.5%) and the Indian river dolphin or susu (*Platanista gangetica*) (HI=0.75%) (Schwerdtfeger, Oelschläger & Stephan, 1984) values can be calculated from the given percentage of total brain volume. These were compared to similar data for insectivores and primates (Stephan *et al.*, 1981) and monotremes and the opossum (Pirlot & Nelson, 1978), by converting the hippocampal formation volume into a hippocampal index (HI), or percentage of the brain occupied by the hippocampal formation. For most mammals (excluding cetaceans) the HI decreases with increasing brain size (Fig. 9). However, the data points for cetaceans fall well below the 95% confidence intervals of the values expected based on the regression line from other mammals. Thus, in both actual and relative terms (based on the available sample of three species), the size of the hippocampal formation in cetaceans is small, supporting the qualitative impression derived from the studies of its architecture (Breathnach & Goldby, 1954; Jacobs *et al.*, 1979). The small relative and actual size of the cetacean hippocampus becomes more

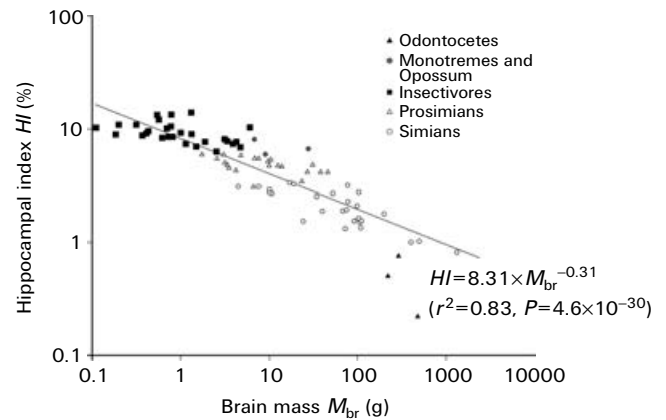


Fig. 9. Allometric plot of hippocampal index (*HI*) (hippocampal volume expressed as a percentage of brain volume) against brain mass (M_{br}). The regression line is based on all data excluding the three odontocetes.

evident when compared to the enormous and highly convoluted hippocampus of the African elephant (Hakeem *et al.*, 2005).

V. SPECIALISATIONS OF THE CETACEAN BRAIN

There are two significant specialisations of the cetacean brain (although neither is limited to the order Cetacea) that to date have not been satisfactorily explained. These are related to their vocal and sleeping behaviours. The neuro-anatomical features involved are the nucleus ellipticus of the periaqueductal grey matter, which is suggested to be involved with vocalisation, and the neural assembly of the pontomesencephalon which is proposed to control unihemispheric sleep phenomenology. The vocal capability of cetaceans is a major factor in the popular assumption that cetaceans represent an aquatic intellectual counterpart of humans (Forestell, 2002). The control of sleep is based upon the release of neurotransmitters from various nuclei in the brain, several of which reside in the tegmentum of the pontomesencephalon. The release of these transmitters in light of the unihemispheric nature of cetacean sleep is discussed here in relation to central nervous system thermogenesis.

(1) Conspecific communication among cetaceans

Any discussion of vocal communication in cetaceans must first place their vocal behaviour within the framework of all conspecific communication between cetaceans. In general, non-human animals communicate about a limited range of topics, which include sex, aggression, predators and food, and they do this *via* a limited set of signals. Communication conveys information about the internal state of an individual to conspecifics by the use of stereotyped vocalisations, postures or movements.

The skeleto-muscular system of cetaceans limits their ability to use body language as an effective means of communicating internal state, or intentionality, to conspecifics. First, the facial musculature of cetaceans has atrophied such that they are no longer capable of facial expressions (Caldwell & Caldwell, 1972). Second, the loss of limbs limits their range of body postures. Third, the evolution of a streamlined body necessary for fast swimming and subcutaneous blubber has resulted in a homogeneous external morphology. Given these limitations, what are cetaceans capable of in terms of body language? Madsen & Herman (1980) list the probable set of body language signals available to cetaceans including: breaching the water surface, displays of the ventral body surface, tail slaps, mouth opening, head nodding and shaking, and some stereotyped gross body postures and swimming patterns. This body language repertoire is clearly limited to gross movements.

Olfaction plays an important role in conspecific communication in numerous species. Odontocetes lack olfactory bulbs, and mysticetes have olfactory bulbs that are atrophied (reviewed in Ridgway, 1990). Thus, olfactory communication among cetaceans is likely to be greatly limited in mysticetes, and absent in odontocetes. Interestingly, the terminal nerve is present in cetaceans, and the ganglia of the terminal nerve are quite large (Ridgway *et al.*, 1987). This structure is thought to be related to chemical signals involved in sexual reproduction; thus, the cetaceans may be able to communicate reproductive state *via* the terminal nerve system, although this may not be intentional communication. The above list should be compared to the estimated set of around 200 paralinguistic elements (plus thousands of facial expressions) found in humans, which only slightly exceeds that available to chimpanzees and rhesus monkeys (Wilson, 1975). It is clear therefore that the cetaceans lack a significant set of non-vocal communication signals.

The majority of cetacean conspecific communication is achieved by the use of sound (Herman & Tavolga, 1980; Ridgway & Au, 1999). The vocal proclivity of cetaceans, combined with the large size of the brain, has led many investigators to believe that cetacean vocalisations may be structurally and functionally as sophisticated as human language. Lilly (1967) maintained that dolphin vocalisations represented a language, that they conversed regularly, and that they were capable of imitating human sounds. However, numerous rejections of these ideas have been published (see review by Herman & Tavolga, 1980). Herman & Tavolga (1980) showed that the repertoire of dolphin vocalisations that may be used for communication is quite small: between 5 and 20. Bullock & Gurevich (1979) concluded that the total vocal repertoire of the bottlenose dolphin was limited to less than 40 distinct vocalisations. The greatest number of identifiable vocalisations classified for a cetacean species is 30 (in seven broad classes) for the pilot whale, *Globicephala melaena* (Taruski, 1976, cited in Herman & Tavolga, 1980).

McCowan *et al.* (1999) used the principles of information theory to examine vocalisations of the bottlenose dolphin as a predictor of their communication capacity. Their results suggested a certain level of internal structure to be present in

dolphin vocalisations; however, it was clear that higher order entropies, typical of human language, were not found. Despite these studies, other investigators still persist with the possibility that dolphins have a language. For example, Janik (2000) concludes that wild dolphins were addressing each other at distances of up to 580 m as individuals to initiate conversation. However, a close inspection of these results reveals that only 39 of 1719 whistles studied (2.27%, or as stated by the author 'less than chance') were classified as matched interactions (i.e. that two whistles of the same type produced within 3 s of each other by different dolphins were judged to be 'relatively similar' by five naïve human observers). Janik (2000) reports that in three instances a dolphin whistle was matched by another individual, and then repeated by the initial dolphin. These matching whistles were limited to the signature whistles of the individual dolphins, which in some instances are the only vocalisations that dolphins produce (Janik & Slater, 1998). Thus, the behavioural evidence for a cetacean language is at present unconvincing.

The neuronal control of vocalisation in various mammalian species has been extensively studied, and the neural circuitry that underlies vocalisation can be described (reviewed by Jürgens, 1998). Neurons from the anterior cingulate cortex project to four locations: the medial nucleus of the amygdala, the hypothalamus, the midline dorsal thalamus and the lateral periaqueductal grey matter. The amygdala, hypothalamus, and dorsal thalamus in turn project to the periaqueductal grey matter. The periaqueductal grey matter then projects to the nucleus ambiguus and nucleus retroambiguus, which constitute the phonatory motoneurons and premotoneurons controlling the vocal cords and respiratory muscles. Two interesting features of the mammalian vocal control system of relevance to the cetaceans are: (1) the majority of the vocal control system of the telencephalon belongs to the limbic system; and (2) all telencephalic control of vocalisation is channelled to the brainstem through the periaqueductal grey matter.

The limbic system of the dolphin telencephalon has been the subject of detailed anatomical study (Breathnach & Goldby, 1954; Kruger, 1959, 1966; Morgane *et al.*, 1982). These observations indicate that the limbic lobe of the telencephalon is greatly reduced in comparative terms (Kruger, 1966; Morgane *et al.*, 1982; Pilleri & Gahr, 1970). The relative volume of the limbic portion of the dorsal thalamus of the bottlenose dolphin is approximately half that seen in other eutherian mammals (Kruger, 1959, 1966); however, the amygdala appears unchanged, apart from a specific loss of olfactory connections (Breathnach & Goldby, 1954).

Previous studies have shown that the anterior cingulate cortex of monkeys is important in the voluntary control of vocalisations (Sutton, Larson & Lindeman, 1974). Thus, as the cetacean limbic system is reduced, and the anterior cingulate cortex is both reduced and lacks a granular region, it is not unlikely that the voluntary control of vocalisation by cetaceans suffers serious deficiencies. However, as the amygdala appears normal, we can also conclude that involuntary species-specific intonations provided to vocalisations by this structure (Jürgens, 1998) are present.

The second relevant feature of importance to emerge is the channeling of all the telencephalic pathways through the periaqueductal grey matter (Jürgens, 1998). This region of the brain controls the activity of the phonatory motoneurons and may act as a vocal pattern generator (Zhang *et al.*, 1994). Studies of mammals and other vertebrates have shown that natural-sounding species-specific vocalisations are produced in response to electrical or chemical stimulation of these neurons (reviewed in Jürgens, 1994). Moreover, specific calls are topographically organised within this region and all calls of a given species are represented here. Lesion or ablation of this region leads to mutism, even in humans; however, in humans mute for this reason, language comprehension and para-linguistic capacities are still present (Esposito *et al.*, 1999).

Within the cetacean mesencephalon is a specialised nucleus, the nucleus ellipticus, which appears to be a parcellated elaboration of the ventral and ventral-lateral periaqueductal grey matter (Fig. 10). This structure is prominent at birth in the bottlenose dolphin (Fig. 10A), at which time the calf can vocalise but not produce echolocation sounds (Herman & Tavolga, 1980). As this structure is a feature of both odontocetes and mysticetes (Jansen, 1969; Ridgway, 1990), it is unlikely to be related to echolocation (only found in odontocetes). Rather, the nucleus ellipticus is likely to be a specialised column of the periaqueductal grey matter related to vocalisation. If this is correct, it can be concluded that vocalisations of the dolphin must be mainly under the control of a mesencephalic structure, with minor telencephalic influence. This feature of the cetacean brain indicates a specialised, but probably non-conscious and involuntary, vocalisation-generation system (probably under significant influence from the amygdala). Interestingly, a nucleus ellipticus is also found in elephants (Cozzi, Spagnoli & Bruno, 2001), another species with a specialised vocal repertoire.

(2) Sleep in cetaceans

One of the more intensely studied specialisations of the cetaceans is the physiological and behavioural phenomenology surrounding sleep. That the dolphin may sleep with half its brain at a time was first suggested by Lilly (1967), and was later demonstrated physiologically by Serafetinides, Shurley & Brooks (1972), Mukhametov (1987, 1988, 1995), Mukhametov & Lyamin (1994), and Mukhametov, Supin & Polyakova (1977). This form of sleep has been identified physiologically in five species (see above references and Mukhametov & Polyakova, 1981; Oleksenko *et al.*, 1994; Lyamin *et al.*, 2002a) and behaviourally (Flanigan, 1974a, b, 1975a, b, c; Lyamin *et al.*, 2000) in several cetacean species, and it is likely to be a common feature of sleep in all extant cetaceans. The generalised sleep pattern observed is alternating approximately 1 h long bouts of slow-wave sleep (SWS) in each hemisphere, with very small (10–60 s) amounts of rapid eye movement (REM) sleep interspersed, either at the end of the SWS period, or in short bursts during SWS. Very little is known of the neuronal control of uni-hemispheric sleep in these species. However, results from other mammals and preliminary observations on cetaceans

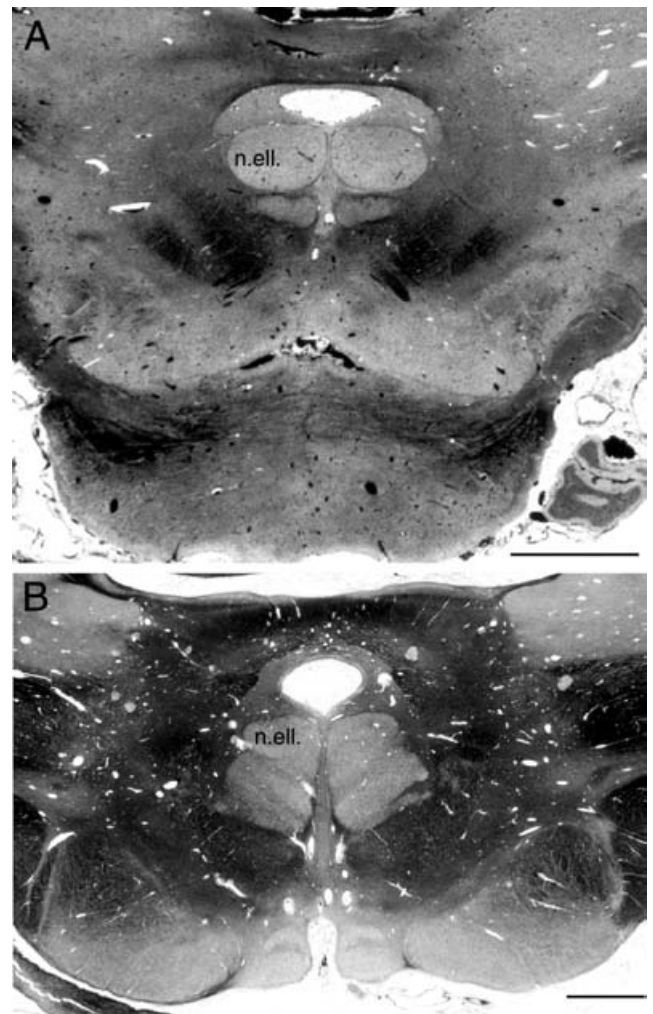


Fig. 10. Photomicrographs of myelin-stained coronal sections through the rostral rhombencephalon in a newborn (A) and adult (B) *Tursiops truncatus*. These photomicrographs demonstrate the extreme nuclear specialisation of the ventral lateral periaqueductal grey matter into the distinct nucleus ellipticus (n.ell.). This region is located in a topologically similar region to the vocalisation column of the periaqueductal grey matter in other mammals, thus, it may be a specialised vocalisation nucleus. At birth bottlenose dolphins can whistle but they cannot echolocate. A nucleus ellipticus has been found in all odontocetes and mysticetes examined. These photomicrographs are from sections belonging to the Comparative Mammalian Brain Collection [<http://brainmuseum.org>]. Scale bars = 5 mm.

