AN EXAMINATION OF NON-MAMMALIAN CYNODONT CRANIAL ENDOCASTS

by

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DECLARATION

I, the undersigned, hereby declare that the work contained in this dissertation is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree. I further more cede copyright of the dissertation in favour of the University of the Free State.

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DEDICATION

To the King of kings, the only living God, the Lord and my Saviour, Jesus Christ. All of the praise, all of the honour, all of the glorification belongs to You. I thank you for Your gifts, blessings and inspiration. Thank you for the three years during which I was blessed with the privilege to work with these animals. Everything that I am, is grace from Your hands. Without You I am nothing.

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SUMMARY

The palaeoneurology (study of the nervous system of extinct animals) of non-mammalian cynodonts, which were the ancestors of mammals, is poorly understood. It is thought that the relative brain size of cynodonts increased with time, and that this change significantly affected their physiology and behaviour. Forty-four cynodont skulls belonging to eleven genera from Permian, Triassic and Jurassic strata were scanned and analysed using neutron computerized tomography (NCT), at the SAFARI-1 Nuclear Research Reactor of the Nuclear Energy Corporation of South Africa (Necsa). Data concerning the endocranial casts was hereby obtained in a non-destructive manner. Four specimens, namely *Galesaurus*, *Platycraniellus*, *Langbergia* and *Tritylodon* produced successful scans and were used for further study. Measurements of the cranial material were used to calculate the size of the brain endocasts and the approximate body masses were determined from an equation using skull length. The encephalization quotient (EQ), a measure of brain size relative to body size, was determined for each specimen using brain volume and body mass. Changes in the position of the brain inside the skull, and an overall increase in size of the brain in the more derived cynodonts indicate some development towards the mammalian condition. Taxonomic variation regarding the shape and size of the olfactory bulbs and other parts of the brain endocasts is discussed and related to differences in ecology or behaviour. The relatively deep and large olfactory bulbs in some cynodonts may be an adaptation to either nocturnal behaviour, dietary or habitat preferences. Relatively large cranial endocasts in *Galesaurus, Platycraniellus, Massetognathus, Tritylodon, Chiniquodon* and the tritheledonts may be related to habitat preference or social behaviour. The basal epicynodonts *Galesaurus* and *Platycraniellus* have the largest cranial endocasts of all the cynodonts studied. Their large cranial endocasts may be related to behavioural or ecological preferences, but the results require confirmation from a larger sample size. The present study provides an important foundation from which further cranial endocast studies on cynodonts can be developed.

Key words: computerized tomography; Cynodontia; encephalization; palaeoneurology

SAMEVATTING

‘n Ondersoek van binneskedelvormafdrukke van nie-soogdieragtige Cynodontia

Min is bekend oor die palaeoneurologie (studie van die senuweestelsel van uitgestorwe diere) van nie-soogdieragtige Cynodontia, wat die voorouers van soogdiere is. Daar word vermoed dat die relatiewe breingrootte van Cynodontia oor tyd toegeneem het, en dat hierdie verandering hulle fisiologie en gedrag aansienlik beïnvloed het. Vier-en-veertig Cynodontia-skedels, wat tot elf genera behoort en uit Permiese, Triassiese en Jurassiese aardlae afkomstig is, is met behulp van neutron gerekenariseerde tomografie (NCT), by die SAFARI-1 Kernnavorsingsreaktor van die Suid-Afrikaanse Kernkragkorperasie (Necsa) geskandeer en ontleed. Inligting rakende die binneskedelvormafdrukke is hierdeur op ‘n nie-vernietigende wyse bekom. Vier eksemplare, naamlik *Galesaurus*, *Platycraniellus*, *Langbergia* en *Tritylodon*, het suksesvolle skanderings geproduseer en is vir verdere studie gebruik. Afmetings van die skedelmateriaal is gebruik om die grootte van die breinafgietsels te bereken en die benaderde liggaamsmassa is bepaal uit ‘n vergelyking wat van skedellengte gebruik maak. Die ensefalisasiekwosiënt (EK), ‘n maatstaf van breingrootte relatief tot liggaamsgrootte, vir elke eksemplaar is bepaal deur breinvolume en liggaamsmassa te gebruik. Veranderinge in die ligging van die brein binne die skedel, en ‘n algehele toename in grootte van die brein in die meer gevorderde Cynodontia dui op ‘n neiging van ontwikkeling in die rigting van ‘n meer soogdieragtige toestand. Taksonomiese variasie rakende die olfaktoriese lobbe en ander dele van die breinafgietsels is bespreek en verbind met verskille in ekologie of gedrag. Die relatief diep en groot olfaktoriese lobbe by sommige Cynodontia is dalk ‘n aanpassing vir naglewende gedrag, dieet- of habitatsvoorkeure. Relatiewe groot breinafgietsels in *Galesaurus, Platycraniellus, Massetognathus, Tritylodon, Chiniquodon* en die Tritheledonta word toegeskryf aan habitatvoorkeur of sosiale gedrag. Die basale Epicynodontia *Galesaurus* en *Platycraniellus* het die grootste breinafgietsels van al die Cynodontia wat bestudeer is. Hulle groot breinafgietsels hou dalk verband met gedrags- of ekologiese voorkeure, maar die resultate benodig bevestiging van ‘n groter monstergrootte. ‘n Belangrike fondering word deur hierdie studie gebied, waaruit verdere breinafgietselstudies by Cynodontia ontwikkel kan word.

Sleutelwoorde: Cynodontia; ensefalisasie; gerekenariseerde tomografie; palaeoneuroëtologie

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CHAPTER ONE
INTRODUCTION

1.1 Introduction

Synapsids include mammals and their 'pelycosaur' and therapsid ancestors. This group first appeared during the Late Carboniferous. Towards the middle of the Permian (267 million years ago (mya)) the therapsids first appeared (Lucas, 2004). The earliest therapsid fossils are found in Russia (Ivakhnenko, 2003; Lucas, 2004; Kemp, 2005, 2006) and China (Liu *et al.*, 2009). Their sudden appearance in the Middle Permian fossil record suggests that they may have evolved from members of the paraphyletic 'pelycosaurs' (Kemp, 2005), most likely the sphenacodontids (Hopson, 1991; Laurin, 1993; Kemp, 2005; Liu *et al.*, 2009), probably 30 million years earlier, during the Early Permian (Kemp, 2006). The history of the therapsids is well known, due to the many Permo-Triassic fossils found in Africa, Asia, South America and Antarctica (Parrish *et al.*, 1986; Behrensmeyer *et al.*, 1992; Milner, 1994; Li *et al.*, 1996; Berman *et al.*, 1997; Li & Cheng, 1997; Langer, 2000; Lucas, 2001; Kemp, 2006). The various groups of therapsids (Biarmosuchia, Dinocephalia, Anomodontia and Theriodontia) (Table 1) acquired increasingly mammal-like structures during their evolution, and exhibit a varying mosaic of reptilian and mammalian stages of organization (Sidor & Hopson, 1998; Kemp, 2005).

Table 1. Classification of the Therapsida. Modified from Rubidge and Sidor (2001), Ray *et al.* (2004) and Kemp (2005).

- THERAPSIDA
  - Biarmosuchia
  - Eutherapsida
    - Dinocephalia
    - Neotherapsida
      - Anomodontia
      - Theriodontia
        - Gorgonopsia
        - Eutheriodontia
          - Therocephalia
          - Cynodontia

Typical mammalian features, that appeared gradually during therapsid evolution, include highly differentiated teeth for various purposes (Osborn, 1973; Kemp, 2005, 2006); a bony secondary palate, allowing simultaneous breathing and chewing (Parrington & Westoll, 1940; Sidor, 2003a); a lower jaw that consists of a single dentary bone (Sidor, 2003b), with increased and specialized jaw musculature, permitting a stronger bite (Crompton & Parker, 1978; Ivakhnenko, 2002; Kemp, 2006); and remodelling of the inner and middle ear bones, permitting a wider range of audible sounds to be heard (Stebbins, 1980).

Postcranial features changed as a result of increasingly erect gait with upright limbs positioned directly beneath the body, allowing greater agility (Kemp, 1969a; Jenkins, 1971a, 1973; Jenkins & Parrington, 1976). The loss of lumbar ribs is correlated with the evolution of a diaphragm and may also have provided greater dorsoventral flexibility of the spinal column (Ruben *et al.*, 1987; Perry *et al.*, 2005). By the Early Cretaceous, the last group of therapsids, the non-mammalian cynodonts went extinct (Watabe *et al.*, 2007; Lopatin & Agadjanian, 2008), some time after giving rise to the first true mammals in the Late Triassic. The earliest mammals were probably for the most part tiny, nocturnal, insectivorous animals (Simpson, 1959; Hopson, 1969).

The non-mammalian cynodonts (herein referred to as cynodonts) are a group of therapsids that, together with the gorgonopsians and therocephalians, form a larger group called the theriodonts (Table 1). The evolutionary track of the cynodonts began late in the Permian, with the most basal genus yet found being *Charassognathus* (Botha *et al.*, 2007). Other basal cynodonts include *Procynosuchus* from South Africa, Zambia, Tanzania, western Germany and Russia (Sues & Munk, 1996), and *Dvinia* from Russia (Modesto & Rybczynski, 2000; Tatarinov, 2004). Their derived features suggest that cynodonts evolved much earlier, probably during the early part of the Permian. Cynodonts are one of the few therapsid groups that survived the end-Permian extinction. By the Triassic, they had a cosmopolitan distribution (Kemp, 2005), although the most complete fossil record of cynodonts is found in the Karoo Basin of South Africa. The Karoo Supergroup (Table 2) is known to contain one of the richest fossil records of therapsids in the world and the genera in the present study form part of these rich fossil assemblages.

Table 2. Biostratigraphy of the Karoo Supergroup, South Africa. The material used in the present study was recovered from the assemblage zones indicated in bold. The *Euskelosaurus* and *Massospondylus* range zones are informal zones and not formal assemblage zones. Modified from Rubidge (1995), Gradstein and Ogg (2004), Mundil *et al.* (2004) and McCarthy and Rubidge (2005). Abbreviations: mya, millions of years ago.

