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The evolution of cognition through deep time

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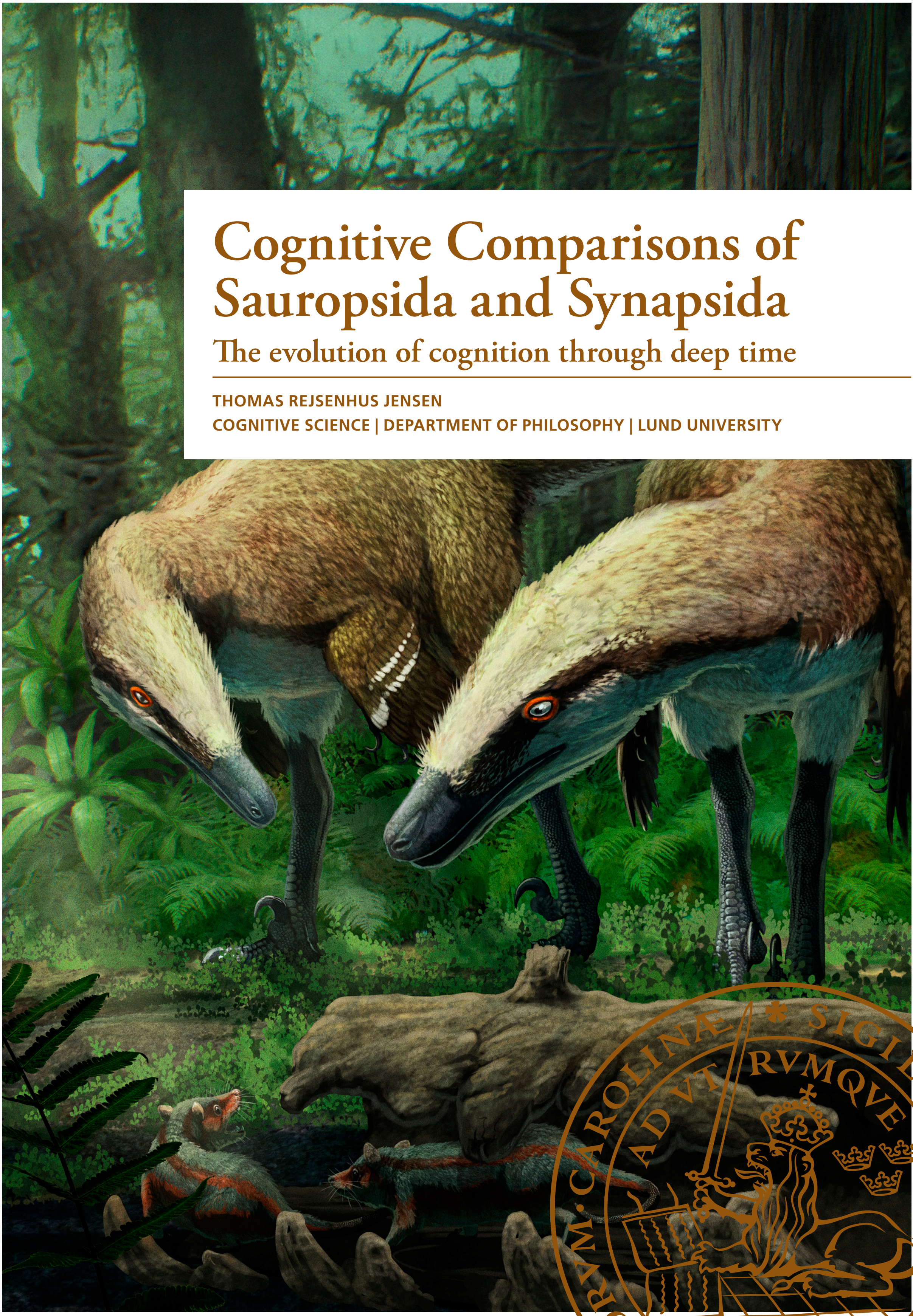

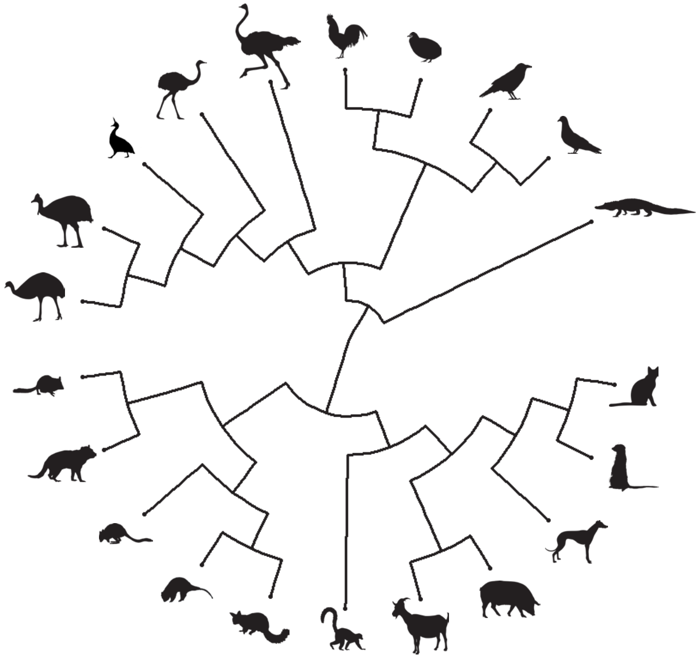

Mammals and birds have independently evolved complex neurocognition despite their phylogenetic separation for 325 million years. This thesis investigates and compares the evolution of core cognitive functions and social cognition in these two lineages through comparative studies of 21 mammal and archosaur species –to shed light on the evolution of cognition through deep time.

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The evolution of cognition through deep time

Thomas Rejsenhus Jensen

DOCTORAL DISSERTATION

Doctoral dissertation for the degree of Doctor of Philosophy (PhD) at the Joint
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Abstract:

Birds and mammals show remarkable convergence in their neurocognition and thermal physiology despite being phylogenetically separated for 325 million years of evolution. This elaboration in neurocognition is hypothesised to be directed at increasing the caloric intake through efficient foraging to power tachymetabolic endothermy. To gain a better understanding of how and why cognitive abilities evolved in today's endothermic birds and mammals, knowledge from several fields is required to provide unique perspectives in the construction of a more complete view of cognitive evolution in deep time. This thesis first introduces the emerging field of Palaeocognition, and how it may be studied, in a largely theoretical paper. Then, we compare species at important phylogenetic positions within Mammalia (Synapsida) and Archosauria (Sauropsida) with focus on core cognitive functions. Three empirical papers are dedicated to study the evolution and ontogeny of inhibitory control and visual working memory, which are thought to increase foraging success the better they are developed. We found that motor control was poor in American alligators compared to mammals and birds and especially common ravens. Furthermore, we found that visual working memory was more complex and developed in American alligators and birds compared to non-primate mammals, and we suggest that visual acuity may be a prerequisite for more complex visual working memory to evolve. We also found that within archosaurs, American alligators had less robust visual working memory representations than birds, which may be due to ectotherms' lower potential to dedicate expensive neurons to such functions. Lastly, we find that both mammals and birds can protect their visual working memory from distractions, but that interfering distractions of value to the subject distract more than non-valuable ones. Lastly, this thesis also dedicated two empirical papers to the study of social cognition, specifically the acoustic basis for individual recognition in American alligators and social cognition associated with allopreening in palaeognath birds. We find that alligators have bellows that are individually distinct, which can provide a basis for the evolution of individual recognition. In palaeognaths, we find no evidence of allopreening. We then discuss this absence in relation to the similarities in neurocognition and reproductive systems with non-avian paravian dinosaurs and make inferences on the grooming behaviours of these extinct animals.

Key words: evolution of cognition, synapsids, sauropsids, palaeocognition, inhibitory control, visual working memory, acoustic individuality, mutual grooming

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MADE IN SWEDEN

To my ever-patient wife, Marie, and our unborn daughter

Table of Contents

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List of Papers

Paper I
Jensen, T. R., Jacobs, I., Reber, S. A., Lalić, L., & Osvath, M. (in prep). *T. rex* cognition was *T. rex*-like: reflections on the emerging field of palaeocognition. Invited for *The Anatomical Record*.

Paper II
Jensen, T. R., Horváth, K., Kabadayi, C. and Osvath, M. (in prep). Cognition with vision: the evolution of motor self-regulation and visual working memory in mammals and archosaurs.

Paper III
Jensen, T. R., Kabadayi, C., Osvath, M. (in prep). The ontogeny of visual working memory in ravens.

Paper IV
Jensen, T. R., Boehly, T., Reber, S. A & Osvath, M. (in prep). Interference control of visual working memory in mammals and birds.

Paper V
Jensen, T. R., Anikin, A., Osvath, M. and Reber, S. A. (2023) Knowing a fellow by their bellow: Acoustic individuality in the bellows of the American alligator. *Animal Behaviour* 207, 157-167. https://doi.org/10.1016/j.anbehav.2023.11.009.

Paper VI
Jensen, T. R., Zeiträg, C. and Osvath, M. (2023) The selfish preen: Absence of allopreening in Palaeognathae and its socio-cognitive implications. *Animal Cognition* 26, 1467-1476. https://doi.org/10.1007/s10071-023-01794-x.

Other papers by the author not included in the thesis

Jensen, T.R., Osvath, M. (2021) Post-conflict Affiliation. In: Vonk, J., Shackelford, T. (eds) Encyclopedia of Animal Cognition and Behavior. Springer, Cham. https://doi.org/10.1007/978-3-319-47829-6_2116-1.

Zeiträg, C., Jensen, T. R., Osvath, M. (2022). Gaze following: A socio-cognitive skill rooted in deep time. *Frontiers in Psychology*. 13:950935. https://doi.org/10.3389/fpsyg.2022.950935.

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1 Introduction

At first glance, mammals and birds are quite different animals. Mammals have fur, (almost) all of them give birth to live young and produce milk to feed them. In contrast, (almost all) birds have feathered wings enabling flight, lay eggs, and have toothless beaks. However, even with 325 million years of separate evolution (Ford & Benson, 2020), they show striking cognitive similarities. Both lineages have independently evolved sophisticated cognitive abilities such as planning, deceit, flexible tool use, behavioural flexibility, and complex sociality (Güntürkün et al., 2024; Lambert et al., 2019). Why did such complex cognition evolve in both groups despite their independent evolutionary paths? The answers to these questions may be found in the evolution of endothermy, as suggested by the endothermic brain hypothesis, which underpins much of this research (Osvath et al., 2024).

1.1 The endothermic brain hypothesis

The endothermic brain hypothesis postulates that the brains of endotherms increased in complexity to increase energy intake through more efficient foraging (Osvath et al., 2024). Tachymetabolic endothermy, the capacity to produce and retain heat produced at a whole-body scale through a high aerobic metabolic rate (Grigg et al., 2022), evolved convergently in both Sauropsida (modern birds) and Synapsida (modern mammals). With the evolution of endothermy, these animals became much less constrained by the temperature fluctuations of the environment, as they produced their own body heat. This opened the possibility to invade and explore previously inaccessible niches (Rosslenbroich, 2014). Alongside this, both sauropsids and synapsids expanded their relative brain sizes by a factor of 10 and the number of neurons by a factor of 20 (Kverková et al., 2022; Osvath et al., 2024). However, such an elaborated nervous system and its associated endothermy results in a ten times higher food requirement compared to an active ectotherm (Nagy, 2005). So, why did such a costly thing evolve?

To begin to understand this, one must explore what cognition is for. For a living organism to uphold itself and propagate, it must maintain its structural integrity, avoid harm, and reproduce. It does so through allostatic processes, by which it acts proactively to meet its needs before its homeostasis is disrupted. Cognition is a key allostatic process for physiological regulation and is thus tightly connected with metabolism (Schulkin & Sterling, 2019). Cognition aids in upholding and maintaining metabolism by processing, valuing, and interacting with information in the environment for the purpose of survival, growth and reproduction (Lyon, 2020). As such, the nervous system is essentially the result of selection pressures for the preservation and expansion of allostatic processes, when a mobile organism becomes large and multicellular. The nervous system and the brain become a necessity when movements need to be coordinated between specialised cells in a multicellular organism (Sterling & Laughlin, 2023). The invention of the brain allowed for the effective acquisition and subsequent storage of information in memory, extending allostasis further into the future.

The nervous system is some of the most expensive tissue in the body (Niven & Laughlin, 2008). Accounting for body mass, mammals must consume eight times the energy as an ectotherm, while birds must consume eleven times as much (Nagy, 2001). This high cost is further signified by the tendency for environments with low or unstable energy to lead to smaller brained animals within it, be they ectotherms or endotherms (Heldstab et al., 2022; Song et al., 2023). However, important aspects of the life histories of ectotherms and endotherms differ fundamentally in relation to brain size. In amniotic ectotherms, species with larger brains have shorter lifespans, whereas in endotherms larger brained species live longer (Stark & Pincheira-Donoso, 2022). This suggests that the energy requirement of the nervous system of ectotherms stands in direct competition with other bodily processes, while the opposite is true for endotherms. Endotherms managed to increase their neuronal densities massively, implying a fundamental shift in how the brain relates to the energetic demands of these animals (Kverková et al., 2022; Osvath et al., 2024). In endotherms, the brain might then pay for its increasingly expensive quantity of neurons through a substantial increase in the efficiency of energy intake (Osvath et al., 2024). The increased acquisition of energy may even be crucial for offspring care, as endothermic brains would allow an animal to sustain their offspring in addition to themselves through the increased energy acquired (Beekman et al., 2019).

For such neuron-rich endothermic brains to outweigh their energetic costs, they must provide cognitive functions that substantially increase the amount of energy gained when foraging. Such cognition may either not exist or may be less developed in ectotherms (Osvath et al., 2024). It is thus likely that the cognitive functions that evolved alongside endothermy and high metabolism assisted in increasing the efficiency of foraging to maximise the intake of energy needed to fuel this circular system: metabolism and endothermy enabled a powerful brain, which improved foraging efficiency, which further fuelled metabolism and endothermy (Osvath et al., 2024). But what does this foraging-oriented cognition look like?

In its essence, the search for energy can be reduced to two mutually exclusive core decisions that an animal must continuously choose between: whether to stay in an area to exploit currently available resources (exploitation), or whether to leave an area in search for better availability elsewhere (exploration) (Cisek, 2022; Hills et al., 2015). Broadly speaking, exploration can either be model-free or model-based. Model-free exploration is the random search for food, driven primarily by previous stimulus-response experiences. Model-based exploration, on the other hand, relies on goal-oriented behaviours and the construction of a mental model of the environment in which an animal may simulate its actions. This allows for informed predictions based on the memory of previously learned information to effectively search for food and maximise the acquisition of energy.

Exploitation involves the extraction of energy from the immediate environment. The efficiency of exploitation likely also increased with the evolution of endothermy to maximise energy intake. Several cognitive capacities seem related to the exploitation of resources and are all likely to be under selection for increased efficiency in endotherms. Just as cognitive abilities associated with exploration may be more elaborate in endotherms than in ectotherms (Osvath et al., 2024), cognitive skills and behaviours such as extractive foraging, object cognition, problem solving, and inhibition may also show a similar trend. It is not hard to imagine how a better understanding of the physical properties of the world allows an animal to exploit it better. The ability to represent objects and know they continue to exist when they are not currently perceived, allows animals to return to an object later, or to search for it if it becomes occluded. Likewise, representing and recognising certain features and qualities of objects assists in making optimal choices when two resources are mutually exclusive (e.g., picking out the optimal individual to pounce during hunting). In the same vein, keeping a goal in mind while capitalising on spontaneous opportunities, or inhibiting the interference from distractions, likely also increases net energy gain.