(Manger, Ridgway & Siegel, 2003; Pillay & Manger, 2004) allow some speculations in terms of cetacean brain evolution and behaviour.

The sleep patterns of mammals (and most vertebrates) are largely under the influence of nuclei located in the pontomesencephalon. In particular, three groups of neurons have been implicated in the control of sleep, especially REM sleep (Siegel, 1994). These are the locus coeruleus complex, which produces noradrenalin, the dorsal raphe nuclei, which produce serotonin, and the pedunculopontine (PPN)

and lateral dorsal tegmental (LDT) nuclei, which produce acetylcholine. Each of these nuclear groups have a specific pattern of discharge that correlates with different sleep/wake phases. During wake, the neurons of each group discharge at a random, high average rate; during SWS, the neurons of each group discharge rhythmically at a slower rate; and during REM sleep, the neurons of the locus coeruleus complex and dorsal raphe cease to discharge, while those of the LDT and PPN fire at a rate and manner similar to that seen during wake.

As the sleep pattern of cetaceans is modified, the neural activity of these cell groups might also be modified. Each hemisphere of the cetacean brain exhibits SWS electroencephalogram (EEG) patterns for approximately 4 h per day, the remainder of the time exhibiting EEG patterns consistent with waking (Mukhametov, 1995). REM sleep in cetaceans is cryptic both physiologically (Mukhametov, 1988) and behaviourally (Lyamin *et al.*, 2002*b*), and is likely to account for a very small amount of total sleep time in cetaceans. Anatomical observations of the locus coeruleus complex (Manger *et al.*, 2003) have not shown features that might relate to unihemispheric sleep phenomenology. As the locus coeruleus complex emerges during the phenotypic stage of development (Clancy, Darlington & Finlay, 2001; Galis & Metz, 2001), alterations in its function, in both the developing and adult animal, are unlikely. It is possible that the firing pattern of locus coeruleus neurons will correspond to hemispheric sleep EEG patterns seen in other mammals. Thus, during wake, the neurons of the locus coeruleus will discharge at a high constant rate, and will slow unihemispherically during SWS. As there is little REM sleep, there will be only very short periods when these neurons are inactive. If these predictions are correct the cetacean brain will be virtually in constant receipt of noradrenalin and serotonin; with no time period when their brain is deprived of these neurotransmitters, as happens in bihemispheric sleeping mammals during REM sleep.

One of the major effects of neuronal production of noradrenalin is the facilitation of skeletal muscle tone (Siegel, 1994; Kiyashchenko *et al.*, 2001). In mammals 30% of the heat production required to maintain body temperature is met by basal muscle tone (Gisolfi & Mora, 2000). The ability to maintain body temperature is likely to be a strong selection pressure on cetaceans, as heat loss in water is 90.8 times faster than in air at the same ambient temperature (Downhower & Blumer, 1988). Continually maintaining muscle tone would be a consistent source of heat production. Unihemispheric sleep, as well as allowing breathing and maintenance of body position in the water, could also facilitate thermoregulation. Combined with other features of cetacean thermoregulation (Hokkanen, 1990) unihemispheric sleep could be an adaptation to ensure maintenance of body temperature in an extremely thermally challenging environment (Pillay & Manger, 2004).

It has been suggested that one role of glia in the vertebrate brain is thermogenesis (Donhoffer, 1980; Széleányi, 1998). The metabolic activity of glia is increased by exposure to noradrenalin, significantly above increases in neural metabolism (Donhoffer, 1980; Stone & Ariano, 1989). If the

cetacean brain does have consistently high levels of noradrenalin the glia may have a consistently higher metabolic rate, in the absence of order-specific alterations in glia function. As discussed previously (Section III. 6), the cetacean brain has a higher glia:neuron index than that of other mammals. A high percentage of glia, and a consistent metabolic influence of noradrenalin, would suggest that the brain of the cetacean is likely to be a proficient thermogenetic organ.

VI. EVOLUTION OF THE CETACEAN BRAIN

The evolutionary history of cetaceans recently has been advanced by the discovery of several key fossils and through molecular techniques. A comprehensive discussion of cetacean evolution can be found in Thewissen (1998).

The only terrestrial cetaceans to be identified were members of the pakicetids, an early Eocene group, which together with the alleged amphibious cetacean *Ambulocetus* and the artiodactyls form the Cetartiodactyla (Thewissen *et al.*, 2001). Although no calculations of brain and body size have been published or endocasts found, the photographs and diagrams of the fossilized skulls indicate that the brain of these species was relatively small (see Fig. 3 of Thewissen *et al.*, 2001; and Fig. 9 of Thewissen, Madar & Hussain, 1996). For example, the terrestrial pakicetid, *Pakicetus attocki*, a wolf-sized animal, appears to have maximal brain dimensions of 4 cm × 3.5 cm × 2 cm (anteroposterior length × width × height) (Thewissen *et al.*, 2001). It would have a brain mass under 20 g, far less than most modern wolf-sized animals that have a brain mass over 100 g. For the amphibious Eocene cetacean, *Ambulocetus natans*, estimated body mass ranges between 140–250 kg (Thewissen *et al.*, 1996) and around 720 kg (Gingerich, 1998). Maximal brain dimensions for this species, as judged from the published figures (Thewissen *et al.*, 1996), are 10 cm × 6 cm × 6 cm (anteroposterior length × width × height). Brain mass for *Ambulocetus natans* would therefore be less than 200 g, small for a mammal with a body mass of around 200 kg and significantly less than the comparable-sized polar bear, which has a brain mass of around 500 g.

The first fully aquatic group of cetaceans is the Archaeoceti. These cetaceans evolved and speciated in the warm Tethys sea, for a period of around 20 million years, from the beginning of the middle Eocene (53 million years ago) to the early Oligocene (32 million years ago) (Fordyce & Barnes, 1994). Several fossil endocasts of archaeocetes have been found. The earliest and best description of these endocasts is provided by Dart (1923), some of whose figures are redrawn in Fig. 11. The cerebellum occupies the largest part while the brainstem and midbrain are of a size appropriate to the body size of these species; however, the most striking feature is the extremely small size of the cerebral hemispheres: a generous estimate of the cortical surface area from the specimens described by Dart (1923) is 20 cm². This is far less than that of modern cetaceans, which have cortical surface areas ranging between approximately 1500 and 14 000 cm² (Table 2). The cortical volume for

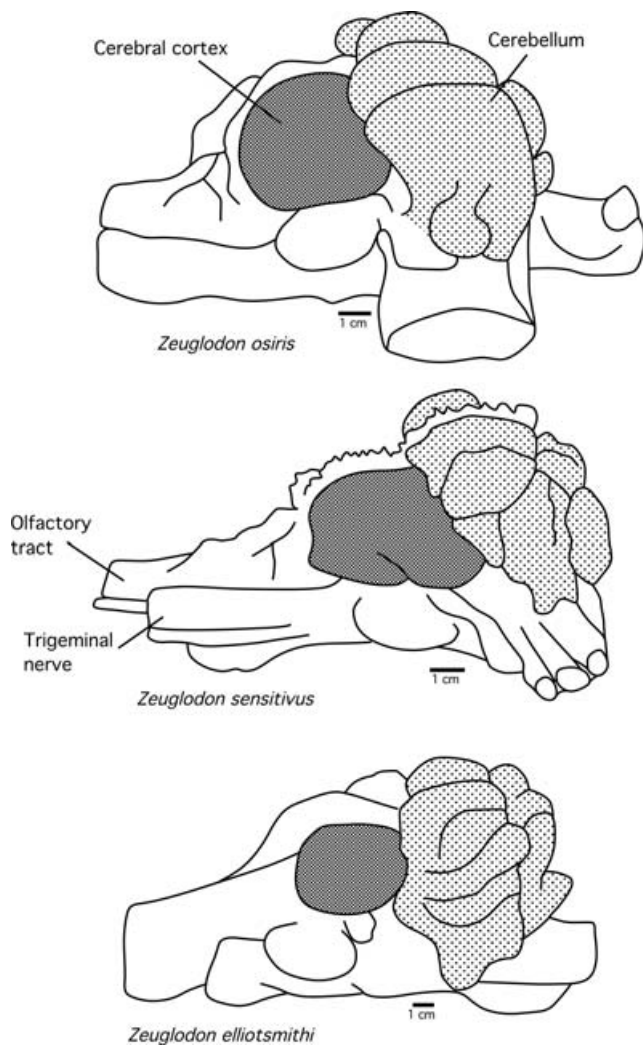


Fig. 11. Diagrams of fossil endocasts of three species of Archaeoceti redrawn from the diagrams presented in Dart (1923). Note the large cerebellum and very small cerebral cortex. The diameter of the cerebral cortex is approximately 4 cm; it occupied less than 2% of the total brain mass.

the Archaeoceti would be around 3–5 cm³ compared to 250–2400 cm³ for modern cetaceans, and the corticalisation index would be 0.3–2%, compared to approximately 40% for modern odontocetes or 20% for the single mysticete for which data are available (Table 2). The rich fossil record of the Archaeoceti, and the relatively high number of species – 25 known genera, six families (Gingerich, 1998), clearly indicates that this group managed to thrive and diversify in their environment. Thus, one can only conclude that a big brain was not necessary for successful adaptation of early cetaceans to an aquatic environment.

The morphology and relative size of the archaeocete brain does not appear to have changed significantly during the 20 million years that these fully aquatic species existed (Fig. 12) (see also Gingerich, 1998; Marino, McShea & Uhen, 2004). Allometric analysis of brain mass and body mass of the Archaeoceti reveal a regression line with a slope

of 0.672. This slope is significantly steeper than that calculated herein for modern cetaceans (0.376, see equation 5, a comparison of the slopes of the regression equations derived for archaeocetes and modern cetaceans revealed a significant difference, $P=0.014$ using the mean squares between and within slopes), and was not significantly different from other contemporary mammals (e.g. a comparison of the slopes of the regression equations derived for archaeocetes and Neogene ungulates revealed no significant difference, $P=1$ using the mean squares between and within slopes).

The sudden extinction of the Archaeoceti and the subsequent evolution of the modern cetacean fauna occurred at the junction of the early and late Oligocene, approximately 30 million years ago. Marino *et al.* (2004) estimated brain and body masses of seven Oligocene cetaceans, all presumably odontocetes (see Table 1). The relative brain size, or encephalisation quotient of Oligocene cetaceans is higher than the archaeocete values, and falls within the range seen for modern cetaceans (see Fig. 13). The scaling of the relationship between brain and body mass is also altered compared to archaeocetes. The slope of the allometric equation derived for the Oligocene cetaceans (Fig. 12) is 0.47, and is identical to that seen for extant odontocetes, suggesting that the selection pressures determining the scaling of extant cetaceans were present in the Oligocene.

Photographs and descriptions of three endocasts of Miocene cetaceans have been published, *Aulophyseter morricei* (18 million years old), *Argyroctetus* sp., and *Schizodelphis* sp. (ages not provided) (Edinger, 1955; Jerison, 1973; Gingerich, 1998). The morphology of the brain, as determined from these endocasts resembles closely that of extant cetaceans (see Figs 15.3 and 15.4 in Jerison, 1973) in the expansion of the cerebral hemispheres. Thus, from being a minor feature in Archaeoceti, the endocasts of the Miocene odontocetes are dominated by the cerebral hemispheres.

The calculated brain and body masses of 38 Miocene odontocetes [see Table 1, data from Gingerich (1998) and Marino *et al.* (2004)] are similar to those of extant odontocetes (Fig. 12). Moreover, the scaling relationship between brain and body mass in the Miocene cetaceans (slope 0.52) is statistically similar to that found for extant odontocetes (slope 0.47, a comparison of these slopes revealed no significant difference, $P=1$ using the mean squares between and within slopes).