Geological periods	mya	Group	Formation	Assemblage zones
Jurassic	199.6	Drakensberg Basalt		
		Stormberg	Clarens	
			Elliot	***Massospondylus***
Triassic	252			*Euskelosaurus*
			Molteno	
		Beaufort	Burgersdorp	***Cynognathus***
			Katberg	***Lystrosaurus***
Permian	290		Teekloof	***Dicynodon***
				Cistecephalus
				Tropidostoma
			Abrahamskraal	*Pristerognathus*
				Tapinocephalus
		Ecca	Whitehill	*Mesosaurus*
Carboniferous	359.2	Dwyka		

Although morphological studies have provided extensive information regarding the phylogeny, food acquisition and processing, locomotion and biomechanical adaptations of cynodonts, little is known about their palaeoneurology (the study of the nervous system of extinct taxa). This information is necessary for understanding the early development and evolution of the mammalian brain.

1.2 Objectives of study

The examination of the brain and associated structures of an animal provides useful information regarding its biology. A comparison of the neurology of extant and extinct animals has improved the understanding of the lifestyle adaptations and indirectly the physiology of extinct animals (Hopson, 1980).

Earlier palaeoneurological studies concentrated mostly on non-avian dinosaur and mammal cranial endocasts (i.e. casts of the endocranial space, which is primarily filled by the brain) (Radinsky, 1977, 1978; Hopson, 1980). The Cynodontia is a large and well-known group and many skulls have been described and figured, but unfortunately, most of the descriptions confine themselves to the superficial bones, resulting in the braincase being poorly known (Figure 1). Furthermore, because only the hindbrain is usually well preserved (Kemp, 2009), and the cartilaginous sides and floor of the fore- and midbrain are not always determinable (Jerison, 1973; Kemp, 2006), previous reconstructions of cynodont brains have been inconsistent (Kemp, 2005).

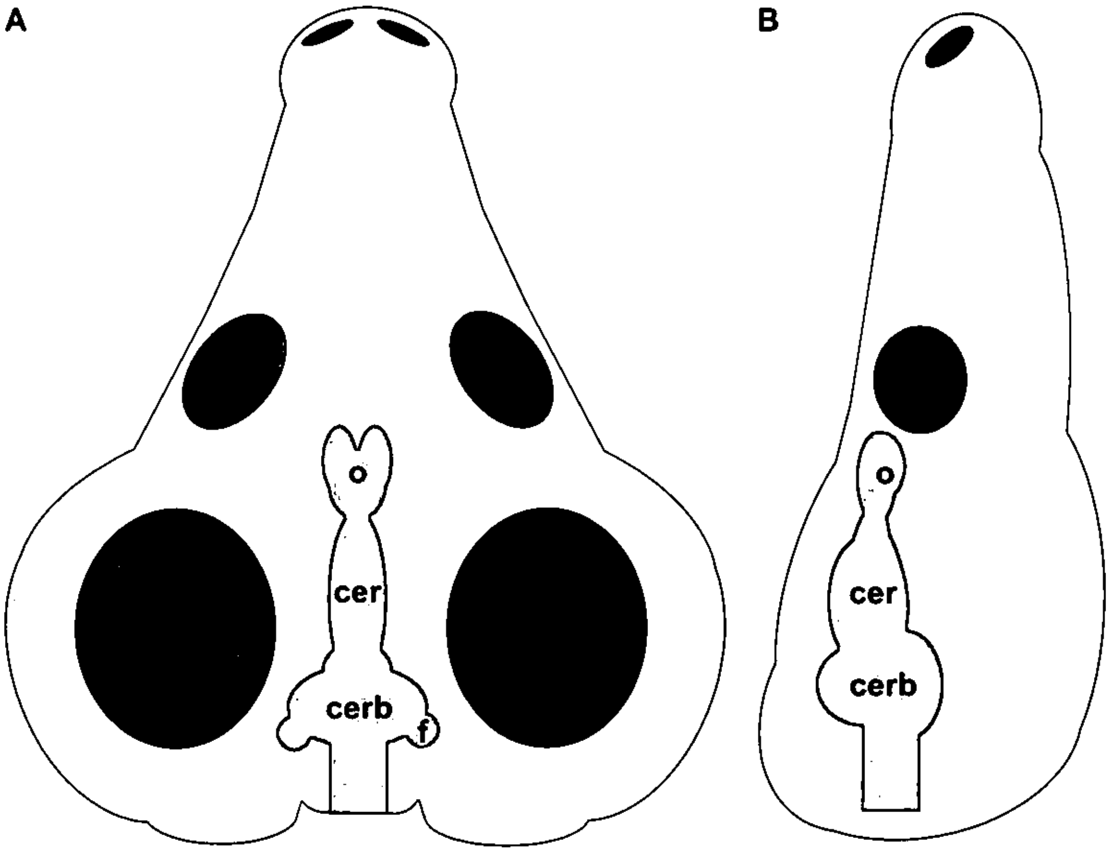

Figure 1. Schematic representation of the position of the brain within the endocranial cavity of a generalized cynodont skull in dorsal (A) and right lateral (B) views. Abbreviations: cer, cerebrum; cerb, cerebellum; f, flocullus; o, olfactory bulbs.

The braincase of *Procynosuchus* (Mendrez, 1972; Kemp, 1979, 1982), *Thrinaxodon* (Watson, 1913; Simpson, 1927; Hopson, 1969, 1979; Gow, 1986), *Diademodon* (Watson, 1913; Gow, 1986), *Trirachodon* (Hopson, 1979; Gow, 1986), traversodontids (Bonaparte, 1966; Kemp, 1982), tritylodontids (Hopson, 1964; Gow, 1986) and several South American genera (Quiroga, 1978, 1979, 1980a, b, c, 1984) have been studied in detail. Kielan-Jaworowska *et al.* (2004) reviewed the literature on the endocranial casts and reconstructed brains of cynodonts, as well as Mesozoic mammals, and tabulated published encephalization quotients (EQ) for these taxa (see **3.5 Assessments: Encephalization quotients**). Using computerized tomography in an attempt to determine the origin of endothermy in these therapsids, Rodrigues (2005) studied the nasal cavities and braincases of Brazilian cynodonts, while Kemp (2009) combined computerized tomography and acoustic transformation to describe the cranial endocast of *Chiniquodon*.

In the present study, the crania of several non-mammalian cynodont genera were selected for comparative analysis using computerized tomography. The genera represent early (basal) to later (derived) forms, which permit an assessment of the changes in cranial endocast shape and size during different stages of cynodont evolution. Eleven genera were assessed for their computerized tomographic compatibility (families indicated in Table 3). *Galesaurus* and *Platycraniellus*, which are basal epicynodonts, and *Langbergia* and *Tritylodon*, which represent more derived eucynodonts, were compatable.

The phylogeny in the present study (Table 3) follows that of Hopson and Kitching (1972), Hopson (1991), Rubidge and Sidor (2001) and Bonaparte *et al.* (2005), all of whom consider the Tritylodontoidea to be the sister group of the Traversodontidae. However, others such as Kemp (1982), Martinez *et al.* (1996), Luo *et al.* (2002) and Abdala (2007) place the Tritylodontoidea as the sister group to tritheledonts and mammals. This controversy has yet to be resolved.

Table 3. Classification of the Cynodontia. The families in bold were sampled for the present study and those used in further analysis are underlined. Modified from Hopson and Kitching (1972), Hopson and Barghusen (1979), Rubidge and Sidor (2001), Sidor and Smith (2004), Bonaparte *et al.* (2005), Sidor and Hancox (2006) and Botha *et al.* (2007).

- CYNODONTIA
  - Procynosuchia
    - Dviniidae
    - **Procynosuchidae**
  - Epicynodontia
    - **Galesauridae**
    - **Platycraniellidae**
    - **Thrinaxodontidae**
    - Eucynodontia
      - Cynognathia
        - **Cynognathidae**
        - Diademodontoidea
          - **Diademodontidae**
          - **Trirachodontidae**
          - **Traversodontidae**
        - Tritylodontoidea
          - **Tritylodontidae**
      - Probainognathia
        - Probainognathidae
        - Chiniquodontoidea
          - ***Lumkuia***
          - Chiniquodontidae
        - Tritheledonta
          - Therioherpetidae
          - Brasilodontidae
          - Tritheledontidae
        - Mammalia

The aim of the present study was to assess evolutionary trends exhibited by the relative brain size of the non-mammalian cynodonts. The examination of cranial endocasts was intended to assess the timing and origin of the mammal-sized brain and to shed light on the development of endothermy in the synapsid lineage, assuming these two events are associated. The following aspects were therefore examined:

1. *the variation of cranial endocast shape and size of the genera of cynodonts*
2. *the variation of cranial capacity (EQ) between basal and more derived genera of Cynodontia*
3. *individual variation of cranial capacity within species*
4. *a comparison with cranial endocasts of cynodonts and mammals in the literature to determine any evolutionary trends*

CHAPTER TWO
PALAEOBIOLOGY LITERATURE REVIEW

2.1 Thermophysiology of the Cynodontia

Terminology

Both the terms 'warm-blooded' and 'cold-blooded' have fallen out of favour with scientists, because of the vagueness of the terms, and due to an increased understanding in thermophysiology. Each term may be replaced within one or more alternatives. Body temperature maintenance incorporates a wide range of different techniques that result in a body temperature continuum, with the traditional ideals of 'warm-blooded' and 'cold-blooded' being at opposite ends of the spectrum.