The study of animal cognition has focused primarily on rats, primates, pigeons, corvids and parrots (van Horik & Emery, 2011). Many of these groups are relatively young and quite derived compared to the rest of the vertebrate tree of life and thus provide more limited insights into the evolution of cognition in deep time. To better cast light on this, we must also study earlier diverging groups of vertebrates which provide insights into how and when specific aspects of cognition evolved. Differences between taxa with plesiomorphic or diverging neuroanatomy, such as palaeognath birds, crocodylians and marsupials, compared to other birds and mammals, can provide valuable insights into the evolution of cognition through deep time. For example, one species might be particularly adept at inhibiting impulse behaviours, while a different species might be less so. Through the study of the neuroanatomy and physiology of such species, together with behavioural experiments, we can shed light on the impulse control and the associated neuroanatomy of their common ancestor, as well as in which diverging lineage this capacity had been selected for. By extension, the study of several such taxa with key phylogenetic positions, might allow us to answer questions about the emergence and tempo of the evolution of cognition, and how it relates to neuroanatomy and thermal physiology, in deep time. Just as importantly, by comparing the evolution of cognition between the bird and mammal lineages, we may be able to describe how similar these two evolutionary trajectories are, and in which aspects they might differ from each other.

Behavioural and cognitive tests need not stand alone in the study of cognition in deep time but can benefit greatly from other avenues of enquiry. Particularly, the comparison of neuroanatomy of extant species from key phylogenetic positions helps shed light on how brains have evolved in deep time, and such information can be compared to their performance in behavioural experiments. Likewise, osteological correlates from palaeontological studies of sensory systems and neuroanatomy of extinct species also provide insights. These correlates hint at what information earlier diverging groups of animals had available to them and how developed their brains were. These different but complementary avenues of research have only just begun to be combined, leading to the emerging field of palaeocognition.

In this thesis I provide an overview of the phylogeny of Synapsida and Sauropsida. I describe the field of palaeocognition, how it could be studied, and the many potential pitfalls that must be avoided. Then, I compare synapsids (mammals) and sauropsids (specifically crocodylians and birds) in a selection of cognitive tasks. Most of the cognition studied in this thesis is of the type that could be described as core cognitive functions. That is, these cognitive capacities are underlying a wide range of both social and non-social behaviours, and many other cognitive abilities may be viewed as expansions upon these (Cisek, 2019; Schurgin, 2018). As such, these cognitive abilities possibly evolved early and are widespread in amniotes. Additionally, much of the cognition explored in this thesis fits within the exploitation side of the exploitation/exploration dichotomy. These are cognitive abilities such as object permanence, memory, and inhibition. However, I also explore cognition within the social domain, namely individuality and individual recognition, as well as the evolution of mutual grooming and the underlying cognition of this behaviour in dinosaurs.

1.2 Structure of the thesis

This thesis focuses on the comparison of cognition between synapsids and sauropsids, more specifically therian mammals and archosaurs. It introduces the field of palaeocognition and how it should be studied (PAPER I) as well as several empirical papers. Focus is laid primarily on inhibition and visual working memory (PAPER II, III and IV), but also on cognition within the social domain, namely individual recognition (PAPER V) and mutual grooming (PAPER VI).

It is worthy of note that many of the paper manuscripts within this thesis are quite interconnected in nature and yet to be published. As such, some manuscripts may assume knowledge that is presented in other manuscripts, while in some others the opposite might be true because they are planned to be published first. The numerical order of manuscripts somewhat reflects this. However, attention has been paid first and foremost to a coherent structure rather than publication order.

Chapter 2 introduces the phylogeny of sauropsids and synapsids, with special focus on the lineages relevant to this thesis, and why they are of interest to the study of cognition in deep time. It describes similarities and differences in the evolution of brains and sensory systems as well as the evolution of endothermy in both lineages.

Chapter 3 provides an introduction into how Palaeontology, Neuroanatomy and Cognitive zoology can contribute to the study of cognition in deep time. It provides a description of the extant phylogenetic bracketing approach and how it should be appropriately used to infer cognition in extinct animals. Here, PAPER I is also introduced, which discusses the emerging field of Palaeocognition, how it should be studied, and posits areas of research that should be pursued.

Chapter 4 describes the social and non-social cognition that is studied within the empirical papers of this thesis and provides a brief background of each topic. PAPER II examines inhibitory control and visual working memory in a wide selection of marsupials, placentals, palaeognaths, neognaths and American alligators in relation to the development of their visual systems and its associated neurocognition. PAPER III investigates the ontogeny of visual working memory in juvenile ravens, providing parallels to how this capacity evolved in sauropsids. PAPER IV examines the visual working memory of mammals and birds when faced with distractions that are either valuable or irrelevant to the animals. PAPER V analyses the bellows of American alligators and finds acoustic individuality between bellows which provides the basis for individual recognition. Lastly, PAPER VI examines and discusses the lack of allopreening behaviours in palaeognath birds and how the lack of this behaviour relates to social behaviours and cognition in non-avian paravian dinosaurs.

2 An overview of synapsids and sauropsids

Roughly 340 million years ago (Ford & Benson, 2020), the first amniotes escaped the confines of water as they evolved thicker skin and the amniotic egg, protecting them and their eggs from water loss. Since then, amniotes have split into two major lineages: Sauropsida and Synapsida. Sauropsida contains all squamate reptiles, crocodylians, pterosaurs, non-avian dinosaurs and birds. Synapsida consist of all extant mammals and their extinct cynodontian, therapsid and pelycosaurian ancestors. Despite the independent evolution of these two lineages for hundreds of millions of years, many of their extant representatives show striking similarities in their cognition and thermal biology. Parts of both lineages underwent a series of similar but independent evolutionary shifts resulting in similar cognitive and physiological developments. Both lineages transitioned from a sprawling gait to a parasagittal stance with their legs positioned directly under their bodies. Additionally, they evolved the capacity to use their metabolism to produce their own body heat. To sustain this, they increased the encephalisation and neuron densities of their brains, as well as the complexity of their neurocognition (Osvath et al., 2024). However, notable differences between each lineage also exist. Throughout evolution, synapsids and sauropsids inhabited largely different ecological niches with little overlap, particularly during the Mesozoic (Gerkema et al., 2013). This led to significant differences in their sensory ecology as well as the tempo and mode of their cognitive evolution. This chapter provides a brief overview of these two lineages, focusing on their respective evolution of brain anatomy and sensory systems. I also briefly discuss the evolution of endothermy in both lineages, as this is tightly linked with the evolution of neurocognition (Osvath et al., 2024) (see Section 1.1).

2.1 Synapsids and Sauropsids on the phylogenetic tree

As this thesis focuses on the extant groups of synapsids and sauropsids and their extinct ancestors, the following sections describe only the lineages leading to today’s mammals and birds. Therefore, pterosaurs, ornithischians and sauropods are not detailed. Likewise, only extinct synapsids close to the evolutionary trajectory toward Mammalia are described (see Figure 1 for an overview of phylogeny of amniotes and Figure 2 for examples of extant species studied in this thesis).

Synapsida consists of three extant orders nested within Mammalia. The first diverging order, splitting from Theria somewhere between 160-250 million years ago, is Monotremata (Flannery et al., 2022). This group is well known for its five species of egg-laying mammals: the platypus and the echidnas. The remaining Therian mammals diverged into the two orders of Marsupialia and Placentalia around 160 million years ago (Williamson et al., 2014). Marsupialia are characterised by their short gestation periods, after which they give birth to very small, “underdeveloped” young that are subsequently protected within a pouch in which they nurse. Lastly, Placentalia is characterised by a highly developed placenta, allowing for long gestation periods and birth of more developed young. This group contains all extant mammals that are not monotremes or marsupials.

Sauropsida consists of reptiles, crocodylians and birds. Sauropsida can further be divided into Lepidosauria containing non-avian reptiles, and Archelosauria. Archelosauria contains Testudinata (turtles) and Archosauria containing the extant crocodylians and their ancestors, pterosaurs, as well as extant birds. Within Archosauria, birds and their non-avian dinosaur ancestors form the clade Dinosauria. Dinosauria is split into two distinct groups: Ornithischia and Saurischia. Ornithischia has no extant members and contains primarily herbivorous dinosaurs, such as *Parasaurolophus*, *Triceratops* and *Stegosaurus*. Saurischia consists of two different groups: Sauropodomorpha (the enormous, all extinct, long-necked dinosaurs) and Theropoda. Theropoda contains all bipedal carnivorous dinosaurs, such as *Tyrannosaurus rex*, as well as birds. Within Theropoda, we find the smaller Maniraptoran dinosaurs, which include well-known species such as *Oviraptor* and the paravian dinosaurs *Velociraptor* and *Troodon*. Within Maniraptora, we find Avialae, which includes dinosaurs that are quite bird-like, such as *Archaeopteryx*, and all living birds. Lastly, within Avialae, we find Aves, which contains all extant birds. Aves is further split into the neuroanatomically plesiomorphic birds of Palaeognathae, and all other birds within Neognathae.

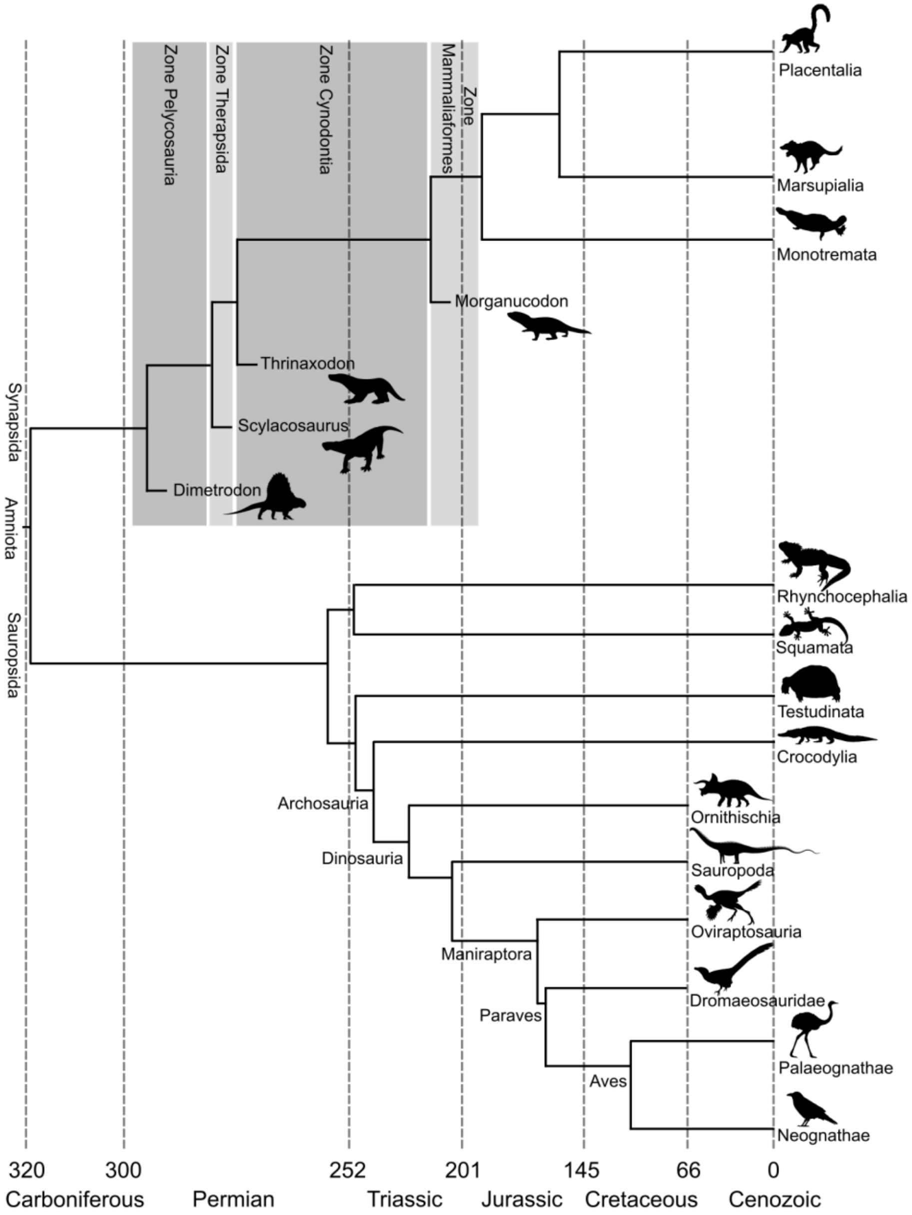

Figure 1: The amniote phylogenetic tree based on Benoit et al., (2023), Brusatte et al., (2015), Gemmell et al., (2020), Rowe (2023) and Zachos (2020). Silhouettes are sourced from Phylopic.org.

2.2 Species in this thesis

This thesis contains several large comparative studies and as a result many different species have been participating in making this work a reality. To compare mammals and birds, we incorporated species from key phylogenetic positions within both Synapsida and Sauropsida.

Beginning with Synapsida, we chose several marsupial and placental species to bracket the last common Therian ancestor of these two groups. Within Marsupialia we chose species from two major orders, namely Dasyuromorpha containing the majority of extant carnivorous marsupials, and Diprotodontia containing almost exclusively herbivorous species. From Dasyuromorpha we included the Tasmanian devil (*Sarcophilus harrisii*; Figure 2) and the kowari (*Dasyuroides byrnie*) as representatives. From Diprodontia we included the ground cuscus (*Phalanger gymnotis*; Figure 2), the brush-tailed bettong (*Bettongia penicillate*), and the common brushtailed possum (*Trichosurus vulpecula*). These species include different families as well as different feeding ecologies within Marsupialia. For Placentalia, we included three species from Carnivora; the meerkat (*Suricata suricatta*; Figure 2), the domestic cat (*Felis catus*) and the domestic dog (*Canis familiaris*). We also included two herbivorous species from Artiodactyla: the goat (*Capra hirus*) and the minipig (*Sus scrofa domesticus*). Lastly, we included a primate: the ring-tailed lemur (*Lemur catta*, Figure 2).

From Sauropsida, the focus has been primarily on the two extant archosaur groups bracketing all extinct dinosaurs: Crocodylia and Aves. Within Crocodylia, we have studied American alligators (*Alligator mississippiensis*; Figure 2). Within Aves, Palaeognathae represents the neuroanatomically most plesiomorphic group of birds and are thus important for comparative work. Within this thesis I have included five species from different families: the common ostrich (*Struthio camelus*), the emu (*Dromaius novaehollandiae*; Figure 2), the southern cassowary (*Casuarius casuraius*), the greater rhea (*Rhea americana*), and the elegant crested tinamou (*Eudromia elegans*). This provided a broad sample of ecologies, social structures and flight capabilities within the taxon. We also worked with three early diverging neognath species: red junglefowl/chicken (*Gallus gallus* [*domesticus*]; Figure 2) and king quail (*Synoicus chinensis*) from the order Galliformes, in addition to ring doves (*Streptopelia risorii*) from Colombiformes. Lastly, the passerine species with the most neurons, the common raven (*Corvus corax*; Figure 2), was included. The two galliform species, together with the ring dove and common raven, were chosen to enable comparisons between palaeognaths and crocodylians to neognaths that are both are both early and newly derived.