To put these alterations in the scaling of the brain-body mass relationship and EQs during cetacean evolution into perspective the cetaceans can be compared with their closest mammalian relatives the ungulates (Thewissen *et al.*, 2001). The brain-body scaling of ungulates during evolution (Fig. 12) shows features in common with the majority of mammalian lineages. First, over time, the mean relative size of the brain increases gradually. Second, the slopes of the allometric equations are close to parallel (a comparison of the slopes of the regression equations derived for the various groups revealed no significant differences using the mean squares between and within slopes: Archaic ungulates and Paleocene ungulates, $P=1$; Paleocene ungulates and

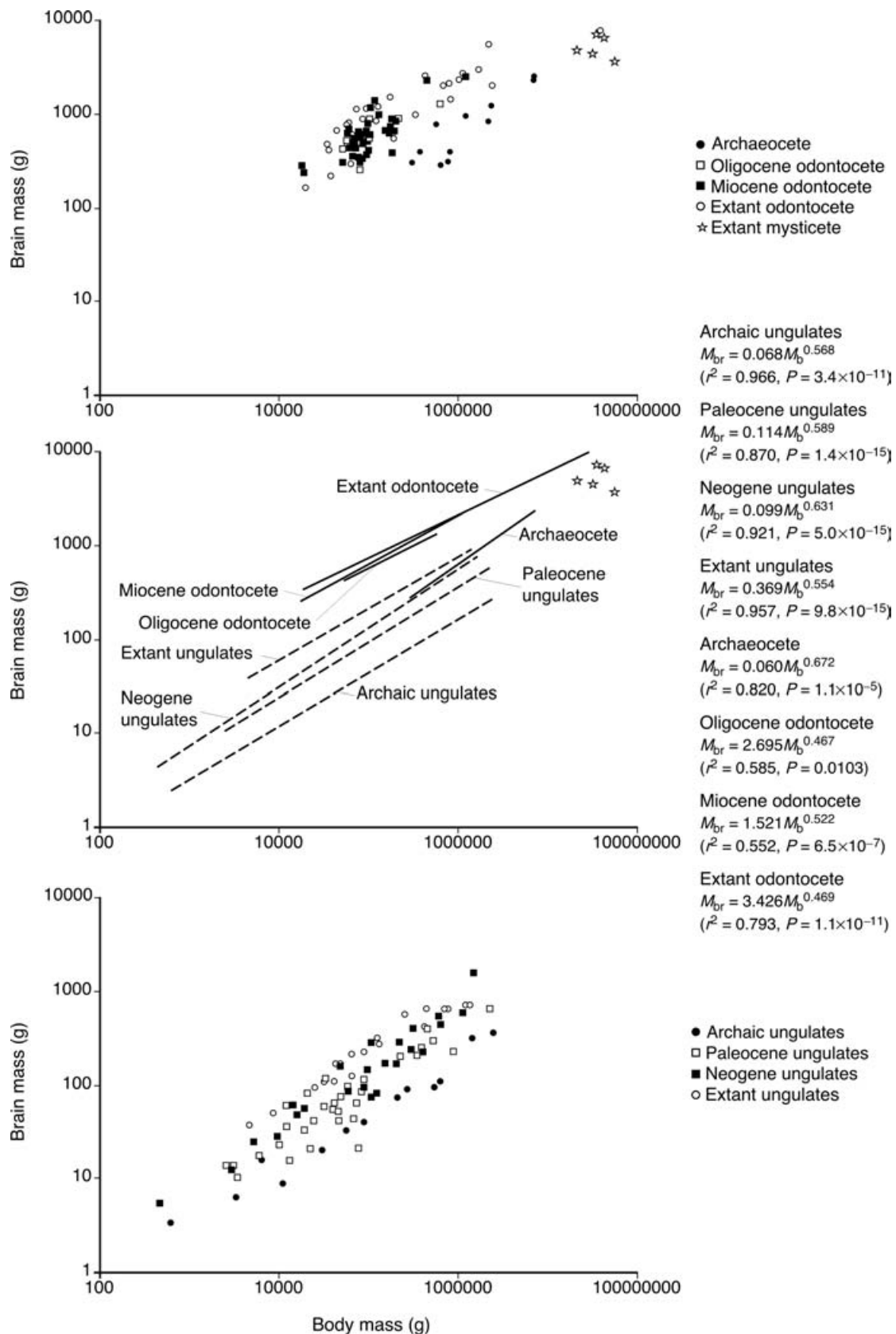


Fig. 12. Changes of brain mass and body mass during the evolutionary history of the cetaceans and the ungulates. Data for these plots are derived from sources listed in Table 1 for cetaceans, and Jerison (1973) for ungulates. Note the increase in brain size relative

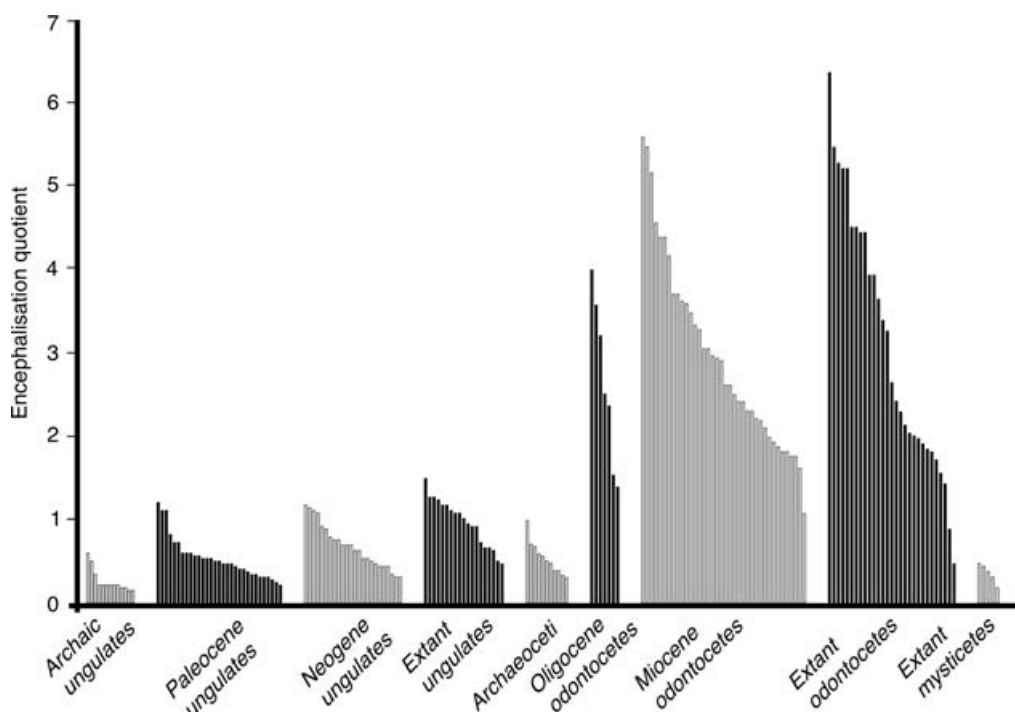


Fig. 13. Encephalisation quotients based on the general extant mammalian regression (see Fig. 2) for extinct and extant ungulate and cetacean species. Note the gradual increase in relative brain size of the ungulates with time. The cetaceans show a dramatic change in relative brain size at the Archaeoceti – modern cetacean faunal transition. This type of logarithmic alteration of brain size is not a common event in mammalian brain evolution; rather, the pattern exhibited by ungulates is more commonly seen.

Neogene ungulates, $P=1$; Neogene ungulates and extant ungulates, $P=1$). Third, the correlation coefficients for these equations indicate that the majority of the variation in brain mass (between 87 and 96 %) can be accounted for by variations in body mass. The ungulate EQ values also show a gradual increase in the relative size of the brain over time (Fig. 13).

The pattern of cetacean brain evolution is dramatically different. Despite limited data, comparison of the Archaeoceti with the contemporaneous Neogene ungulates shows a similar allometric relationship (see above). At the archaeocete – Oligocene cetacean transition there appears to be a punctuation in cetacean brain evolution, which from the fossil endocasts of the Miocene cetaceans appears to be due to the expansion of the cerebral hemispheres. This change in slope and upward shift of the regression line is unlike anything seen in the evolution of the ungulate brain. Following this is a lack of change in the evolution of the cetacean brain both in scaling and relative size. The punctuation in the evolution of the cetacean brain is also demonstrated by the EQ values (Fig. 13) (archeocete EQs average 0.53 and range from 0.31–0.97, while Oligocene cetacean EQs average 2.55 and range from 1.34–3.85, approximately a fivefold increase in average EQ); the EQs of archaeocetes fall within the range seen

for Neogene ungulates, whereas those of the Oligocene and Miocene odontocetes fall in the range of the modern odontocetes.

VII. THE INTELLECTUAL CAPACITIES OF CETACEANS

In the following sections, a synthesis of the available observations is used to formulate a neuroanatomical test of cetacean intellectual abilities.

(1) Actual and relative brain size of cetaceans

Cetaceans have large brains. It is this observation that has led many scientists to regard them as having high intellectual abilities. Why is it that large brain size is considered the equivalent of intellectual capacities? Jerison (1973) influentially related the residual brain size once body mass was corrected for (the encephalisation quotient) to intellectual ability. This led him to propose (Jerison, 1978) that some cetaceans, especially the Delphinidae (see Table 1), possess high intellectual capacities. However, the larger cetaceans, such as sperm whales and the baleen whales, have very low EQs, in fact cetaceans have some of the highest and lowest

to body size over time in the ungulates. There is a major punctuation in this relationship in cetaceans at the transition from Archaeoceti to Oligocene odontocetes. This punctuation is accompanied by a change in the scaling of the brain (slope of regression) relative to body size.

EQs of mammals, plus the entire range between (see Figs 2, 3, 13).

The above examination of the allometry of the cetacean brain raises a series of interesting observations regarding the evolution of a large brain. The volumetrically large brains of the cetaceans evolved more than 20 million years after their ancestors led a fully aquatic lifestyle. The evolution of large brain size in cetaceans seems to have occurred as an evolutionary punctuation, and not as a gradual Darwinian-type increase (as is the case for ungulates and many other mammals). This can be interpreted as indicating a specific evolutionary pressure acting at a particular time. Second, the brain-body scaling of the extant cetaceans differs from that of other extant mammalian species (see Section II.1). For a given increase in body size, the relative increase in brain size in cetaceans is less than it is for other mammals and much less than in hominids: both hominids and cetaceans appear to represent exceptions to the general pattern of brain-body allometric scaling for mammals.

Nevertheless, it is not parsimonious to claim that increases in relative brain size in hominids and some selected cetaceans (Marino, 1998), were both driven by the need for greater information-processing capacity. Moreover, an examination of the intraspecific scaling of cetaceans indicates that the selection pressure causing the intraordinal scaling pattern of cetaceans continues to act upon extant cetaceans.

Previous studies of cetacean allometry have interesting parallels with those of the craniometrists of the 1800s (Gould, 1981). The craniometrists attempted to fit measurements of brain mass and skull size and shape into a preconceived notion of the rank of different races of humans, in an attempt to prove some imagined superiority of the Caucasian male. In doing this, the craniometrists ignored available data, statistically manipulated and misrepresented results, and provided imaginative and often untestable explanations for data that did not fit their preconceived notions. In the study of cetacean allometry parallels can be found in the absence of certain species from analyses, statistical manipulation without sound evolutionary logic (e.g. the grouping of Delphinidae and primates to allow the recalculation of the EQ), and imaginative explanations to account for the observed differences (e.g. 'aquatic weightlessness', and non-innervated blubber) (see Marino, 1998).

Given its importance in thermoregulation the thickness of cetacean blubber is surprisingly low with dolphins only having a blubber layer 2.5 cm thick (Hokkanen, 1990), whereas in adult pinnipeds this blubber layer is commonly 7–10 cm thick (Iverson, 2002). Moreover, the manner in which blubber scales in cetaceans (Ryg *et al.*, 1993), means that subtraction of blubber mass from total body mass, while increasing the EQ, will reduce further the slope of the brain-body mass scaling relationship.

(2) Vocalisations of cetaceans: language or simple species-specific calls?

The vocalisations of cetaceans have been the subject of speculation ever since Lilly (1962) entertained the possibility of a dolphin language, or 'dolphinsese'. Despite extensive

efforts to either impose a language upon cetaceans, or decipher their vocalisations, it is clear that no such language exists (Herman & Tavolga, 1980; Herman, 2002).

Mammals have a common vocalisation pathway (Jürgens, 1998). The only known exception to this is the language areas of the human cerebral neocortex (see Price, 2000, for review). There are no reports of a region of the cetacean neocortex that might be analogous to the language areas of the human neocortex. In fact, given the relatively small size and simple areal organisation of the cetacean cerebral cortex, it is likely that no neocortically initiated vocalisations can be produced by cetaceans. In comparison to other mammals, the anterior cingulate cortex of cetaceans is also small and undifferentiated. This limbic region is involved in the voluntary initiation of vocalisations in mammals (Jürgens, 1998); thus, any cortical origin for vocalisations in cetaceans must be greatly compromised or does not exist.

The region of the vocalisation system localised in the periaqueductal grey matter does appear to be specialised in cetaceans. Within the periaqueductal grey matter of cetaceans lies a large and distinct nucleus, the nucleus ellipticus. If this nucleus is indeed involved in vocalisations, as seems likely (see Section V.1), then the probable centre for controlling vocalisations in cetaceans lies in the brainstem. In humans, the main centres for the control of language lie in the neocortex (Price, 2000). Thus, the study of cetacean neuroanatomy suggests that dolphin 'language' is a uniquely evolved brainstem specialisation, dramatically different from the neocortically based language of humans.

A more parsimonious explanation is that cetaceans do not possess the capacity for language. Rather, they have approximately seven different species-specific vocalisations (Herman & Tavolga, 1980), which are controlled mainly at the brainstem level. Several species of mammals possess an equal or greater range of vocalisations and are not considered linguistically sophisticated. For example, the grey-headed flying fox (*Pteropus poliocephalus*) has over 30 different calls (Hall & Richards, 2000), yet has not been suggested to possess linguistic capacities.

It is a general belief that cetacean vocalisations have a semantic meaning. However, this assumption can be challenged by using a more strict and non-anthropomorphic approach, by asking what the animal accomplishes by vocalising, instead of asking what it is trying to say (Morton, 1977; Morton & Page, 1992; Owings, 1992). The most common vocalisation of bottlenose dolphins is the signature whistle, presumed to be a 'cohesion call' (Janik & Slater, 1998) i.e. it is used for group coherence to keep the pod within acoustic range of each other. The main predators of dolphins are large sharks, and by schooling an individual is less likely to be predated (Acevedo-Gutiérrez, 2002). The vocalisation in itself is not required to have a semantic or symbolic meaning; dolphins just have to learn, by association, that increasing pod coherence in response to a specific vocalisation decreases their chance of being predated.

Vocalisations have also been used to argue that cetaceans possess 'culture', by the transference of information from one individual to another and subsequently to the entire population (Rendell & Whitehead, 2001). The most commonly cited example of 'cultural' transference of

vocalisations across individuals are the ‘songs’ of the humpback whale (Payne, 1999). It has been shown that the majority of breeding humpback whales ‘sing’ nearly the same ‘song’, but that this ‘song’ changes over the course of a breeding season and between breeding seasons. It has been postulated that these changes reflect cultural transmission and learning across the male humpback population (Rendell & Whitehead, 2001). However, it has been shown, using a simple mathematical model, that birds copying each other’s songs but with a low and constant random error rate, can explain regional variations in bird song (Williams & Slater, 1991). It is likely that a constant random error rate in song copying in whales leads to the observed alteration in songs, rather than a meta-cognitive cultural phenomenon (Rendell & Whitehead, 2001).