'Warm-bloodedness' generally refers to three separate aspects of thermoregulation:

1. Endothermy (Greek *endo* = 'within', *therm* = 'heat') is the ability of some taxa to control their body temperatures through internal heat generation such as muscle shivering and fat burning (McNab, 1978, 1997). The meaning of 'endothermy' is sometimes restricted to mechanisms which directly raise the animal's metabolic rate in order to produce heat. When the principal heat source for the body is external, such an animal is called ectothermic (Nelson *et al.*, 1984; Garrick, 2008).
2. Homeothermy (Greek *homoios* = 'similar') is thermoregulation that maintains a relatively stable internal body temperature regardless of external influence (McNab, 1978). This temperature is often higher than the immediate environment. The opposite of homeothermy is poikilothermy.
3. Tachymetabolism (Greek *tachy* = 'fast, swift', *metabol* = 'to change') is the kind of thermoregulation used by taxa to maintain a high resting metabolism (Barrick *et al.*, 1997). Tachymetabolic animals are metabolically active all of the time, and although their resting metabolism

is still many times slower than their active metabolism, the difference is often not as large as that seen in bradymetabolic animals (low resting metabolism). Tachymetabolic species have greater difficulty dealing with limited primary resources, such as food (Barrick & Showers, 1999).

A large proportion of the animals that were traditionally called 'warm-blooded' (mammals and birds) fit into all three of these above-mentioned categories. However, many small mammal and bird species do not fit all of these criteria. These animals become poikilothermic and bradymetabolic when they enter daily torpor and/or hibernation (Bartholomew *et al.*, 1970; Turbill *et al.*, 2003; Maddocks & Geiser, 2007; Cooper & Geiser, 2008; Cory Toussaint *et al.*, 2009) and are thus heterothermic, with different internal body temperatures from when they are more active.

Ectothermy versus endothermy

Living reptiles differ from living mammals and birds in that reptiles obtain heat externally from their immediate environment (Marais, 2004), usually from the sun (heliothermy) or warm surfaces (thignothermy) (Alexander & Marais, 2007). All reptiles bask by absorbing warmth from the environment. Reptiles are also able to vasodilate or vasoconstrict vessels in their circulatory systems to modify rates of heat exchange, and can modify heart rate to reduce or enhance the transport of heat by the circulatory system (Alexander & Marais, 2007). Some species, like crocodilians, are able to pant as a means of evaporative heat loss (Alexander & Marais, 2007).

Birds and mammals use a different strategy in that they maintain a constant internal temperature independently of external conditions. In conditions of excessive heat, body temperature is kept low by evaporative cooling, such as panting or sweating (Hafez, 1964). When environmental temperatures decrease, they raise their metabolic rates to counteract the increased rate of body heat loss. This is achieved by a high and accurately controlled rate of metabolism, rapidly oxidizing carbohydrates and fats as fuel to keep their internal temperature at a constant level of warmth usually relatively higher than their surroundings. Shivering from the cold is one of several ways to increase metabolic rate (Alexander & Marais, 2007). If their internal temperature falls much below the specific constant, death from hypothermia may occur (King & Murphy, 1985).

Reptiles do not generate heat internally (Marais, 2004) by metabolizing food as mammals and birds do. The advantage of ectothermy, therefore, is fuel efficiency. Reptiles lose heat to the environment more quickly when it becomes colder, causing a decrease in metabolic rate and temporary dormancy until the environmental temperature increases again (Alexander & Marais, 2007), and provided they are protected from danger, they need not waste energy. Mammals and birds, on the other hand, may have a metabolic rate several times that of a similar-sized reptile at low environmental temperatures (Speakman, 1997), requiring a constant supply of food, for they convert 90% of the food they eat into heat in order to maintain muscle and biochemical efficiency at all times. This allows them to operate at times (late at night and winter) and in extreme climates (polar tundra and cold seas) that reptiles cannot (Alexander & Marais, 2007).

Evolution of endothermy in synapsids

There is general consensus that basal synapsids, like living reptiles, were ectothermic, relying on their environment and the sun as their primary sources of body heat (Kemp, 1982, 2005; Turner & Tracy, 1986). Progressive changes in the postcranial skeletons of the various therapsid groups suggest increasingly mammal-like activity levels (Jenkins, 1970; Kemp, 1982, 2005, 2006, 2007; Colbert, 1986), although the specific thermoregulatory status of therapsids remains uncertain (Bennett & Ruben, 1986). Features of the earliest mammals (Kemp, 2005), and some derived cynodonts from the Middle Triassic (McNab, 1978), suggest that these cynodonts, based on their phylogenetic proximity to living mammals (Hopson, 1980), may have evolved a basic form of endothermy. However, they probably had a lower body temperature than that of living placental mammals (McNab, 1978), similar to the metabolic rates of living marsupials that are about 70% to 80% the rate of placental mammals

(MacMillen & Nelson, 1969; Dawson & Hulbert, 1970). Because very little information is available for early mammals, Hopson (1980) speculated that all post-Jurassic fossil mammals were most likely endothermic, because their relative brain sizes group closely to that of living endothermic mammals.

Body size

'Pelycosaurs' and early therapsids such as the dinocephalians may have controlled their body temperature simply by increasing their body size (McNab, 1978; Kemp, 2005). Large size provides greater protection against predation (Warren & Lawton, 1987; Pennings, 1990; Reinhardt *et al.*, 2001; Basolo & Wagner, 2004), and permits a more efficient use of resting metabolic rate independent of climatic change (Humphries *et al.*, 2004). This happens because the metabolic rate of a mammal varies is proportional to the surface area rather than to body mass (Woodward, 1988; Speakman, 1997). Surface area equals approximately 0.7 power of body mass, meaning that smaller animals have larger surface areas relative to their mass. As animals become larger, the body surface increases much more slowly than body volume (Kemp, 2005), because surface area increases as the square of body length (L^2), whereas volume (and therefore mass) increases as the cube of body length (L^3) (Hickman *et al.*, 2004).

A small animal has a relatively large surface area, and will thus heat up and cool down more quickly than a large animal. Large, primitive synapsids may have lost and gained heat to and from their surroundings so slowly that even the alternation of night and day would have had a negligible effect on their body temperature. Such animals would probably have been inertially homeothermic (gigantothermic) (Kemp, 2005).

At the end of the Triassic, the first mammals, such as *Morganucodon* and *Megazostrodon*, were minute shrew-like animals (approximately 10-12 cm in length) with an estimated body mass of 5-20 g (Jenkins & Parrington, 1976; Kemp, 2005). Large mammals did not exist during the Mesozoic (Woodward, 1988). *Repenomamus*, a Chinese triconodont, *Steropodon*, an early monotreme, and the Cretaceous marsupial *Didelphodon*, were relatively large for Mesozoic mammals (about the size of a Virginian opossum to a Tasmanian devil (Hu *et al.*, 2005), cat (Johnson, 2006) and badger respectively (Lillengraven, 1979)). This supports the idea of McNab (1978), who suggested that endothermy may have preceded the appearance of mammals by at least 25 million years, based on a reduction in body size. Such a new method of controlling body temperature required many changes, including modified jaws and teeth, locomotion, breathing control, and external insulation to maintain the body's internal temperature. However, Kemp (2005) correctly pointed out that this trend is not all that clear, since there are small, medium and large species in every synapsid order, including cynodonts.

Pelage

Fur is not necessary thermoregulation in larger animals (and many of the therapsids were large, up to the size of oxen or rhinoceroses), because they have a proportionately smaller surface area relative to their body mass through which heat may be lost. There appears to be a mass barrier of approximately 1.5 ton that acts as a natural limit for the absence of pelage, and nearly all birds and mammals below this mass are insulated (Colagrande & Felder, 2000).

It is unknown what kind of skin covering therapsids had. However, fossil skin impressions of the primitive therapsid *Estemmenosuchus* show that these animals lacked scales, and may have had skin glands, similar to living mammals (Bennett & Ruben, 1986; Oftedal, 2002a). Harderian glands, structures associated with grooming and maintenance of the pelage in living mammals (Thiessen & Kittrell, 1980), are thought to have been absent in therapsids, but may already have been present in Late Triassic mammals (Hillenius, 2000), suggesting that hair, and possibly complex grooming behaviour, did not occur before the appearance of the Mammalia (Ruben & Jones, 2000). The oldest fossilized fur is found in Middle Jurassic docodonts (Ji *et al.*, 2006), eutherians from the Early Cretaceous (Ji *et al.*, 2002; Hillenius & Ruben, 2004) and Palaeogene multituberculates (Meng & Wyss, 1997), so hair was probably present in the common ancestor of these mammals.

Vibrissae, commonly called 'whiskers', are modified hairs that provide tactile sense to many mammals, and are especially long in nocturnal, arboreal and burrowing animals (Ahl, 1986; Park *et al.*, 2007). The origin of hair is poorly known, but it is possible that vibrissae may have appeared before insulative fur evolved, because sensory hairs do not necessarily indicate the presence of any form of pelage (Ruben & Jones, 2000). The presence of tiny pits in the bones of the muzzle of *Thrinaxodon* indicates nerve-endings and suggests that these small openings may have held protovibrissae (Chernova, 2006). Similar foramina are, however, present in the skulls of reptiles (Ruben & Jones, 2000).

2.2 Dentition

Parallel evolution of the synapsids and anapsid pareiasaurs resulted in the development the evolution of heterodont dentition (teeth of different sizes and shapes) (Kordikova & Khlyupin, 2001). Even the earliest 'pelycosaurs' had three kinds of teeth in their jaws. In cynodonts the small, sharp nipping incisors at the front were separated from the biting molars at the back by a pair of long, stabbing canines in both the upper and lower jaw (Ziegler, 1969). These teeth were renewed periodically by waves of replacement along each jaw.

The more derived therapsids departed from this regular tooth replacement pattern. Instead, teeth were replaced only a few times during the animal's life (Kermack, 1956; Ziegler, 1969). This was a major development, because it allowed each molar to remain in the jaws for a longer period so that the opposing crowns could develop a complex pattern of blunted points and valleys. These allowed for the development of tooth occlusion, which improved the chewing process (Grine, 1976, 1977). Well-chewed food is digested more quickly, which results in a more rapid release of nutrients needed to fuel the body and allow for a more active metabolism.