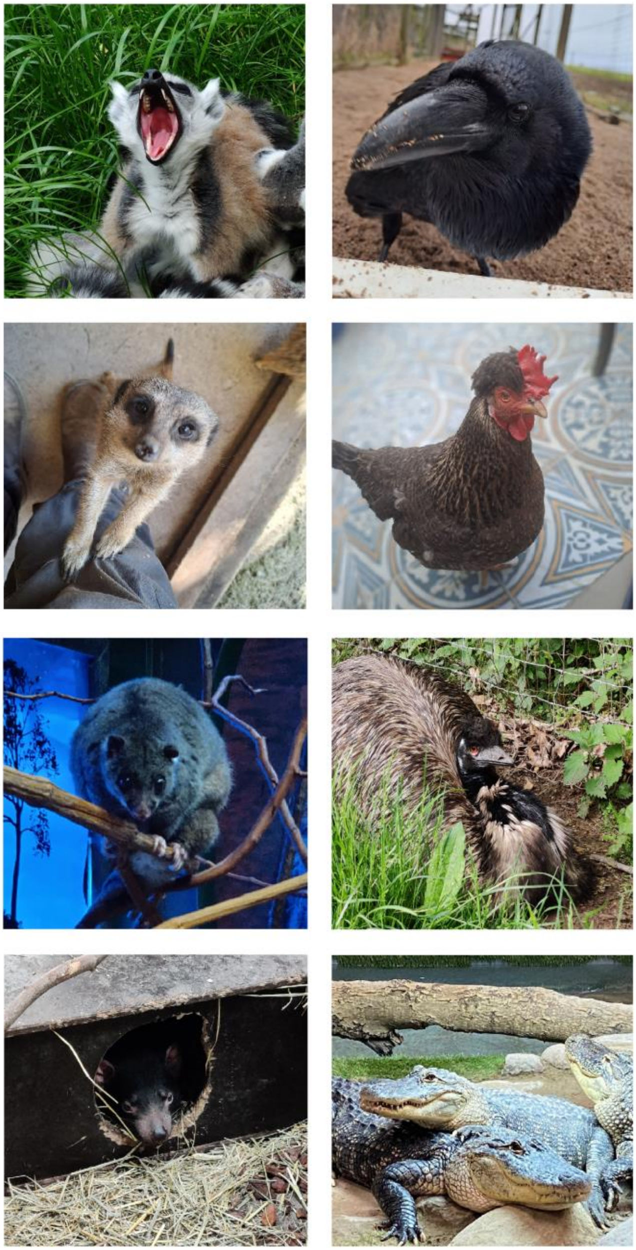

Figure 2: Representatives of species from key phylogenetic groups studied in this thesis. Synapsida (left, from top to bottom): Ring-tailed lemur, meerkat, ground cuscus, Tasmanian devil. Sauropsida (right, from top to bottom): Common raven, domestic chicken, emu, American alligator. Photo credit: Helena Osvath and Thibault Boehly.

2.3 The brains and sensory systems of synapsids and sauropsids

The brain of the first amniote was undoubtedly less elaborated than what we see in today's birds and mammals. It is difficult to know exactly what the brains of early amniotes looked like, but we do have species alive today, as well as fossil endocasts, that provide hints. Fossil endocasts of *Seymouria*, a very reptile-like amphibian and close relative to the first amniote ancestor, show no noteworthy encephalisation of any areas of the brain. This suggests a relatively amphibian-like brain morphology of the first amniotes, with no particular enlargement of any specific brain areas (Bazzana-Adams et al., 2023). In addition to fossils endocasts, we can study one of the oldest extant amniote lineages, Rhynchocephalia, represented by only one species: the tuatara (*Sphenodon punctatus*). This lineage diverged from other reptiles roughly 250 million years ago and have retained many characteristics shared with early anamniotes (Gemmell et al., 2020). The tuatara brain already features the foundational components characteristic of both extant Synapsids and Sauropsids (Figure 3a). The telencephalon, responsible for action selection and motor control, among many other things (Naumann et al., 2015), is notably wider than in amphibians (Striedter & Northcutt, 2020). Likewise, the cerebellum, involved in a wide variety of processes, such as eye movement, body posture and precise body movements (Macrì et al., 2019), is also slightly larger than in amphibians (Striedter & Northcutt, 2020). The tuatara brain also features laminated structures of the dorsal part of the telencephalon which is not present in amphibians (Dicke & Roth, 2007; Striedter & Northcutt, 2020). The tuatara is thus likely the best extant representative of what the common ancestor of synapsids and sauropsids may have looked like.

2.3.1 Sauropsids: Vision during the day

Within Sauropsida, there has been a slow trend towards brain enlargement from early amniotes toward more derived theropod dinosaurs and extant birds. From basal amniotes toward Lepidosauria (lizards and snakes), we find few changes in overall brain morphology. However, relative brain size has increased in some lineages such as varanids (Northcutt, 2013) as a result of an expanded telencephalon (consisting of the cerebrum and the olfactory bulbs). Neuronal numbers have been estimated for a selection of reptiles, including lizards, snakes, monitors and turtles. These numbers vary between 1.7 million neurons in the whole brain of an Algerian sand gecko (*Tropiocolotes steudneri*) to 78 million in the Asian water monitor (*Varanus salvator*) (Kverková et al., 2022). Likewise, the neuronal numbers of the telencephalon and the cerebellum vary. The Algerian sand gecko has 740.000 in the telencephalon and 151.000 in the cerebellum, whereas the Asian water monitor has

41 million and 17 million. In general, the varanid reptiles appear to have the highest number of neurons of the squamate groups (Kverková et al., 2022). The sensory systems of squamates are similar to that of the tuatara. Hearing is generally considered to be weak with frequency ranges between 0.1-5 kHz and a peak sensitivity around 1.6-2 kHz (Brittan-Powell et al., 2010). However, the olfaction and visual systems are well developed (Crowe-Ridell & Lillywhite, 2023).

Crocodylians provide insights into the brain anatomy of early archosaurs (Fabbri & Bhullar, 2022; Green et al., 2014) (Figure 3c). Early archosaurs likely had a telencephalon of comparative size to the previously mentioned large-brained lizards. However, the cerebellum has significantly increased in size compared to other reptiles (Northcutt, 2013). An adult Nile crocodile (*Crocodylus niloticus*) brain contains 81 million neurons, with 30 million and 40 million situated in the telencephalon and the cerebellum, respectively (Kverková et al., 2022). While the absolute neuron numbers are higher than in the gecko and varanid described above, the brain of an adult crocodylian is also larger. Additionally, as only a low number of neurons are added to the brain through neurogenesis as a Nile crocodile grows, the density of neurons in a crocodylian brain lowers as the animal grows into adulthood (Ngwenya et al., 2016). It is, however, still worth noting that crocodylians appear to have almost double the number of cerebellar neurons as an Asian water monitor, and it has been suggested that the absolute number of neurons in a given brain area is important for cognitive performance regardless of brain size (Herculano-Houzel, 2017). The sensory systems of crocodylians are generally similar to other reptiles. An exception is an increased frequency range of hearing when compared to other reptiles, with hearing ranges somewhere between 0.1-8 kHz and peak sensitivity at 1-2 kHz (Higgs et al., 2002). This peak sensitivity overlaps well with the frequency range of juvenile calls (Reber, 2018), which, alongside the increase in cochlear length at the base of Archosauria, has been suggested to be related to the evolution of parental care (Hanson et al., 2021). Vision is also generally good, although with adaptations for nocturnality limiting visual acuity in return for higher light sensitivity (Emerling, 2017; Karl et al., 2018; Nagloo et al., 2016).

Moving away from extant reptile representatives, we then enter a period of ~200 million of years between the last common ancestor of crocodylians and palaeognath birds for which we have no extant species with brains to study. Here, we can only rely on fossils to provide clues as to how brains have evolved. Unfortunately, the brain does not fill the brain case of crocodylians but fills does so almost completely in birds. Vascular impressions on the brain cavity walls of fossil maniraptoran dinosaurs imply that these dinosaurs had larger brains that filled out the brain cavity to a larger extent – perhaps even to a similar extent as modern birds (see below). This difference between crocodylians and birds makes it difficult to infer brain size and anatomy of dinosaurs, as the BEC index (Brain-to-endocranial cavity index - the extent to which the brain fills out the brain case; see Section 3.1.1) could be anywhere from 30% to nearly 100%. Despite these difficulties, several attempts have been made to infer such neuroanatomical features. It appears that the early theropod dinosaurs largely retained linear brains with moderately sized telencephala and cerebella, but that expansions of these brain areas took place in derived coelurosaurians (oviraptorosaurs, dromaeorosaurids, availians). Some indication of this can be seen in the deflection of the optic lobe observed in some theropod endocasts, which is thought to result from the enlargement of the cerebellum and telencephalon (Balanoff et al., 2014; Balanoff et al., 2013; Bever et al., 2011; Torres et al., 2021; Witmer & Ridgely, 2009) (Figure 3c-e). It is thus not unlikely that the BEC index of theropod dinosaurs has steadily increased as evolution progressed towards birds and that this trend had already slowly begun as groups of dinosaurs, such as tyrannosaurids, emerged (Balanoff & Bever, 2017).

Along the lineage towards birds, there appears to have been a trend towards a reduction of the size of the olfactory bulbs (Zelenitsky et al., 2011). Early theropod dinosaurs such as tyrannosaurs, but also many dromaeosaurs had well developed olfaction (Franzosa, 2004; Paulina-Carabajal et al., 2023; Witmer & Ridgely, 2009; Zelenitsky et al., 2008). Although *Tyrannosaurus rex* may have been one of the theropod species with the keenest sense of smell, they have been estimated to have had similar numbers of olfactory receptor genes as domestic cats, and thus may still have had less developed olfaction than today’s dogs and many rodents (Hughes & Finarelli, 2019; Montague et al., 2014; Niimura & Nei, 2007). Regardless, such a trend could be an indicator of a general shift in the primary sensory modality away from olfaction toward vision (Wharton, 2002). Indeed, this is supported by seemingly an increase in the size of the optic lobe throughout theropod evolution toward extant birds (Franzosa, 2004), but also by the discovery of a Wulst in Ichtyornis (Torres et al., 2021). As most extant reptiles today are quite visually oriented animals, it is thus likely that vision has been a modality that Sauropsids have always relied upon. However, within birds, additional areas within the telencephalon processing visual input have substantially enlarged, corroborating the trajectory toward the increasingly more efficient use of visual stimuli along the theropod lineage (Shimizu et al., 2024). The hearing capabilities of dinosaurs also improved compared to reptiles. This is known from studies on relative lengths of cochlear ducts, which correlate well with hearing range and show little overlap between reptiles and birds (Walsh et al., 2009). Indeed, theropod dinosaurs were generally intermediate between reptiles and birds in their hearing ranges, although exceptions existed, such as *Shuvuuia deseerti* which had unusually long cochlear ducts (Choiniere et al., 2021). Theropod hearing ranges have been estimated to be between 2.4-3.2 kHz, with high frequency limits at 5.5-6.9 kHz in smaller theropods such as *Archaopteryx*. Larger theropods of 1000 kg and above are estimated at lower ranges between 0.7-1.5 kHz with high frequency limits at 1.8-3 kHz (Gleich et al., 2005). The further development of hearing ranges in dinosaurs and birds is overall restricted compared to mammals. This may be because sauropsids only have one middle ear bone as opposed to the three found in mammals, which significantly hampers the evolvability of wider hearing ranges (Maître et al., 2020).

By the time maniraptoran dinosaurs emerged, the BEC index appears to have approached values similar to modern birds, as an endocranial cast of an ornithomimosaurian (Maniraptoriformes) dinosaur was described with impressions of vascular canals from the brain (Russell, 1972). Such impressions suggest that the brain was in close contact with the inner surface of the endocranium (Balanoff & Bever, 2017). This has similarly been found in an oviraptorosaur showing clear impressions of brain blood vessels around the cerebellum and the hemisphere of the cerebrum (Osmólska, 2004). Knowing that the brains filled out close to the entire brain case of these animals, we can more easily infer the gross morphology of their brains, as the brain would have a similar shape as the endocranial cavity. These endocasts show an increase in the encephalisation of certain brain areas, especially of the cerebrum and the cerebellum, leading to an increasingly sigmoidal brain shape. as compared to a more linear brain as is typically seen in reptiles (Balanoff et al., 2013). Indeed, endocasts of such dinosaurs look much more like an extant palaeognath brain than that of a reptile, with large expansions of the cerebellum and telencephalon (Balanoff et al., 2013; Widrig et al., 2024). Within Maniraptora, we find the paravians, exemplified by *Velociraptor* and *Archaeopteryx*. These were generally smaller, highly mobile dinosaurs covered in feathers akin to those of modern birds. They relied heavily on vision as their primary sense which many species used to catch similarly mobile prey (Franzosa, 2004). Additionally, their sense of smell was also still well-developed, potentially allowing for the tracking of prey (Zelenitsky et al., 2008). The hearing capabilities of most paravians were, however, still restricted to lower frequency sounds, much akin to other theropod dinosaurs (Gleich et al., 2005).

Many extant groups of birds evolved before the Cretaceous-Paleogene extinction event that wiped out the non-avian dinosaurs 66 million years ago. The species that would lead to modern palaeognath birds, fowl and waterfowl all lived alongside the non-avian dinosaurs (Brusatte et al., 2015). However, once the non-avian dinosaurs were gone, birds diversified rapidly and many of these newly derived groups evolved larger brains relative to their body sizes, driven largely by the reduction in body size (Ksepka et al., 2020). Now that we are on the other side of the gap of extinct dinosaurs between reptiles to birds, it becomes possible to once again look at brains in more detail. The brains of birds are packed with neurons at much higher densities than what is seen in mammals, compensating for their more modest sizes (Kverková et al., 2022). In fact, passerines and parrots have equal or higher numbers of neurons in their telencephalon compared to primates (Olkowicz et al., 2016). Neuronal numbers are especially inflated in the cerebellum and in the telencephalon, and within Telluraves a further shift in the scaling relationship between brain size and neuronal densities led to even higher numbers in this clade, compared to earlier diverging bird lineages (Kverková et al., 2022). To contrast with reptiles, the brain of the greater rhea (*Rhea americana*), a palaeognath bird, contains ~1 billion neurons, of which 367 million and 610 million reside in the telencephalon and cerebellum, respectively (Kverková et al., 2022). More impressive is the brain of the common raven (*Corvus corax*), sporting more than 2 billion, 1.3 billion, and 753 million neurons in the whole brain, telencephalon, and cerebellum, respectively (Olkowicz et al., 2016). In addition, several neural projections connect the cerebellum and telencephalon (Gutierrez-Ibanez et al., 2018). Similar projections also connect the visual input with further visual processing areas within the telencephalon (Pusch et al., 2023), indicating a high reliance on acute vision with high temporal resolution (Bostrom et al., 2016). The olfactory bulbs are increasingly reduced in Neoaves, implying a much-reduced reliance on olfaction in more derived groups of birds (Zelenitsky et al., 2011). As such, hearing has become a more important sensory modality than olfaction in most birds. This is despite that even in modern birds, the frequency range of hearing is marginally narrower than what mammals are capable of. No birds perceive sounds at frequencies much above 12 kHz and most species are most sensitive to sounds between 1-4 kHz (Gleich & Langemann, 2011). Large palaeognath birds appear to have a slightly lower frequency range (kiwi are an exception) with a higher sensitivity towards lower frequency sounds. This may be an ancestral state (Corfield et al., 2013), as this is what would be expected in non-avian dinosaurs (Choiniere et al., 2021; Gleich et al., 2005), or it could be a result of their large body sizes.