(3) The cerebral cortex and hippocampal formation

Any serious proposal concerning the intellectual capacities of mammalian species must be supported by neuroanatomical complexity of the cerebral cortex, the region thought to be involved in complex cognitive behaviours. In the present survey, 15 differences in the structure of the cetacean cerebral cortex in comparison to other mammals were found: (1) cortical lamination is not distinct; (2) there is pyramidalisation of layer 2 neurons; (3) layer 4 recedes during development; (4) the cortex is thin relative to total brain size; (5) neuronal density is low; (6) there is imperfect vertical columnar and microcolumnar organisation; (7) there is low diversity and complexity of neuronal morphologies; (8) the glia:neuron ratio is very high; (9) there is a very small number of cortical areas; (10) there is no apparent prefrontal cortex; (11) the temporal cortex is relatively small; (12) the limbic lobe, especially the anterior cingulate cortex is relatively small; (13) the relative amount of total cerebral cortex is low; (14) the cerebral cortical volume expands proportionally, not allometrically, with increased brain size across cetacean species; and (15) there are altered proportions of the constituents of the neuropil.

These features are intimately linked with the processing capacity of the cerebral cortex. One way in which the mammalian cerebral cortex processes information is by vertical, or interlaminar, connectivity (Jones, 2000). This basic vertical processing unit is seriously compromised in the heterotypical cetacean cerebral cortex. Intercolumnar processing is also compromised due to the paucity of parvalbumin-immunoreactive neurons (Hof *et al.*, 2000). Blurring of the cortical lamination, lack of layer 4, a thin cortex, low neuronal density, and pyramidal cells in layer 2, will all compromise the processing capacity of the mammalian cortical network. No clear alternatives to compensate for these alterations in structure have been identified in cetaceans.

Kaas (1995), states that: ‘All mammals appear to have roughly 20 cortical areas, ..., in common as retentions from an early ancestor ...’. It would appear that cetaceans possess only those areas in common to all mammals, though many of these may be greatly reduced in relative terms (see Fig. 6). Moreover, the general trend for increasing numbers of

cortical areas with increasing cortical size (Kaas, 1995) is not apparent for cetaceans. An increase in the number of cortical areas would increase the sophistication of information processing and reduce the problem of interconnecting circuits (Kaas, 1995), probably resulting in a greater behavioural range and increased cognitive capacities.

In the present analysis, prefrontal cortex is designated as the region of cortex rostral to the distribution of the gigantopyramidal cells that project to the pontine nucleus (found within motor and pre-motor cortex – the origin of the cortico-pontine tract). The definition and homologies of prefrontal cortex across mammalian species is a contentious issue (Divac *et al.*, 1987; Divac & Öberg, 1990; Preuss, 1995). In cetaceans it is difficult to identify any region of cortex rostral to premotor areas, although agranular prefrontal cortex is readily identified in a range of mammalian species, including primates (Brodmann, 1909; Divac *et al.*, 1987; Preuss, 1995). Agranular prefrontal cortex plays a major role in complex cognitive functions.

For mammals in general, an increase in brain size means that a greater proportion of the brain is made up of cerebral cortex (Finlay & Darlington, 1995). This trend is not found in the cetaceans, where the percentage of the brain that is cerebral cortex remains unchanged with changes in brain size.

The altered proportions of the contents of the neuropil discussed in Section III.6 will have a direct impact on the processing power of the cetacean cerebral cortex. The observed higher proportion of glial processes, myelin sheaths, and axons of passage (thalamocortical axons), plus lower spine numbers and less branched dendrites will all impact negatively on its processing power. For example, a lack of dendritic branching will cause lowering of processing/parcellation of inputs in the dendritic tree.

This analysis of the cetacean cerebral cortex makes it clear that cetacean cerebral cortex is unique to these animals, rather than representing a primitive mammalian brain (Glezer *et al.*, 1988). In all aspects investigated to date, the cetacean cerebral cortex can be argued to be deficient in terms of processing capacity, with no unique structures yet identified that could compensate for this.

The hippocampal formation of cetaceans is small in relative and actual terms. The function of this structure in forming enduring memories and the interaction of memory with cognitive functions, again casts doubt on reports of complex cognitive abilities in cetaceans.

One major theory of comparative intelligence is based on the assumption that intelligence is a product of various cognitive modules, and that each species has its own set of cognitive modules, the sum of which describes the intelligence of that species. This is known as the ecological theory of intelligence (Shettleworth, 1998), or neuroecology (Bolhuis & Macphail, 2001). The main experimental focus of the ecological theory of intelligence has been to compare the differences in hippocampal formation size in food-storing birds (which have a comparatively better spatial memory) with related non-food-storing birds. The relatively small size of the cetacean hippocampal formation could suggest that the cognitive module associated with spatial memory is greatly compromised in cetaceans. It appears appropriate

therefore to suggest that functions related to hippocampal processing must be compromised in cetaceans.

(4) Does acoustic specialisation account for the increase in cetacean brain size?

It has been proposed that the increase in cetacean brain size is related to their specialised acoustic system (Langworthy, 1931, 1932). Ridgway & Au (1999) state that: '... the great hypertrophy of the dolphin auditory system – and perhaps the entire cerebrum – may result from the animal's need for great precision and speed in processing sound.' This reasoning has particularly been used for the Delphinidae, which have the highest encephalisation quotients of cetaceans (Table 1). It is hypothesised that specialisations of the delphinoid acoustic system for echolocation may have been the driving force behind the relative increase in brain size of this group above other cetaceans.

The peripheral auditory structures of cetaceans are highly modified (for review see Ridgway & Au, 1999). The dolphin cochlea is rich in outer hair cells, and possesses many ganglion cells. The vestibulocochlear nerve (8th cranial) is large in all cetaceans (Pilleri & Gahr, 1970) consisting of a large number of fibres, e.g. 153 500 in the fin whale, 179 000 in the humpback whale, and 214 500 in the sperm whale, compared with 50 000 in man (Jacobs & Jensen, 1964). All central neural structures associated with auditory processing, such as the inferior colliculus, cochlear nucleus, superior olive, and the medial geniculate body, are relatively enlarged and heavily myelinated (Hosokawa *et al.*, 1969; Glezer *et al.*, 1998). As described above, the proportion of the cortical sheet devoted to auditory processing is also substantial. It is clear that much of the brain of the cetacean is used for processing acoustic information. However, does this mean that the enlargement of the entire brain was driven by acoustic specialisation or that this increase in brain size was accompanied by an increase in the general level of intelligence?

Many mammalian species possess specialised sensory systems and certain regularities in the modifications of peripheral and neural structures are evident. The specialised sensory systems of the bill of the platypus (*Ornithorhynchus anatinus*) and the visual system of primates, including man, can be compared to the cetacean auditory system to highlight these regularities, and also to show where the cetaceans differ compared to other mammals. The bill of the platypus is a highly derived sensory structure containing specialised tactile and electrical receptors (Pettigrew, Manger & Fine, 1998). There are approximately 46 500 push-rod mechanoreceptor complexes and 43 500 electroreceptors (of two types), innervated by a total of 672 000 axons per trigeminal nerve (Manger & Pettigrew, 1996). The primate eye is an elaborate structure with a significant diversity in cell types within the retina (Robinson, 1991); the human optic nerve contains around 1 200 000 axons (Jacobs & Jensen, 1964). The trigeminal ganglion and the ventral posterior medial nucleus of the platypus thalamus are both greatly enlarged (Hines, 1929), as are the lateral geniculate and pulvinar nuclei of primates (Jones, 1985). Approximately two-thirds

of the platypus neocortex is involved with the representation and processing of sensory information obtained *via* the bill (Krubitzer *et al.*, 1995). A major portion of the neocortex of primates is also devoted to processing visual sensory information (van Essen *et al.*, 2001). The primary somatosensory cortex of the platypus is highly derived, and exhibits a mechano/mechano-electro dominance column configuration (Krubitzer *et al.*, 1995; Manger, Calford & Pettigrew, 1996). Similarly, the primary visual cortex of primates is highly derived and exhibits many forms of modules including ocular dominance columns, orientation columns, and blob and interblob zones (Mountcastle, 1997).

Similarities arising from this comparison include: (1) peripheral specialisation with extensive innervation; (2) enlargement and specialisation of all subcortical structures involved with the specialised sense; and (3) occupation of a large portion of the cerebral cortex by the specialised sense. These features are seen in all mammals that possess specialised sensory systems including dolphins.

The first difference of note is that within the auditory cortex of the dolphin, no specialised, anatomically identifiable, cortical modules have been found, despite the range of stains used to examine this region (Glezer *et al.*, 1998; and references therein). Such anatomically identifiable modules are found in the primary sensory cortices of other mammals with specialised sensory systems, e.g. platypus (Manger *et al.*, 1996), insectivores (Catania, 2000), marsupials (Elston & Manger, 1999; Huffman *et al.*, 1999), rodents (Woolsey, Welker & Schwartz, 1975), and primates (Mountcastle, 1997) among many others. Second, mammals with specialised sensory systems do not have the encephalisation quotient (EQ) grossly altered due to brain-body mass scaling differences that is seen in cetaceans. The platypus has an EQ of around 1.07, only slightly above the 'average' mammal [EQ of the average mammal = 1, 95% confidence intervals 0.51–1.99, the platypus EQ of 1.07 falls well within (66%) the Gaussian frequency distribution of mammalian EQs]. Other mammals, such as carnivores or primates, with specialised visual systems similarly lie within the normal range for mammals or primates (see Fig. 4). Third, the volume of the cerebral cortex of mammals with specialised sensory systems does not scale unusually compared with other mammals, i.e. they have the same amount of cerebral cortex as a mammal of the same brain size that lacks the sensory specialisations (Finlay, Darlington & Nicastro, 2001). As shown earlier, cetaceans actually have less cerebral cortex than mammals of similar brain size, so the concept that sensory specialisation has driven a 'hypertrophy' of the cerebrum (Ridgway & Au, 1999) does not fit the anatomical data. Moreover, the number of fibres in the vestibulocochlear nerve is less than half that of the trigeminal nerve in all cetaceans studied (Jacobs & Jensen, 1964), raising a question as to the degree of specialisation of the cetacean acoustic system.

Microchiropteran bats possess similar echolocation abilities to the cetaceans (Covey & Casseday, 1999). As with the cetaceans, the auditory system of the Microchiroptera exhibits peripheral and central specialisations (e.g. Covey & Casseday, 1999; Fitzpatrick, Olsen & Suga, 1998; Sakai & Suga, 2001; and references therein). Within the auditory

cortex of the Microchiroptera, around seven auditory areas have been defined (Fitzpatrick *et al.*, 1998). This is probably matched by the cetaceans, even though on cytoarchitectonic grounds only four areas have been identified (Kesarev *et al.*, 1977). Despite the potential similarities in the organisation of the acoustic system in these two groups of mammals, microchiropteran bats do not have disproportionately large brains: microchiropterans follow normal mammalian allometric patterns and there has been no increase in relative brain size to accommodate their specialised acoustic system (Baron, Stephan & Frahm, 1996).

Echolocation in microchiropterans provides a maximum of 3 m detection range (best range is 1 m), whereas delphinoids have a range of around 100 m (Ridgway, 1990), thus it is possible that echolocation distance is responsible for the relative brain size differences between cetaceans and microchiropterans. However, given that dolphins are some 1000 times larger than Microchiropteran bats, the difference in range could also be accounted for simply by the difference in size. Within the environment of the Microchiropteran, there are numerous surfaces that will reflect sound (Covey & Casseday, 1999), whereas in the open-ocean environment of most cetaceans this is not the case. In both Microchiroptera and the barn owl (*Tyto alba*), specific neuronal groups within the auditory space map of the inferior colliculus have been identified that compensate for echoes (Covey & Casseday, 1999; Keller & Takahashi, 1996). Thus, it is unlikely that physical acoustic properties are acting as a selection pressure resulting in large brain size in cetaceans.

It has been argued that cetaceans must echolocate a sphere of 100 m diameter, whereas in a microchiropteran this sphere is only 3 m diameter, and that this requires an enlarged cerebral cortex (Ridgway, 1990). However, it has been shown that a precise map of auditory space exists within the inferior colliculus of all mammals studied (Park & Pollack, 1994; Grothe, Covey & Casseday, 1996; Wu & Jen, 1996; Zhou & Jen, 2000). This collicular auditory space map has also been intensively studied in the barn owl (Cohen & Knudsen, 1999) in which the space map is based on the tuning features of the individual neurons to such stimuli as interaural time differences and interaural level differences (Moiseff & Konishi, 1981; Mogdans & Knudsen, 1994; Peña & Konishi, 2001). A complete and accurate map of auditory space is created in the midbrain portion of the auditory system.

The formation of the auditory space map in the owl is assisted by an asymmetric morphology of the head, with one ear being lower than the other. Cranial asymmetries are found in the skull of echolocating odontocetes, but not in the non-echolocating mysticetes (Ness, 1967; Ridgway, 1990), which may assist in the creation of the collicular auditory space map. Moreover, the echolocation pulses of cetaceans are often described as being emitted 'directed forward in a narrow pattern' (Ridgway & Au, 1999) making it probable that rather than scanning a 100 m diameter sphere with sound they are instead focussed on a narrow portion of this sphere.

These observations question the need for an exceptionally enlarged cerebral cortex in delphinoids to localise acoustic

stimuli accurately. In fact, the inferior colliculus of the dolphin appears to have a modular organisation of GABAergic neurons (Glezer *et al.*, 1998) that could subserve an accurate map of acoustic space as seen in the Microchiroptera (Park & Pollack, 1994; Zhou & Jen, 2000). Taken together the above discussion shows that echolocation does not provide a satisfactory explanation for the altered brain-body mass scaling of cetaceans.

(5) Can apparent convergences in cognitive behaviour explain the increase in cetacean brain size?

A recent article by Marino (2002) lists three apparently complex cognitive abilities that are implied to infer high levels of intelligence in cetaceans and are suggested to underlie their increased brain size: social group behaviour, language comprehension, and self-recognition ability. In Section VII.2 it was shown that there is little evidence for a language and the vocalisations of cetaceans are more parsimoniously explained by an anatomical specialisation within the rostral brainstem, the nucleus ellipticus.