The teeth in the lower jaw were lodged in a single enlarged dentary bone with a high coronoid process to which jaw muscles were attached (Kemp, 1982; Rubidge & Sidor, 2001). This was a much stronger arrangement than that of earlier synapsids, with several bones in the lower jaw. The dentary development may have been the direct result of the evolution of the synapsid type of skull, with a single pair of temporal fenestrae, set low behind each eye socket that gradually became transformed into the temporal fenestrae of cynodonts that are much larger than those of their ancestors. The widening of the zygomatic arch allowed for more robust jaw musculature supporting the evidence that feeding represents the functional impetys for the development of a more mammal-like skull (Rubidge & Sidor, 2001).

2.3 Senses

Hearing

During synapsid evolution, the dentary progressively enlarged and the bones below and behind it became smaller and moved to the back of the jaw (Kemp, 2005). This freed these smaller bones of the lower jaw to become involved in forming the mammalian middle ear.

The two bones, the quadrate and articular, which formed the joint between the skull and the lower jaw in therapsids (Kemp, 2005) entered into the middle ear in mammals. Here, they became the incus and malleus, and linked up with the already present stapes (Stebbins, 1980), to form a chain of three ear ossicles. Sound vibrations are transmitted and amplified along this chain from the outer eardrum to the fluid-filled canals of the inner ear in living mammals. The progressive reduction of these three ear bones can be traced in cynodonts (Kemp, 2005) and can still be seen during the development of a living mammal embryo (Goodrich, 1915).

Acute mammalian hearing is aided by a pair of fleshy ear-flaps or pinnae on either side of the head, which are able to pinpoint the exact source of any sound, even when faint. It is however, not certain precisely when these external ears evolved, although the external ear canal was present in therapsids (Olson, 1971; Stebbins, 1980). Improved hearing gave these animals a better awareness of their environment and, in turn, this increased amount of auditory information called for a greater capacity for processing in the auditory centres of the brain. The level of development of the sensory organs suggests that at least the early mammals were capable of being nocturnal and/or fossorial (Stebbins, 1980; Kemp, 2005).

Smell

Most mammals make extensive use of smell (Kermack & Kermack, 1984), and this sense is generally more acute and important to the lifestyles of those mammals that are nocturnal or live in subterranean darkness and do not rely on vision. However, many diurnal reptiles also depend largely on their sense of smell (Alexander & Marais, 2007). The well-developed turbinal bones in mammals probably increased the area of the olfactory epithelium (Kermack & Kermack, 1984; Kemp, 2005), in addition to of being involved in the warming of air passing into the lungs, as has been suggested by Hillenius (1992). Other methods of water conservation due to rapid ventilation rates in endotherms are possible, as the maxilloturbinate bones are poorly developed or absent in a small number of mammals (Scott, 1954; Bang, 1971; Sikes, 1971).

Ventilation

Reptiles ventilate their lungs by negative pressure; air is pulled into the lungs by expansion of the thoracic cavity (squamates) or by movement of internal organs (chelonians and crocodilians) (Klein & Owerkowicz, 2006; Perry *et al.*, 2009). Thickening of the thoracic ribs and lumbar rib reduction in cynodonts (Perry *et al.*, 2009), may have provided greater dorsoventral flexibility of the spinal column (Hickman *et al.*, 2004), but it was probably mainly correlated with the evolution of a dome-shaped, muscular diaphragm between the chest cavity and abdomen. Such a development would have allowed larger lungs to be filled and emptied more rapidly and more frequently, enabling cynodonts to breathe more efficiently than their ancestors (Cloudsley-Thompson, 2005). This, in turn, resulted in more oxygen entering the bloodstream, which allowed the tissues to use oxygen more quickly. This development could speed up digestion or increase muscular exertion, when, for example, chasing prey or avoiding predators. It represents an essential development in the evolution of body temperature control. It seems as if at least some Triassic therapsids may have exhibited mammal-like ventilation (Ruben & Jones, 2000).

A secondary palate, which at first was probably membranous (Sidor, 2003a; Kemp, 2006) and then bony, developed in the roof of the mouth in theriodonts, to separate the respiratory nasal passages from the mouth cavity (Oftedal, 2002a). This secondary palate caused air flow from the nostrils to travel above the mouth and enter the throat instead of directly through the mouth. Thus the food or prey item that filled the mouth of an animal did not stop it from breathing, and so it would be able to chew its food in preparation for digestion without depriving its body of oxygen (Maier *et al.*, 1996; Oftedal, 2002a).

The development of a secondary palate helped the animal to maintain a high level of activity and because it allowed for a constant supply of oxygen, which was a necessary feature for the development of endothermy in the derived theriodonts (bauriamorph therocephalians and cynodonts) (Parrington & Westoll, 1940; McLoughlin, 1980). It has also been suggested that a soft secondary palate existed in earlier therapsids as well (Sidor, 2003a; Kemp, 2006). The secondary palate may also have been important to subsequent mammalian evolution by permitting the young to breathe while suckling (Maier *et al.*, 1996; Oftedal, 2002a, b).

2.4 Posture and locomotion

Most extant reptiles walk with their legs splayed outward and their ventral surface close to the ground (Blob & Biewener, 2001; Reilly & Blob, 2003). The 'pelycosaurs' of the Late Carboniferous and Early Permian had a typical reptilian sprawling posture – bending the body from side to side, with the limbs sprawled out horizontally. In the therapsids, flexure of the limbs and body in the vertical, rather than the original horizontal plane, developed. In addition, the orientation of the feet changed, from projecting laterally to facing forward, and the toes became shorter and similar in length (Kemp, 2005).

The cynodont posture differed from the reptilian pattern in that the strong hindlimbs became positioned directly beneath the body (Rubidge & Sidor, 2001), leaving more room for the lungs to develop, an essential trait of endothermic mammals (Carrier, 1987). This new posture greatly improved their agility (Kemp, 1982) and body weight support (Hickman *et al.*, 2004). In addition, the limb bones in cynodonts became increasingly slender and developed bony processes at the joints for firmer muscle attachment (Hickman *et al.*, 2004), allowing for a longer stride and a faster leg swing. The forelimbs were however still sprawling, similar to reptiles (Jenkins, 1971a; Kemp, 1980, 1982; Blob, 2001), and only in the tritylodontids and early mammals did the elbow turn backwards, placing the forelimb below the body (Jenkins, 1971b).

2.6 Brain shape and size

The brain is a metabolically expensive organ, and consumes approximately 25% of the body's metabolic energy. It therefore evolved conservatively and the brain of vertebrate species rarely enlarged in evolutionary history (Jerison, 1969). Isler and Van Schaik (2006) showed that energetics is a problem in maintaining a relatively large brain. Hulbert (1980) pointed out that about 5-10% of a mammal's basal metabolic rate is due to the metabolic activity of its brain. This means that selection for an enlarged brain may have served as a selective pressure for the development of endothermy. The endothermic condition, with its stable optimum temperature, allows for the maintenance of a more highly organized and sensitive nervous system (Manger, 2006). The brain in living endothermic vertebrates, such as birds and mammals, has increased in size, on average ten times more than those of living ectotherms (Hopson, 1980) and completely fills its cavity in the enlarged cranium (Kemp, 2005). This suggests that a link exists between activity levels (and possibly degree of environmental awareness), metabolism rate, and relative brain size (Niven, 2005; Isler & Van Schaik, 2006; Manger, 2006).

Cynodonts are thought to have had better developed brains than most extant reptiles (Hopson, 1979, 1980; Quiroga, 1979; Kemp, 2009). In non-cynodont synapsids the brain was elongated, narrow and tubular, similar to those of extant reptiles (Hopson, 1979; McLoughlin, 1980). It gradually widened and deepened posteriorly during the evolution of cynodonts (Hopson, 1979; Kemp, 1979). In mammals, the brain is expanded (Hopson, 1979) and fills most of the rear of the skull (McLoughlin, 1980). The prominent olfactory bulbs and cochlear region of the inner ear were well-developed in cynodonts (Hopson, 1979), suggesting that smell and hearing played a particularly important role. Because of their phylogenetic proximity to living endothermic mammals (see Table 3) the possession of anatomical characters believed to be related to endothermy, and since their relative brain sizes were intermediate between those of living ectothermic reptiles and endothermic mammals, Hopson (1980) expected cynodont therapsids to have been partially endothermic. Kemp (1969b) attempted to reconstruct a gorgonopsian brain and suggested that it was larger than the average size of ectothermic animals in general. According to Bennett and Ruben (1986), however, the link between brain size and thermoregulation remains speculative, based on Hopson (1980), who showed that the relative brain size of the cynodonts *Thrinaxodon* and *Trirachodon* are closer to those of extant monitor lizards, which are active, intelligent animals, but are still ectothermic.

2.7 Palaeoenvironment and its influence on the palaeofauna

Approximately 300 million years ago, the great ice sheet that had covered most of Gondwana began to melt, and this relatively cool supercontinent (Chumakov & Zharkov, 2002) became populated with basal synapsids that came from Laurasia. These animals arose amongst the temperate Permian forests and evolved to become the dominant land vertebrates. About 260 million years ago, during the Middle to Late Permian, South Africa was a low-lying area with broad meandering rivers. Silt and fine mud were deposited on vast floodplains during periods of catastrophic flooding after heavy rains (McCarthy & Rubidge, 2005).

It was on these Karoo floodplains that the therapsids thrived and diversified to fill various ecological niches.

The end of the Permian Period, about 252 million years ago (Saunders & Reichow, 2009), coincided with a number of factors that gradually, over about 100 000 to 500 000 years (Smith, 1995; Smith & Ward, 2001; Sidor & Smith, 2004), combined to create a world in distress. The formation of Pangaea led to a general lowering of sea levels, and many important shallow coastal areas and coastline habitats were destroyed in the process. The abundant annual rain (Parrish *et al.*, 1986) and mists that rose at sea could no longer reach the central interior of Pangaea, due to the rain shadow effect of the mountains in southern Gondwana (Sidor & Smith, 2004), which caused some parts of Pangaea to become drier. Deserts grew larger (Chumakov & Zharkov, 2003), and animals not adapted for life in arid conditions became extinct.