2.3.2 Synapsids: Audition, tactition and olfaction at night

The first known basal synapsid group that emerged is often called Pelycosauria. Pelycosauria is a paraphyletic grade containing all basal synapsids that are not Therapsids. This grade was dominant during the late Carboniferous into the early Permian around 315-260 million years ago (Angielczyk & Kammerer, 2018). A well-known example of a pelycosaur is *Dimetrodon*, a synapsid of up to 3.5 metres in length with an impressive sail on its back (Bramwell & Fellgett, 1973). Like extant reptiles, pelycosaurs had a sprawling gait with their limbs pointing outwards and likely did not lift themselves much from the substrate when walking (Lungmus & Angielczyk, 2019). Not much is known about the brains of these early synapsids, as the endocranial cavity of these animals was open anteriorly in addition to the forebrain being enclosed by an orbitosphenoid bone that rarely fossilises. This often results in poor endocasts as only a small area near the hypothalamus is enclosed by bone (Rowe, 2023). However, the brain organisation and size likely did not differ significantly from their early amniote ancestors. The brain was likely small, tubular in organisation with no clear encephalisation of any brain regions (Bazzana et al., 2022). Pelycosaurs likely inherited their visual capabilities, adapted for a diurnal lifestyle, from their ancestors. These included tetrachromatic colour vision and a spatial resolution high enough for predation purposes (Benoit et al., 2023). However, studies on sclerotic rings (bony structures that help support the structure of the eye) of pelycosaurs indicate that the diel patterns of this group might have been diverse, with groups being everything from diurnal to nocturnal or crepuscular (Angielczyk & Schmitz, 2014). Not much is known about how well developed the olfaction of these basal synapsids was. However, studies indicate that not much development took place during their early evolution and that olfaction only increased in resolution and sensitivity later (Benoit et al., 2023; Rodrigues et al., 2019; Rowe et al., 2011). The same can be said about the hearing capabilities of early synapsids. They lacked auditory pinnae (external ears) and did likely not have a tympanic membrane (eardrum) (Benoit et al., 2023). The hearing range has been estimated to lie between 2.4-4.8 kHz with a best hearing frequency range at 1.5-2.8 kHz (Bazzana et al., 2022).

In the early Permian, Therapsida emerged. Basal therapsids were quite successful during the period of early Permian until the late Triassic roughly 260-200 million years ago (Benoit et al., 2023). A notable difference between therapsids and their pelycosaurian ancestors was the development of a parasagittal gait (a non-sprawling placement of the limbs directly underneath the animal), which allowed for faster locomotion and manoeuvrability (Preuschoft et al., 2022; Rowe, 2023). Endocasts of early therapsids leave no indication of expanded brain areas and thus appear quite similar to pelycosaur endocasts. Even the olfactory bulbs appear small, and the brain likely did not fill out the endocranial cavity (Benoit et al., 2023; Benoit et al., 2017). However, one can speculate that perhaps the cerebellar regions, which handle split-second motor planning, might have been affected by the change in gait in some way, leading to an enlargement of this particular area to compensate. Like pelycosaurs, therapsids might also have encompassed diurnal, nocturnal and crepuscular ecologies, as is suggested by studies on their sclerotic rings (Angielczyk & Schmitz, 2014). Tetrachromatic colour vision would likely still be present at least in diurnal lineages. In the same vein, therapsids also likely lacked auditory pinnae and a tympanic membrane, indicating generally poor hearing capabilities not much different from pelycosaurs (Rowe, 2023). We now direct our attention to a special group of therapsids: the cynodonts, from which modern mammals descend.

Cynodontia appeared in the late Permian roughly 260 million years ago (Jones et al., 2019). Within this group, there are several signs of a nocturnal bottleneck taking place. The sclerotic rings have been lost, likely due to relaxed selection on the visual system, suggesting that acute vision had less importance for these animals. Likewise, the fossil record indicate facial vibrissae used to gather tactile information via whisking (Benoit et al., 2016), as well as changes in the middle ear (although still attached to the jaw) leading to a slightly improved hearing range to about 1.5 – 5 kHz (Benoit et al., 2023). Endocasts of cynodont braincases indicate an enlargement of the olfactory bulb compared to earlier therapsid ancestors, suggesting an increased reliance on olfaction (Rodrigues et al., 2019). Olfactory bulb size appears to increase further along the cynodont grade, with derived groups such as Trithelodontidae having even larger olfactory bulbs (Kerber et al., 2021). We also see an expansion of the cerebral hemispheres outward and backward, with the median sulcus (indicating bulging and separation of hemispheres) being clearly visible in endocasts of more derived cynodonts (Kerber et al., 2021). Likewise, there's an expansion of the cerebellum, hinting at further improved motor control (Benoit et al., 2023; Rodrigues et al., 2019; Rowe, 2023).

Basal Mammaliaformes are the close relative of mammals that are not quite true mammals. These animals were present around 210 million years ago (Rowe, 2023) during the late Triassic, when dinosaurs had begun their rule. These animals largely continue the trend of the cynodonts. They exhibit further enlargements of the cerebral hemispheres as well as the cerebellum, making the brain largely similar in their appearance to extant mammalian brains (Rowe, 1996; Rowe et al., 2011). Mammaliaformes also improved their hearing for high frequency sounds via the tympanic membrane and the release of the jaw structures that would later become the malleus, stapes and incus bones in the ear (Kemp, 2016). Similarly, olfaction and tactile sensitivity also increased and tetrachromatic vision was lost, as likely most species of early Mammaliaformes were restricted to a nocturnal lifestyle (Benoit et al., 2023). All mammaliaforms were also very small, approximately the size of a shrew, and it is likely that even the cynodont ancestors of mammaliaforms were likewise quite small in size. As such, they filled the niche of being nocturnal, small and likely insectivorous or omnivorous, a niche in which they could remain somewhat safe from their dinosaur and archosaur predators (Benoit et al., 2023; Maor et al., 2017; Rowe, 2023).

Mammalia, the crown group containing all mammals alive today and defined as all species descended from the most recent common ancestor of modern-day mammals, emerged already by the early Jurassic 170 million years ago. Extant mammals generally have a larger telencephalon (which contains the isocortex, among other brain areas, in mammals) than their Mammaliaform, and even mammalian, ancestors (Kaas, 2013). The first phylogenetic split within Mammalia consists of today's monotremes, and this group split further into echidnas and platypuses in the early Cretaceous (Rowe et al., 2008). Echidnas have a folded neocortex with grooves and ridges (Figure 3f), as is common for many mammals, while the platypus does not. The presence of such folds increases the surface area of the neocortex, allowing for faster transmission rates between neurons due to the lowered travel distance of action potentials. Such folds appear to develop in mammals with larger brain volumes (Striedter et al., 2015). Vision in monotremes is generally poor and all species are primarily nocturnal. Instead, they specialise in either olfaction or electroreception (Ashwell, 2013). Uniquely for mammals, platypuses rely on electroreception, which they use to locate prey when hunting in water (Proske & Gregory, 2003). Echidnas in turn rely heavily on olfaction to locate prey, as can be seen by their large olfactory bulbs and laminated olfactory cortex (Ashwell, 2020). When it comes to hearing, monotremes have a wider frequency range than birds (~2-18 kHz, with highest sensitivity at 4-8 kHz), but fall short compared to other mammals (Mills & Shepherd, 2001). This may be explained by all three inner ear bones being less developed in monotremes compared to other mammals in addition to these potentially having evolved independently in this group

(Rich et al., 2005). Additionally, monotremes do not have pinnae as compared to other mammals, suggesting that this feature evolved in therians.

The second group from the first mammalian split is called Theria, which further split into Marsupialia and Placentalia in the late Jurassic ~165 million years ago (dos Reis et al., 2012). The first marsupial brain might have looked a lot like opossum (e.g., *Didelphis marsupialis*, *Monodelphis domestica*) brains, as these differ little despite being distantly related (Duchêne et al., 2018; Kaas, 2013), and may even reflect the brains of early mammals, as gross morphologies appear quite similar to cynodont endocranial cavities (Kemp, 2009). The overall brain morphology of marsupials does not differ much from placentals, although marsupial brains tend to be lissencephalic (non-folded and smooth) more often than placental brains (Todorov, 2020). Additionally, marsupial (and monotreme) brains lack the corpus callosum connecting the two brain hemispheres for more efficient communication (Suárez et al., 2018). When excluding primates, the relative brain sizes of marsupials, however, do not differ much from placentals (Weisbecker & Goswami, 2010). While currently no information on the neuronal densities within monotreme brains exist, some marsupial species have been examined. For example, the brain of the Tasmanian devil (*Sarcophilus harrisii*) contains ~793 million neurons, of which 122 million can be found in the cerebral cortex and 600 million in the cerebellum (Dos Santos et al., 2017). Of the marsupials currently studied the grey kangaroo has the most neurons, with 2.4 billion neurons in the whole brain, 370 million in the cerebral cortex and 1.9 billion in the cerebellum. The scaling relationship between brain mass and neuronal density in marsupials is overall similar to non-primate placental mammals (Kverková et al., 2022).

Many marsupials are nocturnal with poor visual acuity (Arrese et al., 2000; Arrese et al., 1999; Hemmi & Mark, 1998). Marsupials are generally believed to be dichromats, although studies have found evidence of trichromacy in some species, and this may be more widespread than what is currently known (Arrese et al., 2006; Ebeling et al., 2010). Their poor vision is compensated by olfaction and hearing (Croft, 1988). The frequency range of hearing in marsupials is excellent and can be as broad as between 1-40 kHz with highest sensitivity levels between 8-16 kHz, depending on the species (Old et al., 2020). All therians have evolved pinnae, which allows more directed hearing through their orientation toward the location of sound sources (Maître et al., 2020). Both hearing and olfaction would have been reliable senses for ancestral mammals during the nocturnal bottleneck imposed by the larger dinosaurian predators of the Jurassic and Cretaceous (Gerkema et al., 2013).

Placentals represent the vast majority of extant mammals. This group started diversifying rapidly after the Cretaceous-Paleogene extinction event. Freed from the predation pressure of dinosaurs, both brain size and body size increased rapidly throughout the Paleocene, although the former increased at a lower rate than the latter (Bertrand et al., 2022). This led to a period of lower relative brain sizes in placental mammals, which was caught up on again by the time of the Eocene. The placental brains experienced an expansion of the neocortex and petrosal lobules, the former suggesting an increased reliance on vision, potentially from a shift to more diurnal lifestyles, a transition further corroborated by the decrease in the relative size of olfactory bulbs (Bertrand et al., 2022). Especially artiodactyls, perissodactyls, carnivorans, euprimates and rodents increased their relative brain size at this time, with omnivorous and carnivorous species experiencing a higher rate than herbivores. The increase in brain size was accompanied by an increase in neuronal numbers of especially the cerebellum and the telencephalon (Kverková et al., 2022). The increased rate of speciation of placental mammals also led to some groups evolving highly specialised brains for their niches. Examples of this are specialisations of the brains of bats as they evolved echolocation and flight (Covey, 2005). Whales, elephants and apes experienced an above-average increase in relative brain size, although this does not necessarily imply an accompanying shift in cognition (Smaers et al., 2021). In fact, in all non-primate placentals there does not appear to be a notable relationship between neuronal density and relative brain size – this association only exists in reptiles, birds and primates (Kverková et al., 2022). The difference between primates and other mammals lies in a shift in the scaling relationship between the neuron numbers and brain mass, leading to much higher neuronal numbers per brain volume in primates, the epitome being humans (Kverková et al., 2022; Kaas, 2013). The number of neurons found in a placental mammal's brain depends on the species in question. A short-tailed shrew (*Blarina brevicauda)* has ~55 million neurons in the whole brain, 13 million in the cerebral cortex, and 33 million in the cerebellum, whereas an African elephant has 257 billion neurons in the whole brain, 5 billion in the cerebral cortex, and 250 billion in the cerebellum (perhaps to control the highly flexible trunk) (Herculano-Houzel et al., 2015). Generally, however, the two placental groups with the highest neuronal numbers are carnivorans and primates (Kverková et al., 2022). Domestic dogs and cats have 2.2 billion (249 million in the cortex, 326 million in the cerebellum) and 1.2 billion (528 million in the cortex, 848 million in the cerebellum) neurons in their brains (Jardim-Messeder et al., 2017), whereas humans have 86 billion (16 billion in the cerebral cortex and 69 billion in the cerebellum) (Herculano-Houzel, 2009). Incidentally, carnivorans and primates also have the most developed vision.

The reliance on vision varies in placental mammals. Primates in particular have highly developed visual processing areas in the neocortex, specialised for reaching, grabbing, sophisticated eye movements and colour perception (Kaas, 2013). No non-primate placentals have trichromatic colour vision. All old world monkeys and apes (and some other primate species) have trichromatic colour vision, enabling them to see red (Jacobs, 2009), a likely result of their highly diurnal lifestyle and reliance of fruit in their diet (Onstein et al., 2020). Despite the switch to diurnality of many placental mammals, the sensory modalities of many species still show signs of their nocturnal ancestry. Olfaction is still well developed in most placentals, although primates have significantly reduced the size of their olfaction bulbs to the point that they are hardly visible on the gross morphology of the brains of some species (Gonzales et al., 2015). In terms of hearing capacity, placental mammals show marginal variation in hearing capacity. Large species hear and produce mostly low frequency sounds, but also small mammals are able to hear relatively low frequency sounds. For example, the African elephant can hear infrasound down to 1Hz (Garstang, 2010), while rodents may still hear sounds below 100 Hz despite their small sizes (Heffner et al., 2001). Specialised species such as echolocating bats and whales have upper frequency limits well above 100 kHz (Morell et al., 2020). Less specialised mammals such as sheep, cats and humans have upper frequency ranges at 22-60 kHz (Fay & Popper, 1994). Mammals in general are thus the undisputed kings of vertebrate hearing, largely thanks to the evolution of the three inner ear bones.

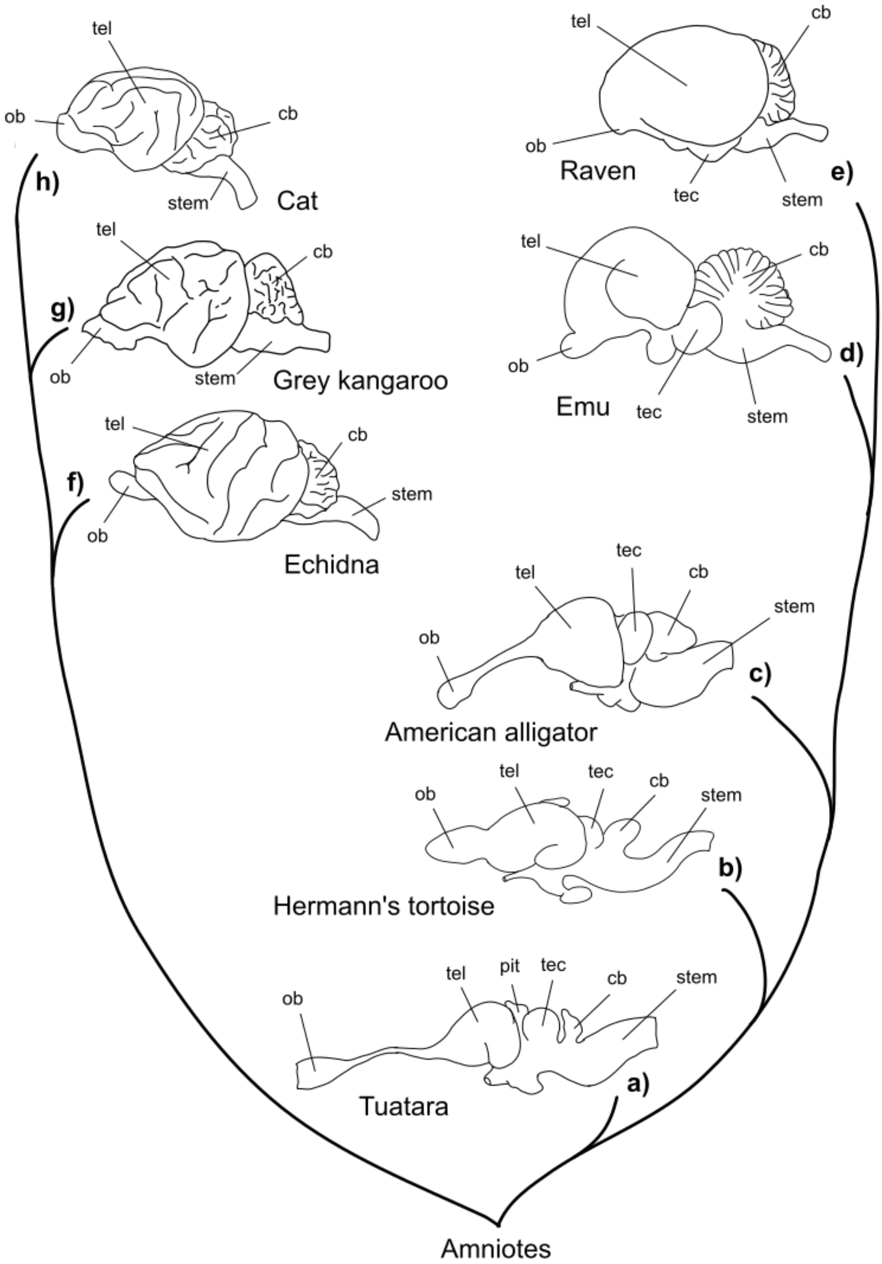

Figure 3: The diversity of extant amniote brains within a phylogenetic context. a), c), f), g) are redrawn from Striedter and Northcutt (2020), b) and h) from Nieuwenhuys et al. (1998), d) and e) are based on Olkowicz et al. (2016). Abbreviations: ob = olfactory bulb; tel = telencephalon; pit = pituary gland; tec = optic lobe (tectum); cb = cerebellum; stem = brainstem.

