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HENRY PIHLSTRÖM**The Size of Major Mammalian Sensory Organs as Measured from Cranial Characters, and Their Relation to the Biology and Evolution of Mammals**DIVISION OF PHYSIOLOGY AND NEUROSCIENCE
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**THE SIZE OF MAJOR MAMMALIAN SENSORY ORGANS
AS MEASURED FROM CRANIAL CHARACTERS, AND
THEIR RELATION TO THE BIOLOGY AND EVOLUTION
OF MAMMALS**

Henry Pihlström

ACADEMIC DISSERTATION

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ABSTRACT

The basic functional principles of the major sensory systems of mammals (e.g., vision, hearing and olfaction) are fairly well understood. Within certain limits, increasing the size of the structures that collect the adequate physical signals and transduce them into neural responses is *a priori* expected to improve sensory performance, and the relative size of a sensory organ might provide a simple measure of the relative importance of the corresponding sense. If investments into complex sensory organs can be expressed by simple anatomical measures, this would facilitate large-scale comparative studies of the ecology and evolutionary history of the sensory modalities in different groups. Although sensory organs mainly consist of soft tissues, they are embedded in bony structures and some include functional bony components. Thus it is possible to define potentially relevant osteological dimensions that can be measured from both extant and extinct (fossil) species, and this is the point of departure of the present thesis.

The original measurements focus on two senses, olfaction and vision. In the first study, the area of the cribriform plate of the ethmoid bone is defined, measured, and validated as a useful hard-tissue anatomical proxy for the sensitivity of olfaction in various mammalian groups. It is shown that cribriform plate area (representing olfactory organ size) grows proportionally to skull area (representing animal size), with no sign of levelling off in the highest range. There are only a few taxa that have smaller olfactory organs than 'expected': these include monkeys and apes on the one hand, and the aquatic dugong on the other. The semi-aquatic pinnipeds, by contrast, have cribriform plate areas comparable in size to those of similar-sized terrestrial carnivores.

In the second study, the analysis of orbit size as a proxy for eye size, which has previously been used for primates by several authors, is applied to a comprehensive mammalian data base of 355 species representing most major orders, largely based on new original measurements. It was first shown that the eyes of the groups included are effectively spherical and that the relation between eye and orbit size is regular enough for the orbit to be informative of eye size and thus visual sensitivity/acuity. The earlier primate studies have found that (small) nocturnally active species have relatively larger orbit diameters than diurnally active species of similar size. While this was confirmed for primates, no general diurnal/nocturnal difference in orbit size at the same skull size was found in non-primate mammals. The allometric growth of orbit size with increasing skull size was steeper for nocturnal than diurnal mammals, but the significance of this is unclear, as the former sample was dominated by smaller species compared with the latter sample. In 'catheMERal' species (i.e., species active during both night and day), the allometric relation of orbit size to skull size was more similar to

that of nocturnal than of diurnal species. Taken together, the results suggest that relative orbit diameter is not a useful indicator of the diel activity pattern of non-primate mammals, and cannot be used to infer the pattern of fossil species.

In the third study, the question of the trade-off relations between three major senses, vision, hearing, and olfaction, was investigated. The proxy measure used for the auditory organ was the size of the middle ear bones as reported by Nummela et al. (1995). The 'residual' size of each organ in each species was calculated as its deviation from the global mammalian regression line relating the respective organ proxy size to body size. The residuals were plotted into a three-dimensional 'sensory space', where the coordinate axes represent vision, hearing, and smell. This provides a graphic representation of correlations between organ sizes, both positive and negative. The results suggested that good vision and hearing are often positively correlated in mammals; thus, it seems that investments in eyes and ears are likely to cooperate rather than compete. By contrast, it appeared that a keen sense of smell rarely occurs together with equally keen vision and/or hearing.

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A formative experience in my youth was the reading of the late Professor Björn Kurtén's many popular books on palaeontology. My interest in this field of science (so difficult to pursue in this country with a nearly non-existent fossil record) has lasted to this day. Via Professor Mikael Fortelius at the Department of Geology, I have been able to gain at least a small insight into the study of the ancient past, and for this I am grateful. On this subject, I want to extend my thanks also to the participants at the meetings of the Björn Kurtén Club for many interesting talks and discussions.

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following original studies:

I Pihlström, H., Fortelius, M., Hemilä, S., Forsman, R. & Reuter T. (2005) Scaling of mammalian ethmoid bones can predict olfactory organ size and performance. *Proceedings of the Royal Society of London B* 272:957-962.

II Pihlström, H. Relative orbit size and diel activity pattern in mammals. Submitted. With Supplementary material.

III Nummela, S., Pihlström, H., Puolamäki, K., Fortelius, M., Hemilä, S. & Reuter, T. Exploring the mammalian sensory space: co-operations and tradeoffs between senses. Submitted.

The papers are referred to in the text by their roman numerals.

ABBREVIATIONS

CT	computer tomography
EPB	extant phylogenetic bracket
LS	least-squares
LWS	long-wavelength sensitive
MOB	main olfactory bulb
MWS	middle-wavelength sensitive
MYA	millions of years ago
OR	olfactory receptor
PIC	phylogenetically independent contrasts
Rh	rhodopsin
RMA	reduced major axis
SWS	short-wavelength sensitive

1 INTRODUCTION

1.1 GENERAL

In terms of evolutionary success, the mammals are unquestionably one of the most notable extant animal groups. A crucial factor in this evolutionary success story has been their sophisticated capacities for collecting and processing information about their environment. This is based primarily on four main sensory modalities: smell, touch, hearing and vision. The relative importance of these senses varies widely between groups. Arguably, investment in improved performance is always costly in some way, and therefore the relative sophistication of the different senses is likely to reflect what types of information are of primary importance to the mammal, which must, in turn, reflect its ecology and mode of life.

The functionality of senses may, and indeed needs to, be studied at many different levels; for example, behavioural ecology, psychophysics, neurophysiology, genetics, and molecular biology. The ultimate processing unit for sensory information is the brain, but, at the most distal point of contact with the external world, a sensory system is dependent on the anatomical structures that collect and channel the adequate physical signal to transducing neurons. Roughly speaking, it might be said that the larger these organs are, the greater is the amount of information that the signal may potentially transmit, other things being equal. More specific anatomical features may give us insight into the use of that information. The study of these distal organs may therefore, if judiciously analysed, tell us much about the corresponding sensory capacities of its owner.

The empirical studies in this thesis focus especially on functional measures that can be obtained from skeletal structures, which may potentially allow us to extrapolate conclusions to the biology of extinct species that can be studied only in fossil material. Soft-tissues are normally not preserved as fossils, but if anatomical correlates to the performance of various sensory organs exist in extant taxa, we may reasonably presume similar correlates to have existed in extinct taxa as well. In other words, we may use our knowledge about modern species to make inferences about the sensory capacities of fossil species. Recent years have seen great advances in mammalian phylogenetics; in particular, the publication of large-scale morphological and, especially, molecular studies of the relationships of extant mammals (e.g., Bininda-Emonds et al., 2007). Such studies have greatly increased our understanding of the evolutionary history of the class Mammalia and its various orders, and they now allow us to reconstruct the mammalian evolutionary tree with a considerable degree of confidence. Our increased understanding of the phylogeny of extinct mammals allows us to place many of these, too, in their respective places in the mammalian family

tree, and, thanks to methodologies such as the principle of the extant phylogenetic bracket (EPB) (Witmer, 1995), we may apply our knowledge of extant taxa to reconstruct behavioural and soft-tissue morphological characters of fossil species.

The fundamental question behind part 1 of this thesis is whether some simple anatomical measures, with special emphasis on skeletal measures, may be useful for assessing the performance of two of the main sensory modalities of mammals, olfaction and vision (Papers I and II). The question is approached by a broad comparison across a wide range of body sizes, ecological adaptations, and phylogeny.

Part 2 (Paper III) deals with the relative allocation of sensory resources to different modalities, based on a large body of literature including (I) and (II). The paper introduces the concept of the *sensory space* of an animal. This is viewed against the hypothesis that, given a number of fundamental constraints (e.g., neural resources, energy usage, anatomy), improving performance of one sense generally necessitates evolutionary trade-offs; in other words, it often occurs at the expense of other senses.

1.2 MAMMALIAN SENSES

Very roughly speaking, sensory organ performance is size-dependent: as a rule of thumb, the larger the organ is, the more efficiently it functions. Naturally, this is true only as a general rule within limited size ranges. Due to biophysical factors alone, the marginal returns from increasing size in most systems dwindle so as to become, from some limit, outweighed by increasing disadvantages. For the most part, though, 'bigger is better' within the size ranges encountered in Nature, and natural selection may be expected to favour a size increase of biologically important sense organs over evolutionary timescales.

However, sensory organ size is also constrained by other factors than relatively simple biophysical limits. Sensory information is ultimately processed in the brain, and the processing capacity of the mammalian brain has its limitations (e.g., Laughlin, 2001). Therefore, animals must often 'choose' which sense(s) to develop at the expense of other(s).

Notably, such *trade-offs* need not only take place between different sensory modalities (e.g., vision and olfaction), but they may also take place between different aspects of the same sensory modality. For example, the physiological requirements for excellent colour vision may have to compete with requirements for equally excellent scotopic vision (seeing in low-light conditions) (cf. Osorio and Vorobyev, 2005).

The general biology of any given species will influence the particular nature of its sensory specialisations. A predator has different needs than a prey animal, and an aquatic species has needs that are different from those of an arboreal species. On the other hand, some species may possess sensory

adaptations inherited from their ancestors which, in their current mode of life, are suboptimal. This highlights the need to take the phylogeny of animals into account when considering their sensory biology.

1.3 ANATOMICAL INDICATORS OF THE SIZE OF SENSORY ORGANS

While the mammalian sense organs themselves are ‘soft-tissue’ structures, many of them correspond closely to some particular skeletal (or sometimes cartilaginous) structures. For example, it is obvious that the size and shape of the eye are in some ways constrained by the bony orbit; likewise, it is apparent that the middle ear bones are involved in mammalian hearing. Less intuitively, perhaps, these are also important components of the mammalian equilibrioception, or sense of balance. The tactile sense, or the sense of touch, also has identifiable hard-tissue correlates. E.g., the size of the infraorbital foramen in the cranium correlates with the number of vibrissae (Muchlinski, 2010). In Paper (I), it is shown that the area of the cribriform plate correlates with olfactory sensitivity.

Given the existence of such skeletal correlates to sensory modalities, scientists have attempted to study said structures biometrically in order to gain measures of sensory capacities that might be read even from fossil bone material. The earliest comparative studies of relative sensory organ size were hampered by the failure of investigators to properly address issues of scaling, the fact that different parts of an organism may grow differently in relation to its other parts (*allometry*). To take a simple example, a mouse has smaller eyes than an elephant in *absolute* terms, but the eyes of the mouse are larger *relative* to its body size. Thus, without correcting for the effect of body size, raw data on (say) eye size alone are not sufficient to inform us about the relative investment in eye function in different animals.

There is a large body of data from earlier studies of mammalian eye morphology, including research on the functional relation between soft- and hard-tissue structures. Some of this will be summarised in later sections. It gives the point of departure for my analysis of a greatly expanded database on orbit size, largely based on my original skull measurements (II). The anatomical basis of mammalian hearing has been fairly thoroughly studied by Nummela and co-workers, especially the scaling and functional role of the middle ear bones (e.g., Hemilä et al., 1995; Nummela, 1995; Nummela et al., 1999), and I present no new measurements here. However, no comparable studies of the olfactory organ across mammals exist. Thus I have collected extensive original data on the size of the cribriform plate of the ethmoid bone, its relation to the size of the olfactory epithelium, and the relation of the latter to olfactory sensitivity (I). The results from these studies on ‘eye’ and ‘nose’ (I, II) size are finally synthesised with, in particular, those from the ‘ear’ size studies of Nummela and co-workers (III).

1.4 NOTE ON THE NOMENCLATURE AND PHYLOGENY USED IN THIS THESIS

“Nothing in biology makes sense except in the light of evolution.”

(T. Dobzhansky, 1973)

“Nothing in evolution makes sense except in the light of phylogeny.”

(Society of Systematic Biologists/Sytsma and Pires, 2001)

While the main focus of this thesis is on comparative sensory biology, taking a stand on some issues regarding mammalian phylogeny has been necessary. The reason for this is that different species, or indeed any taxa, cannot be treated as independent data points of equal weight in comparative analyses. Their present characters depend to different extents on shared vs. separate evolutionary histories. Thus, in order to meaningfully perform comparative analyses it is imperative to have a wholly or mostly resolved evolutionary tree at one's disposal. The composite mammalian 'supertree' published by Bininda-Emonds et al. (2007, 2008) has formed the basis of all comparative analyses in this thesis. However, as this 'supertree' contains a large number of polytomies (that is, unresolved nodes within the tree) which complicate calculations of phylogenetically independent contrasts (see below), I have, where necessary, complemented it with phylogenetic trees that offer resolution to polytomies. Inevitably, introducing data from several trees that have been compiled by different workers using different methodologies and data sets, may introduce error into the data. In order to minimize such effects, I have restricted myself to using only trees based on molecular data, and, where topologies have differed between trees, I have preferentially followed the most recently published ones.