On the floodplains of the Karoo Basin, during the deposition of the Katberg Formation, lush riparian vegetation disappeared (Retallack *et al.*, 2003), due to reduced channel bank strength and increased siltation, as the river systems changed from meandering to braided (Ward *et al.*, 2000; Smith & Ward, 2001). The floodplains, which were at least seasonally moist (Parrish *et al.*, 1986), became seasonally to predominantly dry (Smith, 1995). This caused the extinction of small herbivorous dicynodonts and small carnivorous gorgonopsians (Sidor & Smith, 2004). Subsequently, the replacement of gallery forest trees and shrubs (mainly *Glossopteris*) by a diverse *Dicroidium*-dominated flora (Kemp, 1982; Steiner *et al.*, 2003; McCarthy & Rubidge, 2005) took place. This resulted in the demise of the larger dicynodonts, therocephalians and gorgonopsians (Kemp, 1982; Sidor & Smith, 2004).

As the Early Triassic continued, Pangaea began to drift northward until it lay right across the equator. Although wetlands were still widespread, as indicated by the occurrence of lycopsids (Rayner, 1992; Retallack, 1997) and labyrinthodont amphibians (Parrington, 1948; Rubidge, 1995; Damiani, 2004), the vast lowland swamps that had dominated the supercontinent for so long slowly disappeared, and gymnosperms began to dominate instead (Kemp, 1982). As the period progressed, Sahara-sized, semi-arid to arid areas with seasonal rainfall began to appear (Robinson, 1973; Tucker & Benton, 1982; Anderson & Anderson, 1983, 1985; Parrish *et al.*, 1986; Kutzbach & Gallimore, 1989; Smith *et al.*, 1993; McCarthy & Rubidge, 2005; Pires *et al.*, 2005; Smith & Botha, 2005), especially in the interior of the immense landmass. The Karoo Basin experienced warm, dry summers followed by cool, wet winters (Kiehl & Shields, 2005). The beginning of the Jurassic Period was characterized, not only by increasing temperatures (Wignall & Bond, 2008), but also by a sudden rise in humidity, which is attributed to widespread volcanism (Svensen *et al.*, 2007; Aarnes et al., 2009; Ruckwied & Götz, 2009).

2.8 Use of computerized tomography

Computerized tomography (CT) (*sensu* Kak & Slaney, 2001) is an imaging method that employs digital radiography (Whitehouse, 2000). Digital geometry processing is used to generate a three-dimensional image of the inside of an object from a large series of two-dimensional transmission digital images (radiographs). These radiographs, taken around a single axis of 360° rotation, are formed based on the attenuation of the radiation (related to density and/or chemical composition) as it passes through an object (DeVore *et al.*, 2006). The primary benefit of this technique to palaeontology is that features of the inside of a skull (fossil or extant) can be examined and endocasts can be extracted without destroying the specimen (Rowe *et al.*, 1999; Marino *et al.*, 2000; Ketcham & Carlson, 2001; Tykoski *et al.*, 2002; Brochu, 2003; Witmer *et al.*, 2003; Alonso *et al.*, 2004; Macrini *et al.*, 2006, 2007a, b, c). Volumetric reconstructions show far more structural detail, although they are superficially similar to conventional photographs (Tykoski *et al.*, 2002).

Penetrating radiation, X-rays and gamma rays or neutrons, is generated using a continuous potential X-ray source, radio-isotope or nuclear research reactor, respectively. The radiation passes through inanimate specimens, which are slowly and smoothly rotated (Sutton, 2008). A scintillator transforms the radiation image into a visible photon image (radiograph), which is then captured by a two-dimensional charge couple detector (CCD) array. The detector captures the digital data streams that represent varying radiographic intensities of the sample from every degree in a 180° rotation (Sutton, 2008).

Thus, in conventional radiography, an integrated shadow image of the object is compressed into a single plane (radiograph), but in CT, the radiographs are used to produce a very high-quality three-dimensional computer model or isosurface-based virtual fossil which can be manipulated and dissected within digital space (Sutton, 2008). This dissection in digital space is done through a process known as segmentation, and is done in order to demonstrate various structures based on their ability to absorb or scatter the beam of radiation. Differences in physical density of fossil and matrix can be distinguished, even where materials are similar (Dominguez *et al.*, 2002), although there are cases where attenuation contrast is unsufficient (Sutton, 2008).

Detailed internal structures, such as the shape of the brain, that can usually only be examined when a fossil is physically dissected can be viewed in this way (Smith *et al.*, 2009). Although historically, the images generated were in the axial or transverse plane, modern visualisation software programs allow this volume of data to be reformatted in various planes or even as three-dimensional representations of structures.

The data scans are obtained by using an inverse Radon transform (Kak & Slaney, 2001) and are combined with the mathematical procedure known as tomographic reconstruction. The resolution of a tomographic dataset from a scan is directly proportional to the resolution of the detector, but the range of volume element (voxel) sizes a scanner can achieve depends on the configuration and precision of the device (Sutton, 2008). This data can then be displayed, photographed, or used as input for further processing.

Although computerized tomography is a relatively accurate procedure, it can produce artefacts (Wang & Vannier, 1994; Shikhaliev, 2005; Meganck *et al.*, 2009). These artefacts are caused by sudden transitions between materials of low and high attenuation (Baissalov *et al.*, 2000; Preuss *et al.*, 2008). This results in data values exceeding that of the dynamic range of the processing system (Bieberle & Hampel, 2006).

The increased availability of CT facilities has been responsible for an increase in popularity and its utilization as a moderate to high radiation diagnostic technique (Watkin *et al.*, 2009). Although technical advances have improved radiation efficiency, there has been pressure to obtain higher-resolution imaging and to use more complex scanning techniques, both of which normally produce higher induced doses of radioactivity in samples when thermal neutrons are used as a radiation probe (F.C. de Beer, *pers. comm.* 2009[1]). The quality of the radiograph produced in the detector of a particular study depends on multiple factors: the volume of the specimen, its shape, density, the number of rotational projections, resolution and image contrast (Davis & Wong, 1996; Bayraktar *et al.*, 2008; Gomi & Hirano, 2008).

New software technology uses filters that significantly reduce random noise and enhance structures. In this way, it is possible to obtain high quality images. Careful editing of digital volumes also allows for the removal of noise (Sutton *et al.*, 2001).

A new technique called synchrotron X-ray tomographic microscopy (SRXTM) allows for detailed three-dimensional scanning of fossils. It prevents beam hardening and geometric artefacts in the images (Olejniczak *et al.*, 2007) and allows non-invasive high definition scans of objects, that result in data of exceptional resolution and clarity (Sutton, 2008), making it easier to take measurements (Olejniczak *et al.*, 2007). SRXTM has been applied in the field of palaeontology to perform non-destructive internal examinations of small fossils, including fossil embryos (Donoghue et al., 2006) and teeth (Olejniczak *et al.*, 2007).

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Whereas high-resolution X-ray CT maps regions of different densities within an object, neutron computerized tomography (NCT) is sensitive to differences in the concentration of some light organic materials containing hydrogen and carbon (Graf *et al.*, 1983; Schwarz *et al.*, 2005). The image quality is therefore strongly influenced by the resinous materials used for the reconstruction and conservation of the objects. Metal inclusions used to satabilize bone usually scatter the X-rays in CT, but these inclusions can be penetrated far better in NCT. However, NCT cannot be used for specimens with a cross-sectional thickness above 120 mm, and its resolution is far lower (100 μm) than that of research X-ray CT in terms of minimum voxel size (approximately 50 μm) (Winkler, 2006). High-density neutron bombardment can furthermore induce hazardous radioactive levels in some geological materials (Sutton, 2008), requiring specimens to be kept in quarantine for a period of time after NCT study. Generally, a high intensity of radiation through a specimen results in high quality images. A lower intensity leads to increased image noise and results in blurred images. Although Sutton (2008) states that X-ray CT remains the most useful tomographic technique, Rant *et al.* (2002) and Schwarz *et al.* (2005) found that by combining X-ray and neutron CT data, the information on internal structures can be improved.

2.9 Palaeoneurology and interpreting lifestyles

Fossils can preserve evidence of physical and biological activity within a prehistoric population (Pandolfi, 1992; Boyce *et al.*, 2001). Studying the anatomy of fossils can provide information on aspects of the lifestyle, diet, movement, and growth of extinct animals. By combining information from other, comparable finds with a detailed knowledge of the anatomy of extant animals, the appearance, behaviour and environment in which fossil organisms lived, can be reconstructed (Barrett & Rayfield, 2006).

The braincase is one of most poorly understood regions of the fossil vertebrate skeleton (Serrano-Brañas *et al.*, 2006), because other parts of the cranium often partially or completely obscure the braincase from view. Cranial endocasts (*sensu* Colbert *et al.*, 2005; Macrini *et al.*, 2006) are three-dimensional representations of the space within the cranial cavity (i.e. the endocranial space), which is filled primarily by the brain in vivo. In birds and mammals, an endocast reflects the external surface of the brain relatively well (Jerison, 1969). Reptilian endocasts do not closely follow the shape of the brain, but are adequate for comparing the forebrain, midbrain and hindbrain with each other and for identifying some of the cranial nerves, blood vessels and inner ear strcutures. In the fossil record, natural cranial endocasts are rare (Serrano-Brañas *et al.*, 2006). Soft tissue structures, such as organs, only fossilize under extraordinary conditions. Because of the extreme rarity of this type of soft tissue preservation, palaeontologists often rely mostly on cranial endocasts to study the brain and associated sensory systems in extinct animals. These three-dimensional fossils of the braincase are an important source of palaeontological information, but can be difficult to visualize and study (Macrini *et al.*, 2007c; Sutton, 2008), since they represent the soft anatomy. This branch of palaeontology dealing with the nervous system of fossil animals is known as palaeoneurology (Jerison, 1973; Buchholtz & Seyfarth, 1999).