2.4 The evolution of endothermy in synapsids and sauropsids

Sauropsids and synapsids evolved tachymetabolic endothermy independently of each other sometime during the Mesozoic (Benton, 2021). The exact period in which it emerged is hard to pinpoint, both due to the fossil record leaving incomplete and often only correlational cues as to the presence of endothermy, but also because such a capacity likely evolved gradually over millions of years. Endothermy, and the physiology required to sustain it, likely played a pivotal role in the evolution of cognition (Osvath et al., 2024) (see Section 1.1), and so here I provide a brief overview of what is known about its evolution in deep time. I begin with describing the extant ectothermic sauropsids and the dinosaurian transition to endothermy. Then, I discuss what is known about the evolution of endothermy in mammals and their synapsid ancestors.

2.4.1 Sauropsids: Heating for tiny bodies?

Uniquely, as compared to synapsids, the sauropsid clade still contains extant ectotherms – the reptiles. All extant non-avian reptiles are ectotherms and primarily increase their body temperature via external heat sources, such as the sun. However, large crocodylians and leatherback sea turtles have achieved relatively stable, higher-than-ambient body temperatures in adulthood through various combinations of blood shunting, muscle heat generation, and large sizes (Legendre & Davesne, 2020). In addition, some smaller reptiles have evolved physiological ways of generating heat. The most famous example of this is the Indian python (*Python molorus bivittatus*) which can generate body heat via muscle contractions, akin to shivering thermogenesis in mammals and birds. They do this only when they incubate their eggs, ensuring optimal developmental temperatures for the embryos (Hutchison et al., 1966). Additionally, thermogenesis has also been found in a tegu lizard during reproductive seasons, although it is not yet known what exact physiological mechanism generates this heat (Tattersall et al., 2016). However, such facultative heat generation, combined with the selection for more leaky cell membranes, have been proposed to be important precursors for more permanent heat generation to evolve (Grigg et al., 2004).

While ectothermic reptiles stayed within their niches and kept their sprawling gait and their low metabolisms, other groups went in a different direction. These groups shifted their postures to a parasagittal gait, with their legs placed underneath their bodies, which would have required a much more sustained use of leg musculature, and perhaps a higher metabolism (Benton, 2021). Tachymetabolic endothermy, as seen in birds and mammals, likely evolved somewhere during archosaurian evolution. It is generally agreed upon that theropod dinosaurs exhibited some level of endothermy (Benton, 2021; Grigg et al., 2022; Lovegrove, 2017; Rezende et al., 2020). The exact nature and degree of endothermy is still debated. Historically, several possible modes of endotherm have been suggested, ranging from gigantothermy as a result of high, stable body temperatures from large body sizes (Paladino et al., 1990), to fully developed tachymetabolic endothermy (Wiemann et al., 2022). Currently, the consensus appears to be that all theropod dinosaurs were capable of some level of internal heat production from an intermediate metabolic rate, helped along by their large body sizes (Benton, 2021; Grady et al., 2014; Rezende et al., 2020). The initially large sizes of dinosaurs might have allowed for an endothermic body at an energetically cheap price. However, not all dinosaurs were enormous. Many Cretaceous dinosaurs were quite small and would have lost their body heat to the environment much more rapidly as a result of their higher surface to volume ratio. The trend towards a reduction in body sizes throughout the Mesozoic along the dinosaur lineage leading to birds (Benson et al., 2014), could have posed a selection pressure toward increased metabolic rates, heat production and feathers, essentially countering increased heat loss with increased heat production and insulation (Rezende et al., 2020). When exactly feathers emerged is still debated. Fossil evidence suggests that monofilamentous feathers may have been a frequent feature as early as in coelurosaurian dinosaurs (Benton et al., 2019), a clade which emerged in the early-middle Jurassic (Brusatte et al., 2015). Early feathers have also been identified in an ornithischian dinosaur (Godefroit et al., 2014), and several fossils of pterosaurs appear to have been covered in pycnofibers and branched epidermal structures resembling simple dinosaur feathers, which might share a common origin with feathers seen in birds (Cincotta et al., 2022; Jagielska & Brusatte, 2021; Yang et al., 2019). Insulation may thus have been a present in archosaurs. It is also of interest that protofeathers and feathers have generally been found in smaller dinosaurs, whereas only direct skin impressions have been found in the much larger *Tyrannosaurus rex* so far *(Bell et al., 2017)*. It should, however, be noted that the settings in which *T. rex* has been preserved is not ideal for the preservation of feathers. It may thus still be that tyrannosaurs had feathers covering parts of their bodies. The largest feathered dinosaur found is *Yutyrannus huali* which weighed approximately 1400kg but also lived in colder climates of 10°C on average (Xu et al., 2012). This is largely in agreement with the hypothesis that smaller dinosaurs may have needed the insulation, while larger dinosaurs did not.

Maniraptoran dinosaurs had well developed feather plumages and may likely have been tachymetabolic endotherms (Chiarenza et al., 2024; Rezende et al., 2020). However, some studies have indicated that these animals may have fluctuated more in their body temperatures than what is typically seen in extant birds, somewhat akin to extant echidnas (Brice et al., 2002; Grigg et al., 2004; Tagliavento et al., 2023). This would imply a gradual shift toward higher metabolism, higher body temperatures, and perhaps also a gradual shift toward smaller fluctuations around an optimal body temperature, as is seen in many endotherms today.

All extant birds are tachymetabolic, homeothermic endotherms. Their body temperatures vary between 37-39°C in flightless palaeognaths to about 42°C in passerines at rest (Gavrilov et al., 2023; Maloney, 2008; Prinzinger et al., 1991). Most birds require their body temperature to be kept at a constant optimal temperature, and deviations from a narrow temperature range is potentially lethal. Some smaller birds (<100g), however, are able to go into torpor for short periods, allowing for lower body temperatures and metabolic rates (Schleucher, 2004). This allows them to save energy that would have otherwise been lost as heat, but also makes them sluggish and vulnerable to predation (Shankar et al., 2023). From this, it appears that even in mammals and the most derived dinosaurs, the birds, endothermy is not a binary feature and may be highly flexible according to what is adaptive. Even so, throughout sauropsid evolution, the generation of internal body heat through metabolic means has followed a trend towards higher and higher prominence. Today, very few animals exist that could be considered intermediate forms between ectothermy and endothermy (Grigg et al., 2004), perhaps because they have been outcompeted by more developed endothermic species, while ectotherms have been able to stick to their low metabolic niches without such competition.

2.4.2 Synapsids: Heating for cold nights?

The earliest synapsids, the Pelycosaurs, were obligate ectotherms, acquiring all of their body heat form the external environment, with likely little capacity for generating body heat internally (Benton, 2021; Faure-Brac & Cubo, 2020). However, evidence of such capacities has been found in therapsids, a group emerging from a pelycosaurian ancestor.

Therapsids show early signs of an elevated metabolism and an associated internal heat generation. It has been suggested that the Permian-Triassic extinction event wiped out all non-parasagittal therapsids (and by extension all the pelycosaurs), leaving only the faster, more agile therapsids alive. The evolution of more agile gaits took place in both synapsids and sauropsids parallelly at the same point in geological time. These two events may thus have set the stage for a physiological arms race between the two clades (Benton, 2021). These improved movement capabilities would likely have required an increased metabolic rate and might thus be one of the first signs of such accompanied by elevated rates of body heat generation in synapsids (Benton, 2021).

In cynodonts, we find fossilised respiratory turbinates, which are labyrinthine structures in the nasal cavity of extant mammals. These structures aid in reducing heat and vapour loss when breathing and could be indicators of endothermy in synapsids (Benton, 2021; Owerkowicz et al., 2015). An additional indicator of endothermy can be found in the differentiation of lumbar and thorax vertebrae in cynodont fossils. The ribs of the lumbar vertebrae have been reduced, either heavily or completely, which would have allowed for a diaphragm to actively pull air into the lungs to sustain a higher oxygen consumption resulting from an elevated metabolism (Buchholtz et al., 2012). Finally, the presence of facial vibrissae, which are likely to be modified hairs, would suggest that these animals had fur. Although, even if vibrissae came before fur, a layer of subcutaneous fat could also have served a similar role in insulation (Benton, 2021). Endothermy may have provided a significant advantage as cynodonts were pushed through a nocturnal bottleneck. The ability to generate their own body heat would have allowed for higher activity levels during cold nights with no external heat sources available (Angielczyk & Schmitz, 2014). Likewise, as a small animal with a high surface to volume ratio, a layer of insulating fur would have been significant in helping these small animals retain their heat. Fur may therefor have been a stable feature in cynodonts but could have evolved even earlier in the Permian according to hair-like findings in coprolites (Bajdek et al., 2016). However, whether these structures indeed are hairs is still uncertain.

It is unlikely to be a coincidence that it is in the cynodonts that we also find substantial brain enlargements. In the fossil record, increased encephalisation appears to go hand in hand with higher metabolism and increasingly more signs of endothermy. This correlation is in agreement with the endothermic brain hypothesis which links the evolution of cognition to the evolution of endothermy (Osvath et al., 2024) (see Section 1.1). Importantly, each degree Celsius increase of body temperature would in theory provide benefits to an animal, allowing for the gradual evolution of higher body temperatures as well as more homeostatic endothermic tendencies (Benton, 2021; Grigg et al., 2004). This trend appears to continue towards the emergence of Mammalia.

All extant mammals are tachymetabolic endotherms, although monotremes possess some quite unique traits when it comes to their thermoregulation. Monotremes generally have a modal body temperature of ~32°C. While platypuses appear to maintain their body temperature well with little fluctuation (Grant & Dawson, 1978), echidnas are unique in their relaxed thermoregulatory precision, allowing for fluctuations in body temperatures of up to 10°C, which can save metabolic costs (Brice et al., 2002; Grigg et al., 2004). Such lax thermoregulation (or perhaps the lack of ability to maintain stable body temperatures) might have been an important precursor for the evolution of constant higher body temperatures via metabolic means. Echidnas are thus reminiscent of findings on the fluctuating temperatures of maniraptoran dinosaurs (Tagliavento et al., 2023). Indeed, the standard metabolic rates of the platypus and the echidnas also differ substantially, with the platypus approaching marsupial levels at a standard metabolic rate more than double the rate of echidnas (Dawson et al., 1979). Marsupials generally have body temperatures around 35°C which is kept with little fluctuation. Just as their body temperatures are lower than placentals, their metabolism is also approximately 30% lower (Dawson & Hulbert, 1969). As such they appear somewhat intermediate between monotremes and placentals. Placental have body temperatures at ~37°C (Mortola, 2013). However, just like in birds, mammals of very small sizes may lower their body temperature and metabolism by going into torpor. Additionally, some larger mammals that can gather sufficient energy storage may hibernate for extended periods of time, reducing both temperature and metabolism (Ruf & Geiser, 2015).

3 How to study the evolution of cognition in deep time

It is one thing to study living animals, designing experiments, and getting behavioural results. But how does one study extinct animals that lived long ago and have been extinct for millions of years? Studying the evolution of cognition in deep time naturally comes with some challenges. For one, most species that have ever existed on Earth are long extinct and thus do not exhibit much cognition. Fortunately, as evolution primarily builds upon- and alters already existing structures, homology can be used to infer traits of extinct animals, by examining extant outgroups still alive today. By studying extant species at specific phylogenetic positions, we can infer characteristics of their common ancestor by means of comparison. This approach is called Extant Phylogenetic Bracketing (Witmer, 1995) and provides a framework for establishing the extent and limits to the inferences that are made. In this chapter, I describe how the EPB approach has traditionally been used in palaeontology and how it may be used to shed light on the evolution of cognition in extinct animals, through the combination of palaeontology, neuroanatomy and cognitive zoology.

3.1 Phylogenetic bracketing in cognitive research

Phylogenetic bracketing involves the inference of traits of extinct animals, by examining extant species at relevant placements on the phylogenetic tree, that bracket an extinct common ancestor of interest (Witmer, 1995). An example of commonly used extant groups of animals used for phylogenetic bracketing are crocodylians and birds, which together bracket all extinct theropod dinosaurs. Through comparisons between such two groups and the fossils of extinct animals, palaeontologist use this approach to infer soft-tissue traits such as anatomy and biomechanics of extinct species. Fossil bones often provide the foundation for bracketing inferences as these allow for the connection between extinct and extant anatomical characters in combination with the concept of biological homology. For example, the presence of certain muscles in extinct animals might be inferred by examining muscle attachment site on fossil bones and comparing them with homologous bones in extant species that bracket the extinct taxon in question.

Depending on the presence of similar attachment sites (and their corresponding muscle) on bones of extant species, one can infer homologous muscles in the extinct ancestor. There are three levels of inference that one may arrive at, depending on the presence or absence of characters in the extant bracketing groups (Witmer, 1995):

Level I inferences

A level I inference finds the trait of interest in both extant outgroups, thereby requiring minimal speculation on a similar presence in the extinct ancestor. By virtue of maximum parsimony, it is likely that osteological traits and their associated soft tissue in extant species were similar in extinct species because such traits must have been inherited by the common ancestor of the two extant groups. An example of such an inference, as was also given by Witmer (1995), is the presence of eyeballs in *Tyrannosaurus rex*. The EPB of *T. rex* are crocodylians and birds, and both of these groups have eyeballs. Moreover, the osteological correlates of eyeballs – such as the eye sockets and foramina for the optic nerves in the skull – are present in both bracket groups as well as in *T. rex*.

Level II inferences

When a trait of interest is only found in one of the two bracketing outgroups, a level II inference can be made. Such an inference indicates the emergence of a trait along the evolutionary line leading to one of the two outgroups and makes it difficult to pinpoint the exact place in time that a trait evolved. An obvious example that has seen lively debate for decades is tachymetabolic endothermy. One bracketing outgroup, the crocodylians, are ectotherms, while the birds are endotherms. As such, endothermy must have evolved sometime during the evolutionary trajectory toward birds, but when exactly is impossible to pinpoint from extant phylogenetic bracketing alone.

Level III inferences

If a trait is found in none of the extant outgroups of an extinct ancestor this leads to a level III inference. The lack of a trait in extant outgroups does not necessarily mean that a trait did not exist in an extinct ancestor, but such inferences would be speculative and require a great deal of compelling morphological evidence and/or evidence from other sources to support it.