Related to the issue of choice of phylogeny is the choice of appropriate nomenclature. I have mainly followed the most recently published edition (2005) of Wilson and Reeder's *Mammal Species of the World*. In a few cases, I follow more recent nomenclatural proposals.

Information on the ecology, including especially diel activity patterns, of mammals is mainly based on Nowak (1999).

2 REVIEW OF THE LITERATURE

2.1 MAMMALIAN OLFACTION: THE OLFACTORY ORGAN

Olfaction is one of the most fundamental sensory modalities for animals in general, and for mammals in particular. Via scent detection, mammals may, for example, receive vital information about food, water, shelter, direction, conspecifics, prey, and predators (e.g., Ralls, 1971; Eisenberg and Kleiman, 1972; Stoddart, 1980; Doty, 1986; Apfelbach et al., 2005). In some mammals, however, the relative importance of olfaction has diminished during the course of evolutionary history and other sensory modalities have increased in importance. Notably, an apparent reduction of olfactory capacity has taken place in the anthropoid primates, the clade to which we humans belong. Thus, human beings tend to experience the surrounding world primarily via vision rather than olfaction. Perhaps at least partly for this reason, olfaction has received less scientific attention than vision (or hearing, for that matter).

However, recent years have witnessed an upsurge of research interest in mammalian olfaction. This has to a great extent followed the breakthrough in the molecular genetics of the olfactory receptors that started in the early 1990's (Buck and Axel, 1991); an accomplishment which, in 2004, was rewarded with the Nobel Prize in Physiology or Medicine. Many subsequent studies have focused on sequencing the mammalian and, especially, the human olfactory receptor gene repertoire (e.g., Glusman et al., 2000, 2001; Zozulya et al., 2001).

2.1.1 OLFACTORY RECEPTORS

Volatile odorants are detected by the olfactory receptor (OR) molecules in the membranes of olfactory epithelial cells (Firestein, 2001). To a lesser extent, OR genes are also expressed on other tissues (Vanderhaeghen et al., 1997; Feldmesser et al., 2006). Genes that code for olfactory receptors form the largest identified gene superfamily in mammals (Buck and Axel, 1991; Issel-Tarver and Rine, 1997; Mombaerts, 2001; Buck, 2004; Zarzo, 2007). This supports the widely held notion that olfaction is an especially important sensory modality.

The number of functional vs. non-functional OR genes varies considerably between different mammal groups. In some taxa, such as humans, the proportion of pseudogenes is very high. The most recent studies suggest that slightly more than 50% of the OR genes in humans are nonfunctional (Niimura and Nei, 2003, 2005, 2006, 2007; Malnic et al., 2004). In odontocetes, the proportion of OR pseudogenes may be as high as 80-85% on

average (McGowen et al., 2008; Hayden et al., 2010). In contrast, in many bats the fraction of non-functional OR genes is very low. For example, in the lesser horseshoe bat *Rhinolophus hipposideros* as many as 90% of the OR genes appear to be functional (Hayden et al., 2010). For comparison, in such keen-scented species as rats and dogs, respectively, ‘only’ ca. 80% of the OR genes are functional (Quignon et al., 2005).

Having a relatively large number of non-functional OR genes is characteristic not only of humans, but also of other anthropoid primates thus far investigated, such as callitrichines (Whinnett and Mundy, 2003), and the chimpanzee *Pan troglodytes* (Gimelbrant et al., 2004). Early studies (Gilad et al., 2000, 2005) suggested that the olfactory receptor pseudogenisation process had been much less extensive in the chimpanzee lineage (as well as in other ape and monkey lineages) than in the human lineage, suggesting that olfactory sense reduction had accelerated in the human lineage since its split from the lineage leading to the chimpanzee. Later studies have necessitated a modification of this view. Go and Niimura (2008) have shown that the number of functional OR genes is, in fact, very similar in humans and chimpanzees. However, the specific gene repertoires differ considerably between these two species, suggesting that the evolutionary selection pressures in their respective lineages have been somewhat different.

2.1.2 THE MAMMALIAN OLFACTORY ORGAN AND ITS STRUCTURE

The mammalian olfactory organ consists of various hard- and soft-tissue components, which together form a functional whole. By ‘olfactory organ’ is here meant the complex of olfaction-related morphological structures in the mammalian snout and brain, including the nose, the olfactory epithelium which contains the odorant receptors, the turbinates in the nasal cavity, the cribriform plate of the ethmoid, the olfactory nerves, and the main olfactory bulb (cf. Allison, 1953; Negus, 1954, 1958; Adrian, 1956).

In addition to the main olfactory organ, mammals also have other olfaction-related chemosensory structures. The accessory olfactory bulb is the main anatomical component of the vomeronasal organ (also known as Jacobson’s organ), which detects pheromones rather than non-social volatile odorants (Keverne, 1999). The vomeronasal organ was traditionally considered to be a part of the olfactory organ, but subsequently opinion shifted to regarding it as a wholly separate sensory system (e.g., Estes, 1972; Scalia and Winans, 1975). Later discoveries have shown that there is functional overlap between the mammalian olfactory and vomeronasal systems, and that both olfactory and vomeronasal receptors may detect both pheromones and other odorants (e.g., Breer et al., 2006; Munger et al., 2009; Touhara and Vosshall, 2009; see also Laska et al., 2006; Savic et al., 2009). However, neither the vomeronasal organ nor three other putatively olfaction-related components that have been described, namely, the septal organ of Masera (Ma et al., 2003), the Grüneberg ganglion (Storan and Key, 2006;

Brechbühl et al., 2008), and the trigeminal system (Finger et al., 2003) will be considered further in this thesis.

2.1.3 THE NASAL CAVITY AND THE OLFACTORY EPITHELIUM

Inhaled respiratory airflow transports volatile odorants into a mammal's nasal cavity. The animal may also actively sample odorants from the air by sniffing (Sobel et al., 1998; Kepecs et al., 2006; Mainland and Sobel, 2006). Inside the nasal cavity, the air flow transports the odorant molecules across the nasal turbinates. The turbinates are extremely thin and highly convoluted bony scrolls, which are classified as maxillo-, naso-, or ethmoturbinals depending on their point of origin. Among extant vertebrates, ossified turbinates are only found in mammals (Hillenius, 1992; Rowe et al., 2011). However, among extinct taxa, respiratory turbinates were present in the immediate ancestors of true mammals, the pre-mammalian synapsids, (Hillenius, 1994). The evolution of turbinates in the mammalian lineage has been associated with the evolution of endothermy and the increased requirements of respiratory efficiency (Hillenius, 1992, 1994). Surprisingly, putative olfactory turbinates have also been identified in at least one group of Mesozoic dinosaurs, the herbivorous, armoured ankylosaurians (Witmer and Ridgely, 2008; Miyashita et al., 2011). However, this intriguing suggestion still needs the support of additional anatomical evidence.

The surface of the turbinates is covered by both respiratory and olfactory epithelia. The epithelia are composed of ciliated receptor cells, supporting cells, basal cells, and microvillar cells in a mosaic-like arrangement (Lauruschkus, 1942; Müller, 1955; Andres, 1966, 1969; Dodd and Squirrell, 1980; Neuhaus, 1981; Keverne, 1982; Moran et al., 1982; Morrison and Costanzo, 1990, 1992; Mombaerts, 1996; Dryer, 2000; Kumar et al., 2000; Craven et al., 2007, 2010). The respiratory epithelium predominantly covers the maxilloturbinals, whereas the naso- and the ethmoturbinals are mainly covered by olfactory epithelium (Morrison and Costanzo, 1990, 1992).

In most mammals, the surface of the olfactory epithelium is greater than that of the respiratory epithelium (e.g., Adams, 1972; Schmidt and Nadolski, 1979; Gross et al., 1982), but there are also species where the opposite is true. Many microchiropteran bats, for example, have greater respiratory than olfactory epithelium surfaces (Gurtovoi, 1966; Bhatnagar and Kallen, 1975; Smith et al., 2012). Yet, this is not a universal chiropteran trait, as the Jamaican fruit bat *Artibeus jamaicensis* has the common mammalian pattern (Bhatnagar and Kallen, 1975; see also Bhatnagar and Kallen, 1974b). In shrews, most investigated species conform to the common pattern, with the exception of the semi-aquatic Eurasian water shrew *Neomys fodiens* (Söllner and Kraft, 1980; Larochelle and Baron, 1989). The respiratory epithelium surfaces are usually larger than olfactory epithelium surfaces also in aquatic and semi-aquatic carnivores (Van Valkenburgh et al., 2011). This

has been suggested to reflect a relatively lesser reliance on olfaction in aquatic and semi-aquatic species (Van Valkenburgh et al., 2011).

2.1.4 THE OLFACTORY BULB

From the olfactory epithelium, the axons of the olfactory receptor cells pass to the main olfactory bulb (MOB), *bulbus olfactorius* (Mori, 1993) through perforations in the cribriform plate (see below). The MOB is a paired lobe that is situated anteriorly to the rest of the brain, in a depression of the braincase known as the olfactory fossa. The MOB is the centre for the coding and processing of olfactory information (Mori et al., 1999; Leon and Johnson, 2003; Lledo et al., 2005). On its surface are located the glomeruli to which the axons from the sensory neurons of the olfactory epithelium project (Yoshihara and Mori, 1997; Mori et al., 2000). In some species (e.g., the rat; Heine and Galaburda, 1986), the left and right MOB hemisphere volumes are asymmetric, in other mammals, including humans, no such asymmetry has been found (Hirano et al., 1989).

An enlarged MOB is a primitive mammalian character, already present in Early Jurassic pre-mammals, which lacked many other olfaction-related morphological structures that characterise modern mammals (Rowe et al., 2011).

Comparatively many studies have been undertaken on the mammalian MOB, including its relative size across several major mammal clades (e.g., Stephan et al., 1981; Baron et al., 1983; Gittleman, 1991; see also Marschner, 1970). However, detailed information about the cytostructure and ontogenetic development of the MOB is available for far fewer species, among which are the common laboratory species such as mouse (e.g., Williams et al., 2001; Mirich et al., 2002), rat (e.g., Smith, 1935; Andres, 1965; White, 1965; Rehmer et al., 1970; Hinds and McNelly, 1977, 1981), golden hamster (Schoenfeld et al., 1994), rabbit (Allison and Warwick, 1949), and grey short-tailed opossum *Monodelphis domestica* (Brunjes et al., 1992; Rowe et al., 2005; Macrini et al., 2007).

2.1.5 THE CRIBRIFORM PLATE

The *lamina cribrosa* or the cribriform plate of the ethmoid bone is a sieve-like bony plate that is situated in the olfactory fossa of the base of the skull, where it separates the cranial and the nasal cavities from each other (Gray, 1997) (Figure 1). In many mammal species, notably larger ones, the left and the right halves of the olfactory bulb are separated by a bony wall, the *crista galli*, which projects upwards from the cribriform plate. In olfactory bulb endocasts, the *crista galli* forms a groove which acts as a clear separating line between the left and the right hemispheres of the bulb. The various perforations found across the cribriform plate are the reason why, in some languages, the name of this bone literally means ‘sieve bone’ (e.g.,

Siebbein in German, *silben* in Swedish, and *seulahuu* in Finnish). Through these perforations, the olfactory nerves project from the nasal cavity onto the olfactory bulb.



Figure 1 Cranium of *Ovis orientalis* with the cribriform plate exposed. Figure from (I). Photo by Simo Hemilä.

The presence of a cribriform plate seems to be a synapomorphy for mammals, i.e., a character that has evolved only in the mammalian lineage. However, it should be noted that, depending on the exact phylogenetic definition, some of the taxa that probably possessed a cribriform plate (e.g., the multituberculates; Hurum, 1994) may be outside the crown mammalian clade, and, therefore, in a strictly phylogenetic sense they are not members of 'Mammalia' (e.g., Wible, 1991).

The shape of the cribriform plate varies between different groups, even between closely related species. This is the case in, for instance, some extinct and extant bears of the genus *Ursus* (García et al., 2007). Moreover, there may also be intraspecific shape variation. In humans, cribriform plate shape variations appear to be particularly pronounced (Schmidt, 1974). Some studies (Schmidt, 1974; Teatini et al., 1987) have also reported differences in relative height between the left and the right halves of the cribriform plate in humans. However, Jones et al. (2002) later failed to replicate these findings in a computer tomography study.

As is the case with other components of the mammalian olfactory organ, the cribriform plate may also undergo morphological change and functional deterioration at advanced age. In old humans, the perforations may be reduced in size or even close completely (Krmpotić-Nemanić, 1969; Kalmey et al., 1998).

2.1.6 PREVIOUS COMPARATIVE STUDIES OF THE CRIBRIFORM PLATE

The medical literature on the human cribriform plate and, especially, its various pathologies is large. However, it falls outside the scope of this review.

On the other hand, studies of the cribriform plate specifically in other mammals are much scarcer. This may at least partly be explained by the relative inaccessibility of this bone. Only by fairly new techniques (suitable cast-making materials or computer tomography) has it become possible to measure the cribriform plate without breaking open the specimen's cranium (which is rarely an option when one studies museum material). In an early comparative study on the sensory organs of domesticated mammals, Klatt (1913) even claimed that it would be "quite impossible" ("*ganz unmöglich*" in the original, p. 420) to measure the area of the cribriform plate accurately. I aim to show in this thesis that Klatt's pessimism was somewhat unfounded.