In the past, studies of fossil brains were restricted to natural endocasts (Jerison, 1973) or specimens from which artificial endocasts could be easily extracted, by filling the cleaned braincase with clay (Schoch, 1983) or liquid latex (Boonstra, 1968; Radinsky, 1977). However, the cavities of many fossil skulls are filled with matrix and could previously only be studied through the destructive method of serial sectioning (Sollas, 1904; Olson, 1944; Boonstra, 1968). Recently, however, computerized tomography has proved to be effective to replace physical extraction of endocasts from skulls, fossil or extant, without damaging the specimens (Marino *et al.*, 2000; Witmer *et al.*, 2003; Macrini *et al.*, 2006, 2007a, b, c).

In extant reptiles, the brain is small, never exceeding 1% of the body weight (Hickman *et al.*, 2004), and does not completely fill the cavity in which it lies, thus an internal cast of the cavity does not represent either the real size or the exact shape of the brain (Edinger, 1951). In contrast, the brain shape of mammals is closely applied to the surrounding membranes and the endocranial space (De Beer, 1937), and leave impressions of its gross structures on the internal surfaces of skull bones. The importance of cranial endocasts for studying the evolution of the brain in extinct mammals has, for this reason, long been recognized (Edinger, 1964; Radinsky, 1977).

Macrini *et al.* (2007b) found that more than one-third of the phylogenetic characters of the endocranial cavity examined in their study of opossums showed some kind of variation (ontogenetic, individual, or both). This suggests that although endocasts are potentially informative for systematics, both ontogenetic and individual variation affect how endocranial characters are scored for phylogenetic analysis. Several earlier studies (Luo *et al.*, 2002, 2003) used central nervous system characters to determine phylogenetic relationships of extant animals. Relatively few studies have incorporated exclusively endocranial space characters into phylogenetic analyses of extinct and extant taxa (Kielan-Jaworowksa *et al.*, 2004). Because endocasts, especially those of fossil taxa, are difficult to visualize and study, the internal cranial morphology is poorly represented in phylogenetic analyses (Macrini *et al.*, 2007c).

Examining the sensory system is important for understanding the lifestyles, ecological niches and behavioural evolution of organisms (Coria & Currie, 2002; Macrini *et al.*, 2007c), especially because endocasts tend to be more conservative than those parts of the skeleton more directly associated with feeding, locomotion or other highly adaptive functions (Bakker *et al.*, 1988). Behaviour is often a response to environmental stimuli (Hickman *et al.*, 2004), that are processed and coordinated by the brain (Makeig *et al.*, 2009). The evolution of behaviour and the brain is therefore correlated (Macrini *et al.*, 2007c).

Comparisons of the relative sizes of major structures of the brains of extant animals are used to infer the degree of evolution of different sensory systems (Rupp *et al.*, 1996). Therefore, comparative studies of different portions of endocasts of extinct and extant mammals provide information about the evolution of different sensory systems (Edinger, 1964; Macrini *et al.*, 2007b, c).

For instance, it is known that the hypothalamus regulates food intake (Schmidt-Nielsen, 1983). The medulla oblongata and the pons control the rhythmic movements of the diaphragm in mammals (Milsom *et al.*, 2004; Safonov & Tarasova, 2006), and the cerebellum controls muscular coordination (Biggio *et al.*, 1977; Hickman *et al.*, 2004; Gowen & Miall, 2005). The small size of the facial cranial nerve in *Diademodon* corresponds more closely with that of a living crocodile than with that of any living mammal, suggesting that there was little facial musclature, implying that this species did not have an expressive face (Watson, 1913). Similarly, increases in different brain regions would therefore influence cynodont biology in various ways.

Comparative studies based on these types of the regions of the cranial cavity can be crude, but endocasts often represent the best available information about the central nervous system and sensory systems of extinct taxa. Endocasts do not provide any direct information about the internal structure of the brain such as morphology of the neurons, number of neurons, neuron density, or neuron connectivity. However, differences in endocast shape offer valuable information based upon the comparative neuroanatomy of extant mammals (Macrini *et al.*, 2007c).

Allometric growth should also be considered when examining and interpreting cranial endocasts because the brain volume : body mass ratio diminishes with age (De Beer, 1937). There may then be appositional growth observed on the internal surface of the bony braincase, which leads to a thickening of its wall, unless this process is accompanied by erosion on the external surface of the braincase, leading to a general diminution in skull size (De Beer, 1937). Macrini *et al.* (2007c) found that changes in cranial endocast shape during ontogeny may account for the greatest amount of morphological variation between individuals of different ages. Overall endocast length, width, and volume increase with age, but the relative size of the parafloccular casts of the cerebellar area shows a slight negative allometric trend through ontogeny (Macrini *et al.*, 2007c).

Harvey *et al.* (1986) positively correlated brain size among terrestrial mammals with a number of life history variables, including gestation period, weaning age, length of the juvenile period, and the lifespan length. Among terrestrial mammals, particularly primates, large relative brain sizes and long juvenile periods of dependency are associated with a prolonged period of brain development (Harvey *et al.*, 1986; Joffe, 1997).

Hopson (1977) found that, except for the groups with the smallest and largest body masses, relative brain size showed a poor correlation with body size. Small brain sizes are therefore not attributable merely to large body size. A close correlation between relative brain size and certain behavioural parameters has, however, been found in species ranging from sharks (Northcutt, 1981) to primates (Clutton-Brock & Harvey, 1980). Apart from being correlated with the endothermic status, Hopson (1980) also found a correlation between the relative brain size and the degree of behavioural complexity among dinosaurs. The significance of these correlations related excludsively to brain size cannot be tested.

A comparison of different species shows that the ratio of their brain and body mass is correlated with intelligence (Hickman *et al.*, 2004). The actual brain mass, however, is only a rudimentary indicator of intelligence, because many other factors also affect intelligence. The ratio between brain mass and the spinal cord mass affords a better criterion of intelligence (Hickman *et al.*, 2004). Although larger brains are seemingly associated with higher intelligence, smaller brains might be advantageous from an evolutionary point of view in terms of its metabolic use if they are equal in intelligence to larger brains. Higher ratios of brain to body mass on the other hand may increase the amount of brain mass available for more complex cognitive tasks.

Increased relative brain size may be related to factors other than intelligence, such as longevity (Passingham, 1975; Sacher, 1975; Hammer & Foley, 1996), and social, rather than mechanical, skill (Hopson, 1977; Sawaguchi & Kudo, 1990; Dunbar, 1993). Pérez-Barbería *et al.* (2005) found evidence that changes in relative brain size and sociality are closely correlated over evolutionary time for ungulates, carnivorans, and primates. A similar correlation may perhaps also be present among living reptiles, because several southern African cordylid lizard species have an array of complex social interactions (Alexander & Marais, 2007). Marino (1996, 1997, 1999) and Marino *et al.* (2000) positively correlated the social group size of primates and cetaceans with brain size. According to Schultz and Dunbar (2006), monogamous and harem/seasonal ungulates have larger brains compared to solitary species and those living in large mixed groups.

A large brain is required in social animals, since it is necessary to track the behaviour of other group members more closely to avoid becoming separated from the group. The individuals therefore need to compromise on personal foraging or time budget demands to maintain social cohesion, and develop complex social and cognitive strategies (behavioural innovation and capacity for social learning) (Reader & Laland, 2002) to reduce the natural costs of group-living (i.e. foraging competition, social harassment, stress due to crowding). Group-living also offers ecological advantages. These include protection against predators and optimizing feeding and breeding opportunities. Although sociality is cognitively demanding, sociality and brain size sometimes become decoupled, for example in the Carnivora (Pérez-Barbería *et al.*, 2005; Finarelli & Flynn, 2009) and some of the ungulates under the influence of their habitats (dense bush, or burrows).

Bats and ungulates that live in mixed habitats (savannah woodland) have the largest brains, followed by those in closed habitats (forests), whereas species in open habitats (plains) have the smallest relative brain size (Hutcheon *et al.*, 2002; Schultz & Dunbar, 2006). There are several possible explanations why habitat could be related to brain size: (1) it is more difficult to detect predators in mixed and closed habitats so that increased sensory ability, anti-predator defences and general awareness will benefit individuals in risky environments, and (2) increased habitat complexity will demand better spatial awareness for individuals to be able to negotiate their way within a home range (Niven, 2005). Resource limitation and the absence of predation pressure on the other hand may play important roles in the reduction of brain size (Niven, 2005).

Complex dietary strategies are positively correlated with brain size in terrestrial mammals (Eisenberg & Wilson, 1978; Clutton-Brock & Harvey, 1980; Eisenberg & Wilson, 1981; Mann *et al.*, 1988). Hutcheon *et al.* (2002) suggested that brain size in bats is affected by foraging ecology, because habitat complexity is correlated with relative brain size of predatory species, but not of herbivorous species. Carnivorous theropod dinosaurs possessed the largest brains relative to body size of the dinosaurs, although large herbivorous ornithopods fall within the theropod range (Hopson, 1980). Active predatory lizards (Platel, 1974, 1975) and mammals (Jerison, 1973) tend to have large brains, but Radinsky (1978) found no evidence for such a tend in carnivores relative to their ungulate contemporaries. Browsers have been found to have larger relative brain sizes than either frugivores/omnivores or grazers (Schultz & Dunbar, 2006).

The energy requirements of herbivorous dinosaurs may be indirectly estimated from the degree of specialization of the dentition for processing vegetation (Bakker, 1971). The amount of oral food-processing is strongly and positively correlated with an increase of the relative brain size (Hopson, 1977).

Relative brain size increases with an inferred increase in the speed and degree of agility in dinosaurs (Hopson, 1977). This association has also been described in lizards (Platel, 1975). Large brains in some species of coelurosaurs have been associated with binocular vision (Hopson, 1977; Hopson, 1980). Hopson (1980) suggested that selection acted upon the central nervous systems of these active animals and improved the coordination between rapid movements and visual information about the spatial position of both small rapidly-moving prey and agile enemies. Cranial endocasts indicate that the forebrain of hadrosaurs and *Iguanodon* were also notably large for dinosaurs that may be explained by their possible reliance on acute visual and acoustic senses during display, and escape from predators (Hopson, 1980).