Not all characters that may be studied in extant bracketing groups have osteological evidence available. However, such characters may still be hypothesised strictly on a phylogenetic basis, without osteological evidence. In such situations, a parallel scheme to the three levels of inference described above exists: Level (I'), (II'), and (III') inferences. These inferences are given a prime (') designation, which denotes an inference with no osteological evidence. Several examples of such inferences exist, such as the four chambered heart found in both crocodylians and birds. A heart leaves no osteological evidence in the fossil record, yet we are still quite confident that the hearts of theropod dinosaurs also had these features, given their existence in both bracketing outgroups. Likewise, cognition such as gaze following behaviour and model-based exploration, or neuroarchitecture such as neuronal counts, have no direct osteological evidence, but may be inferred based on strictly phylogenetic grounds. To support such inferences, corroborating studies from other fields can provide further assistance. Neuroanatomical studies on extant neuron numbers and brain morphology as well as indirect osteological data, especially cranial endocasts, provide information on brain size and morphology which aids in supporting inferences on cognition. These three avenues of palaeontology, neuroanatomy, and behavioural studies used for studying the deep time evolution of cognition are described further below.

3.1.1 Palaeontology

With the ongoing technological development in palaeontological research, more and more information has become available from examining fossil evidence. An especially impactful development is that of Computed Tomography (CT) scanning techniques, allowing non-invasive scans of both the inside and outside of fossils, without having to fragment or break them. Before the development of CT scans, to create an endocast of a fossilised skull, the insides needed to be hollowed out and coated with a layer of latex. Once dry, this latex could then be pulled out to produce an endocast of the cranial cavity (Witmer et al., 2008). Such procedures posed great risks to the fossil and could break it in the process. Often, the value of the fossil was higher than the value of the information gained from breaking it. With CT scans, the fossils are no longer at risk, and as a result, more and more information on the endocranial morphology of a large number of extinct dinosaur and mammal species has become available (Balanoff & Bever, 2017; Rowe et al., 2011; Witmer et al., 2008). However, information from such endocranial scans come with important caveats: It is not all species that have brains that fill out the entirety of the braincase. For example, the brains in non-archosaur sauropsids and crocodylians do not fill out the cranial cavity, but they do so in all birds living today. The percentage of the braincase that is taken up by the brain is usually reported in either percentages or proportions in a Brain to Endocranial Cavity (BEC) index. Reptiles typically have BEC indexes of 33-50% (Balanoff & Bever, 2017). Hurlburt et al. (2013) made an attempt at estimating the brain sizes of extinct theropod dinosaurs based on the encephalisation quotient (EQ; a measure of the relative brain to body size in relation to what is expected from a given taxa) of reptiles and birds, and the BEC index of American alligators (*Alligator mississippiensis*) of different sizes typically encountered in the wild. From this he calculated the brain sizes of extinct tyrannosaurids from an estimate of a BEC index of 37%, putting tyrannosaurids slightly above the expected EQ of reptiles.

Not all dinosaurs appear to have had BEC indexes like non-archosaurian reptiles and crocodylians. Some fossil endocasts have been found with vascular impressions on the inside of the skull, indicating that the brain filled out almost the entire braincase (Hurlburt et al., 2013). Such impressions have been found in the endocasts of maniraptoran dinosaurs such as oviraptors, ornithomimosaurs and troodontids (Currie & Zhao, 1993; Osmólska, 2004; Russell, 1972), and thus appears to be a common feature of all maniraptoran dinosaurs (Balanoff et al., 2014; Witmer & Ridgely, 2009). Hurlburt et al. (2013) also found that this group of dinosaurs fall into the same scaling relationship between brain as body size as is observed in extant birds today. As such, there appears to have been a trend towards larger brains and a larger ratio of the brain case being filled when moving up along the archosaurian phylogenetic tree towards theropod dinosaurs and birds.

All brains of extant mammals fill out close to the entire braincase (Ashwell, 2010; Ashwell et al., 2014; Balanoff & Bever, 2017), and thus it is likely that this was also the case in the last common ancestor of all extant mammals. It is difficult to speculate on when exactly the brain came to fill the entire brain case in synapsids. Nevertheless, it probably did not always do so, as the common amniote ancestor of mammals and birds likely did not have a high BEC index. Unfortunately, as there is no extant outgroup within synapsids with potentially lower BEC indexes, speculating on when the brain started filling out the brain case is problematic. That being said, an increase in BEC index must have happened somewhere (or in several separate bursts) on the trajectory from the first amniotes, along the lineage of therapsids and cynodonts, reaching mammalian levels before or as the common ancestor to extant mammals arose. EQ has also been studied in mammals and appears to be generally comparable between marsupial and placental mammals with the exception of primates (Weisbecker & Goswami, 2014). Endocranial casts of extinct mammals have also been examined in this context but are less relevant for behavioural comparisons of cognition because no extant outgroups within synapsids that diverged before today's mammals exist, leaving no opportunities for comparisons in deeper geological time.

3.1.2 Neuroanatomy

The encephalisation quotient (EQ) has been a widely used metric for inferring the level of cognitive abilities of a species: the larger brain size relative to what is expected from a given body size, the more cognitively sophisticated the animal is generally thought to be. This relationship does seem to hold for some groups of animals, especially if comparing closely related species. This is primarily because the neuronal scaling relationships are similar between closely related taxa, leading to a higher absolute numbers of neurons in species that have larger brains (Kverková et al., 2022). When comparing lineages of vertebrates that have been phylogenetically separated for longer, this relationship becomes less and less convincing due to these scaling relationships differing to larger and larger extents.

This is exemplified by the much higher neuronal densities of bird brains compared to mammals, resulting in similar cognitive complexity in birds and mammals despite their large brain size differences (Olkowicz et al., 2016). Instead of looking at relative brain sizes, it may instead be more fruitful to examine specific brain areas, and in particular the number of neurons dedicated to these (Herculano-Houzel, 2017; Kverková et al., 2022). Additionally, the connections between brain areas as well as their function might tell us much about their neurocognition (Güntürkün et al., 2024). The isotropic fractionator method allows for accurate estimations of neuron numbers of gross brain areas, while the optic fractionator allows for estimations of smaller brain areas that can be reliably sectioned (Herculano-Houzel & Lent, 2005; Mouton et al., 2017). This is done by transforming brain areas of interest into an isotropic suspension containing all the nuclei of brain cells, including neuronal cells. The neuronal nuclei are then stained immunocytochemically to differentiate them from non-neuronal cells, allowing accurate estimations of neuron numbers. With knowledge on the neuronal numbers within brains and particular brain areas of species alive today, in addition to knowledge on brain anatomy of extinct species from palaeontological endocasts, it becomes increasingly feasible to infer how the distribution of neuron numbers in vertebrate brains might have evolved throughout geological time. Of particular interest, once again, are the phylogenetically important archosaurian groups of crocodylians and birds, which together bracket the extinct dinosaurs.

The neuroanatomy of these two groups differs in many aspects. For example, a crocodylian brain is, as in other reptiles, quite small. The brain consists primarily of the brainstem, a cerebellum, optic lobes, the telencephalon, and the olfactory bulbs. All brain areas, except the olfactory bulbs, are relatively small and are organised in an almost sequential fashion along the length of the brain (Figure 3c). Conversely, the avian brain has reduced olfactory bulbs, while the cerebellum and telencephalon have increased in size substantially, leading to these two brain areas almost enclosing the rest of the brain and making it much more rounded in shape (Figure 3d-e) (Jarvis, 2009). Likewise, the number of neurons in the brains of crocodylians is also humble, an example being a 5.81g brain of a Nile crocodile with around 81.5 million neurons (Ngwenya et al., 2016). In comparison, a 5.43g brain of an adult magpie has 897 million neurons (Olkowicz et al., 2016). As such there's been a trend towards increased encephalisation and neuron numbers during the archosaur evolutionary trajectory towards modern birds. This increase primarily took place in the telencephalon and the cerebellum, while the neuron numbers in other brain regions increased much less (Kverková et al., 2022). The telencephalon expanded and differentiated substantially leading to the emergence of several important areas for complex cognition, such as a much-enlarged dorsal ventricular ridge, a hyperpallium, and the nidopallium caudolaterale (NCL) (Striedter & Northcutt, 2020). These areas perform many of the same functions as the neocortex does in mammals (Güntürkün et al., 2024). Additionally, birds have neural pathways between cerebellar and telencephalic areas, which likely allow for the involvement of the cerebellum in other cognitive functions other than tightly controlling movements and locomotion (Gutierrez-Ibanez et al., 2018; Osvath et al., 2024). All of these brain areas and their associated cognitive functions have been suggested to have evolved to fuel the energetic needs related to endothermy (Osvath et al., 2024) (see Section 1.1). Narrowing the possible periods in time that such brain areas are likely to have evolved will help us understand the extent of the cognition that various dinosaurs may have possessed, which in turn may inform us on their metabolism and thermal biology. However, the neuroanatomical changes that took place during the transition from reptiles to birds are difficult to describe in detail, as fossil endocasts are difficult to interpret when it comes to identifying specific brain areas. We are thus largely left with inferences on the presence of such pallial areas. Here, the EPB can assist by further examining the neuroanatomy of crocodylians, other reptiles and birds. For example, it has recently been discovered that crocodylians may possess a rudimentary NCL as well as projections between the telencephalon and the cerebellum, similar to what is found in birds, although less elaborated (Billings et al., 2020; Gutiérrez-Ibáñez et al., 2022). Such findings would shift the inference of the NCL from Level II' to Level I' and would indicate that these brain structures were available to expand upon in all dinosaurs. On the other hand, crocodylians lack many other brain structures that birds possess (Güntürkün et al., 2020), and for now we can only infer that they must have evolved at some point during the evolutionary path leading to birds.

Within birds, palaeognaths in particular can similarly provide insights into the neurocognition of non-avian dinosaurs. This is due to their plesiomorphic neuromorphology and their phylogenetic placement. The palaeognaths and the neognath clades containing fowl (Galloanserae) and pigeons and allies (Columbaves) had already emerged before the Cretaceous-Paleogene extinction event that wiped out the non-avian dinosaurs 66 million years ago. After this event, a subsequent acceleration of brain size evolution took place in the telluravian neognaths (Ksepka et al., 2020). Palaeognaths and early neognath clades have not undergone the same selection pressure on brain evolution as telluravians. Consequently, palaeognaths and early neognaths have lower neuronal densities compared to the Telluravian clades that emerged after the extinction event. For example, as compared to the previously mentioned 5.43g magpie brain with 897 million neurons, an almost four times larger 21.3g brain of a greater rhea contains approximately only roughly 1 billion neurons (Kverková et al., 2022). Palaeognaths have also retained similar scaling relationships between body and brain mass as has been described in paravian dinosaurs (Ksepka et al., 2020). This makes palaeognaths our best extant model for inferring what cognitive abilities might have been present in these dinosaurs. Increased knowledge from their neuroanatomy as well as information on endocranial morphology from palaeontological research may further be combined with cognitive and behavioural experiments to provide insights into the cognition of non-avian paravian dinosaurs.

3.1.3 Cognitive zoology

The contents of this thesis lie predominantly within the realms of cognitive zoology. Unfortunately, it is not yet possible to directly measure the neurological processes associated with cognition in a non-invasive way. Likewise, linguistic reports are not obtainable from animal subjects. Because of this, the field of animal cognition primarily uses behavioural experiments, constructed in ways that can provide insight into the underlying cognitive processes of the behavioural responses of animals. Cognition has no direct reference to osteological material and extinct animals cannot be tested in behavioural tests. However, the EPB approach may still be used to infer the likely cognitive capabilities of extinct species by using the results of behavioural tests on cognition in extant ones. For behavioural testing to provide insights into the deep time evolution of cognition, the phylogenetic context must be central to the study setup.

The most important outgroups for Sauropsida in this thesis are crocodylians and birds, with palaeognath birds being of particular interest due to their plesiomorphic neuroanatomy highly similar to the extinct paravian dinosaurs (Balanoff et al., 2013; Ksepka et al., 2020). Due to the early split between crocodylians and birds, we can go roughly 250 million years back to their common ancestor by comparing the cognition of these groups (Figure 1). Additionally, Sauropsida contains several other extant reptile lineages which allow us to go further back in geological time in the study of cognitive evolution. In contrast to sauropsids, the synapsid lineage is much sparser in extant groups, making inferences of cognition in deeper time much more difficult. The only three extant synapsid lineages had already separated 200 million years ago (Figure 1). Nevertheless, the study of placentals, marsupials and monotremes can still provide valuable insights into similarities and differences in tempo and mode of cognitive evolution between the synapsid and the sauropsid lineage. The study and comparisons of mammals with birds may therefore allow us to identify general trends in tempo and mode that might be universal steps in cognitive evolution.

To increase the reliability of inferences of cognition back in time, focus should be on core cognitive functions. These are cognitive abilities that are unlikely to be lost once gained, because they provide substantial benefits to the behavioural repertoire of an animal (see Chapter 4). Additionally, other more complex cognitive abilities likely expand upon these, integrating them further into the cognition of an animal. Because of this, differences in various core cognitive capacities between species at key phylogenetic positions are likely to be informative on the evolution of cognition in deep time. Recently, the evolution of gaze following in archosaurs was studied using the EPB approach on crocodylians and palaeognath birds (Zeiträg et al., 2023). Both low level (reflexive co-orientation with a conspecific's gaze) and high level (an understanding of the viewpoint of others) gaze following were examined in both outgroups. Crocodylians were found to possess only low-level gaze following, while palaeognath birds possessed both. From this, we can infer that all non-avian dinosaurs likely also possessed low level gaze following, while high-level gaze following must have originated at some point during dinosaur evolution on the trajectory toward birds. Some core cognitive functions do not only manifest themselves as being either wholly present or wholly absent. Many executive functions rather vary in degrees of development or “mastery”. For example, behavioural inhibition in animals differs between many animal groups (PAPER II). If one outgroup is mediocre at inhibiting impulses, but the other is highly skilled, we can infer that the increased capabilities in the highest performing outgroup likely developed after the two extant outgroups split, and that the extinct ancestor also may have possessed mediocre or less developed capabilities. Similarly, such inferences allow us to identify which lineages may have benefitted most from developing stronger inhibition. Such inferences should then be further corroborated by evidence from other avenues, such as studies on brain evolutionary rates, metabolic physiology, thermal biology, among others, to provide further support and explanatory power on why such cognition evolved (see Section 1.1). The study of cognition in deep time is, however, not necessarily restricted only to core cognitive functions. Behaviours that are easily identifiable and which have strong theoretical and empirical connections to complex cognition may also be studied. For example, mutual grooming is readily identifiable when expressed and is associated with other behaviours such as strong pair bonding, cooperation and sociality in extant species (Kenny et al., 2017). The presence or absence of this behaviour in key phylogenetic groups similarly allows for inferences about the behaviours and cognition of extinct animals (PAPER VI).

Given the nature of studying extinct animals, it will always be subjective to what extent evidence is deemed “convincing” enough to support that an extinct animal possessed certain cognitive skills. However, the combination of evidence from several avenues of enquiry can increase the support for or against any inferences made through the EPB approach. The emerging field of palaeocognition aims to combine the knowledge from evolutionary neurobiology and cognitive zoology (and other fields) on extant animals to infer the neurocognition of extinct animals. Palaeontology provides the link between the extant and the extinct through the identification of osteological correlates and reconstructions of extinct brains and sensory systems. The identification of fruitful approaches and most relevant research questions is still ongoing. The evolution of cognition must be understood in the light of its allostatic function (Lyon, 2020) and how the evolution of tachymetabolic endothermy affected how cognition performed this function (Osvath et al., 2024) (see Section 1.1). In PAPER I, we discuss and propose how comparative studies on extant species can elucidate cognitive evolution in deep time and suggest new angles of research that might further support cognitive inferences in extinct animals.