Bhatnagar (1971) and Bhatnagar and Kallen (1974a) performed the first modern, large-scale comparative study on cribriform plate area in mammals. They presented data on 40 species of Neotropical bats. Instead of making endocasts they removed the cribriform plates from the crania and, after having removed all soft tissue covering the cribriform plates, made camera lucida drawings of their surfaces. In addition to estimating the surface areas, Bhatnagar and Kallen counted the number of foramina on the cribriform plates; furthermore, they also dissected the various bats' olfactory bulbs in order to estimate their respective volumes. Bhatnagar and Kallen's (1974a) results suggest that there is a positive relationship between cribriform plate area (more precisely: the perforated area of the cribriform plate) and olfactory acuity. This is in good general agreement with the conclusions in (I).

In recent years, the availability of computer tomography (CT) scanning equipment has made it possible to study fragile or valuable material in a non-invasive way. However, to date, CT studies of the cribriform plate have only been carried out on individual species (e.g., humans, Jones et al., 2002), rather than across a wide range of taxa.

This thesis presents the first large-scale comparative studies on the relative size of the cribriform area (I, III). The technique was to make meltable vinyl composition casts of the cribriform plate, from which the area was calculated (see the Materials and Methods section).

2.1.7 THE IMPACT OF DOMESTICATION ON MAMMALIAN OLFACTION

Some mammals have phenomenal olfactory capacities. Domestic dogs, in particular, have been utilised for millennia by humans for scent-detection. While dogs are truly impressive in their olfactory performance (e.g., Kauhanen et al., 2002; Pickel et al., 2004; Willis et al., 2004; Browne et al., 2006), they do not, by mammalian standards, have unusually large

functional OR repertoires. Although far superior to humans, they are comparable to mice in this regard (Olender et al., 2004). Some data suggest that the proportion of non-functional OR genes is higher in the domestic dog than in its wild ancestor, the grey wolf *Canis lupus*; this difference, however, may not be statistically significant (Zhang et al., 2011). It should be noted, however, that the number of *different* ORs is likely to correlate with the diversity of smells that can be detected and maybe with discrimination acuity, but not necessarily with the sensitivity to particular odorants.

Domestic pigs, too, have an extremely keen sense of smell (which, in some cultures, humans have utilised for centuries to locate truffles). Whether there are differences in the relative number of OR pseudogenes between the domestic pig and its ancestor, the wild boar *Sus scrofa*, is currently unknown. However, Güntherschulze (1979) noted that the olfactory epithelium surface of the wild boar is much greater than that of the domestic pig. From this he concluded that domestication has had a negative influence on sensory, or at least olfactory, capacities.

2.1.8 OLFACTION IN AQUATIC AND SEMI-AQUATIC SPECIES

Among non-primate mammals, a notable reduction of the size of the olfactory organ has taken place in certain aquatic and semi-aquatic taxa. Fish have a perfectly functional sense of smell in water (Hara, 1994), but this is served by a class of receptors (Class I) distinct from those that serve tetrapods olfaction in air (Class II). Class I receptors are the phylogenetically more 'primitive' and are present in amphibians (as well as in fish). In amniotes, including mammals, Class II receptors predominate (Freitag et al., 1995, 1998). They are adapted to detecting airborne odorants, and are non-functional when washed by water. For long it was therefore thought that mammals are totally unable to use the sense of olfaction while submerged (Freitag et al., 1998). However, it has recently been shown that at least some mammals may circumvent this genetic constraint by holding on to air bubbles underwater (see below).

The functional reduction of the olfactory organ is apparent already in such partially aquatic taxa as the various semi-aquatic 'insectivores': the afrotherian otter shrews and aquatic tenrecs on the one hand, and various water shrews and semi-aquatic moles on the other (Pihlström, 2008). In all these taxa, the relative size of the main olfactory bulb is smaller in semi-aquatic species than in their terrestrial relatives (Stephan & Bauchot, 1959; Stephan and Andy, 1964; Bauchot and Stephan, 1966, 1968; Stephan, 1967; Stephan et al., 1981, 1986; Stephan and Kuhn, 1982; Baron et al., 1983; Barton et al., 1995; Sánchez-Villagra et al., 2002). Interestingly, it has been discovered that at least two different lineages of semi-aquatic insectivores have evolved the ability to detect odorants underwater. While diving, both star-nosed moles *Condylura cristata* (Catania, 2006) and American water shrews *Sorex palustris* (Catania, 2006; Catania et al., 2008) are able to hold

on to captured air bubbles at the tips of their noses, and inside these bubbles they sample odorants via sniffing.

In contrast to the ‘insectivores’, reduction of olfactory organ size in semi-aquatic rodents (e.g. beavers) *vis à vis* terrestrial rodents is much less pronounced or even non-existent (Pilleri, 1959, 1983). However, relative reduction of the olfactory organ is evident also in semi-aquatic carnivores such as otters and minks (Ferron, 1973; Estes, 1989; Gittleman, 1991).

In sirenians, both the size of the olfactory bulb (Genschow, 1934; Pirlot and Kamiya, 1985) and the area of the cribriform plate (I) are reduced. In the extant cetaceans and the platypus *Ornithorhynchus anatinus*, a perforated cribriform plate is completely absent in adult individuals (Paulli, 1900; de Beer and Fell, 1936; Zeller, 1988, 1989; Pihlström, 2008). This and other olfaction-related morphological structures are, however, more fully developed during earlier ontogenetic stages (Oelschläger and Buhl, 1985; Oelschläger et al., 1987; Zeller, 1988, 1989; Oelschläger, 1989; Pihlström, 2008). In cetaceans, an interesting distinction exists between odontocetes and mysticetes, as the olfactory structures, specifically the olfactory bulbs, are less completely reduced in the latter (Gruhl, 1911; Edinger, 1955; Breathnach, 1960; Morgane and Jacobs, 1972; Cave, 1988; McGowen et al., 2008; Pihlström, 2008), and at least some mysticetes still seem to have the ability to detect air-borne scents (Thewissen et al., 2011).

In recent decades, spectacular fossil discoveries have offered insight into the evolution of the olfactory organ in monotremes. The Miocene platypus *Obdurodon*, which is the closest known relative of the extant *Ornithorhynchus* and morphologically similar to it, already had reduced olfactory bulbs (Macrini et al., 2006). The extant, strictly terrestrial echidnas, by contrast, possess relatively large cribriform plates as well as fairly large olfactory bulbs (Kuhn, 1971; Pirlot and Nelson, 1978; Ashwell, 2006). Interestingly, fossil and molecular evidence suggest that echidnas may have evolved from platypus-like ancestors and are thus secondarily terrestrial (Musser, 2003; Phillips et al., 2009). If the last common ancestor of platypus and echidnas did indeed already lack a perforated cribriform plate, then this structure has re-evolved in the echidna lineage. This would be an interesting parallel to the apparent independent evolution of another sensory structure, the middle ear bones, in monotremes and in therians (Rich et al., 2005).

In the fully aquatic cetaceans, the number of functional olfactory receptor genes is reduced compared with terrestrial artiodactyls, whereas the semi-aquatic pinnipeds do not differ as much from terrestrial carnivores in this regard (Kishida et al., 2007; Hayden et al., 2010). This suggests that pinnipeds possess considerable olfactory capabilities. The idea that pinnipeds are able to detect air-borne scents is, in fact, supported by both observational (Burton et al., 1975; Dobson and Jouventin, 2003; Phillips, 2003; Pitcher et al., 2011) and experimental (Kowalewsky et al., 2005; Laska et al., 2010) data.

Reviews of the olfactory sense in aquatic and semi-aquatic mammals can be found in Lowell and Flanigan (1980), Brown (1985), and Pihlström (2008).

2.1.9 PRIMATE OLFACTION

Primates have traditionally been considered to have a reduced sense of olfaction (but see below). This has often been linked to their primitively arboreal way of life, which supposedly placed less demands on olfactory acuity. Arboreality by itself is not a sufficient explanation, however, as other tree-living mammal taxa (e.g., sciurids) do not have correspondingly reduced olfactory organs (cf. Cartmill 1974).

As a rule, the various olfaction-related morphological structures, such as olfactory bulb volume, are relatively larger in strepsirrhines than in haplorhines (e.g., Stephan et al., 1981; Baron et al., 1983; Barton et al., 1995; Barton, 2006). This holds true also for various fossil 'prosimians', which have been shown to possess relatively large olfactory bulbs (e.g., Radinsky, 1979; Takai et al., 2003; Kay et al., 2004a, b; Kay, 2005). These observations, combined with behavioural studies of extant strepsirrhines (Schilling, 1980), suggest that primates are, indeed, originally olfaction-reliant animals.

Anthropoid primates have often been thought to have a particularly strongly reduced sense of smell, especially when compared to strepsirrhines (e.g., Negus, 1957; Cave, 1973; Radinsky, 1974; Fobes and King, 1977; Heymann, 2006b; cf. Keverne, 1980, and Bush et al., 2004). However, this notion is not entirely accurate. Observational data suggest that some New World platyrrhines, for example, use scent marks for social signalling (Heymann, 2006a). In addition, several empirical studies suggest that many anthropoid primates have considerable olfactory capabilities (e.g., Laska and Hudson, 1993; Laska and Freyer, 1997; Hübener and Laska, 1998; Laska et al., 2000, 2004, 2005; Laska and Seibt, 2002; Smith and Bhatnagar, 2004; Smith et al., 2004, 2007). Even human olfactory discrimination potential may be considerably greater than is often believed (Shepherd, 2004, 2005). Laska and Teubner (1998) and Laska et al. (1999) showed that humans and squirrel monkeys *Saimiri sciureus* perform approximately equally well in many olfactory discrimination experiments. Porter et al. (2007), in turn, demonstrated that, with some training, humans may even be able to follow a scent trail outdoors.

2.2 MAMMALIAN VISION: EYE STRUCTURE AND VISUAL ECOMORPHOLOGY

Eyes of various kinds (ranging from simple light-sensitive skin cells to the complex lens eyes of vertebrates) have evolved numerous times in the animal kingdom (Land and Nilsson, 2002). This fact alone shows how beneficial

vision is for animals, and that, once eyes have evolved, natural selection only relatively rarely ‘allows’ them to become rudimentary or disappear completely. In the vertebrate lineage, it appears certain that lens eyes have evolved only once, probably in the Cambrian Period more than 500 MYA, and that they have since been retained (Land and Nilsson, 2002; Lamb et al., 2007). The hypothesis that vertebrate eyes are homologous is strongly supported by fact that the development of the eyes in all thus far investigated vertebrates is controlled by the same gene, *Pax6* (Gehring and Ikeo, 1999; Fernald, 2004; Kozmik, 2005).

Among vertebrates, birds in particular are famous for their keen eyesight, as well as for their often gaudy colours which indicate the presence of well-developed colour vision. By contrast, mammals are not usually thought of as particularly vision-oriented animals, although in fact, many mammalian species, especially among primates, have excellent vision.

2.2.1 THE MAMMALIAN EYE AND VISUAL PIGMENTS

The basic structure of the mammalian camera eye is well known, and described in great detail in the literature (see, e.g., the seminal study of Walls, 1942, and Land and Nilsson, 2002). Here, only the barest outline of mammalian eye morphology and function is presented.

The eye is situated in and protected by the bony orbit (which is not a single bone but consists of several cranial bones). In the posterior part of the orbit are found three foramina: the superior orbital fissure, the inferior orbital fissure, and the optic canal. Through these openings, the various visual nerves and vessels are in connection with the eye and the brain. In many vertebrates the eyeball is further protected and stabilised by the sclerotic ring, which consists of either bones or cartilage. In mammals, however, a partial (cartilaginous) sclerotic ring is found only in monotremes (Newell, 1953).

The outer layer of the eyeball consists of a protective layer known as the sclera (in humans, much of the light-coloured sclera is visible and is known as the “white of the eye”). The posterior part of the sclera is perforated and sieve-like in structure (as it acts as both entrance and exit site of retinal ganglion axons and retinal vessels) and known as the *lamina cribrosa*; this, obviously, should not be confused with the similarly named component of the mammalian olfactory organ.

The dilations and the contractions of the pupil regulate the amount of light that, passing through the iris and refracted by the lens, ultimately reach the retina. It has been suggested that the variations of pupil shape in terrestrial mammals (round, horizontally slit, or vertically slit) may be related to diel activity pattern differences (Malmström and Kröger, 2006).

The size and shape of the lens are also variable among mammals, and these variations seem to be ecologically correlated. In terrestrial species including humans, the lens is typically fairly flat, but in aquatic mammals

such as cetaceans and pinnipeds, the lens is very large and spherical to compensate for the lack of refractive power at the corneal surface when the eye is submerged in water (Mass and Supin, 2007).

The retina which covers the inner surface of the eye consists of several cell layers. In many nocturnal mammals, one of the layers behind the neural retina is the *tapetum lucidum*. It contains cells that reflect back light through the retina, thereby creating a 'second chance' for absorption of photons passing through the retina (Schwab et al., 2002). The *tapetum lucidum* is responsible for the familiar 'eyeshine' of cats and many other animals when an artificial light is shone at their eyes at night.