CHAPTER THREE
MATERIALS AND METHODS

3.1 Study material

Fourty four specimens that belong to 11 cynodont genera from the Permian, Triassic and Jurassic Periods of South Africa, the Zambian *Luangwa* (Middle Triassic Ntawere Formation) and Argentinean *Massetognathus* (Middle Triassic Chañares Formation), were tested for CT compatability (Table 4). A juvenile *Procynosuchus* specimen, BP/1/2244 (see Appendix, Table 1 for institutional abbreviations), was also included in the present study to investigate possible ontogenetic variation. Not all the specimens were successfully scanned and digital endocasts obtained for only four cynodonts. These four scanes were compared to descriptions of digital endocasts, natural endocasts, and brain structures of various extinct and extant synapsids in the literature.

Table 4. The cynodont specimens sampled in the present study, their localities and geological zones. The *Massospondylus* range zone is an informal geological zone and not a formal assemblage zone. Abbreviations: Fm, Formation; juv., juvenile.

Genus and specimen	Locality (farm, district)	Assemblage Zone
Procynosuchus		*Cistecephalus* or *Dicynodon AZ*
BP/1/226	Ringfontein, Murraysburg	
BP/1/1545	Lumku, Murraysburg	
BP/1/2244 (juv.)	Oudeberg, Murraysburg	
BP/1/2600	Ringfontein, Murraysburg	
BP/1/5895	Oudeberg, Murraysburg	
NMQR280	Grampian Hills, Philippolis	
Cynosaurus		*Dicynodon* AZ
BP/1/47	Toorberg, Graaff-Reinet	
Galesaurus		*Lystrosaurus* AZ
NMQR135	Oviston, Venterstad	
RC845	Fairydale, Bethulie	
SAM-PK-K9956	Donald, Bethulie	
SAM-PK-K10468	Donald, Bethulie	
Platycraniellus		*Lystrosaurus AZ*
NMQR860	Harrismith	
NMQR1632	Harrismith	

Table 4 (continued)

Genus and specimen	Locality (farm, district)	Assemblage Zone
Thrinaxodon		*Lystrosaurus* AZ
BP/1/4280	Fairydale, Bethulie	
BP/1/4942	Bethulie	
NMQR24	Zeekoeigat, Venterstad	
NMQR810	Harrismith	
SAM-PK-K1468	Harrismith	
SAM-PK-K1498	Harrismith	
Cynognathus		*Cynognathus* AZ
BP/1/1181	Matyantya, Lady Frere	
NMQR1444	unknown	
SAM-PK-K10497	Slootkraal, Rouxville	
SAM-PK-K11264	Winnaarsbaken, Burgersdorp	
SAM-PK-K11484	Tsoaing Stream, Mafeteng	
BP/1/990	Winnaarsbaken, Burgersdorp	
BP/1/3639	Upper Luangwa Valley	
BP/1/3754	Lady Frere	
BP/1/3771	Cragievar, Burgersdorp	
BP/1/3773	Cragievar, Burgersdorp	
Langbergia		*Cynognathus* AZ
NMQR3255	Langberg, Paul Roux	
Trirachodon		*Cynognathus* AZ
BP/1/4200	Winnaarsbaken, Burgersdorp	
BP/1/4201	Winnaarsbaken, Burgersdorp	
NMQR1298	Harrismith	
NMQR3256	Langberg, Paul Roux	
NMQR3280	Eerste Geluk, Kestell	
Luangwa		Ntawere Fm
BP/1/3731	Upper Luangwa Valley	
Massetognathus		Chañares Fm
BP/1/4245	Los Chañares, La Rioja	
Tritylodon		*Massospondylus* RZ
BP/1/4265	Dunblane, Clarens	
BP/1/4876	Mequatling, Clocolan	
BP/1/4965	Twee Zusters, Ladybrand	
BP/1/5047	Winnaarsbaken, Burgersdorp	
BP/1/5089 a	Emmaus, Ladybrand	
BP/1/5167	Bramleyshoek, Bethlehem	
Lumkuia		*Cynognathus* AZ
BP/1/2669	Lumku, Lady Frere	

3.2 Computerized tomography scanning

Neutron computerized tomography (NCT) and high-energy X-ray computerized tomography (HEXCT) technology are proven analytical techniques for studying the internal cranial osteology and cavities of fossils and other unique specimens (Macrini *et al.*, 2006; Macrini *et al.*, 2007a; Macrini *et al.*, 2007b; Macrini *et al.*, 2007c; Macrini, 2009). HEXCT is sensitive to different densities within specimens, whereas NCT utilizes differential attenuation of neutrons that had passed through a specimen to differentiate between bone and other material. Both methods produce two-dimensional images (i.e. slices) that reveal internal details of specimens. Consecutive two-dimensional slices can be linked to provide a three-dimensional digital map of the specimen that can be manipulated through the use of a variety of image processing techniques and software.

In the present study, most of the skulls were NCT scanned, although HEXCT was used in some cases. Scanes were done at the SAFARI-1 Nuclear Research Reactor of the Nuclear Energy Corporation of South Africa (Necsa) near Pretoria in July 2008 and May 2009. The characteristics of the South African Neutron Radiography (SANRAD) facility (De Beer, 2005) are summarized in Table 5, and Figure 2 depicts the neutron tomography setup of this facility.

Table 5. Collimator specifications, neutron and X-ray beam characteristics and imaging properties for beam port no. 2 of the SAFARI-1 Nuclear Research Reactor at Necsa, Pretoria. Modified from De Beer (2005).

Neutrons	
Distance from aperture (L)	2 465 mm
Beam diameter at outlet of collimator	300 mm
Neutron flux (based on Au activation foils) at object in center of beam (n cm^{-2} s^{-1}) at 20 MW reactor power and pinhole aperture (D) = 21 mm	1.2 x 10 7
Approximate collimation ratio L/D for pinhole aperture (D) = 21 mm	150
Theoretical geometric unsharpness with pinhole aperture (D) = 21 mm and sample detector distance = 600 mm	3.3 mm
Beam divergence at pinhole aperture (D) = 21 mm	3.2°

Table 5 (continued)

X-rays	
Distance from aperture to scintillator (L)	1 000 mm
Approximate cone beam diameter at	728 mm
X-ray tube voltage	0-100 kV
Approximate collimation ratio L/D for focal spot (D) = 1 mm	800
Geometric unsharpness (mm) with sample thickness = 50 mm and sample distance = 600 mm from focal spot (D) = 1 mm	0.07 mm
Beam divergence	40°

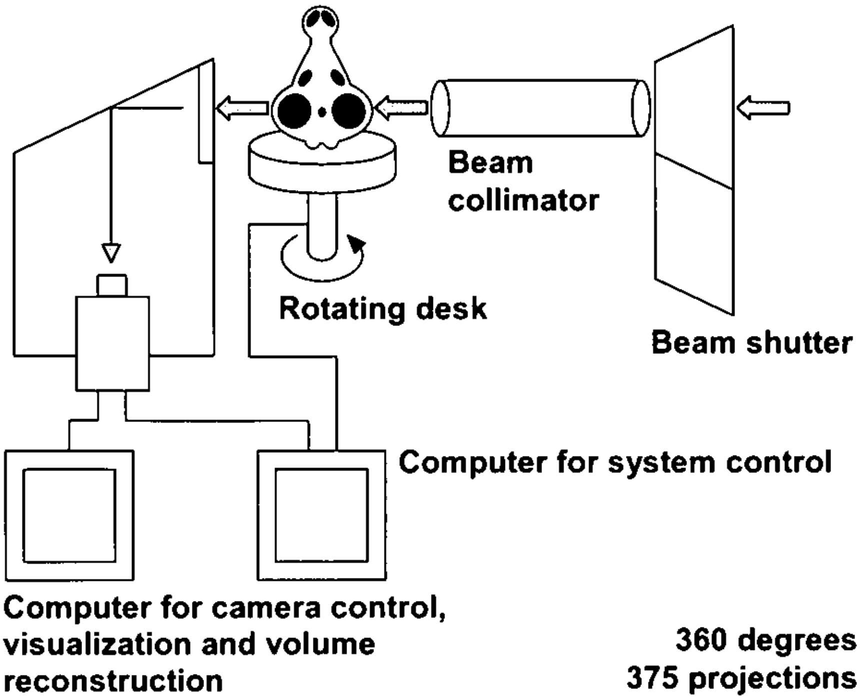

Figure 2. Schematic representation of the tomography setup of the SANRAD facility at Necsa, Pretoria. After De Beer (2005).

All specimens were scanned completely and the orientation of the scans was in the coronal (transverse) slice plane. Due to the length and width of some skulls, the number of frontal and coronal slices in these specimens had been reduced, without affecting the area that contains the endocast.

The samples were scanned with an acquired slice thickness of 0.088 mm, and an interslice spacing of 0.9 mm. The image field of reconstruction varied between 9 x 9 cm, 10 x 10 cm and 20 x 20 cm. The 16-bit range of greyscales was used to maximise the output ranges and calibrate the reconstruction parameters. The time necessary for a NCT scan was up to 3 hours per specimen, based on the recommendation of Schwarz *et al.* (2005). The data were archived as individual slices and are stored at Necsa.

Unsatisfactory scans were produced when the fossil bone (apatite) and sediment matrix (particularly mudstone) apparently had similar attenuation values (see Schwarz *et al.*, 2005 and Sutton, 2008), the skull bones were too thick to allow adequate penetration of the neutron beams, or the fossils were too poorly preserved.

Where adhesives were extensively used in the reconstruction and preservation of the fossil material, the scan images were blurred (also observed by Schwarz *et al.* (2005)), and this reduced the amount of information that could be obtained from the cranial endocast. The plastocene used to fasten the material to the mounting table led to a similar reduction in image quality, and the affected parts (usually on the snout, such as *Langbergia* NMQR3255 (see Figure 5)), but also at the back of the skull, were removed digitally. Even when adequate penetration had been achieved, scans of many of the skulls revealed that only partial information regarding the cranial endocast was obtained because the fragile bones that define the bottom and sides of the endocranial space were rarely preserved. In such cases, volumetric calculations (see Table 6) could not be done.