4 The cognition in this thesis

Cognition and life itself are intimately linked. Cognition is a process that makes the survival, reproduction and growth of an organism possible through the collection and processing of information in order to interact adaptively with the environment (Lyon, 2020). It functions as an allostatic extension of metabolism: it aids an organism in avoiding structural damage and sustains it by working to locate and acquire nutrients (Osvath et al., 2024). Allostasis allows for the anticipation of future needs, such as food or warmth, allowing an organism to satisfy such needs *before* they become critical (Schulkin & Sterling, 2019). The advent of multicellularity further led to the evolution of the nervous system, allowing the coordination of large quantities of cells in a body for locomotor purposes (Sterling & Laughlin, 2023), and a wide selection of sensory organs followed suit, which gradually became more and more sophisticated. This allowed for allostasis to be extended further and further into time. (Schulkin & Sterling, 2019; Sterling & Laughlin, 2023). Through further evolutionary iteration, cognitive capacities such as memory and associative learning emerged, aiding in allostasis by allowing for an organism to remember favourable contexts and associating certain events with positive outcomes (Ginsburg & Jablonka, 2010). Such cognitive capacities, along with all others, likely all aid in the upholding of the organism in some way.

Much of the cognition studied in this thesis is discussed in relation to the exploration/exploitation dichotomy of foraging (Hills et al., 2015). In foraging situations, there will always be a trade-off between exploiting known resources or exploring the environment to locate better resources in a different location. Alongside the evolution of tachymetabolic endothermy, the need for energy must also have increased to fuel its associated metabolism (Nagy, 2005). The brain elaborations of endotherms has here been hypothesised to have evolved to enable the neurocognition necessary for an increased caloric intake through more efficient foraging (Osvath et al., 2024) (see Section 1.1). As such, one can imagine an increased selection pressure on the development of cognitive abilities that allow more efficient exploration and exploitation of the environment to increase energy intake. Much of the cognition in this thesis falls under the exploitation side of this dichotomy. That is, cognition that allows an animal to maximise the extraction of energy from their environment. However, it must be noted that many cognitive abilities might also provide benefits during exploration (e.g., object permanence would very likely be crucial for constructing cognitive maps of the environment and its features).

Within this framework, focus is laid primarily on cognitive capacities that have emerged early and have been developed upon further during the evolution of amniotes. They are here termed core cognitive functions, which are cognitive abilities that likely evolved early in animals and which provides the basis for many other cognitive capacities. Specifically, this thesis focuses primarily on the executive functions of inhibitory control and visual working memory (PAPER II, III and IV). Executive functions is a term encompassing many both highly complex and more fundamental cognitive abilities. Examples of complex executive functions are cognitive flexibility ("creative thinking" and adaptation to changing circumstances), problem-solving, planning and reasoning (concept formation and creativity) (Cristofori et al., 2019; Diamond, 2013). Many of these capacities, however, also contain aspects that are fundamental and widespread in vertebrates. Cognitive capacities such as working memory, inhibitory control and interference control may vary in the degree to which it is mastered by a given species and may by extension have gradually increased in complexity throughout evolution. Working memory, for example, is a process that holds and manipulates limited information to solve problems, a skill required for any task that involves more than basic associative or fixed behaviours (Hahn & Rose, 2020). It is thus highly beneficial in many situations and likely widespread in vertebrates, but at varying degrees of complexity depending on the species (Bloch et al., 2019; Hahn & Rose, 2020; Lind et al., 2015; Wilkinson & Huber, 2012).

In addition to non-social cognitive abilities, I also look at core socio-cognitive functions. While living beings naturally also conform to the rules of the physical world (a predator in hiding does not stop existing just because it can no longer be perceived), they are additionally complicated because they are driven by their own needs, which makes them unpredictable, self-governing agents. These agents all have similar needs to survive, such as finding food, avoiding predators, and reproducing. Because of this, there are several situations in which even very asocial species may draw benefits from core socio-cognitive abilities. One example is gaze following into distant space, which is considered a reflexive behaviour, leading to the adjustment of ones direction of gaze to that of a conspecific (Zeiträg et al., 2022). By doing this, an observer can gather information about what a conspecific had its attention directed at (e.g., food to be obtained or a predator to be avoided). Another example that is explored in this thesis is individual recognition. Being able to discriminate between conspecifics based on features unique to them provides a basis for many other social behaviours and interactions (Tibbetts & Dale, 2007). Social relations such as pair bonding or hierarchical group structures would fall apart if individuals could not tell their partner apart from other conspecifics. Once such social relations emerge in a species, it becomes beneficial to be able to maintain and repair them if disagreements or conflict should arise. Mutual grooming has independently evolved in both sauropsids and synapsids to serve such a function, and in many derived birds and primates it has been further built upon as a social currency. The last two parts of this chapter are dedicated to individual recognition (PAPER V) and mutual grooming (PAPER VI).

4.1 Motor self-regulation

An essential component of executive functions is inhibitory control, which involves the control of impulses and habitual behaviours in favour of more appropriate goal-oriented ones (Beran, 2015). A core aspect of such inhibitory control is motor self-regulation which specifically involved inhibiting unproductive motor movements (Kabadayi et al., 2018). Motor self-regulation has been studied for more than 100 years using various iterations of the detour paradigm (Hobhouse, 1901; Kabadayi et al., 2018). A detour task involves the inhibition of motor impulses that emerge as a result of a visible reward placed behind a see-through barrier. To obtain the reward, the subject must inhibit the visual pull of the reward and the impulse to move directly towards it (and thus colliding with the barrier), and instead move around the obstruction. The detour paradigm may be separated into two main categories: initially visible goal detours and continuously visible goal detours (Kabadayi et al., 2018). The continuously visible goal detours involve only barrier sections that are see-through, whereas initially visible detours additionally involve a section in which the reward is obstructed from view, either by an additional opaque obstruction, or from the subject having to direct its field of vision away from the reward in order to detour. Within this thesis, only the continuously visible goal setup has been used, although we also work with the obstruction of direct visual connections in different setups (see Section.3). The single barrier setup is the most simplistic but has still seen several iterations in how the obstruction is shaped and constructed, such as the use of material with different transparencies or wires/mesh (Juszczak & Miller, 2016; Kabadayi et al., 2017), as well as the shape of e.g., a cylinder, a simple barrier, or barriers of various shapes (Kabadayi et al., 2018; Kabadayi et al., 2016; Nawroth et al., 2016). Particularly, the different types of barriers have been suggested to affect performance depending on the primary sensory modalities of a species (Kabadayi et al., 2018). Additionally, some setups require only the subject to reach around a barrier, while others require the movement of the entire body (Kabadayi et al., 2017; Vlamings et al., 2010).

The detour task has been used to study the inhibitory capabilities of a wide variety of species, although there has been a bias toward studying birds and placental mammals, especially primates (MacLean et al., 2014). This has, however, more recently begun to be remedied by studies on more bird species, marsupials, reptiles and fishes (Kochen et al., 2022; Sovrano et al., 2018; Wilkinson et al., 2010; Wynne & Leguet, 2004). The performance of corvids appears to be much better than would be expected from their brain size (Kabadayi et al., 2016; MacLean et al., 2014), highlighting that it is the brain architecture and not brain size per se that correlates with cognitive performance. Birds have much higher densities of neurons in the brain than mammals do, allowing for more processing power per gram brain weight (Kverková et al., 2022; Olkowicz et al., 2016). The high performance of primates and corvids may particularly relate to the well-developed telencephalon of both groups. Not much is known about the exact neural basis of inhibitory performance, but lesion studies on several primate species seem to indicate that the prefrontal and temporal areas of the neocortex are involved in at least detour-related behaviours (Kabadayi et al., 2018). The avian nidopallium caudolaterale is a functional analogue to the mammalian prefrontal cortex and is similarly well developed in corvids as the prefrontal cortex is in primates, potentially explaining their high performance (Güntürkün et al., 2024).

In PAPER II we test the motor self-regulation of several marsupial and placental mammals, several palaeognath and neognath birds, as well as the American alligator. To maximise comparability between species, we used two versions of one of the simpler iterations of the detour paradigm - a standard barrier. We had two conditions of this setup – one mesh and one transparent, as it has previously been suggested that different barriers might influence the performance of a species depending on its sensory modalities (Kabadayi et al., 2018). The species that stood out the most was the American alligator which showed poor motor self-regulation. By contrast, the ravens reached ceiling levels in the task with performance above palaeognaths and the other neognaths tested, which suggest an increase in inhibitory control throughout evolution. A similar but less pronounced trend is also seen in the mammals, with non-primate placentals passing more trials than marsupials, but fewer than lemurs. However, when looking at the number of touches made between marsupials and placentals, only the lemurs make fewer. As such, marsupials may possess comparable capabilities for motor self-regulation to non-primate placentals, but their lack of acute vision may be insufficient to prevent an initial touch which signifies a failed trial. Additionally, our data supports the suggestion that different types of barriers may influence how a given species performs depending on its primary sensory modalities. We found that mammals in general performed worse on mesh trials, which is consistent with their higher reliance on olfaction and the fact that scents can diffuse through the wire mesh. Likewise, we found lower performance in the primarily visual archosaurs in transparent trials, which may be harder to navigate compared to mesh barriers that partially obscure the visual access to the food item.

4.2 Visual working memory

In a foraging context, situations continuously arise in which features in the environment that were previously perceivable become occluded or unavailable. In such situations, an animal benefits from being able to uphold representations of food items in working memory so that they might still be pursued. Additionally, the ability to store information on the features of objects (such as the quality of food) in memory may also increase foraging success, because an animal is able to make optimal decisions on what to pursue to maximise caloric intake. The knowledge that objects continue to exist when they are not directly perceived is termed object permanence (Zewald & Jacobs, 2021). Object permanence has been shown in a wide variety of birds and mammals (Majecka & Pietraszewski, 2018; Pepperberg & Funk, 1990; Singer & Henderson, 2015). Additionally, our group has recently discovered object permanence in leopard geckos (*Eublepharis macularius*) (Lalić, 2023) and American alligators (Osvath et al., in prep). Whether or not object permanence is present in fish is more mixed, as it has been argued that it is necessary for detour behaviours (Sovrano et al., 2018). However, the cleaner wrasse (*Labroides dimidiatus*) was recently tested in both the detour task and in an object permanence task and was only able to perform detours, suggesting that these tasks require different cognitive processes (Aellen et al., 2022). In humans and apes, object permanence has been suggested to be a type of visual working memory (Hulme & Zeki, 2007), which involves a wide selection of visual and neocortical areas of the brain (Erlikhman & Caplovitz, 2017; Ungerleider et al., 1998). As such, it is likely that these animals also possess some level of visual working memory in which to store and process visual information.

Within this thesis we study the evolution of visual working memory through a large object permanence test battery. Some of the tasks we use are modifications of the classic object permanence battery (Užgiris & Hunt, 1975), while others are novel, designed to test the strength of visual working memory. Basic object permanence is tested using a classic forced-choice double barrier setup in which a desirable food item is hidden behind one of two barriers. The consistent retrieval of the occluded food behind the correct barrier would indicate the capacity for object permanence. To further challenge visual working memory capacities, the battery contains several iterations of this setup which consist of the addition of successive visible displacements of the food, as well as the A-not-B task. We also test the capacity to store feature information of objects by means of an object individuation task. Here, a preferred high-quality and a mediocre quality food item are hidden behind a barrier each, and if an animal can consistently retrieve the hidden preferred food, this would suggest an ability to store information on object quality in visual working memory.

The novel tasks in this thesis focus on testing memory guided inhibition when faced with competing direct visual input. The experimental setup involves two tasks: the Vision-Memory competition task and the Vision-Memory priority task. The Vision-Memory competition task aims tests the ability of an animal to inhibit themselves from going for a directly perceived food of mediocre quality in favour of the representation of hidden high-quality food in working memory. This is tested by presenting a situation in which highly desirable food is occluded behind an opaque barrier, but a less desirable food item is within visual access behind a transparent barrier. In this situation, an animal must inhibit the visual pull of the mediocre food and instead be guided by its visual working memory. The Vision-memory priority task further tests the robustness of visual working memory by changing the rewards to have equal value but one of them is hidden while the other is visible. A highly robust visual working memory that shows representational strength on the same level as direct visual input will lead to a ratio of hidden/opaque choices close to 50/50, whereas a weaker visual working memory results in ratios that favour more transparent choices.

In PAPER II we tested the visual working memory of a large selection of palaeognath and neognath birds, placental and marsupial mammals, and the American alligator. All species tested possessed visual working memory and were able to locate food hidden behind one of two barriers consistently, which suggests visual working memory that is developed enough to support basic object permanence as has also been found in many other species vertebrate species. However, all mammals tested except the ring-tailed lemurs were unable to locate their preferred food when both food of high and mediocre quality was hidden behind each their barrier, suggesting that they are unable to attribute object features to their visual working memory. In contrast, all archosaur species passed this task, including the American alligators. This is a surprising finding given the highly elaborated neurocognition in mammals as compared to crocodylians. This suggest that the differences in visual acuity between non-primate mammals compared to primates and archosaurs may place constraints on the degree to which visual working memory can increase in complexity. In the Vision-Memory competition task we found that the lemurs and archosaur species all were capable of using visual working memory to inhibit the visual input of mediocre food in favour of occluded food of high quality. However, American alligators stood out in the Vision-memory priority task. When the quality of the reward was identical between the transparent and the opaque barriers, alligators would almost exclusively choose the transparent barrier. Taken together with the Vision-memory competition task, this suggest that alligators are able to use visual working memory as a guide to inhibit visual input when quality differs, but that these representations are generally weak and lose out when the visual input is identical to what is represented in memory. Lemurs and ravens showed a ratio close to 50/50, indicating strong visual working memory that can compete with direct visual input, whereas palaeognaths and junglefowl were intermediate. The increase in robustness of visual working memory from alligators to palaeognaths and junglefowl to ravens suggests an evolutionary trend toward more complexity in this skill.

In PAPER III we tested juvenile ravens in both Vision-Memory tasks in order to examine how visual working memory develops during early ontogeny in a neurocognitively derived bird. We found that juvenile ravens were able to represent objects of different qualities in visual working memory immediately along the emergence of basic object permanence. Additionally, one juvenile also passed the Vision-Memory competition task immediately after the onset of object permanence, while the others required more time. We tested one raven in the Vision-Memory priority task across several weeks of development and found that the ratio between transparent and opaque barrier choices began at 100% transparent but moved toward a 50/50 ratio as the raven developed over the weeks. When tested at week 23 the ratio was comparable to what we found in adult ravens in PAPER II. This ontogenetic development of visual working memory complexity mirrors the evolutionary progression of the skill seen in archosaurs, further suggesting an evolutionary component to this skill.

4.3 Interference control

Animals are constantly interacting adaptively with their environment through the use of their sensory systems (Gibson, 2014). However, a lot of the information received from sensory systems is irrelevant noise that needs to be filtered out in favour of information that is relevant to a particular situation and/or species (Lev-Ari et al., 2022). Cognitive mechanisms such as selective attention and cognitive inhibition, which together constitute interference control, aid in the filtering of such information to protect working memory. Selective attention involves the processes of focusing the sensory attention toward one or few select stimuli, while cognitive inhibition is a process that deletes irrelevant information and prevents it from being stored in working memory (Diamond, 2013). Crudely described, selective attention thus involves controlling what to focus on, while cognitive inhibition involves the inhibition of attention toward unimportant stimuli. Interference control has predominantly been studied in humans and primates via visual search experiments, but selective attention in chickens has also been demonstrated (Beran et al., 2016; Sridharan et al., 2014). In such experiments, response times or success rates are compared between conditions in which a distracting stimulus is presented alongside what must be located in the experiment, and animals generally show poorer performance when distractions are present (Clapp et al., 2010; Wagener et al., 2023; Washburn & Taglialatela, 2012). Cognitive inhibition has also been studied in dogs through the use of reversal learning tests. Here, more specifically, the dogs' ability to inhibit prior knowledge represented in working memory, in order to not pick a stimulus that is no longer rewarded, is tested (Brucks et al., 2017). Because of the obvious benefits of interference control, components of such capacity likely evolved early in vertebrates (Krauzlis et al., 2018). Some aspects of selective attention might be hard-wired in the brain of amphibians and reptiles, leading to a bias toward movement that is jerky instead of smooth (i.e., prey movements vs. irrelevant movements) (Pallus et al., 2010), or predator/avoidance behaviours depending on the size of the moving object (Ewert, 1970). Such basic responses appear to be the result of stimuli processes in the optic tectum, thalamus and brain stem. The evolution of the prefrontal cortex in mammals, and the nidopallium caudolaterale in birds, may have led to increased top-down control of such capacities, allowing for an increased rate of flexibility in attention (Güntürkün & Bugnyar, 2016; Krauzlis et al., 2018).