The deepest layer of the neural retina (relative to the direction of entrance of the light) is formed by the light-sensitive photoreceptor cells: the rods and the cones. (There are also light-sensitive ganglion cells in the most superficial layer of the mammalian retina (Berson, 2003) but these are far less numerous than rods or cones.) Somewhat simplified, rods are made for seeing at low light levels by having long outer segments containing great amounts of visual pigments, rhodopsin, ensuring efficient photon catch. The rhodopsin is adapted for reliable detection of small numbers of photons by being thermally highly stable but having instead a slow 'visual cycle' of regeneration after photoactivation ('bleaching'). Cones, by contrast, generally have smaller outer segments which thus contain smaller amounts of visual pigments. Cone visual pigments are much more quickly regenerated after bleaching, but are thermally less stable ('noisy') instead. Cones are therefore better adapted to functioning at higher light levels. In other words, a mainly night-active species might be expected to have relatively more rods than cones in its retina than a mainly day-active species, and vice versa. Generally speaking, this seems indeed to be the case in mammals.

Five families of visual pigments, or opsins, are expressed in vertebrate rods and cones. One, rhodopsin (Rh1) is expressed in rods and is responsible for vision in dim light. The other four families are expressed in spectrally different cone classes: rhodopsin-like (Rh2), short wavelength-sensitive type 1 (SWS1), short wavelength-sensitive type 2 (SWS2), and long- and middle-wavelength-sensitive (LWS/MWS) opsins (Yokoyama, 2000, 2002; Bowmaker and Hunt, 2006; Bowmaker, 2008; Jacobs, 2008). Compared with other vertebrates, opsin diversity in mammals tends to be reduced, and typically, only Rh1, SWS1, and LWS opsins are present. Rh2 cone opsins seem to be absent in all mammals. As for SWS2 opsins, it has recently been shown that monotremes possess these instead of SWS1 (Davies et al., 2007; Wakefield et al., 2008; Warren et al., 2008; Zeiss et al., 2011). In a few placentalian lineages, such as cetaceans, pinnipeds, raccoons, pteropodid bats, certain rodents, lorisiform prosimians, and the platyrrhine *Aotus*, even the SWS1 opsins have become nonfunctional; such mammals have monochromatic vision and they are thus truly 'colour blind' (Peichl et al., 2001; Griebel and Peichl, 2003; Levenson and Dizon, 2003; Newman and Robinson, 2005; Peichl, 2005). Most mammals, however, are dichromats,

possessing LWS and SWS1 cone opsins (Jacobs, 1993); thus, dichromatic colour vision is probably the ancestral condition for Mammalia. Dichromatic colour vision is the norm also in strepsirrhine primates, which are predominantly nocturnal. Even such a highly specialised and strictly nocturnal species as the aye-aye *Daubentonia madagascariensis* is apparently able to discriminate between different colours (Perry et al., 2007).

In a few mammal lineages, functional trichromacy has re-evolved. These include, on the one hand, several marsupial (Arrese et al., 2002; Cowing et al., 2008) and, on the other hand, several primate lineages (Jacobs, 1993, 2008; Tan and Li, 1999; Surridge et al., 2003). In the case of primates, the re-acquisition of trichromatic vision follows from duplications and mutations of the LWS gene. Studies of platyrrhine primates suggest that trichromacy is related to foraging, and, specifically, to being able to discern subtle differences in colouration between young versus old leaves and between ripe and unripe fruit (Regan et al., 1998; Dominy and Lucas, 2001; Dominy et al., 2001; Lucas et al., 2003). However, that the relationship between life history and trichromatic vision in mammals is not a simple one is attested to by the fact that among marsupials, closely related species may differ in this regard even when there are no obviously significant ecological or physiological differences between them (Ebeling et al., 2010).

In addition to the above-mentioned ‘classical’ rod and cone opsins, there are other types of opsins that are expressed in the mammalian eye and brain. One of them, the relatively recently discovered melanopsin, has a known function, underlying the intrinsic photosensitivity of retinal ganglion cells that regulate circadian rhythms by signalling shifts in the general illumination level (Peirson and Foster, 2006; Hankins et al., 2008). Thus, even rodents that lack functional rods and cones are able to differentiate between light and darkness (Freedman et al., 1999). Melanopsin is also expressed in the eyes of fossorial mole-rats *Spalax*, which have strongly reduced eyes, yet can detect changes in light intensity (Hannibal et al., 2002).

2.2.2 PRIMATE VISION

In contrast to both strepsirrhine prosimians and most other mammals, the anthropoid primates are widely regarded as predominantly vision-oriented animals. Visual signals play an important part not least in their intraspecific communication (Emery, 2000), and many primate species are, by mammalian standards, very colourful (Sumner and Mollon, 2003). The eyes themselves may act as powerful and effective signalling devices. This is particularly the case in humans, whose extensively exposed white sclera seems to have evolved primarily for social communication (Kobayashi and Kohshima, 1997, 2001).

Anthropoids, in particular, have relatively large eyes but relatively small olfactory organs. The combination of large eyes and reduced olfactory organs

is also characteristic of the probable extant sister group of the anthropoids, the nocturnal tarsiers (Ross, 2000; Kay et al., 2004; Miller et al., 2005; Williams et al., 2010). Relative to body size, the eyes of tarsiers are, in fact, larger than those of any other known mammals (Rosenberger, 2010). Fossil data suggest that extreme ocular hypertrophy has characterised the tarsier lineage at least since the Eocene (Rossie et al., 2006; Chaimanee et al., 2011).

However, in the other main group of extant primates, the strepsirrhines, the olfactory organ is relatively large, suggesting that the sense of smell is of greater importance to them than it is to haplorhines. This apparent sensory difference between the two main extant primate groups has for a long time been of great interest to primatologists and palaeontologists alike. The traditional assumption (e.g., Clark, 1914; Park, 1940; Cave, 1973; Cartmill, 1974; Fobes and King, 1977) is that the night-active strepsirrhines are more 'primitive', that is, morphologically and/or behaviourally closer to the primates' immediate ancestors among mammals.

Detailed information on the visual acuity of primates, particularly strepsirrhines, is sparse, but there are some data suggesting that nocturnal and cathemeral primates do have poorer visual acuity than diurnal species. For example, the cathemeral blue-eyed black lemur *Eulemur macaco flavifrons* performs less well in visual acuity experiments than the diurnal ring-tailed lemur *Lemur catta* (Veilleux and Kirk, 2009). Other behavioural and anatomical data suggest that fully nocturnal strepsirrhines have even poorer visual acuity (Langston et al., 1986; Veilleux and Kirk, 2009).

In many vertebrates, visual acuity is enhanced by a foveal pit on the retina, where cone cells are concentrated and the neural retina is especially transparent (Walls, 1942). Among mammals, retinal foveae are with certainty known to be present only in apes, monkeys, and tarsiers (Provis et al., 1998; Franco et al., 2000). In addition, foveae are probably present in certain loriform strepsirrhines (DeBruyn et al., 1980; Hendrickson et al., 2000; Ross, 2004), and possibly also in some lemurs (Pariante, 1975). In the secondarily nocturnal owl monkeys, the fovea is either entirely absent or "degenerate" (Webb and Kaas, 1976:1252). Dyer et al. (2009) have shown that prenatal formation of retinal cells in the owl monkey occurs at a different pace from that in other platyrrhines, and suggest that a fovea may not normally have time to form during owl monkey embryogenesis.

In the likewise secondarily nocturnal tarsiers, however, the fovea is more prominent, although the question whether it is fully functional is still not settled (Kirk and Kay, 2004; Ross, 2004). Thus, it seems reasonably certain that the independent evolution of retinal foveae in different vertebrate lineages is strongly, though not exclusively, associated with diurnal habits (Ross, 1996, 2004). All extant strepsirrhines, including the diurnal species, apparently possess *tapeta lucida*, whereas tarsiers and anthropoids uniformly lack them (Schwab et al., 2002; Martin and Ross, 2005). While there is some disagreement regarding the ancestral diel activity pattern of primates (Tan and Li, 1999; Ross, 2000; Beard, 2004; Heesy and Ross,

2004; Ni et al., 2004; Tan et al., 2005; Ankel-Simons and Rasmussen, 2008), it is generally agreed that the two surviving lineages of night-active haplorhines, the tarsiers and *Aotus*, respectively, are secondarily nocturnal (Ross, 1996; Joffe and Dunbar, 1998; Collins et al., 2005). Interestingly, both tarsiers and owl monkeys are known to increase their activity on moonlit nights (Erkert, 1974, 1976; Erkert and Gröber, 1986; Wright, 1989; Fernández-Duque, 2003; Gursky, 2003; Fernández-Duque et al., 2010), and owl monkeys are known to rely heavily on vision while foraging (Bicca-Marquez and Garber, 2004; Fernández-Duque et al., 2010). This suggests that vision is still the primary sensory modality in nocturnal haplorhines, and the fact that tarsiers have retained at least rudimentary retinal foveae further suggests that the selective pressure to maintain relatively acute vision has been maintained for millions of generations in the tarsier lineage. In this regard, nocturnal haplorhines differ from other nocturnal mammals, including strepsirrhines, which rely more on the olfactory, tactile, and auditory senses. However, it is possible that strepsirrhines, at least, utilise vision in the night-time to a greater extent than is usually assumed (Bearder et al., 2006). Conversely, haplorhine olfactory capabilities may be more substantial than is commonly thought (Smith et al., 2007).

2.2.3 DIEL ACTIVITY PATTERNS: DIURNALITY, NOCTURNALITY, AND CATHEMERALITY

Animals that are active exclusively or predominantly during daylight hours are called diurnal, whereas animals that are active exclusively/mainly at night are called nocturnal. Naturally, such a dichotomy is an oversimplification that does not adequately reflect the diversity of mammalian diel activity patterns. There are, in fact, many species that cannot be neatly categorised as either diurnal or nocturnal, as they are active to an almost equal extent both during the day and during the night. For such species, Tattersall (1988, 2006) coined the term ‘cathemeral’, which has since been adopted by most workers. ‘Cathemeral’ is *not* synonymous with ‘crepuscular’, which refers to diel activity that is specifically concentrated around the twilight hours at sunrise and sunset. Whether there are general functional differences between the eyes of crepuscular and cathemeral species is not known. *A priori*, they may be expected to show similar physiological adaptations, as they all need to make a ‘trade-off’ between good scotopic and photopic vision (Schmitz and Motani, 2010). Thus, it may be speculated that the eyes of crepuscular and cathemeral species should be functionally similar.

There are several possible reasons for adopting a cathemeral diel activity pattern. These include avoidance of predators and interspecific competitors, a more flexible and thus more effective utilisation of food sources, and thermoregulation (Erkert and Gröber, 1986; Engqvist and Richard, 1991; Fernández-Duque, 2003; Kappeler and Erkert, 2003; Erkert and Kappeler,

2004; Colquhoun, 2006; Curtis and Rasmussen, 2006a, b; Donati and Borgognini-Tarli, 2006; Hill, 2006; Curtis, 2007; Tattersall, 2008). Many species are also flexible enough to switch their activity pattern when needed, e.g., to avoid contact with humans (e.g., Russo et al., 1997).

Among extant primate taxa, the Malagasy lemur genera *Eulemur* and *Prolemur* are cathemeral (van Schaik and Kappeler, 1996; Curtis and Rasmussen, 2006a, b; Donati and Borgognini-Tarli, 2006; Curtis, 2007). In addition, at least some populations of the primarily nocturnal owl monkeys *Aotus* (Wright, 1989) and of the primarily diurnal baboons *Papio* (Hill et al., 2003; Hill, 2006) may exhibit cathemeral behaviour under certain circumstances. It is likely that field studies of wild primates will reveal further examples of anthropoid primate species displaying similar flexibility in their diel activity patterns.

2.2.4 THE MAMMALIAN ORBIT AS A PROXY FOR RELATIVE EYE SIZE

“The eye, in short, can never be very small and need never be very big; it has its own conditions and limitations apart from the size of the animal.”

(D’Arcy Thompson, 1961)

Direct study of the evolutionary history of the mammalian eye is difficult, as soft-tissue components of animal bodies fossilize only under extremely rare circumstances. Thus, investigation of sensory capacities of extinct taxa mainly relies on measurement of fossil cranial components, and on comparisons of such data with those of extant taxa. This method is based on the assumption that the size and/or shape of some particular character correlates with sensory performance.

It is not self-evident that vertebrate eyes are spherical. Many taxa, including some birds, reptiles, and fish, have noticeably non-spherical eyes (Walls, 1942; Ritland, 1982), the most extreme perhaps being the tubular eyes of certain deep-sea teleosts (Warrant and Locket, 2004). Moreover, a near-circular shape of the orbit cannot be taken for granted either. For example, many large theropod dinosaurs had orbits that were strongly elongated vertically and sometimes even keyhole shaped (Chure, 1998; Henderson, 2002). In those vertebrates which eyes are surrounded by a bony sclerotic ring, the diameter of this ring is a better approximator of eye size than orbit diameter (Franz-Odenaal and Vickaryous, 2006; Hall, 2008, 2009; Schmitz, 2009; Schmitz and Motani, 2010, 2011). However, mammals, as mentioned, lack ossified scleral rings.

The shape of the eyeball in most extant mammals is practically spherical (II). There are only a few known exceptions to this general pattern. The peculiar, subterranean naked mole-rat *Heterocephalus glaber* of Africa has a “stalk-like” eye (Hetling et al., 2005:321). Most cetaceans, too, have distinctly

non-spherical eyes (Walls, 1942; Mass and Supin, 2007; Kröger and Katzir, 2008).