It has been reported that there is a significantly positive correlation between EQ and pod or group size in cetaceans and primates (Marino, 1996, 2002). For cetaceans, Marino (1996) provides a plot of data from a limited number of species (of which only two are solitary), no equation is given for the regression line, or any correlation statistics, making it impossible to judge the validity of the relationship. Fuller examination of the available data supports only a weak positive relationship for primates and cetaceans (Fig. 14). For all cetaceans there is no significant relationship between EQ and pod size ($r^2=0.063$, $P=0.138$), although with the removal of the solitary living cetaceans, the regression just reaches significance ($r^2=0.167$, $P=0.026$). Note that the three solitary-living species used in this analysis, *Platanista gangetica*, *P. minor* and *Pontoporia blainvillei*, have EQs ranging from 1.83 to 2.38 (Table 1), which are in the middle of the observed range of cetacean EQs. The allometry for primates ($r^2=0.205$, slope = 1.43) indicates a slightly better predictability of group size from EQ, with a steeper slope, and a significant correlation ($P=7.1 \times 10^{-5}$). This analysis suggests that while there are weak relationships between EQ and social group size in both primates and cetaceans it is likely that other factors such as levels of predation, food abundance, and other life-history variables also determine cetacean pod size.

Cooperative feeding strategies have also been used as evidence for intelligence in cetaceans. Marino (2002) cites three examples: water-surface trapping of fish by dusky dolphins [genus *Lagenorhynchus*, EQs ranging from 4.43 to 6.32 (Table 1); the EQ of *Lagenorhynchus obscurus* is unknown], 'strand feeding' by bottlenose dolphins (*Tursiops truncatus*, EQ = 4.47), and bubble-net feeding by humpback whales (*Megaptera novaeangliae*, EQ = 0.35). It is clear from this comparison that cooperative feeding strategies in cetaceans are not related to encephalisation levels. Other social behaviours listed by Marino (2002), such as alloparental care, cultural transmission, fission-fusion societies, interpod 'warfare', and intrapod alliances, all rely on behavioural

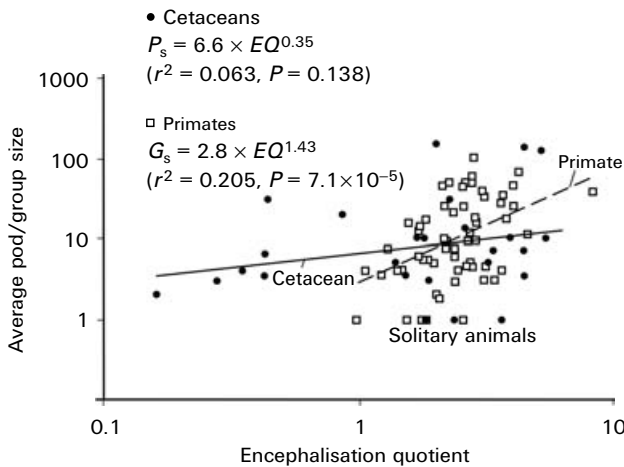


Fig. 14. Plots of average pod (P_s) or group (G_s) size against encephalisation quotient (EQ) of cetaceans and primates. EQ was calculated using equation (1) in Section II.1. In cetaceans, there is a trend towards increasing group size with increasing brain size but this relationship is not significant ($r^2=0.063$, $P=0.138$). For primates the relationship does reach significance ($r^2=0.205$, $P=7.1 \times 10^{-5}$). These results indicate that there is no relationship between encephalisation level and pod size as previously reported (Marino, 2002); and those for primates, while reaching statistical significance, do not have a high level of predictability (Reader & Laland, 2002). Average pod/group sizes used in this plot were taken from Nowak (1999).

observations and have not been sufficiently documented to allow independent scrutiny. Many of these apparently primate-cetacean convergent social behaviours are found in other species of mammals and do not support her artificial grouping. A serious cladistic analysis of these behaviours is required to test the conclusions of Marino (2002). Many of these behaviours occur in a range of cetacean species, with a range of EQ levels, thus, it may not be parsimonious to relate them to increased relative brain size. For example alloparental care, or ‘babysitting’, is said to occur in bottlenose dolphins (*Tursiops truncatus*, EQ=4.47), sperm whales (*Physeter catadon*, EQ=0.44), killer whales (*Orcinus orca*, EQ=2.62), and harbour porpoises (*Phocoena phocoena*, EQ=3.23).

Mirror self-recognition has been used as evidence for sophisticated cognitive abilities, and has been consistently found in chimpanzees, however, findings in other species are limited and controversial. Reiss & Marino (2001), claim to have presented the only convincing evidence for mirror self-recognition in dolphins (*Tursiops truncatus*), despite other studies of cetaceans such as *Orcinus orca* and *Pseudorca crassidens* with similar claims (e.g. Delfour & Marten, 2001). Again, the range of EQ levels for these species indicates that EQ and mirror self-recognition ability are unlikely to be related; this also applies to primates: the chimpanzee (*Pan troglodytes*) has an EQ of 2.76 which is far lower than that of the capuchin monkey (*Cebus capucinus*, EQ=4.55) which does not have mirror self-recognition abilities. Moreover, the methodology (Delfour & Marten, 2001), interpretation (Mitchell,

1995), and controls (Anderson, 1995) in studies of mirror self-recognition in cetaceans have been questioned. The conclusions of Reiss & Marino (2001) are greatly weakened by not addressing these issues and their reliance on measures of latency to infer cognitive activity. Moreover, their data show that unmarked dolphins spent almost as much time in front a mirror as marked individuals, and that the target behaviour was increased dramatically even in the absence of a mirror (see Fig. 3b of Reiss & Marino, 2001).

In summary, the features listed by Marino (2002) that led her to conclude that ‘Cetacean brains and primate brains represent alternative ways brains can increase in size and complexity and arrive at similar cognitive or even computational abilities’ are questionable.

VIII. WATER TEMPERATURE AND THE LARGE CETACEAN BRAIN

If the large brain of modern cetaceans did not evolve to increase its information-processing capacity (i.e. intelligence) then why do they have such large brains? A serious deficiency in modern evolutionary thinking in regards to brain evolution is that the evolution of large brain size is assumed solely to effect an increase in intelligence. So can an evolutionary increase in brain size be related to a specific selection pressure without the need for increased intellectual capacity? In this section neuroanatomical features of cetaceans, the evolution of modern cetacean brain size, intraordinal and intraspecific brain-body mass scaling, encephalisation quotients, the glia:neuron index, and uni-hemispheric sleep phenomenology are related to past and present oceanic temperatures, in which cetaceans evolved and now live. It is suggested that oceanic temperature was the selection pressure that drove the evolution of, and continues to influence, the brain size of modern cetacean fauna.

(1) Water temperature during the archaeocete/Oligocene cetacean transition

In Section VI it was argued that a punctuated change occurred during evolution in the relative size of the cetacean brain. This occurred at the demise of the Archaeoceti and the rise of the modern cetacean fauna, as represented by the Oligocene cetaceans (Gingerich, 1998; Marino *et al.*, 2004). The Archaeoceti lived, for the most part, in the equatorial Tethys sea which is described as a shallow, nutrient-rich, warm sea with low water temperature gradients (Fordyce & Barnes, 1994). The Archaeoceti diversified, both at the species and family level, in this environment, for around 20 million years. During this period, they had a brain with a tiny cerebral cortex (Dart, 1923). During the last 1–2 million years of the archaeocete radiation, significant cooling of the oceanic waters occurred, and this is associated with a decline in archaeocete diversity (Fordyce & Barnes, 1994). At the extinction of the Archaeoceti and the evolution of the modern cetacean fauna there was a major cooling of oceanic temperatures (Whitmore, 1994), with increased latitudinal

thermal gradients, and the closure of the Tethys sea by the suturing of India and Africa to the Eurasian landmass (Fordyce & Barnes, 1994).

(2) Neuroanatomical features of the cetacean brain related to thermogenesis

It has been shown in a variety of mammals, especially ungulates, that the temperature of the brain is regulated separately to the temperature of the body (reviewed in Gisolfi & Mora, 2000). During increased thermal pressure, body temperature increases dramatically while brain temperature remains relatively stable. The pioneering studies of Donhoffer (1980) showed that during exposure to cold, the body temperature of a mammal decreases but the brain temperature remains stable due to increased cerebral heat production (Szelényi, 1998). Szelényi (1998) reviewed the thermogenetic mechanisms allowing brain temperature to remain stable, or even increase, during exposure to cold. Thermogenesis within the central nervous system (CNS) results from glycolysis within the glial cells.

The cetacean cerebral cortex contains an abundance of glia compared to other mammals (Section III.6). The cerebral cortex was the part of the brain that changed most during the period of oceanic cooling that coincided with the archaeocete/Oligocene cetacean transition. This part of the brain probably has a major thermogenetic role in the cetacean CNS due to its higher glia:neuron index. However, in the absence of further data, it is likely that the whole brain is probably involved in thermogenesis, and not just the cerebral cortex. In fact, the increased size of the cetacean brain could have been achieved by simply doubling the number of glia present throughout all regions of the brain.

In Section V it was argued that cetacean sleep patterns, i.e. unihemispheric sleep with a small proportion of REM sleep will effectively bathe the cetacean brain with higher levels of noradrenalin than found in other mammals. Noradrenalin is known to increase glial metabolism by stimulating the breakdown of glial glycogen (Stone & Ariano, 1989). It therefore appears that the greater number of glia in the cetacean brain are also bathed in higher levels of noradrenalin, which will together lead to increased heat production. These observations link the anatomy of the cetacean brain and sleep phenomenology (Manger *et al.*, 2003; Pillay & Manger, 2004) with a thermally challenging environment in which heat loss is likely to be a significant factor.

(3) Brain-body mass scaling in modern cetaceans and its relation to water temperature

Two features characterise the punctuation in cetacean brain evolution at the archaeocete/Oligocene cetacean transition: an increase in actual brain size and an altered brain-body mass scaling. The intraordinal allometric slope of cetacean brain-body mass scaling is lower than either interspecific or intraordinal slopes found for other mammalian groups (see Section II.1) presumably due to a selective force different from those acting on other mammals. It is also of interest that the intraspecific scaling of cetacean species is similar to

the intraordinal scaling (see Section II.2), implying that the factor causing altered brain scaling in cetaceans is still influencing extant cetaceans.

In Fig. 15 brain mass, body mass and EQ are plotted against the upper, lower and range of water temperatures (yearly average water temperatures for 1998 from the National Oceanographic Data Center, Fig. 16) in which the various cetacean species are found [distributional limits for cetaceans derived from Gaskin (1982), Ridgway & Harrison (1985, 1989, 1994) and Waller (1996), see Table 1 and Fig. 16]. Fig. 15 shows there is a trend for larger cetaceans to inhabit environments with lower average maximum and minimum temperatures and these relationships are significant ($r^2=0.56$, $P=1.9 \times 10^{-6}$ for T_{\max} ; $r^2=0.35$, $P=4.0 \times 10^{-4}$ for T_{\min}), but the predictability of these regressions is low. This might be taken as evidence for the concept of thermal inertia – large bodies lose heat less rapidly than do small bodies, thus providing greater tolerance to lower water temperatures. A similar pattern is found for brain mass: there is a significant relationship between brain mass and T_{\max} ($r^2=0.39$, $P=0.0002$) or T_{\min} ($r^2=0.30$, $P=0.0012$), but again the predictability of the regressions is low. The EQs in Fig. 15 were calculated for cetaceans using mammals in general as a reference group (Table 1) as this is an attempt to uncover factors influencing the scaling of cetacean brain-body mass compared to other mammals. Again, there is a trend for an increase in relative brain size (i.e. an increased EQ) to be associated with greater maximal and minimal environment temperatures. These relationships do reach significance: T_{\max} , $r^2=0.54$, $P=3.4 \times 10^{-6}$; T_{\min} , $r^2=0.29$, $P=0.0015$), but the predictability of the regressions was low.

When the range of environmental temperatures was used on the y axis trends for increasing body size with lower environmental temperature ($r^2=0.53$, $P=4.3 \times 10^{-6}$), and increasing brain size with lower environmental temperature ($r^2=0.22$, $P=0.0057$) were seen, but the predictability of the regressions was low. The relationship between environmental temperature range and EQ for cetaceans was strongly statistically significant, and the predictability of the regression was higher ($r^2=0.7$, $P=9.9 \times 10^{-9}$). Thus the strongest relationship exists between the environmental temperature range and EQ with temperature range accounting for around 70% of the variability in EQ.

These analyses suggest that the altered scaling of brain and body mass of cetaceans may be linked to environmental water temperature. A similar conclusion can be reached by qualitatively comparing the distribution of modern cetacean species with oceanic temperatures (Fig. 16): the distributional limits of cetacean species in many cases match isothermal lines of oceanic water temperature.