In PAPER IV, we test emus, domestic chickens, ring doves, ravens, domestic dogs, domestic pigs and ring-tailed lemurs in a new experimental setup designed to test the ability to protect visual working memory from interfering and distracting stimuli. We differentiate between two types of distractions (Clapp et al., 2010): an interference which has relevance to the subject and should be attended to (e.g., a food item) and a distraction which has no value to the subject (e.g., an inedible item). The experimental setup involves two barriers, one of which hides a desirable food item. The task consists of three conditions in which, as the test subject is approaching the barriers in order to retrieve the food item, it is distracted by either 1) another identical food item 2) two identical food items in quick succession, or 3) a non-valuable distraction. The setup was designed such that the distracting stimuli would break the subject's established line of sight to the location of the hidden food, requiring it to specifically rely on visual working memory to solve the task. The animal passes a trial if it retrieves the hidden food behind the correct barrier.

In general, all species had visual working memory sufficient for object permanence. Similarly, all species except the ring doves were able to protect their visual working memory from an interfering stimulus and find the hidden food above chance levels, although performance was reduced compared to the baseline. When faced with two interfering stimuli in quick succession, performance was similar in all species apart from the emus which now performed at chance levels. This suggests that an additional interference has diminishing returns on the distracting effect, perhaps because the second interference only adds handling time, while the first also breaks the visual connection with the hiding location. When we used a non-valuable distraction, performance in all tested species were comparable to the baseline except for the dogs, which may be due to their experience with thrown items always being food or toys. This first step established the presence of well-developed visual memory protection capabilities in birds and mammals and provides the foundation for further comparative studies on marsupials as well as reptiles to examine the evolution of the interference control of visual working memories.

4.4 Individual recognition

The capacity to identify and discriminate between conspecifics is a fundamental cognitive skill required for more complex sociality to evolve (Wiley, 2013). Individual recognition has been found at various levels of complexity in a wide variety of animal taxa (Yorzinski, 2017), depending on the evolutionary needs of a species. A species that raises its young in solitude might not benefit much from being able to differentiate its own offspring from others, while a species that breeds in colonies would ensure that they feed the correct chicks if they can recognise their own (Beecher et al., 1986). The recognition of one's own offspring does not, however, necessarily imply that parents can differentiate between each of their offspring, or that the offspring can differentiate between their two parents (Wiley, 2013). Recognition can thus vary in specificity and multiplicity, where specificity is the number of individuals in a given set (e.g., the recognition of all members of a species, or just one reproductive mate), and multiplicity is the number of units that may be recognised (e.g., merely kin vs. non-kin, or separate recognition of every individual within a group) (Wiley, 2013). True individual recognition – recognising a particular individual based on its unique features – is thus the most complex level of recognition (Tumulty & Sheehan, 2020; Wiley, 2013).

Being recognised by conspecifics as an individual comes with a potential array of advantages and disadvantages. Advantages may include inbreeding avoidance, ensuring offspring survival within a colony, or avoiding wasting energy on repeated interactions with conspecifics e.g., harassment of territorial neighbours, or repeated interactions with either rejecting females or large, aggressive males (Fischer et al., 2015; Lai & Johnston, 2002; Werba et al., 2022). Social species also benefit from more stable dominance hierarchies across time, as well as reciprocity in positive interactions, resulting from the attribution of prior experience to specific conspecifics (Tibbetts & Dale, 2007). However, being recognisable also reduces the anonymity of an individual, which provides fewer opportunities for deceit and theft, and more opportunities for retaliation or avoidance from conspecifics when such deceit is discovered (Clayton & Emery, 2007).

Depending on a species' life history and ecology, one or several modalities might be utilised for individual recognition and communication. The most common communication systems in animals are olfaction, vision, and audition. Scent marks are readily used, especially by mammals, to signal the general presence and identity of an animal for territorial or advertisement purposes (Gosling & Roberts, 2001). While such signals may persist in the environment for an extended time, they are less functional for immediate and direct communication (Eisenberg & Kleiman, 1972). Individual recognition via visual cues provides a more direct way of communication and is likely widespread in the animal kingdom. Most individuals of a species will vary in their phenotypes leading to slight differences in bodily shape and structure, or different colours or patterns (Baciadonna et al., 2024; Kondo & Izawa, 2014), providing grounds for individual recognition. However, such recognition requires visual access between the recogniser and the recognised, leading to the deterioration of recognition accuracy with distance, depending on the visual acuity of the species. In contrast, sound has the capacity to carry information across long distances in environments of low visibility, such as dense forests or aquatic habitats. Sound also provides relatively fast transmission, allowing for immediate and fast paced communication between individuals. Due to these advantages, it is not surprising that acoustic communication is found in all major groups of vertebrates (Chen & Wiens, 2020). Some highly social species will actively incorporate unique acoustic signatures into their vocalisations. For example, some parakeet species have individualised contact calls, and are even able to establish a direct communicative connection to a particular other individual through the imitation of their contact call, whilst still maintaining their own individual signatures (Thomsen et al., 2019). Likewise, bottlenose dolphins actively learn their identity signals almost reminiscent to a unique name (Janik et al., 2006). However, such advanced individualisation is not required for individual signatures to be encoded into vocalisations. More likely, the initial evolution of recognition would result from “byproduct distinctiveness” - subtle differences in genetics or anatomy that lead to differences between individuals and thus provide the basis for individual recognition to evolve. Such differences might be found in the components and composition of scents, differences in the visual appearance of an individual, or differences in acoustic features as a result of anatomical differences of the vocal apparatuses (Boughmann & Moss, 2003). In PAPER V, we examine such byproduct distinctiveness in American alligators. Using machine learning algorithms, we find acoustic individuality in the bellows of a crocodylian for the first time. We discuss our findings in relation to the potential use of acoustic individuality for conservation purposes, but also that acoustic individuality may provide a foundation upon which the evolution of recognition could evolve. We thus provide the basis for further studies examining individual recognition in this taxon. If future studies find individual recognition in crocodylians, this suggests similar capacities might have also been present in extinct dinosaurs.

4.5 Allogrooming and social relations

Evolution often modifies, repurposes, and builds upon existing morphological traits rather than producing entirely new ones. For example, during the evolution of flight in both mammals and birds, forelimbs were repurposed into leathery wings in bats, and feathery wings in birds. Similarly, some cognitive abilities may provide the foundation for others to evolve. For example, cognitive capacities such as object permanence, memory, and inhibitory control may lay the foundation for capacities such as cache pilfering in corvids to emerge (Bugnyar & Kotrschal, 2002; Bugnyar et al., 2007). The presence or absence of such behaviours in a given species or group of species might thus provide insights into their cognitive capabilities. By observing such natural behaviours, it then becomes possible to infer the presence of absence of cognitive abilities that underpin their behaviours. An example of such a complex social behaviour that evolved on a foundation of core cognitive functions is described below: allogrooming as a social currency.

The capacity for individual recognition and long-term memory of conspecifics lays the foundation for a wide variety of more complex social behaviours and socio-cognitive capacities (Boeckle & Bugnyar, 2012; Tibbetts & Dale, 2007). Once an animal can differentiate between other individuals and is able to attribute characteristics and previous experiences to others, friendships can emerge, long-term pair bonding can occur, and cooperation between individuals or within groups is possible. If it is possible to remember and differentiate between good and bad individuals, it becomes highly adaptive to maintain the relationships with cooperative individuals while reducing interactions with uncooperative ones (Muller et al., 2017). Such relationships are valuable and necessary for doing well in complex social groups (Thompson, 2019), which has led to the evolution of behaviours that help maintain and repair crucial relationships between individuals. For example, in primates and corvids, after agonistic encounters between members of a group, opponents will often seek out each other for reconciliatory purposes (Arnold et al., 2010; Fraser & Bugnyar, 2011), or they may seek out a third party for consolation (Romero et al., 2011; Sima et al., 2017). Both such behaviours have relationship mending and/or maintenance functions. A behaviour most often seen during such post-conflict situations, but also during other, more calm occasions, is social grooming, also called allogrooming in mammals and allopreening in birds.

Social grooming appears to have evolved separately in Sauropsids and Synapsids. It is widespread in mammals and can be found in a wide selection of marsupials and placentals (Connor, 1995; Dunbar, 1991; Kutsukake & Clutton-Brock, 2006; Matsuno & Urabe, 1999; Russell, 1984; St. John & Banks, 1970; Stieger et al., 2017; Val-Laillet et al., 2009; van den Bos, 1998), but has to my knowledge not been described in monotremes. In primates, allogrooming can function as a social currency that can be used to acquire favours in the future, or form alliances between group members (Schroepfer-Walker et al., 2015). The use of allogrooming for such purposes has so far not been observed in any non-primate mammal. However, it appears that some species have other, similar mechanisms that will be co-opted for similar purposes as anatomy allows, e.g., coalition forming dolphins "petting" each other for seemingly similar relationship maintenance benefits (King et al., 2021). It is not hard to imagine the potential of such a currency system when it comes to appeasing powerful individuals within a group hierarchy. The choice of who to groom then becomes a matter of politics, with favours and improved relations gained through grooming. An individual might thus gain favours and support from key members within their group to win hierarchical fights, or be offered food by others in the future when times are hard (Anza et al., 2021; Chapais, 1995; de Waal, 2000; de Waal, 1997).

In non-primate placentals, allogrooming seems to be primarily involved in the maintenance of relationships or group coherence, thus lacking a function as a social currency in a broader sense. In meerkats and rats allogrooming has been shown to be used to appease higher ranking individuals within a group (Kutsukake & Clutton-Brock, 2006; Schweinfurth et al., 2017), whereas in ungulates the direction of allogrooming is less clear (Hodgson et al., 2024) and may serve as a general behaviour for maintaining good relations (Val-Laillet et al., 2009). Allogrooming has also been found to be an affiliative behaviour for reconciliation and third-party consolation in horses (Cozzi et al., 2010). It is thus not unreasonable to assume that allogrooming might quickly become a useful appeasement tool if a strict social hierarchy evolves to become the dominant social structure within a species.

Within marsupials, little is known about allogrooming and its function. In marsupials, allogrooming occurs at lower frequencies compared to placentals, with large families such as Didelphidae and Dasyuridae seemingly lacking or showing very little evidence of this behaviour (Dempster, 1995; Dickman, 1988; González & Claramunt, 2000; Russell, 1984). Macropodids, such as kangaroos and wallabies, appears to be the only group in which allogrooming is observed regularly (Cordoni & Norscia, 2014; McLean et al., 2009; Russell, 1984). The exact function of such grooming is not known but is likely to serve similar functions as in placental mammals. When it comes to monotreme mammals, virtually nothing is known about their grooming behaviours. All five extant monotreme species are considered to be solitary species (Makuya & Schradin, 2024), although platypuses might share dens with conspecifics (Makuya et al., 2022). Whether or not monotremes allogroom has not been explicitly examined.

Within Sauropsids, reptiles, including crocodylians, do not appear to allogroom. However, all major groups of neognath birds have species members that allopreen (Kenny et al., 2017). Although allogrooming has evolved separately in mammals and birds, they share a common theme, namely relationship maintenance. While birds might aggregate and form flocks regularly, more complex social relationships tend to occur mostly between pair-bonded individuals with whom they reproduce, either for the year, or for life (Kenny et al., 2017; Picard et al., 2020). It is thus likely that allogrooming in birds, perhaps in concert with its anti-parasite advantages (Clayton et al., 2010), evolved as a means of facilitating strong relationships between parents, as some birds evolved a reproductive strategy involving altricial young that require a much-prolonged duration of parental care (Emery et al., 2007; Kenny et al., 2017). However, in some birds we also find behaviours that are comparable to the scheming primates. Many corvid species form socially complex non-breeder groups with complicated fission-fusion dynamics, until a life-partner is found, and a territory is established (Chen et al., 2022; Loretto et al., 2017; Uhl et al., 2019). In these species, we find similar behaviours such as the formation of alliances (Fraser & Bugnyar, 2012) and deceptive behaviours (Bugnyar & Heinrich, 2006; Bugnyar & Kotrschal, 2002). Fission-fusion dynamics are also found in many parrot species, and thus similar behaviours might also be found there (Balsby et al., 2012; Hobson et al., 2014; Schwing et al., 2016).

Palaeognath birds have been largely ignored when it comes to allopreening, with only sparse information and unsupported claims of allopreening existing in the literature. This is in spite of their unique reproductive mode consisting of paternal care of eggs and offspring produced by several females (Brennan, 2012), which is widely different from the reproductive systems of neognath birds. In PAPER VI we attempt to remedy this, by looking for allopreening in four species of palaeognath birds as well as an outgroup species known to allopreen: the common raven. We find no allopreening in any of the palaeognath birds, but these birds do preen themselves at comparable rates to common ravens. These findings fit well with the reproductive system seen in palaeognaths involving precocial young and paternal care with almost no cooperation between parents. Such a reproductive systems likely demands fewer behaviours directed at relationship maintenance (Kenny et al., 2017). Similar reproductive systems have been suggested in non-avian paravian dinosaurs (Varricchio et al., 2008) and as such it is likely that these animals also lacked allopreening behaviours.

5 Concluding remarks

Palaeocognition is an emerging interdisciplinary field which combines cognitive zoology, palaeontology and evolutionary neurobiology with the purpose of studying the evolution of cognition through deep time. While this interdisciplinary field opens for the exciting possibility of better understanding the evolution of cognition and why it has evolved the way it has, the nature of inferring what can no longer be directly observed also comes with an array of pitfalls that must be avoided. Only through a solid theoretical framework together with the combination of evidence from several avenues of research can we hope to be able to more accurately describe the likely cognition of extinct animals. These avenues relate to the comparative studies of the neurobiology and cognition, but also fields within developmental psychology, physiology, anatomy and other aspects of biology may aid in providing support for, or against, hypotheses on the cognition of extinct animals. Knowledge on the cognition of extant animals should then be tightly connected to osteological correlates, which provide the link between the past and the present.

This thesis provides some of the first large-scale cognitive comparisons of synapsids and sauropsids, and it only scratches the surface of what knowledge we might gain. Mammals and birds have strikingly similar neurocognition, but also show differences in their cognition and sensory modalities. While the synapsid lineage provides fewer opportunities for cognitive comparisons in deeper time due to their sparsity of extant outgroups, the understanding of mammalian cognitive evolution still provides valuable insights into how cognition evolved in the three extant mammalian lineages of monotreme, marsupial and placental mammals. Additionally, comparisons between synapsids and sauropsids might allow us to better understand whether cognition always evolves in a set order of steps, or whether it might differ between lineages but still allow for similar end points to be reached. In the future, neurobiology should be integrated more tightly with cognition through studies with specific focus on the neurobiology behind cognitive phenomena, such as visual working memory.

While this thesis contains a wide selection of species, certain groups are conspicuous in their absence, namely the non-archosaurian reptiles. These groups are of great importance for the understanding of cognitive evolution. I strongly encourage the study of these groups in a comparative framework, as they provide a cornerstone for the understanding of the evolution of endothermic neurocognition. Knowledge on the neurocognition of these animals allows us to better understand which cognitive processes were essential cornerstones for the evolution of endothermic cognition.

6 References

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