The size of the eyeball is usually defined in the literature as its *axial length*; less often, data on the *transverse width* are also given (e.g., Ritland, 1982). The mammalian eyeball is known to fluctuate slightly in size with diurnal variations in light intensity. In rabbits and in adult marmoset monkeys, axial length is at its peak during the night (Liu and Farid, 1998; Nickla et al., 2002), whereas in humans and juvenile marmosets, by contrast, axial length reaches its maximum during the day (Nickla et al., 2002; Stone et al., 2004; Wilson et al., 2006; Read et al., 2008). However, these fluctuations are tiny, μm -scale changes.

In order to draw meaningful conclusions from the size relationship between orbits and soft ocular structures, one must compare functionally important variables. Among soft-tissue variables, the axial length of the eye has been frequently investigated in vertebrate eye studies (e.g., Ritland, 1982; Howland et al., 2004). The functional importance of this measure derives from the fact that an increase of the axial diameter of the eye generally leads to an increase of the eye's focal length, which may improve visual acuity. Orbit diameter, in turn, is functionally informative only under certain conditions. The most fundamental condition is that there should be a close correlation between the size of eye and the orbit. Possible conclusions regarding visual *acuity* further require, specifically, that there be a close correlation between the axial length and the width of the eye (which is the measure constrained by the orbit). To assess to what extent eye parameters can be derived from skeletal structures, it is also important to establish whether orbit height and width can be used interchangeably as proxy measures of eye size. It is therefore necessary to study the relations between the optical axis and the transverse diameter of the eye, the width and height of the orbit, and the size of the eyeball and the orbit in such mammal species for which relevant data are available. All these relations are investigated in Paper (II).

2.2.5 PREVIOUS COMPARATIVE STUDIES ON MAMMALIAN EYE/ORBIT SIZE

Not all seminal studies on mammalian relative eye size have been done on osteological material. Some influential works (e.g., Hughes, 1977; Howland et al., 2004; Burton, 2006) have investigated soft-tissue variables. By and large, their results agree fairly well with those obtained from osteological studies, although there are some exceptions.

In a landmark study, Ritland (1982) presented an enormous amount of original data on the size of vertebrate eyes (axial length, and minimum and maximum transverse diameter). He established that, of all extant vertebrate classes, mammals have the greatest range in both absolute and relative eye size. When Ritland's entire mammalian data set is plotted (log eye diameter

vs. log body length), the relation is represented by a curved, rather than by a straight (allometric) line. This means that the allometric slopes are different in different parts of the size range. The eyes of small mammals, generally speaking, scale with positive allometry, whereas those of the very largest species (notably, large ungulates) scale with negative allometry ('mid-sized' mammals seem to scale more or less isometrically). Moreover, in small species eyes are relatively larger than 'expected', suggesting a biological constraint on the minimum size of functional lens eyes. The negative allometry in the upper size range means that, conversely, very large species tend to have smaller eyes than expected from their body size. This suggests that from a certain range of *absolute* size, the increasing costs of maintaining a bigger eye begin to outweigh the benefits in terms of improved visual performance.

Ritland's results were largely confirmed by Kiltie (2000), who also found that eye size (measured by axial length) scales differently in different ranges of body size. More precisely, the eye vs. body size relation was found to be isometric or positively allometric in species weighing less than 1 kg and negatively allometric above that.

There have been a considerable number of studies on relative orbit size in mammals, but the majority of these have been mostly or wholly focused on primates (e.g., Schultz, 1940; Kay and Cartmill, 1977; Lanèque, 1993; Ross, 1996, 2000; Kay and Kirk, 2000; Heesy and Ross, 2001, 2004; Kay et al., 2004; Kirk, 2004, 2006a, b; Kirk and Kay, 2004; Bloch and Silcox, 2006; Ross et al., 2006; Ross and Kirk, 2007; Ross and Martin, 2007). What essentially all such studies have found is that the orbits of nocturnal primates are larger than those of diurnal primates of comparable size. In contrast to the wealth of data on primates, however, published measurement data for other mammals are scarce. Notable exceptions include Fitzgerald (2006) and Cox (2008), who present orbit diameter data for several phylogenetically, morphologically and ecologically distinct taxa. These authors did not, however, try to relate orbit size to diel activity pattern.

The fossil record shows that some extinct lemur species on Madagascar far exceeded in size any of the extant species, and that some of these extinct giant lemurs persisted even into historical times (Walker, 1967; Godfrey and Jungers, 2003). By extrapolating from data on the relative orbit sizes of extant lemur species, Walker (1967) speculated that the largest extinct lemurs were diurnal. However, Walker's study was criticised by Kay and Cartmill (1977), who were sceptical of the possibility of using the much smaller extant lemurs as points of comparison to their extinct giant relatives.

Not all previous workers have considered orbit size to be a good indicator of eye size, or to be a universally useful predictor of diel activity pattern. Schultz (1940) investigated orbit volume in primates, and related it to body mass. He concluded that "the size of the orbit is not closely determined by the size of the eyeball" (p. 406) and that "the two structures can vary in size independently to a surprising extent" (p. 408). MacPhee and Horovitz

(2004), in their study of the fossil platyrrhine *Xenothrix*, did not consider incompletely preserved orbital rings to be sufficiently informative for reliable orbit diameter estimation, and they also stated that “primate orbital rings are rarely perfectly circular” (p. 34). Kappelman (1996:263), in turn, stated that hominid orbits “vary dramatically” in shape. Similar sentiments were expressed by Köhler and Moyà-Solà (2004) regarding orbit shape in bovids. These authors cautioned that in insular mammals, sensory organs may be reduced to an extent that equals what happens under the domestication process (see below), and that island-living mammals thus may not be ‘representative’ in this regard. Specifically, Köhler and Moyà-Solà (2004) based this claim on their study of the peculiar, so-called ‘cave goat’ *Myotragus balearicus* that lived on the Balearic Islands in the Mediterranean until historical times. These authors suggested that relaxation of predation pressure and interspecific competition resulted in morphological changes similar to those in domesticated ungulates.

That mammalian orbits are, geometrically speaking, rarely or never “perfectly” circular is not in dispute. However, as shown in Paper (II), in the majority of those extant primates and other mammals for which such data are available, orbit length and orbit height are similar enough as to be almost interchangeable in practice. Thus, one can use either measure as a reliable indicator of mammalian eye size. This allows the use of much published data, where orbit diameter has been variably measured/reported. Some researchers have measured it vertically (e.g., Simons, 1997; Kay and Kirk, 2000; Bloch and Silcox, 2006; Kirk, 2006a; Cox, 2008), others horizontally (e.g., Ma, 1986; Maffei et al., 1988; Lanèque, 1993; Heesy and Ross, 2001), and some have given both measurements (e.g., Riggs, 1934; Tejedor et al., 2006). Yet others (e.g., Hill and Beckon, 1978; Flannery, 1991; Parnaby, 2002) do not specify their measurement dimension.

Some authors (e.g., Kay and Cartmill, 1977; Kay and Kirk, 2000; Bloch and Silcox, 2006) caution against the use of orbit size as a predictor of diel activity pattern under certain circumstances. Specifically, they caution against extrapolating data on relative orbit size–diel activity correlations obtained from extant, small-bodied species to extinct, large-bodied species. Their data sets, however, have included few or no non-primates. In contrast, Radinsky (1981a, b), who investigated carnivores, found a strong correlation between eyeball size and orbit size (“orbit area”), and thus considered the latter to be a good indicator of visual ability.

Finally, while this thesis is restricted to mammals, it is worth noting that similar studies on the relation between diel activity pattern and eye/orbit size have been performed also on other vertebrates. For example, Hall and Ross (2007) found that in extant birds, nocturnal species have the relatively largest eyes while diurnal species have the smallest and cathemeral species, in turn, have intermediate eye sizes. Hall and Ross also suggested that the large-eyed nocturnal birds represent an adaptation to high visual sensitivity, whereas the eyes of diurnal birds are optimised for visual acuity instead.

2.3 THE 'TRADE-OFF' HYPOTHESIS

Neural tissue is energetically expensive to produce and to maintain (Laughlin, 2001; Niven and Laughlin, 2008). Therefore, it is likely that a given organism cannot allocate an equal amount of cortical space for processing information from all main senses, and that animals must therefore 'choose' which sense(s) to 'prefer'.

Several authors have made suggestions to the effect that investment in different sensory systems resembles a zero-sum game, so that improving one occurs at the expense of another. For example, in a study of fossil pinnipeds, Repenning (1976) suggested that during evolutionary history, there has been a general trend of improving vision and deteriorating olfaction: in the pinniped lineage, eyes have grown and the olfactory organ has been reduced. However, as mentioned earlier, pinniped vision has, in a way, become 'poorer' as colour discrimination has been lost (Peichl et al., 2001; Griebel and Peichl, 2003), while, on the other hand, a fairly respectable olfactory capacity has been retained (Kowalewsky et al., 2005; Kishida et al., 2007; Hayden et al., 2010; Laska et al., 2010). Thus, any putative evolutionary trade-off between vision and olfaction in Pinnipedia would seem to have been a fairly complex affair.

Okawa et al. (2008) compared the ATP consumption of rod and cone cells in the mammalian retina. Their results show that cones are energetically more costly than rods, and these authors therefore suggested that, circumstances allowing, it would be advantageous for a mammal to reduce the number of the former. Specifically, Okawa et al. (2008) suggested that diurnal mammals might benefit from having a smaller number of cones in the retina. This seems indeed to be the case with diurnal primates.

Comparison of the genetic structure of the rod pigment rhodopsin among various phylogenetically distant and ecologically different mammals led Zhao et al. (2009a,b) to suggest that there may be a trade-off between opsin structure and the presence of so-called 'special senses'. In high-duty-cycle echolocating bats, such as the horseshoe bats, the SWS1 (blue-sensitive cone) gene has become non-functional through a frame shift mutation, and mutations in the rhodopsin gene predict a spectral shift of the rod pigment that would make it less sensitive in nocturnal conditions. This stands in clear contrast to the case in megachiropterans and in low-duty-echolocating microchiropterans and may indicate relaxed selection on the rhodopsin gene in this particular chiropteran evolutionary lineage.

On the other hand, Matsui et al. (2010) showed that the possession of trichromatic colour vision does not exclude a keen sense of olfaction (as implied by the possession of a relatively large number of functional olfactory receptor genes) in primates. Indeed, it might be argued that if trichromatic colour vision in primates is linked to foraging for differently-hued fruits and leaves olfaction might also be of considerable importance for the same animals, as they assess the quality of the putative food (Regan et al., 1998;

Dominy and Lucas, 2001; Dominy et al., 2001, 2003; Lucas et al., 2003). However, having a high discrimination acuity for some combinations of odorants does not necessarily imply having a high sensitivity to odorants as well. Thus, frugivorous primates presumably use their keen sense of smell only at close range, not to detect food items over long distances.

Nozawa et al. (2007) have suggested that genetic drift affects pseudogenisation of (specifically) olfactory receptor genes in humans as much as, or perhaps even more than, selection does. If this is correct, the (arguably) relatively poor human sense of smell may, in some sense, be said to have come about by 'chance'. From another viewpoint, however, relaxed selection allowing drift may be seen as one mechanism whereby a sense that has become relatively less important is allowed to 'fade'. Also, it would be interesting to see whether Nozawa et al.'s results are applicable to other mammals and to other sensory systems.

3 AIMS OF THE STUDY

The general purpose of this study is (i) to identify morphological structures that are directly associated with sensory perception, (ii) to identify skeletal measures that may be used as proxies for the physiologically relevant soft structures (with special reference to palaeobiological application), (iii) to investigate which features of sensory morphology may be related to the mode of life of an animal, and (iv) to compare representatives of different clades and different ecomorphological adaptations (with special emphasis on *a priori* interesting taxa such as species that have adapted to living in a radically different environment than their closest relatives).

The main specific questions are:

1. Is there a simple functional relation between the size of the olfactory epithelium and the olfactory sensitivity of mammals?
2. Is cribriform plate area a suitable proxy measure of olfactory sensitivity in mammals?
3. How closely do eye size and orbit diameter correlate with each other in mammals? In other words, is orbit diameter a suitable proxy measure of eye size (and thereby of visual sensitivity/acuity, in agreement with previous literature)?
4. How does relative orbit size differ between diurnal, nocturnal, and cathemeral mammals?
5. How do vision, hearing, and olfaction interact with each other in the mammalian 'sensory space'?

Paper I has two main objectives. It investigates whether there is a simple functional relation between the size of the olfactory epithelium and olfactory sensitivity/acuity, and whether the area of the cribriform plate of the ethmoid is a suitable proxy measure of olfactory sensitivity (Questions 1 and 2, respectively).

Paper II has three main objectives. First, it investigates how closely eye size and orbit diameter correlate, and thus whether orbit diameter is a suitable proxy measure of eye size (Question 3). Second, it investigates to what extent relative orbit diameters correlate with diel activity pattern (diurnal, nocturnal, cathemeral) (Question 4). Third, it investigates to what extent phylogenetic relatedness influences the results of a large-scale comparative analysis, and whether the conclusions that are mainly based on previous studies on primates have more general validity across Mammalia.