To illustrate the above points we can examine two species whose distributions cover the same range of temperatures, but whose body size is dramatically different. *Neophocaena phocaenoides* and *Tursiops truncatus* both inhabit an environmental temperature range of 16 ° (12 °–28 °C and 13 °–29 °C, respectively). They have a similar EQ of 4.49 and 4.47, respectively, however, *T. truncatus* is around five times larger with a body mass of 165 kg and a brain mass of 1530 g, whereas *N. phocaenoides* has a body mass of 32.4 kg

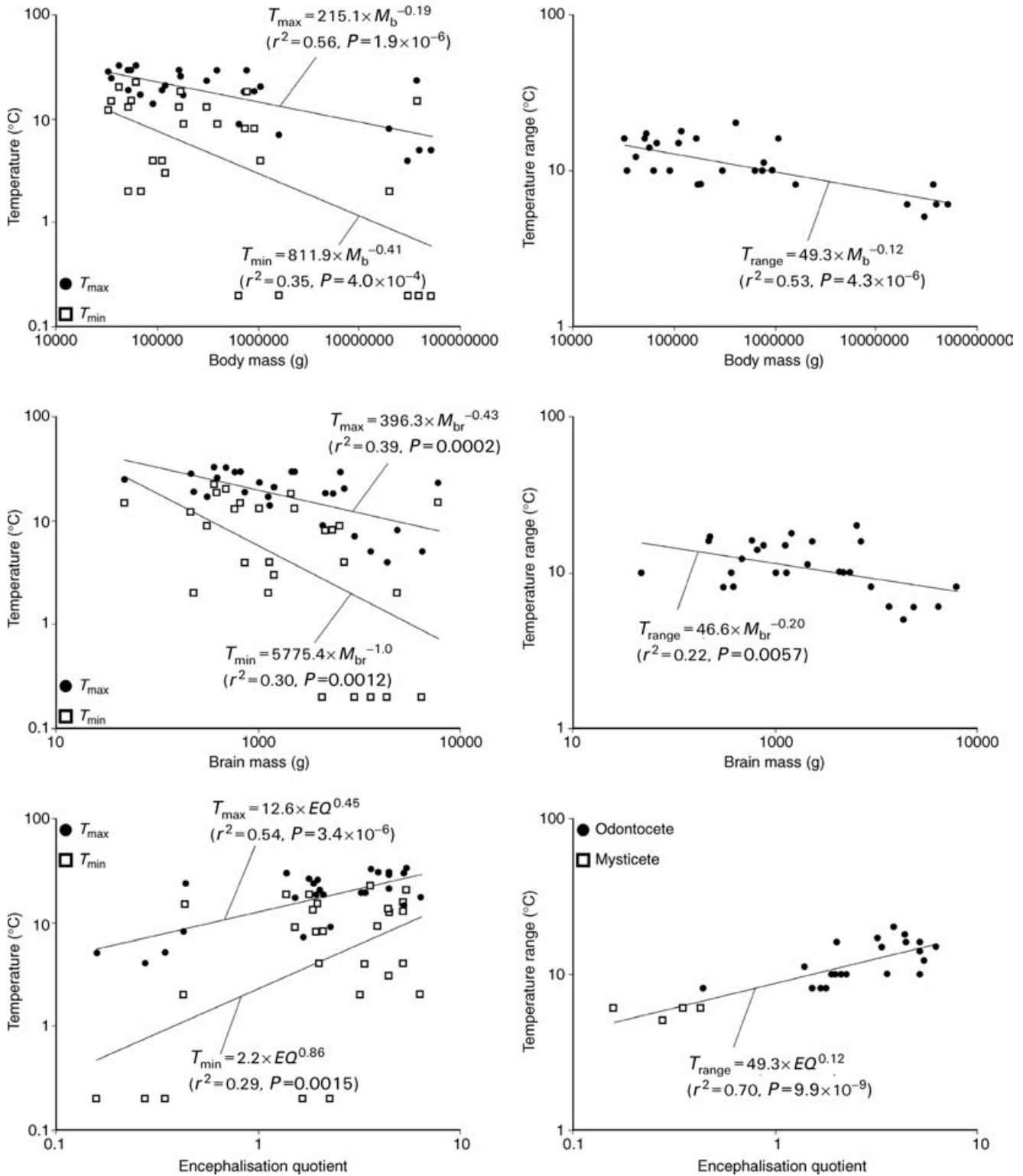


Fig. 15. Plots of body mass, brain mass and encephalisation quotient (EQ) against mean high (T_{max}) and low (T_{min}) temperature extremes and range (T_{range}) of water temperatures encountered by cetaceans. Body mass, brain mass and EQ show statistically significant trends associated with absolute water temperatures, but none of these have a high predictability. The strongest relationship is between EQ and the environmental temperature range ($r^2 = 0.7, P = 9.9 \times 10^{-9}$), with a positive slope indicating an increasing EQ with increasing range of environmental water temperatures. The data in these plots are derived from Table 1.

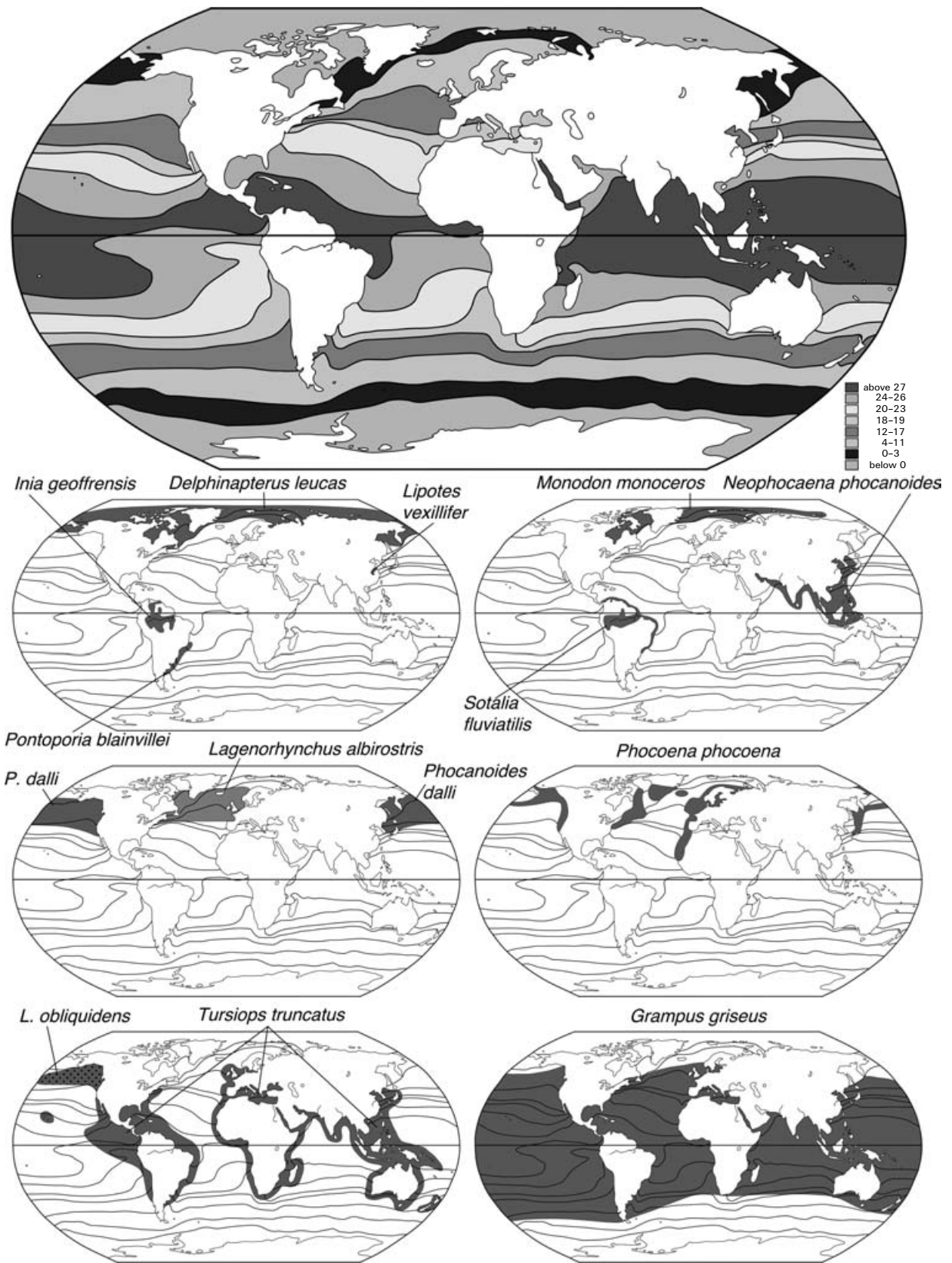


Fig. 16. Continued.

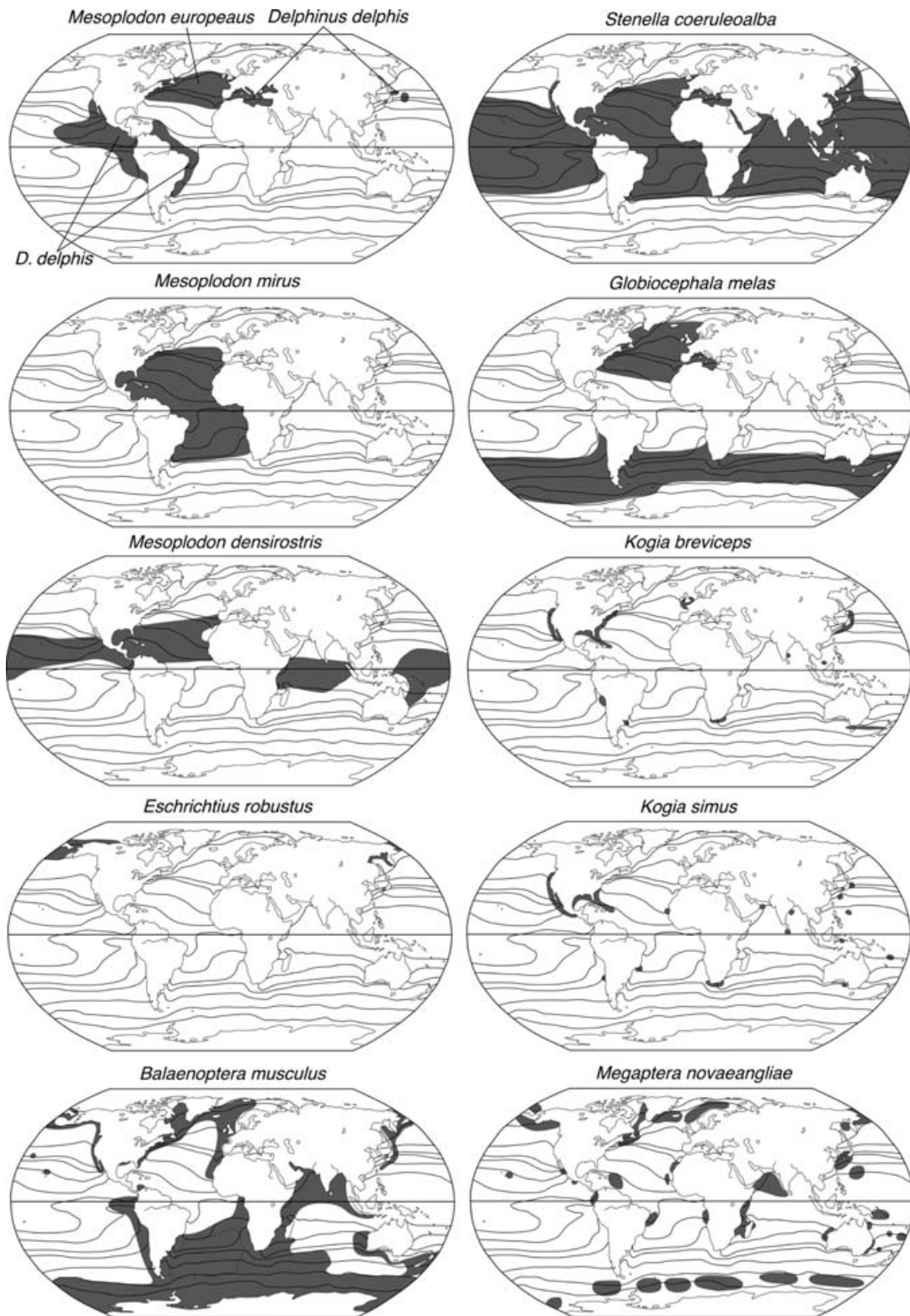


Fig. 16. Global water temperatures and the distribution of cetaceans. The upper figure shows average water temperatures at depths between 0 and 10 m from the surface in 1998. (Derived from the National Oceanographic Data Center web page using the World Ocean Atlas Interactive Image Access for 1998 [http://www.nodc.noaa.gov/OC5/WOA98F/woof_cd/search.html].) The lower figures show the distribution of various cetaceans and their relationship to the isothermal lines of water temperature. Note that many of the edges of the distributions match isothermal lines, often on both sides of a continent. Distributional data were taken from Gaskin (1982), Ridgway & Harrison (1985, 1989, 1994), and Waller (1996).

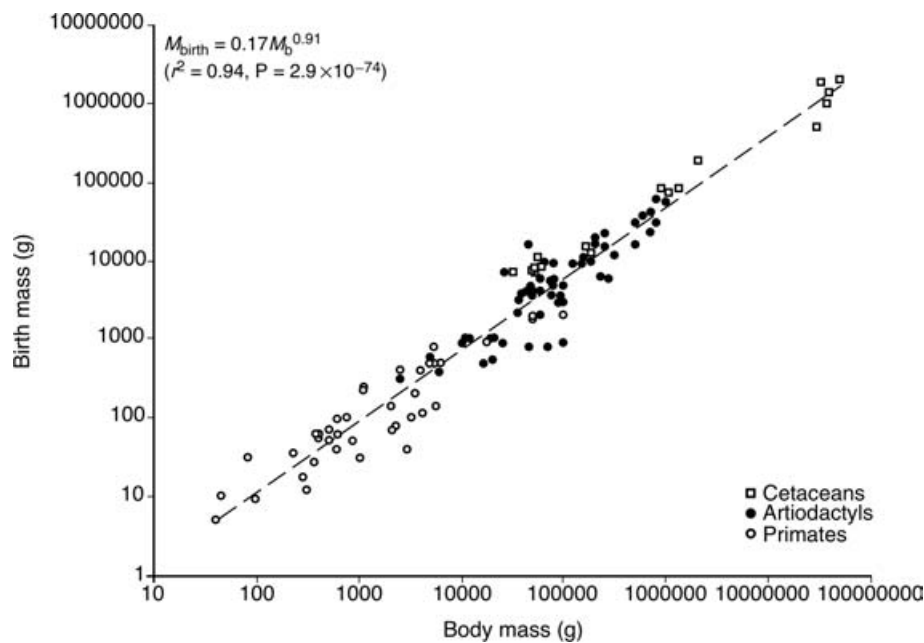


Fig. 17. Allometric plot of the relationship between neonatal (M_{birth}) and adult body mass (M_b) in three orders of eutherian mammals. The data used in this plot are derived from that given in Nowack (1999).

and a brain mass of 468 g. Thus, although inhabiting similar environmental temperatures (both absolute and range), these two species differ greatly in size. The same level of encephalisation in these two species may explain this observation, enabling them to inhabit the same geographical/oceanic range despite differences in body size.

(4) The size of the cetacean brain

The sheer volume of the cetacean brain has been one of the main reasons for attaching high intellectual abilities to cetaceans. However, the size of the cetacean brain can also be explained in terms of water temperature.

Downhower & Blumer (1988) calculated that the rate of heat loss in water is around 90.8 times faster than in air and demonstrated that the smallest body size for neonate cetaceans (~ 6 kg) is limited by this rate of heat loss. Cetaceans are eutherian mammals, and as such, to produce a young of at least 6 kg, the adult cetacean must weigh more than 30 kg (Fig. 17) this allometric relationship applies to all eutherian mammals. This adult cetacean must also have a brain-body mass scaling that allows it to cope with thermal loss to the environment. Given these two factors, it becomes impossible for smaller cetaceans to produce offspring without large brains for their body size, hence having high encephalization quotients. Larger cetaceans will produce larger offspring, resulting in actual larger brains. However, due to the altered scaling of brain and body mass, the encephalisation quotients of these larger species will be smaller.