Paper III has one main objective: to establish the concept of a mammalian sensory space, which provides a graphic method to quantify the relative 'importance' of three main sensory modalities: vision, hearing, and olfaction, by the animal's co-ordinates in this three-dimensional space (Question 5). To test the concept, a large number of mammalian species are mapped into this space.

4 MATERIALS AND METHODS

4.1 CHOICE OF TAXA AND SPECIMENS

The original material on which this thesis is based is skeletal (cranial). The form of the skull changes in mammals as they grow from juveniles to adults, as does relative brain size, including the size of the olfactory bulb at least in some species (e.g., Macrini et al., 2007). In order to avoid possible confounding ontogenetic effects on the results, only data from adults were utilised in this thesis. In some sexually highly dimorphic species (e.g., baboons, eared seals) sex may be an important factor in body size–organ size comparisons (Kappelman, 1996; Kirk and Kay, 2004); however, the material was not sorted by sex, as this information was unavailable for many of the specimens studied.

Domestication is also known to influence relative brain size in mammals. The brains of domesticated animals are generally smaller than those of their wild relatives. This decrease in brain size is visible even in basically non-domesticated animals that have been bred in captivity for only a few generations (Kruska, 2005). Furthermore, at least in domestic dogs, the position of the olfactory bulb relative to the rest of the brain differs between breeds and may be considerably different than in their wild relatives (Roberts et al., 2010). Therefore, we did not include any domesticated taxa in our study of cribriform plate size (I). However, there is relatively little information on how, or if, domestication affects eye size or visual capacities. McGreevy et al. (2004) did show that the domestic dog differs from its ancestor, the grey wolf, in that its eyes are positioned relatively more frontally. Furthermore, McGreevy et al. (2004) showed that there are differences between various dog breeds in eye structure. The visual streak of the retina is more densely packed with cells in dolichocephalic (long-headed) breeds than in brachycephalic (short-headed) breeds. Brachycephalic breeds, by contrast, possess a more strongly developed *area centralis*. Evans and McGreevy (2007), in turn, showed that breed-specific differences in eye structure also exist in the domestic horse. In this species, too, the visual streaks in the retinae of dolichocephalic individuals are more densely packed with cells than are those of more brachycephalic individuals.

Mindful of the possibility that domestication might influence mammalian orbit size, too, I nevertheless included orbit size data for some domesticated species (e.g., dog, cat, horse, cattle) in (II). This was done because there is a relatively large body of data on various aspects of vision and eye morphology in domesticated mammals.

The focus on various *cranial* variables as anatomical proxies of sensory organ size, and cranial length as a measure of overall animal size (rather than, e.g., body mass) serves two main purposes:

1) To find measures that can be applied also to extinct species. In fossils, only skeletal measures are available (save in some exceptional cases). Besides constraining the choice of anatomical proxies of sensory organs, it also constrains the choice of measures of the size of the whole animal. Body mass, obviously, cannot be reliably recovered. Even the bone material is frequently incomplete, with postcranial elements partly or completely missing. Then, e.g., “whole body length” cannot be used. By contrast, if orbits can be measured, the cranium is likely to be reasonably well-preserved and measurable. The size of the cranium is also a more relevant variable than general body size for assessing the relative investment in eyes and other cephalized sense organs, as the spatial resources for which they compete (head space and brain space) are located there rather than, e.g., in the body cavity.

2) To facilitate comparison with previous studies. For example, in eye/orbit size studies, “skull length” (or “cranial length”) is a variable which has been used by many authors, e.g., Kay and Cartmill (1977), Ross (1996) (who related skull length to orbital convergence), Kay and Kirk (2000), Ravosa et al. (2000), Heesy and Ross (2001), Kirk (2006a), and Cox (2008).

In Paper (I), we relate cribriform plate area to ‘skull area’, defined as the greatest length of the skull (which, in most species, equals the prosthion–inion distance) multiplied by condylobasal width (measured at the base of the skull). In Paper (II), I relate the transverse width and the axial length of the eye to each other (based on soft-tissue data from the literature), to establish eye sphericity; orbit height and orbit width against each other, to establish orbit circularity; eye diameter against orbit diameter (defined in my original measurements as the vertical distance between the bony orbit’s superior and inferior margins, perpendicularly to the tooth row), to establish how closely these two correlate; and orbit diameter to skull length (defined as prosthion–inion length) (Figure 2), to study scaling effects. In Paper (III), we utilize measurement data from both Paper (I) and (II), as well as middle ear size data from Nummela (1995), and map (variables derived from) these proxy measures against each other.

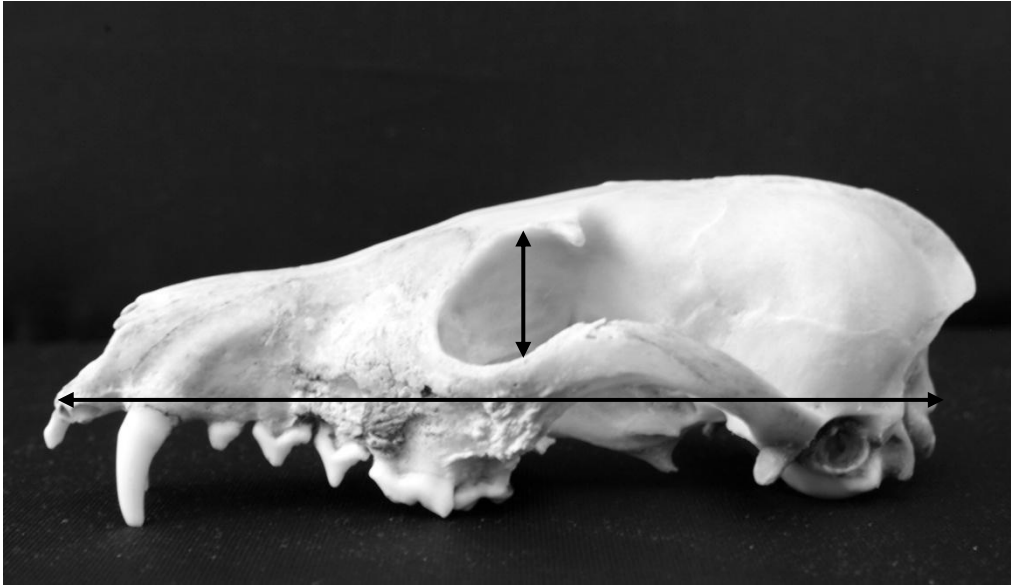


Figure 2 *Vulpes vulpes* cranium, showing the orbit diameter and skull length measurement dimensions. Figure from (II). Photo by Minna Pihlström.

4.2 ENDOCASTS

A traditional method of making endocranial casts is using liquid latex (e.g., Radinsky, 1968). Instead of latex, meltable red Vinamold rubber was used (softness 1; Bang & Bonsomer Company); however, the endocast making procedure is fundamentally the same in both cases (I).

The rubber is first heated in a kettle or another such vessel until it melts and turns into a liquid state. Next, enough of it is poured into the cranium (in the case of intact crania, through the foramen magnum) to cover the cribriform plate and/or fill the olfactory fossa. The rubber is then allowed to cool and solidify, after which it is removed with the help of forceps; the rubber-like consistency of the cast allows it to retain its shape. A practical advantage of using meltable rubber instead of latex is that the former coagulates faster than the latter dries. The making of a latex cast therefore takes several minutes (as described by Radinsky, 1968), whereas the red Vinamold casts become sufficiently solid for removal much more quickly in room temperature.

Before cooling, small amounts of liquid gel may begin to seep through the perforations on the surface of the cribriform plate. This typically results in small knobs and irregularities on the cast's surface (Figure 3), which allows delimitation of the cribriform plate's borders.

From the cast, linear measurements of the length, width, and 'height' (or, rather, 'depth') of the ellipsoid-like surface were obtained with digital callipers. Measurements were taken of 150 species of extant mammals by a

single person (myself) in order to reduce possible variation from slightly different habits of different observers (Palmeirim, 1998; Herr et al., 2000). The surface area of the cribriform plate was calculated as the area of an ellipsoid described by the equation:

$$(1) \quad x^2/a^2 + y^2/b^2 + z^2/b^2 = 1.$$

In this equation, the axes x , y , and z correspond to length (L), width (W), and height (H), respectively. If b is larger than a , the ellipsoid is flattened out along the x -axis (that is, it is shaped like a discus), whereas if b is smaller than a , it is flattened out along the x -axis (that is, it is shaped like a cigar).

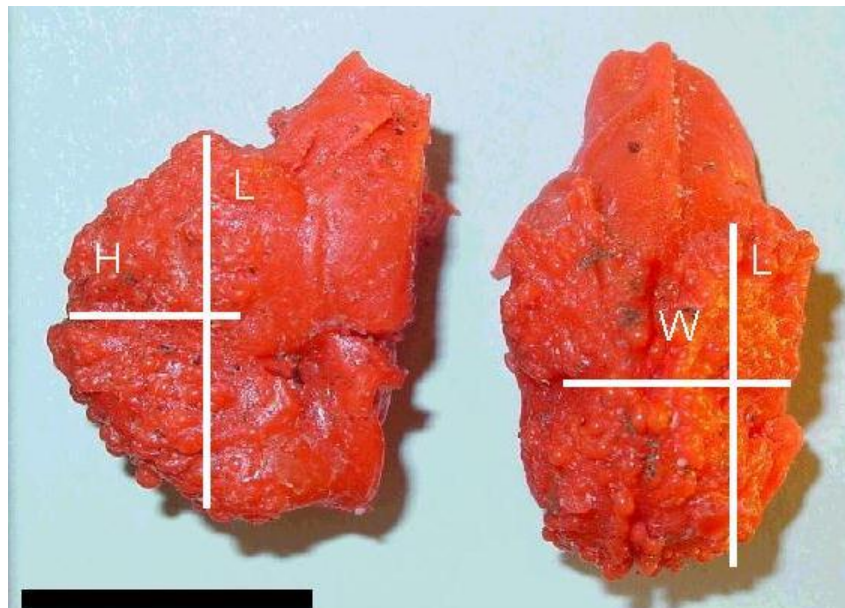


Figure 3 Vinamold endocast showing the measurements used in (I). Photo by Simo Hemilä.

4.3 STATISTICAL ANALYSIS AND PHYLOGENETICALLY INDEPENDENT CONTRASTS

There has been much debate on which type of regression analysis is the most appropriate to use in interspecific allometric analyses (e.g., Seim and Sæther, 1983; Calder, 1987; McArdle, 1988; Martin and Barbour, 1989; Aiello, 1992; Smith, 1994; Gauld, 1996; Martin et al., 2005). Traditionally, ordinary least-squares (LS) regression has been widely used, but many argue that it is preferable to use other methods, particularly reduced major axis regression (RMA) (e.g., Martin and Barbour, 1989; Aiello, 1992; Martin et al., 2005) – a method sometimes called the standardised major axis regression (Warton et al., 2006). However, it has also been shown that when correlation coefficients are high (about 0.90 or higher), results obtained from LS and RMA regression analyses are usually not significantly different, and thus the

use of LS regression is appropriate under such circumstances (McArdle, 1988; Gauld, 1996).

In the last decades, methods have been developed that ‘correct’ for phylogenetic relatedness between taxa in comparative studies. Conventional, or phylogenetically uninformed, analyses regards all data points as completely independent and therefore cannot distinguish to what degree similarities and differences are due to relatedness rather than e.g. functional adaptations. Therefore it is desirable to have methods that take into account evolutionary distances, i.e., the topology and branch lengths of phylogenetic trees. Among the various comparative methods developed to date, the phylogenetically independent contrasts (PIC) method (Felsenstein, 1985) is one of the most versatile and, hence, most commonly used (e.g., Gittleman and Luh, 1992; Garland et al., 1999; Nunn and Barton, 2001; Carvalho et al., 2005; Nunn, 2011). The PIC method is based on the assumption that character change occurs in the fashion of Brownian motion (Felsenstein, 1985; Nunn, 2011), that is, a character value (e.g., orbit diameter) may change over evolutionary time in any direction, independently of previous character changes. The Brownian motion model also assumes that the rate of evolutionary change is constant; in other words, the longer the evolutionary time, the greater the number of character changes (both positive and negative). Brownian character variation is, therefore, proportional to time. Thus, the PIC values are effectively related to ‘reconstructed’ ancestral trait values that are generated by averaging actual trait values.

It has been claimed that comparative studies in biology must always take phylogenetic relatedness explicitly into account (e.g., Garland et al., 2005, and references therein). However, many studies (Weathers and Siegel, 1995; Ricklefs and Starck, 1996; Martin et al., 2005; Muñoz-Garcia and Williams, 2005) have shown that the results obtained by conventional and phylogenetically corrected analyses do not always differ significantly, and that, therefore, traditional non-phylogenetic methods may often be *de facto* sufficient. In Paper (II) of the present thesis, I have applied both methods and compared the results.

The application of the PIC method requires an at least partially resolved phylogeny for the taxa under study. The mammal phylogeny used in (II) is based on the most complete published tree, the composite supertree of Bininda-Emonds et al. (2007, 2008). In order to resolve polytomies found in this tree, I have complemented it with other sources (see Paper (II) for details). All source trees are based on molecular data. Where the additional sources differ regarding their topologies, I have consistently preferred the most recently published source. The PIC analyses were performed with the PDTREE module of the PDAP package (Garland et al., 1993, 1999; Garland and Ives, 2000). With this software, one creates a phylogenetic tree with modifiable branch lengths; it is, however, preferable to use real evolutionary branch lengths (i.e., ‘standardised’ branch lengths) whenever possible, because PDAP uses branch lengths to calculate the PIC values.

5 RESULTS

5.1 CORRELATION BETWEEN THE SIZE OF THE OLFACTORY EPITHELIUM AND OLFACTORY SENSITIVITY

For a few mammal species ($n = 8$), data in the literature provides information both on their detection thresholds for certain odorants (notably, butyric acid), and on the surface areas of their olfactory epithelia. Empirical data (Paper (I) and references therein) show that these odorant detection thresholds correlate with olfactory epithelium surface areas, in that the larger the epithelium surface of a mammal is, the lower is its odorant detection threshold. In other words, mammals with large olfactory surface areas have a greater sensitivity for odorants.

5.2 OLFACTORY SENSITIVITY AND CRIBRIFORM PLATE AREA

In Paper (I), we compared original data on cribriform plate area with literature data on olfactory epithelium areas for 16 species of mammals. Our results showed that there is an isometric relationship between these two traits (Figure 4). In other words, the areas of the olfactory epithelia and the cribriform plates are directly proportional to each other. We have thus established that cribriform plate area is indeed a suitable proxy measure of a given mammal's olfactory sensitivity. Thus, cribriform plate area measured from fossils may be used to infer olfactory sensitivity also in extinct species.

It should be kept in mind that high olfactory sensitivity for certain odorants (i.e., the ability to detect low concentrations of these odorants) is not the same as high olfactory acuity (i.e., the ability to differentiate between many odorants). Olfactory acuity cannot be deduced from skeletal material, at least not directly. However, based on the results of Paper (I), it may be concluded that a species with a large cribriform plate area, and therefore a high olfactory sensitivity, does indeed rely on olfaction to a great extent.

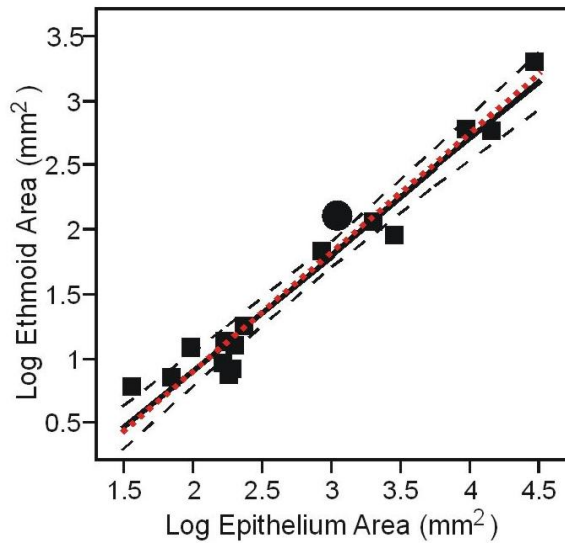


Figure 4 Olfactory epithelium area – cribriform plate area (“ethmoid area”) in 16 species of mammals. The slope of the regression line is $\log(\text{ethmoid area}) = -0.883 + 0.900 \log(\text{epithelium area})$, indicating isometry. The large dot represents *Homo sapiens*. Figure from (I).

5.3 ORBIT DIAMETER AS A PROXY MEASURE OF MAMMALIAN EYE SIZE

It has previously been established in the literature that both visual sensitivity and acuity strongly correlate with the size of the eye. However, with the exception of primates, which have been fairly extensively studied, it has not been shown previously how closely eye size correlates with orbit size in mammals.

In Paper (II), I first showed that, functionally speaking, the eye shape of the majority of mammals may be considered as spherical (which is not the case in all vertebrates, or even in a few mammals such as cetaceans; representatives of the latter, however, were not included in the data set). Thus, axial length and transverse width may be used interchangeably as measures of mammalian eye size. Next, I showed that the orbit of those mammals where both height and width can be reliably measured is, effectively, circular in shape. In these, orbit height and width (variably given in the literature) may be used interchangeably as measures of orbit size. By combining these results, I was able to compare the ‘fit’ between the axial length of the eye and the diameter of the orbit. With the exception of a few taxa such as the fossorial moles (which have much smaller eyes than orbits), this fit was found to be reasonably close. Although the eye/orbit relation did vary with the animal’s absolute size, the relation was regular enough for orbit diameter to be used as a good indicator of actual eye size.

5.4 RELATIVE ORBIT SIZE IN GENERAL AND RESOLVED FOR LOWER-LEVEL TAXA

In Paper (II), the diameter of the orbit relative to the length of the skull was analysed in 355 species of mammals. These relations were investigated with both LS and RMA regression, and both conventional species values-based analyses (Figure 5A) and PIC analyses (Figure 5B) were performed and compared. Overall, the relationship between orbit diameter and skull length is negatively allometric in the entire mammalian data set, regardless of the choice of regression analysis method.

When the data set was broken up into smaller taxonomic units, or when certain taxa were excluded from the main data set, some new patterns emerged. For example, the disproportionately large number of primate species ($n = 102$) in the data set might be expected to bias the all-mammalian regression results. When primates were removed, the LS regression slope still indicated negative allometry for the non-primate data set, whereas the RMA regression analysis recovered a relationship that did not differ significantly from isometry. In other order-level taxa, still finer subdivision of the material sometimes revealed interesting within-taxon differences. Notably, in the chiropterans, the overall orbit – skull relationship is strongly positively allometric, but in the so-called megabats, this relationship is, in fact, *negatively* allometric. In microchiropterans, by contrast, the orbit – skull relationship is isometric according to LS regression, and positively allometric according to RMA regression. This highlights the potential importance of considering taxonomy (that is, phylogenetic relatedness) in comparative analyses.

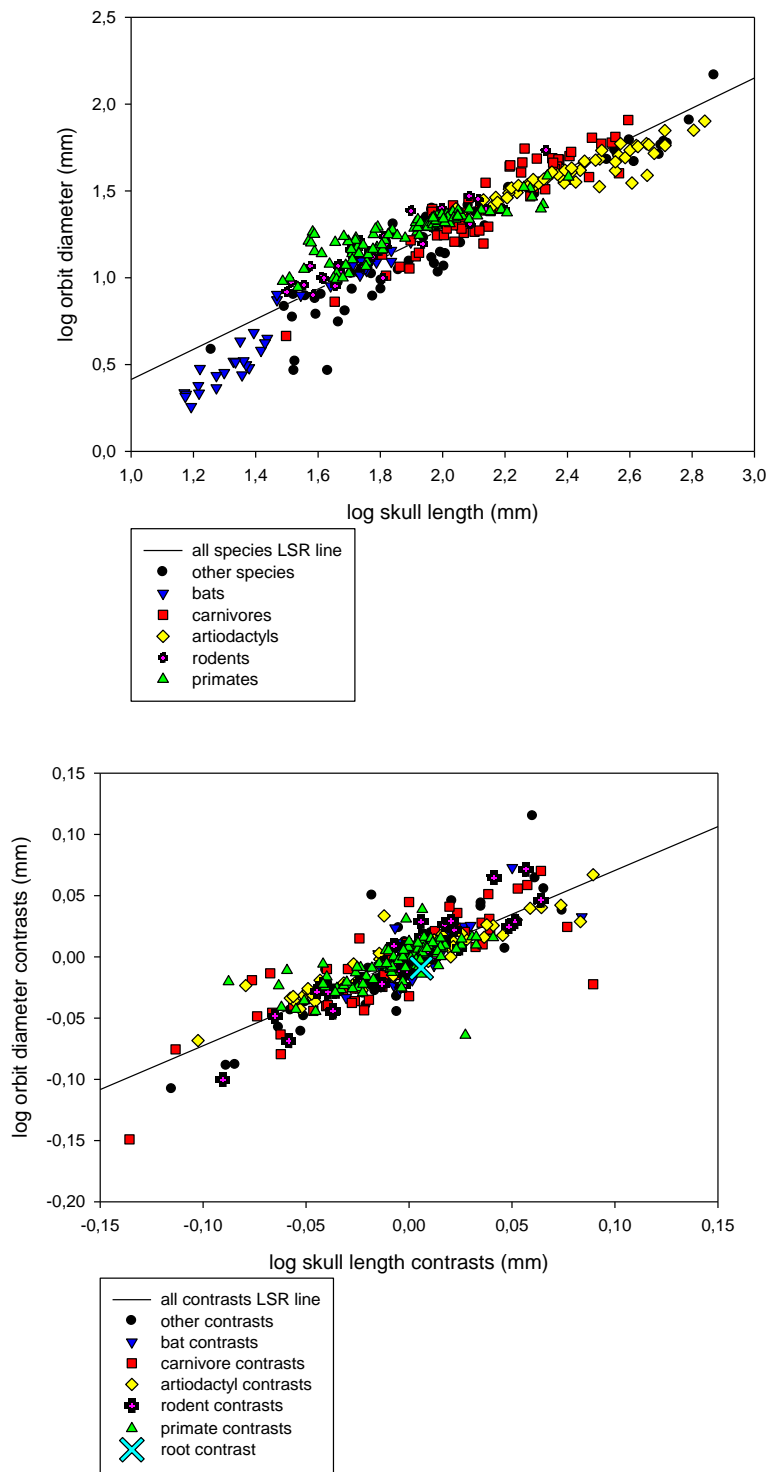


Figure 5A-B (A) Orbit diameter–skull length relation in mammals, data for individual species. The RMA slope of the regression line is $\log(\text{orbit diameter}) = -0.57 + 0.93 (\log \text{skull length})$, indicating negative allometry. Figure from (II). (B) Orbit diameter–skull length relation in mammals, data for PIC values. The RMA slope of the regression line is 0.86, indicating negative allometry (as the regression is through the origin, there is no intercept). The X represents the root contrast. Figure from (II, Supplementary material).

5.5 RELATIVE ORBIT SIZE AND DIEL ACTIVITY PATTERN

The most interesting question in Paper (II) was if and how orbit diameter may be correlated with diel activity pattern (that is, the time of a 24-hour cycle when an animal is most active). All species in the data set had been assigned to one of three diel activity pattern categories (nocturnal, cathemeral, or diurnal). PIC analysis was used to detect ‘outliers’ in the data set. ‘Interesting outliers’ are cases where significant contrasts between sister taxa (seen as strong deviations of data points from the regression line) coincide with shifts in diel activity pattern.. Only few data points meeting these criteria were detected, and most of them were between recently diverged sister species of no outstanding biological interest. Thus, for the most part, correction for phylogeny does not make much difference, and it appeared justified to use ‘raw’ species data in the main analyses of diel activity patterns.

Previous investigations on primates have shown that nocturnal species have larger orbits than diurnal species of similar size. These findings for primates were supported in Paper II. The data for other mammals showed that, while cathemeral species have orbits that are intermediate in size to those of nocturnal and diurnal species, they are nevertheless significantly more similar in size to those of the former. Both nocturnal and cathemeral mammals have orbit diameters that scale roughly isometrically with skull length. Diurnal mammals, by contrast, have orbits that scale with negative allometry to skull length. The last-mentioned result was very robust, as the pattern was nearly identical for primates and non-primates, On the whole, however, great caution is called for when generalisations are made. Differences in, e.g., allometric slopes may easily arise just because the sets of species (eyes) that are compared cover different ranges of *absolute* size.

5.6 INTERACTION BETWEEN VISION, HEARING AND OLFACTION

In Paper (III), we utilised previously established anatomical proxies for the relative investments into different sensory modalities: axial length of the eye for vision, middle ear size for hearing, and cribriform plate area for olfaction. Here, body mass was used as the independent variable. The sensory organ proxy data were recalculated into “residuals”, expressing the (positive or negative) *differential* investments compared with the (“average”) regression of organ size on body mass, and these residuals were mapped onto a three-dimensional “sensory space” with three coordinate axes: “eye”, “ear”

and “nose”. In these plots, ‘eye’ and ‘ear’ data tended to cluster together (meaning that animals with large eyes frequently have large ears too), suggesting a co-evolutionary link between vision and hearing. Olfaction, by contrast, did not show such clear correlations with the two other senses. However, it did show an “ecological” gradient on the terrestrial-arboreal axis, terrestrial mammals tending to have larger olfactory organs than arboreal mammals.

Our results suggested that both phylogeny and ecological factors such as diet and habitat may influence sensory organ interaction. For example carnivores, which mostly have large olfactory organs but medium-sized eyes, tended to cluster together in the sensory space.

6 DISCUSSION

6.1 THE MAMMALIAN OLFACTORY ORGAN AT ECOLOGICAL THRESHOLDS

The main finding of Paper (I) was that, with only a few exceptions (see below), mammalian olfactory organ size scales isometrically relative to skull size. Paper (I) also showed that the cribriform plate area correlates with olfactory epithelium area, which, in turn, correlates with olfactory sensitivity. Thus, simply put, these results show that the larger the olfactory organ, the keener is the sense of smell. In other words, absolute size matters, and there is no obvious saturation point (at least not among extant terrestrial mammals) beyond which it is no longer optimal for a mammal to increase olfactory organ size.