(5) Evidence from other aquatic mammals

Cetaceans are not the only mammals that have adopted a secondarily aquatic mode of life. Both pinnipeds (seals, sea

lions and walrus) and sirenians (manatees and dugongs) have successfully adapted to semi-aquatic and fully aquatic lifestyles. If the hypothesis proposed here that water temperature is a significant evolutionary pressure on cetacean brain evolution is correct, then convergent features may be found in both these groups. Comparable data to those presented here for cetaceans are not available for pinnipeds or sirenians, but some data are available for consideration.

(a) Pinnipedia

The pinnipeds (Order Carnivora) are generally subdivided into three families: the Otariidae (eared seals, sea lions), Odobenidae (walrus) and Phocidae (earless seals). Despite previous disagreements, these groups are now thought to be monophyletic (Bininda-Emonds, Gittleman & Purvis, 1999). Neuroanatomical data are scarce. The external structure of the brain (Fig. 18) shows a highly convoluted cerebral cortex, with a somewhat enlarged cerebellum; however, systematic quantification of the size of regions of the brain has not been undertaken. A recent examination was made of trends in adaptation to an aquatic environment of pinnipeds, compared with terrestrial carnivores (Bininda-Emonds *et al.*, 2001). Few systematic differences were observed, however, features such as a streamlined body, smaller litter sizes, shorter interbirth interval, and shorter lifespan were reported for aquatic carnivores. Of most interest to the present study is that Bininda-Emonds *et al.* (2001) reported that aquatic carnivores had larger brain sizes than their terrestrial relatives, indicating to those authors an increased need for cognitive and sensory abilities: the aquatic carnivores are really semi-aquatic, with an amphibious lifestyle encompassing both aquatic and terrestrial environments.

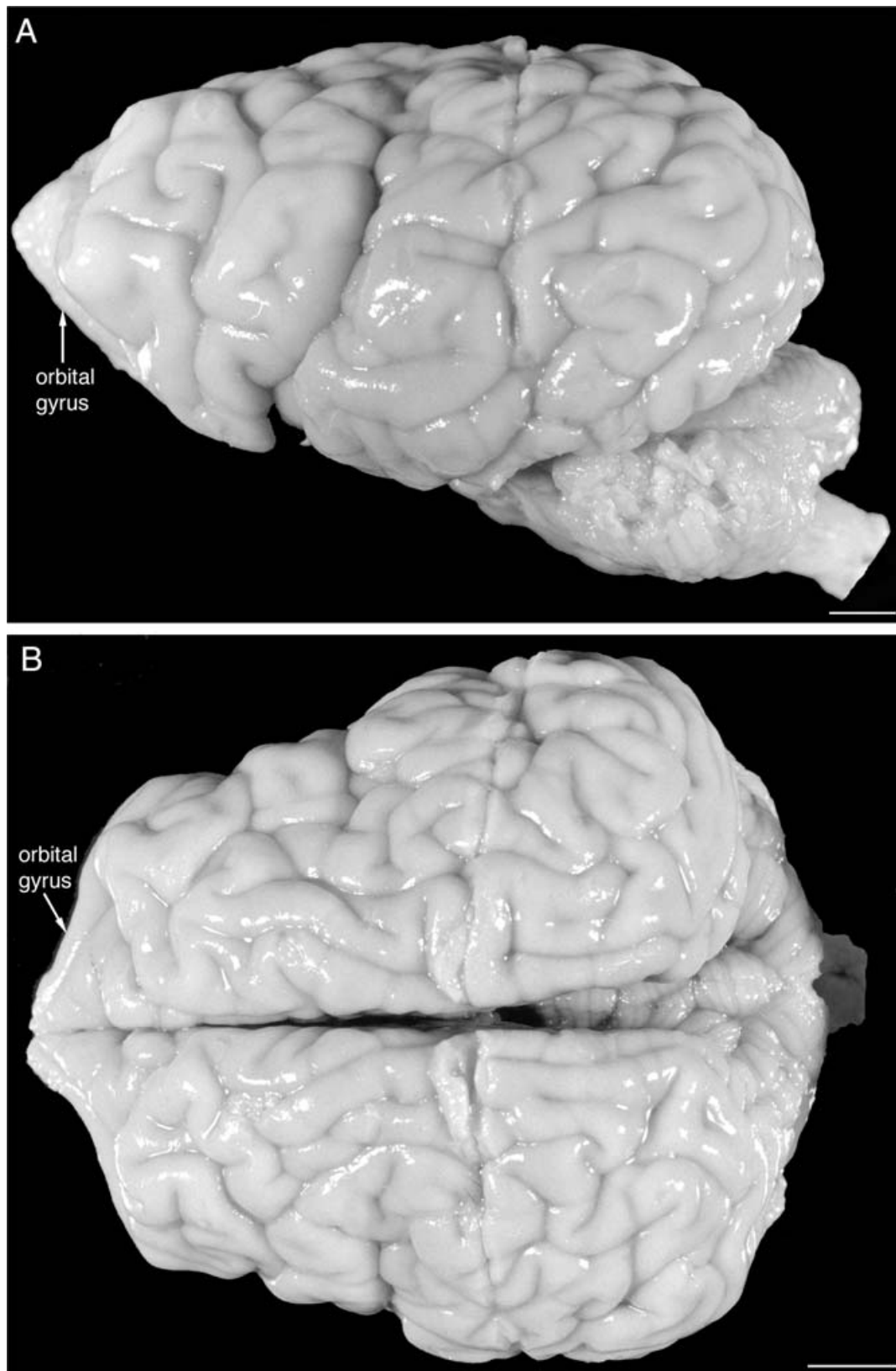


Fig. 18. Photographs of the lateral (A) and dorsal (B) surfaces of the California sea lion (*Zalophus californianus*) brain. Scale bar = 1 cm. Note the extensive gyrfication of the cortex, especially when compared to terrestrial carnivores of similar brain sizes (*c.v.* African lion, *Panthera leo*, brain, Fig. 62 in Welker, 1990). Also note the very anterior location of the orbital gyrus, indicating a proportionately very small amount of prefrontal cortex. The brain photographed here is from the collection of Dr Sam H. Ridgway.

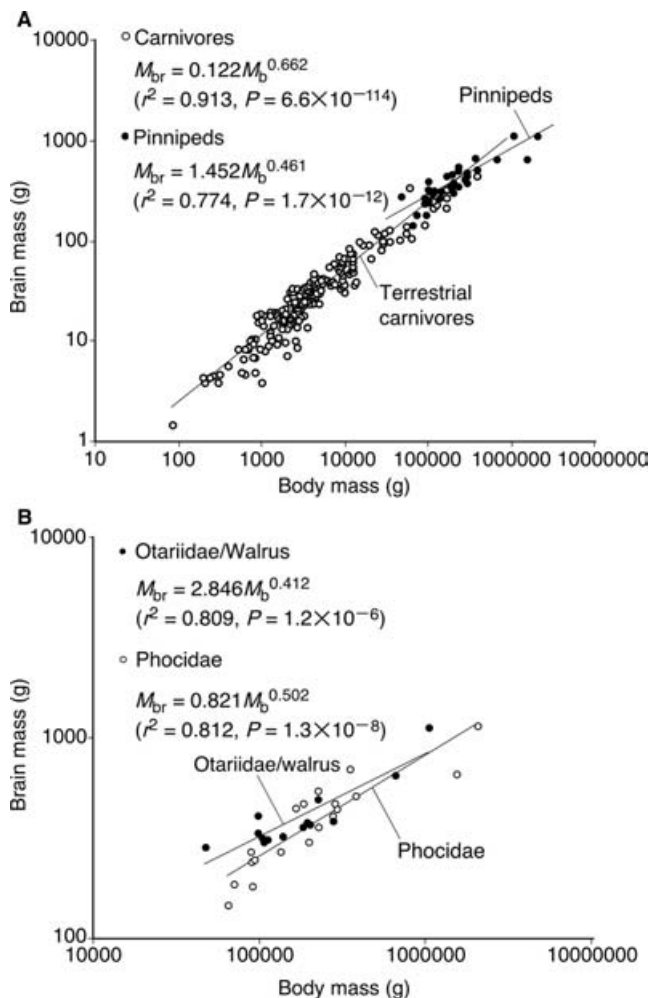


Fig. 19. Allometric plots of brain mass versus body mass for (A) pinnipeds and terrestrial carnivores, and (B) Otariidae and walrus which have unihemispheric sleep patterns, and phocidae (bihemispheric sleepers). Data are derived from Bininda-Emonds *et al.* (2001).

A reanalysis of carnivore brain and body size data was undertaken here to examine if trends similar to those described above for cetaceans were evident. The data used were generously supplied by Olaf Bininda-Emonds from that used by Bininda-Emonds *et al.* (2001). Two groups of carnivores were examined: unambiguously terrestrial carnivores and pinnipeds. Other 'aquatic' species as defined by Bininda-Emonds *et al.* (2001) were excluded. Allometric equations describing the brain-body mass scaling of these groups were calculated (Fig. 19).

The terrestrial carnivores show a typically mammalian intraordinal scaling of brain and body mass (see Armstrong, 1990, and the present analysis of ungulates in Section VI) with a slope of 0.66 ($r^2 = 0.91$, $P = 6.6 \times 10^{-114}$). However, the relationship for pinnipeds has a much shallower slope of 0.46 ($r^2 = 0.77$, $P = 1.7 \times 10^{-12}$; $P = 0.004$ for a comparison using the mean squares between and within slopes of the regressions for pinnipeds and terrestrial carnivores). This

slope is not significantly different from that calculated for odontocetes (equation 4, Figs 2 and 12) where the slope was 0.469 (a comparison of the regressions derived for pinnipeds and odontocetes revealed no significant difference using the mean squares between and within slopes, $P = 3.46$). This implies that similar selection pressures act on the scaling of pinniped brains to those of odontocete cetaceans, lending support to the hypothesis that water temperature is a significant evolutionary pressure on homeotherms inhabiting an aquatic environment. Fig. 19A shows that smaller pinnipeds have higher EQs than most carnivores whereas larger ones would have lower EQs than a hypothesized carnivore of similar body size.

The eared seals and sea lions (Otariidae) and walrus (Odobenidae) exhibit unihemispheric sleep, while the non-eared seals (Phocidae) do not (Lyamin, 1987, 1993; Lyamin & Chetyrbok, 1992; Lyamin, Oleksenko & Polyakova, 1989, 1993; Lyamin *et al.*, 1996; Mukhametov, Supin & Polyakova, 1984; Mukhametov, Lyamin & Polyakova, 1985). Intrasubordinal analyses of these groups indicates no difference in scaling that might be attributable to this difference in unihemispheric sleep phenomenology (Fig. 19B). The unihemispheric sleepers have a slope of 0.41 ($r^2 = 0.81$, $P = 1.2 \times 10^{-6}$) compared to 0.50 ($r^2 = 0.81$, $P = 1.3 \times 10^{-8}$) for bihemispheric sleepers; the difference between these slopes is not significant ($P = 0.235$).

The pinnipeds evolved more recently than the cetaceans (Bininda-Emonds *et al.*, 1999); however, there are some fossil endocasts available. As summarised by Edinger (1975), the general form and shape of the brain of extinct pinnipeds does not differ dramatically from their modern representatives, although the cerebral hemispheres are not as gyrencephalic as in extant pinnipeds. Thus, there appears to have been an increase in the gyrencephalic nature of the cerebral hemispheres of pinnipeds over time. While the evidence is not extensive, the trends exhibited in pinnipeds are similar to those discussed above for cetaceans, implying that water temperature is a significant selective force.

(b) Sirenia

The Sirenia are represented by two families the Dugongidae and the Trichechidae, all inhabiting shallow coastal equatorial waters. The Dugongidae is represented by only one extant species, *Dugong dugon*; the Stellar's sea cow, *Hydrodamalis gigas*, a member of the Dugongidae, was hunted to extinction in the 1700s. There are three extant species of the Trichechidae. The brain of the West Indian, or Florida, manatee (*Trichechus manatus*) is the subject of a special research project (<http://www.manateebrain.org>).

Like other aquatic mammals, the superficial structure of the manatee brain appears unusual, being lissencephalic except for one major sulcus (Fig. 20). Extant sirens have extremely enlarged lateral ventricles. O'Shea & Reep (1990) recorded brain and body masses for the sirens, which can be used in an allometric analysis: *Dugong dugon* ($N = 2$) brain mass 250–282 g, body mass 262–300 kg; *Trichechus manatus* ($N = 13$) 309–445 g (mean 364 g) and 449–1620 kg (mean 756 kg) respectively; *Hydrodamalis gigas* ($N = 3$)

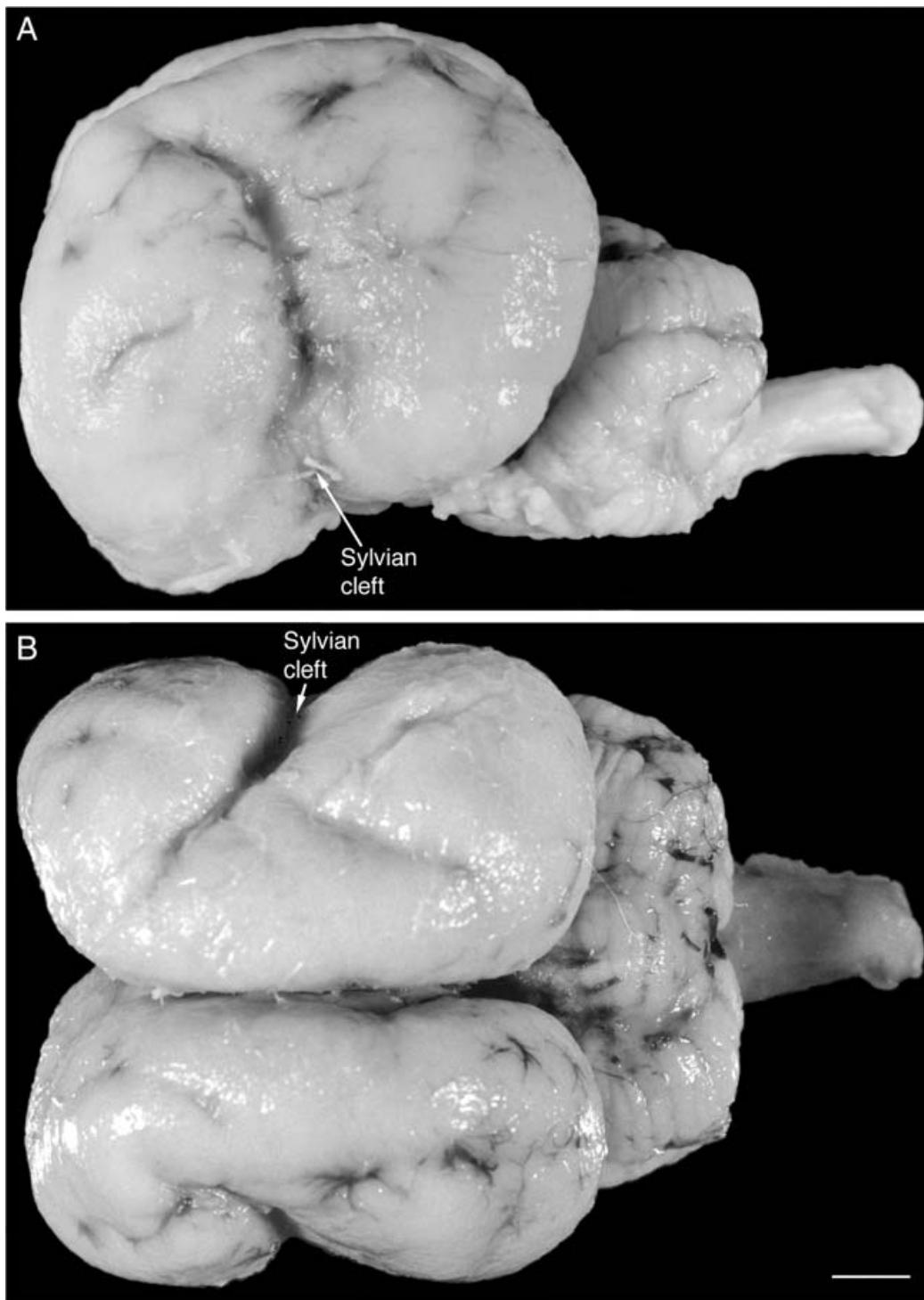


Fig. 20. Photographs of the lateral (A) and dorsal (B) surfaces of the brain of the Florida manatee (*Trichechus manatus*). Scale bar = 1 cm. Note the unusual form of the brain, with the large Sylvian (or lateral) cleft (or fossa) on the lateral aspect of the cerebral hemisphere, resembling human agyria pathology (see Fig. 26 in Welker, 1990). The brain photographed here is from the collection of Dr Sam H. Ridgway.

1014–1129 g (mean 1068 g) and 5335–8870 kg (mean 6929 kg).

The allometric equation derived from these data (Fig. 21) shows a strong resemblance to those derived previously for

cetaceans and pinnipeds; the slope (0.43) is not significantly different from that calculated for odontocete cetaceans (slope = 0.47, comparison between slopes $P = 1$) and pinnipeds (slope = 0.46, comparison between slopes $P = 0.96$),

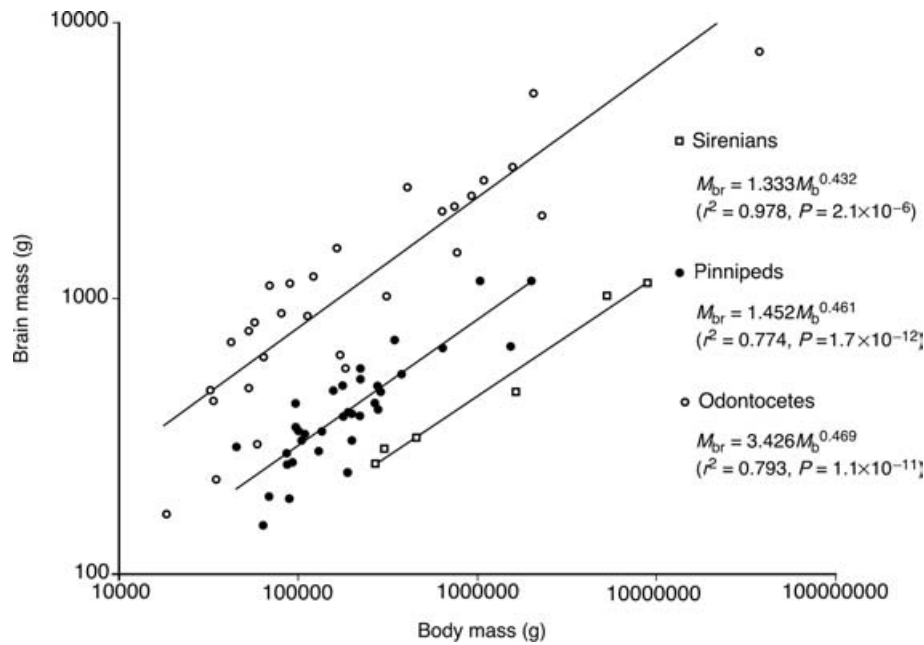


Fig. 21. Allometric plot of brain and body mass in sirenians, pinnipeds and odontocetes (data derived from O'Shea & Reep, 1990; Bininda-Emonds *et al.*, 2001; and Table 1). Note that all three aquatic mammalian groups scale similarly, and that the sirenians have the lowest relative brain sizes.

indicating that the brain-body mass scaling is similar in all three groups of aquatic mammals. The correlation coefficient (r^2) is higher for sirenians (0.978 , $P = 2.1 \times 10^{-6}$) than for other aquatic groups.

Encephalisation quotients calculated using the general mammalian regression (see Section II.1, equation 1), were found to be 0.52 – 0.53 for the dugong, 0.25 – 0.43 for the manatee, and 0.18 – 0.23 for the Stellar's sea cow. These values are slightly higher than those reported by O'Shea & Reep (1990) due to the different equations used to derive them.

A cytoarchitectural analysis of the manatee cerebral cortex available at <http://www.manateebrain.org> reveals features in common with cetaceans. There appears to be very few cortical areas. There also appears to be a very small amount of cortex at the anterior pole of the brain that might be prefrontal cortex, the primary motor cortex being located very close to the anterior pole. Given that premotor cortex must be rostral to this region, any prefrontal cortex must be small. However, published proportions of various structures of the manatee brain indicate that the corticalisation index is 63.96% (see Fig. 8, and Reep & O'Shea, 1990, who give telencephalic volume as 71% of total brain volume, and the cerebral cortex as 90% of this volume). As noted by Reep & O'Shea (1990), the percentage of the brain that is cerebral cortex is within the range of mammals of similar brain size, but from Fig. 8 is somewhat below the values observed in simians.

Another interesting parallel is the unihemispheric nature of sleep in the manatee (Mukhametov *et al.*, 1992). Unihemispheric slow-wave sleep occupies approximately 25% of total sleep time, and REM sleep approximately 1%

of total sleep time in the Amazonian manatee (*Trichechus inunguis*), with the remainder made up of bihemispheric slow-wave sleep. This sleep behaviour might relate to environmental temperature: dugongs (*Dugong dugon*) reportedly avoid water temperatures below 19°C (Anderson, 1986), Amazonian manatees (*Trichechus inunguis*) have been kept successfully in water temperatures between 22° and 30°C (Husar, 1977), West Indian manatees (*Trichechus manatus*) prefer water temperatures above 20°C (Lefebvre *et al.*, 1989), and the West African manatee (*Trichechus senegalensis*) is distributed in waters with a temperature minimum of 18°C (Husar, 1978). Moreover, the sirenians have an extensive blubber layer, ensheathed in a skin that is up to 5 cm thick, even though they have been shown to have a high rate of thermal conductance (Irvine, 1983), which is thought to limit their distribution to warmer waters.

Behavioural tests examining the cognitive abilities of the sirens have not been performed. However, it has been observed that dugongs can 'gang up' to drive sharks from their shallow-water feeding locations by butting them with their heads (Lekagul & McNeely, 1977). Similar behaviour is seen in some cetaceans, suggesting that it is not a behaviour that requires unusually large cognitive abilities.

Several fossilized endocasts of the Sirenia have been described, and Edinger (1975) provides a summary of sirenian brain evolution. Sirenians first appeared in the Eocene (Savage, 1976); endocasts of Eocene to Recent sirenians show few changes: the lissencephalic nature of the sirenian brain and its size are unaltered over time. The sirens evolved in an aquatic habitat over approximately the same length of time as the cetaceans, but in contrast to the punctuation in brain size evolution seen for cetaceans, the brain size of

sirenians has remained stable. This contrast might be related to the lack of environmental expansion of the sirenians compared to cetaceans. Both groups were abundant and diversified in the Tethys sea and were also found in equatorial Central America and Asia (Savage, 1976) during the Eocene. At the Oligocene transition of Archaeoceti to modern cetaceans, several new species of Sirenia appeared (Savage, 1976). However, no change in brain size and structure, and no expansion of their distribution occurred in the sirenians.

The sirens have a similar brain-body mass scaling as other marine mammals (Fig. 21), but it appears that they arrived at this common scaling in a different manner. O'Shea & Reep (1990) provide data on the growth rate of the manatee (*Trichechus manatus*) brain and body. They show that the majority of postnatal brain growth occurs within the first two years of life (prior to weaning). There is then further enlargement of the body, with no enlargement in brain size, for the next eight years. Thus, in the sirens brain growth ceases early, with an extended period of body growth (O'Shea & Reep, 1990). A contrasting pattern of brain growth occurs in cetaceans. The most comprehensive data set was compiled by Pirlot & Kamiya (1982) for the striped dolphin (*Stenella coeruleoalba*) and indicates that brain and body size growth rates are not uncoupled as seen in the manatee but brain growth continues into adulthood.

IX. CONCLUSIONS

(1) This paper provides a comprehensive review of the salient features of the cetacean brain in relation to behaviour and evolution of this mammalian order. It is demonstrated that there are no neurological correlates for the purported intellectual abilities of cetaceans, and that the evolution of the extant cetacean brain, in terms of size, micromorphology and unusual sleep phenomenology, can be explained in terms of water temperature being a significant selection pressure.

(2) The scaling of cetacean brain mass in relation to body mass differs to that of other mammalian orders, leading to relatively large encephalisation quotients (EQ) for smaller cetaceans and relatively small EQs for larger cetaceans. Individuals of the same species show similar scaling trends of brain and body mass to that of the entire order, indicating that a similar selection pressure shapes this relationship in extant cetaceans.

(3) The neuroanatomical features of the cetacean cerebral hemisphere do not indicate a structure supportive of high levels of intellectual capacities. In particular, the high glia:neuron index, the poorly differentiated neuronal morphology, the low number of neurons and cortical areas, the lack of a distinct pre-frontal cortex, the small hippocampal formation, and the altered proportions of the neuropil, will all impact negatively on the processing capacity of the cerebral cortex.

(4) The vocalisations of cetaceans appear to be under the control of a specialised brainstem system of the periaqueductal grey matter, the nucleus ellipticus, which may in

fact be a vocal pattern generator. This differs to the cortically based language found in humans, and argues against suggestions of cetacean linguistic and cultural abilities.

(5) It is hypothesised that unihemispheric slow-wave sleep and lack of REM sleep in cetaceans functions to compensate for heat loss to the water during sleep. As significant thermogenesis is downregulated during sleep in normal mammals, this altered sleep pattern will allow thermogenesis to be maintained in both the brain (through increased glial metabolism *via* noradrenergic stimulation) and the body (through increased muscular movement). The restorative function of sleep can then be enabled in an aquatic environment where heat is lost approximately 90 times faster than in air.

(6) It is shown that during the course of cetacean evolution there was a major punctuation in brain size, seen mainly as an increase in the size of the cerebral hemispheres. This punctuation occurred at the transition of the ancestral cetacean faunal assemblage (the archaeocetes) to the modern cetacean fauna (the Oligocene cetaceans) approximately 32 million years ago. At this transition there was a dramatic increase in both actual and relative brain size that coincided with the loss of a warm and nutrient-rich environment (the Tethys sea) and global oceanic cooling of water temperatures. Following this the size of the brain remained stable. Such a marked change in brain size does not occur in the closely related ungulates over the same time period.

(7) It is demonstrated that previous proposals of the causal factors underlying large relative brain size in the smaller cetaceans do not explain the full range of observable data. Theories associating relative brain size with an increase in general levels of intelligence rely upon unproven assumptions. Vocalisations are shown to consist of seven species-typical calls and not a language. The anatomy of the acoustic system demonstrates that while it is specialised, this is to a similar degree as specialised sensory systems in other mammals with standard brain sizes and therefore cannot be a contributing factor to increased relative brain size. Finally, it is shown that apparent convergences in primate and cetacean behaviour and the behavioural assumptions upon which these are based are unreliable.

(8) The observations made are drawn together to demonstrate that water temperature as a selection pressure may explain all facets of the evolution of the modern cetacean brain. The archaeocete/Oligocene cetacean transition, which coincided with major changes in brain mass and scaling, is coincident with a significant reduction in oceanic temperatures. The microanatomy of the cetacean brain, and their altered sleep phenomenology, indicates that the cetacean brain may be an effective thermogenetic organ. The scaling of brain to body mass in cetaceans (or the EQ as based on a mammalian regression) is found to be significantly linked to the range of oceanic temperatures inhabited by the various extant cetacean species. Lastly, it is shown that the actual size of the cetacean brain may be due to the combination of three constraints: the allometric birth mass of eutherian mammals, the minimum birth mass required to prevent lethal hypothermia in aquatic mammals, and the

allometric relationship between EQ and water temperatures in adult cetaceans.

(9) Along with supporting evidence from other marine mammals, this thermogenetic hypothesis of cetacean brain evolution represents a credible and testable alternative to explain actual and relative brain size, brain micro-morphology, behaviour, and sleep phenomenology in the extant and extinct cetaceans.

(10) It is the first hypothesis to relate these features to a specific and significant environmental selection pressure during evolutionary history.

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