Further, the results of Paper (I) suggest that relative olfactory organ size does not vary significantly between most of the various mammalian clades, or between ecologically different taxa. In other words, once they have evolved a keen sense of smell during their evolutionary history, mammals do not seem to easily give it up. A significant reduction of olfactory sensitivity only seems to happen in the most extreme cases of crossing a novel ecological threshold, as when, for example, terrestrial mammals become adapted to an aquatic environment (Thewissen and Nummela, 2008). Even in such a case, the process of olfactory organ reduction seems to require a substantial amount of time, and a functional sense of smell may be retained for tens of millions of years. In the data set of Paper (I), the most extreme outlier (with the relatively smallest cribriform plate area) is the fully aquatic dugong *Dugong dugon*. The fossil record shows that its ancestors had become aquatic already by the early Eocene, circa 50 MYA (Domning, 2001). By contrast, the pinnipeds (seals, sea lions, and walruses) are a significantly younger clade, which did not diverge from terrestrial carnivores until the late Oligocene or the early Miocene, that is, at most circa 25 MYA (Rybczynski et al., 2009). Pinnipeds are not as fully aquatic as sirenians are, and they spend considerable parts of their lives on land, where they are exposed to air-borne odorants. This difference in the degree of aquatic adaptation is highlighted by the fact that pinnipeds, in contrast to sirenians, have retained fairly large olfactory organs (and thus, a decent sense of smell).

Cetaceans and the platypus were not included in the data set of Paper (I) due to the fact that these mammals lack a perforated cribriform plate altogether. Of these clades, aquatic adaptations of cetaceans are certainly very ancient, having started evolving approximately as long ago as those of sirenians (e.g., Thewissen et al., 2007). It is interesting, therefore, to note that the degree of reduction of the olfactory organ and its various morphological components is far more extensive in extant cetaceans than in

sirenians (Pihlström, 2008). Apparently, the selection pressures acting on the reduction of the olfactory organ in cetaceans have been stronger than they have been in sirenians, but why this should be the case is not entirely clear. Sirenians are admittedly much less well adapted to life in the truly pelagic zone than whales and dolphins are, and, in fact, extant sirenians are rather strictly coastal/estuarine species living in shallow water, including freshwater rivers. However, there are a number of extant cetaceans that live in similar (or, in some cases, the very same) habitats, but which have olfactory organs that are as structurally reduced as those of their ocean-living relatives (e.g., Schwerdtfeger et al., 1984). Thus, a preference for shallow-water habitats is unlikely to be the main explanation for the cetacean-sirenian difference in the degree of olfactory organ reduction.

Due to incompleteness of the fossil record, the origin of (semi-)aquatic adaptations in the monotreme lineage is less clear than in the case of cetaceans or sirenians, but fossil platypus species that were morphologically very similar to the extant species are known to have existed in the late Oligocene–early Miocene (Musser, 2003). This implies that the ultimate origin of the platypus lineage is significantly earlier. In fact, monotreme fossils are known already from the Cretaceous (Rowe et al., 2008), although due to the fragmentary nature of these remains it cannot be ascertained with any degree of certainty whether these early monotremes were aquatic or not. (That some mammalian, or at least near-mammalian, clades had in fact evolved semi-aquatic adaptations already during the Mesozoic was demonstrated by the discovery of the well-preserved fossil remains of the Jurassic docodont *Castorocauda* (Ji et al., 2006).)

The other major group of mammals with a significantly reduced cribriform plate area is the anthropoid primates: tarsiers, monkeys, and apes (including humans). As in the cases of the various aquatically adapted mammalian lineages, the evolutionary origin of primates is intimately connected to a major substrate change: namely, a shift from terrestrial to arboreal living. However, as in the case of aquatic taxa discussed above, arboreality by itself does not seem like a sufficient explanation for the reduction of primate olfactory capabilities. Other arboreally adapted mammals such as opossums (Rowe et al., 2005), sciurids (Cartmill, 1974) and tree-shrews (Meinel and Woehrmann-Repenning, 1973) possess olfactory organs of respectable size. Also, the other main lineage of extant primates, the strepsirrhine ‘prosimians’, generally show much less reduction in olfactory organ size than anthropoids do. Thus, having a sensitive sense of smell is not incompatible with arboreal living, and the reasons for the relative reduction of this sensory system in anthropoids need to be sought for elsewhere.

6.2 RELATIVE ORBIT SIZE AND MAMMALIAN ECOLOGY

Paper (II) showed that orbit diameter can be used as a proxy measure of eye size. Orbit diameter related to skull size showed different allometric growth rates between diurnal mammals on the one hand and nocturnal and cathemeral mammals on the other. The relationship was strongly negatively allometric in the former, but near-isometric in the two latter categories. The linear regression slopes (in log-log plots) of nocturnal and cathemeral mammals are statistically indistinguishable. Removing the large collection of primates from the analysis in Paper (II) did not significantly change the overall results. According to the RMA regression analyses, the orbit–skull relationship remained negatively allometric for the diurnal non-primate species, and isometric for both the nocturnal and the cathemeral ones.

A problematic aspect with relating relative orbit sizes with diel activity patterns across Mammalia is the fact that the various diel activity pattern categories (nocturnal, cathemeral, and diurnal) do not cover entirely similar animal size ranges. For example, most of the smallest species in the data set of Paper (II) are microchiropteran bats which, obviously, are almost universally nocturnal. (Under certain circumstances, even microchiropteran bats may regularly be active during non-scotopic conditions: such circumstances may occur on isolated, predator-free islands (Moore, 1975), or during the middle of the summer at high latitudes (Speakman et al., 2000). However, such exceptions are relatively rare and most microchiropterans may indeed be regarded as *de facto* strictly nocturnal.) Visual inspection of the all-mammal data set shows that the smallest bats (blue inverted triangles in Figure 5A in this thesis) are positioned clearly below the general mammalian regression line. When Chiroptera is analysed separately (Paper (II)), it is seen that relative orbit size does indeed scale differently in this clade than in the rest of Mammalia. In bats as a whole, relative orbit size increases much more steeply, with a stronger positive allometry, than in other mammals. In other words, the smallest bats have relatively smaller orbits than ‘expected’, possibly because the small skull size acts as a very severe constraint on all sensory resources, including eye size. Mammalian lens eyes may here simply be approaching their functional lower size limits, and when this constraint is reduced (that is, when absolute skull size increases), it may again pay off to increase relative eye size more steeply than the general relations in larger mammals would predict. This could explain the steeply increasing orbit diameter–skull size relation observed in chiropterans. At the maximum size range reached by extant bats, the fruit-eating megachiropterans, they do in fact scale similarly to mammals in general, suggesting that the largest bats have ‘escaped’ the severest size constraints that prevent their smaller relatives from evolving a more efficient visual system.

However, this simple scenario is confounded by the presence of compensating sensory modalities in the smaller chiropterans, namely, their ability to echolocate (megachiropterans, with few exceptions, do not echolocate). It is not yet known whether echolocation is, in fact, a less energetically ‘costly’ (*sensu* Niven and Loughlin, 2008) sensory system than vision. If this is indeed the case, perhaps the smallest bats’ apparent handicap of having small eyes is actually more than adequately compensated for by their echolocation capabilities. To gain insights into the optimal eye size of bats, it would be very interesting to investigate the relative eye sizes of hypothetical, truly diurnal microchiropteran species. Unfortunately, however, on this point we are forced to remain ignorant in the face of biological reality.

At the upper end of the size range, the strongly negative allometry of orbit size vs. skull size in diurnal mammals (virtually identical in primates and non-primates) suggests diminishing returns of investment into higher potential acuity. There may be several reasons for this. In some respects, the costs of maintaining a larger eye probably grow with volume (i.e., proportional to the third power of diameter), while acuity, at best, grows proportionally to area (the second power of diameter). Moreover, the biological advantage of very acute vision at large distances is limited by optical factors (refraction, scattering) of the intervening medium, the air.

The results of Paper (II) show that relative orbit diameter is not a reliable indicator of diel activity pattern in extant non-primate mammals. The overlap in morphospace between the various diel activity pattern categories is so extensive that individual species cannot be confidently assigned into such categories simply on the basis of their orbit diameters. Considering that this pattern holds true across virtually all of extant Mammalia (exclusive of Primates), it is reasonable to assume that this was the case also in extinct species of mammals. Thus, it seems that relative orbit diameter can unfortunately not be used with any degree of confidence to reconstruct diel activity patterns in fossil mammals.

6.3 SENSORY TRADE-OFFS

Paper (III) shows that there is some justification for the widely held, though hitherto rarely substantiated, belief that there has been a sensory trade-off between different senses in mammals. That is, throughout evolutionary history, some sensory systems have increased in importance at the expense of others whereas some seem to ‘co-operate’ (or, at any rate, not ‘compete’ with each other). Specifically, the data in Paper (III) suggest that a mammal may simultaneously possess both good vision and acute hearing, but that these, in turn, are rarely coupled with an especially keen olfactory sense.

It should, of course, be kept in mind that vision, hearing, and olfaction are only three of the several distinct mammalian sensory modalities. Conceivably, other senses might interact differently in the sensory space. As noted in Paper (III), the tactile sense (the sense of touch) is of particular importance to many mammals. It has been shown that in mammalian crania, the number of whiskers correlates with the size of the infraorbital foramen (Muchlinski, 2010). Thus, the infraorbital foramen seems to be yet another cranio-osteological proxy measure that can be used to quantify sensory capacities.

In chiropterans and odontocetes, respectively, echolocation has independently evolved to be a major sensory system. As mentioned in the previous section, large eyes may not correlate closely with echolocation capabilities in chiropterans. Pedersen (1998) has shown that the *presence* of echolocation capabilities in chiropterans can be deduced by measuring the angle of the orientation of the rostrum relative to the skull (and that by this method, microchiropteran crania can be further subdivided into species emitting their echolocation calls nasally versus orally). However, as of yet there are no comparable methods of similarly quantifying chiropteran echolocation capabilities as has now been done for vision, hearing, and olfaction.

7 CONCLUSIONS

In this thesis, it has been shown that cribriform plate area is a reliable indicator of olfactory organ size, and thus olfactory acuity, in mammals.

Further, it has been shown that orbit diameter is a reliable indicator of eye size, and thus visual acuity, in mammals.

Taken together, these results suggest that the measurements of judiciously selected morphological structures can act as informative proxies for the acuity of the respective sensory systems that they are parts of.

These results have implications for the study of mammalian evolution. Given that there are clear functional relationships between morphology and sensory acuity (and/or capacity) across the phylogeny of extant Mammalia, we may reasonably presume such relationships to have been present throughout mammalian evolutionary history. Thus, by applying the concept of the EPB (Witmer, 1995), we may infer size and structure of soft-tissue sensory organ structures, as well as diel activity patterns and other similar ecomorphological traits, in fossil taxa (for similar views, see Bryant and Russell, 1992). This approach offers, among other things, an opportunity to gain insight into the conditions surrounding the emergence of the human evolutionary lineage. It has traditionally been thought that a pivotal moment in the evolution of anthropoid primates was their switching from olfaction to vision as their primary sensory modality; the assumption being that these two sense organ systems, so to speak, cancel out each other. Our *sensory space* concept offers a method of quantifying this trade-off situation in mammalian sensory modalities. We have been able to show that, at least among three of the most central sensory systems (olfaction, vision, and hearing) there are notable, taxon-specific patterns in sensory organ allocation among extant mammals. Again, we may reasonably infer that similar patterns were to be found in fossil taxa.

Of particular interest in this context are major ecological transitions, such as the shift from terrestrial to aquatic living, which has taken place in several mammalian lineages. In cetaceans, the sensory changes have been the most dramatic: here, a total or near-total reduction of olfaction has taken place, while there correspondingly has been an increase in the relative importance of hearing. Additionally, in toothed whales, a wholly new sensory modality, echolocation, has partly replaced olfaction. Recently it has been shown that electrosensation, too, is present in at least some odontocetes (Czech-Damal et al., 2012).

In the semi-aquatic platypus and in the sirenians, respectively, olfaction would also seem to have been reduced in importance, albeit not to the same extreme degree as it has in whales. Both the platypus and the sirenians possess compensating, 'special' senses: electroreception in the platypus, and the sense of touch in the sirenians. Notably, in the sirenians the touch-

sensitive hair cells are positioned along the animals' flanks, effectively forming a 'lateral line' (Reep et al., 2002, 2011).

In the pinnipeds, on the other hand, a relatively keen sense of olfaction seems to have been retained; however, their sense of taste has been at least partially reduced, as the pinnipeds' sweet taste receptor genes are nonfunctional (Jiang et al., 2012). As in sirenians, the pinnipeds' tactile sense, in the form of whiskers, is especially well-developed (Dehnhardt et al., 1998).

In bats, olfaction has been retained; indeed, judging by the number of functional olfactory receptor genes that they possess, some chiropteran species might even have a particularly keen sense of smell (Hayden et al., 2010). Most bats do, however, also have a 'special' sense system, echolocation, which is intimately connected with the bats' extremely acute sense of hearing. Perhaps surprisingly, however, the chiropteran visual system is not rudimentary, even though the relative eye size is reduced in the very smallest species.

Finally, it is shown that humans, while not particularly well-endowed when it comes to olfactory capabilities, nevertheless scale similarly to their great ape relatives regarding cribriform plate area, and that they are, similarly, quite alike the other great apes regarding their relative orbit diameters.

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