3.3. Extraction of digital endocasts

Matrix was digitally removed from the NCT scans using the program VGStudioMax © (version 1.2; Volume Graphics GmbH, 2004). VGStudioMax © is a program designed for the analysis and visualization of voxel data that allows the user to digitally individuate or segment portions of the volumetric datasets. VGStudioMax © had also been used to calculate volumes and partial volumes, to take linear measurements, and to generate movie frames of the rotating skulls and endocasts. The movie frames were exported to the National Institute of Health (Bethesda, MD) ImageJ for cropping and rotation. The frames were then exported to QuickTime TM (Apple, Cupertino, CA) and compiled into self-contained movies.

3.4 X-ray diffraction

To determine whether some of the unsatisfactory scans were due to similar attenuation values of materials in the fossils, a preliminary X-ray diffraction (XRD) analysis was performed at Necsa on *Trirachodon* BP/1/4200, in which both NCT and HEXCT proved unsuccessful. XRD analysis is used for chemical phase identification. Measurements were taken at three different positions, namely the right canine tooth, the skull bones of the snout, and at the mudstone matrix at the back of the skull. The results were compared with the estimated mass attenuation values for thermal neutrons that had been calculated at the high-energy X-ray (HEXCT) facility at Necsa.

3.5 Assessments

Body mass

Body size (volume or weight) estimates in vertebrate fossils are usually determined through the use of accurate scale models (Colbert, 1962; Bakker, 1975) or from equations, derived from extant species that relate body mass to skeletal measurements. Anderson *et al.* (1985) and Egi (2001) used the proportions of the limb bones to determine the body mass (P) (in g) of mammals, whereas Jerison (1973) made use of skeletal body length measurements (L) (in cm). Kielan-Jaworowska (1983) used a small mammal equation of $0.025\ L^3$ for *Kryptobataar.* Radinsky (1977, 1978) calculated the body mass of both living and extinct carnivorans, as well as ungulates:

$P = 0.08\ L^{2.73}$ (carnivorans) and $P = 0.0027\ L^{3.45}$ (ungulates)
(P = body mass (g); L = body length (cm))

Unfortunately, postcranial material was not always available for all cynodont genera and therefore a method that uses skull length was also required in the present study. Macrini *et al.* (2007a), following Gingerich and Smith (1984) and Luo *et al.* (2001), estimated the body weight of the extinct theriiform *Vincelestes* from an equation that relates body mass and skull length in extant insectivorans:

$y = 3.68x - 3.83$ ($y = \log_{10}(\text{body mass})$ (g); $x = \log_{10}(\text{skull length})$ (mm))

However, Macrini *et al.* (2007a) admitted that a formula based on a sample of larger extant mammals would probably be more appropriate. Quiroga (1980c) studied the skull length : body length relationships of six cynodonts and other therapsids and proposed a more reliable non-mammalian therapsid equation:

$P = 2.7\ S^3$ (P = body mass (g); S = skull length (mm))

The equation (Quiroga, 1980c) was based on the generalized therapsid skull length : body length relationship of 1 : 4 (Quiroga, 1979). In order to obtain the body mass of each individual investigated in the present study, the last equation discussed above (Quiroga, 1980c) was used.

Because *Platycraniellus* NMQR1632 consists only of a partial posterior skull roof fragment with the impressions of the braincase on its ventral surface, the skull lengths of similar-sized *Platycraniellus* specimens TM25 and NMQR860 (Abdala, 2007; F. Abdala *pers. comm.*, 2008[2]) were used in the present study (see Appendix Table 4).

Endocast measurements

In all of the skulls from which cranial endocasts could be obtained, the maximum linear measurements (length, width and height) of the olfactory bulbs and brain (excluding the olfactory bulbs) (herein referred to as the brain) were obtained through the use of ImageJ (Figure 3). These measurements are presented from the left cerebral hemisphere only because, according to Macrini *et al.* (2007a), measurements from the right cast tend to be identical. The width and height of the foramen magnum were measured, because it was unknown

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whether this opening should be circular (see Appendix Table 4). The pineal complex had not been included as a part of the cranial endocast, because the pineal would in life have consisted mainly of glandular tissue (Hickman *et al.*, 2004).

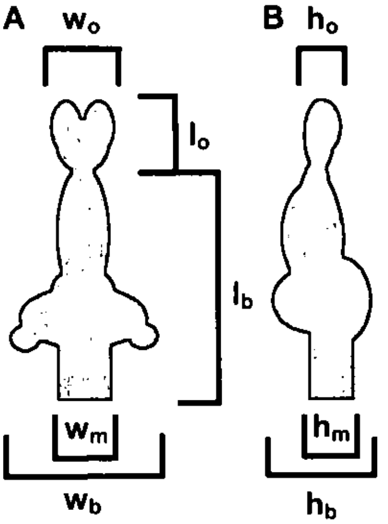


Figure 3. Schematic representation of a generalized cynodont cranial endocast in dorsal (A) and right lateral (B) views that illustrate the position where measurements were taken. Abbreviations: b, brain; h, height; l, length; m, foramen magnum; o, olfactory bulbs; w, width.

In the case of *Platycraniellus* NMQR1632 in which height measurements could not be obtained from the endocast, Jerison's (1973) suggestion to use 80% of the width as an indication of possible endocast height in Mesozoic mammals was followed. This was estimated by an analogy with living species (Jerison, 1973). Errors could, however, be expected, due to the small sample size (n = 6) used by Jerison (1973) and thus a more reliable measure was therefore needed. For *Platycraniellus* NMQR1632 in the present study, average height : width proportions of the cynodonts examined at first hand and data from the literature were used (see Appendix Table 9).

Endocast volume

In the past, the volume of fossil endocasts had been determined by water displacement (Jerison, 1973; Radinsky, 1978) and graphic or numerical double integration (Jerison, 1969, 1973). Jerison (1973) and Kielan-Jaworowska and Lancaster (2004) estimated the endocast volume of Mesozoic mammals through the use of the equation:

$E = 0.25\,\pi\, l\, w\, h$ (E = endocast volume (cm^3); l = endocast length (cm);
w = endocast width; h = endocast height)

The volume of the endocast is therefore modelled on that of an elliptical cylinder (Jerison, 1973), although its size can be overestimated by the use of this equation. Making use of ImageJ, the dorsoventral surface area of the brain and olfactory bulbs were calculated and the result multiplied by the height measurements to give a more accurate estimated endocast volume. In *Platycraniellus* NMQR1632, which is represented by only a partial skull roof, a lack of height measurements did not facilitate a calculation of the exact endocranial volume.

Brain volume

Cranial endocasts provide better approximations of the brains of some vertebrates than others, based on the degree to which the brain would have filled the endocranial space. Because the surfaces of cynodont endocasts are closely moulded to the endocranial surface (Hopson, 1969), Hopson (1980) used 80-100% of the endocast volume to represent the brain volume. Quiroga (1980c) used different brain volumes for various cynodonts, ranging from 75% in *Exaeretodon* to 100% in *Probainognathus.* The brain volume of cynodonts and mammals had therefore been estimated to represent no less than 90% of the total endocranial volume, because the average endocranial rete volume can account for up to 10% of the total endocranial volume (Marino, 1999).

Brain mass

The methods to determine brain mass based upon brain volume vary. Coria and Currie (2003) used a density of 0.9 g/cm^3 for the brain of the theropod dinosaur *Giganotosaurus*. Witmer *et al.* (2003) preferred 1.036 g/cm^3 for pterosaurs and Saveliev and Alifanov (2007) used 1.087 g/cm^3 for *Tarbosaurus*. The present study has followed that of Marino (1999), in which a brain density of 1.0 g/cm^3 is used to determine the brain mass of dolphins, based on the assumption that cynodonts should be more similar to mammals than reptiles.

Encephalization quotients

The encephalization quotient (EQ) was developed by Jerison (1973), and represent the ratio of actual brain mass : expected brain mass for the body mass of a particular taxon. These ratios were determined using plots of $\log_{10}$(body mass) to $\log_{10}$(brain mass) among various closely related taxa (Jerison, 1973).

The size (mass or volume) of the vertebrate brain is exponentionally related to that of the body (Jerison, 1969), and this empirically determined relationship is represented by the power function:

$E = k.P^{0,67}$ (E = brain size (g or cm^3); P = body mass (g))

k represents a proportionality constant equal to the value of E when P = 1 on a log-log plot (Jerison, 1969, 1973; Hopson, 1977). A higher k value implies that the brain is larger for any given body mass. Jerison (1969) found that when brain size for a variety of living vertebrates is plotted against body mass on a log-log scale, two parallel clusters both with slopes of approximately 0.67 appear. The y-intercept of the lower cluster that contains fish, amphibians and reptiles is, approximately ten times less than that for the upper cluster containing the more derived birds and mammals (for further detail, see Jerison (1969: 579)).

An indication of the relative brain size, the encephalization quotient (EQ), is determined by comparing the measured brain size of a closely related animal with the brain size expected for an animal of the same body mass (Jerison, 1973):

$EQ = E_i / E_e$ (Ei = measured brain mass; Ee = expected brain mass)

EQ values below 1.0 indicate relatively small-brained animals, and above 1.0, species with relatively large brains (Jerison, 1973). The standard against which all mammals and cynodonts had been compared in previous studies was the expected brain size (excluding the olfactory bulbs) (E_{eb}) for an 'average' living mammal of the same body size (Jerison, 1973), based on the equation:

$E_{eb} = 0.12 P^{0.67}$ (P = body mass (g))

while that of the olfactory bulbs (E_{eo}) (Jerison, 1973) is based on:

$E_{eo} = 0.015 P^{0.67}$ (P = body mass (g))

The EQ values obtained in the present study were compared to those obtained for other therapsids, as well as a wide range of fossil mammals, such as *Vincelestes* (Macrini *et al.*, 2007b), multituberculates (Kielan-Jaworowska & Lancaster, 2004) as well as living monotremes (Macrini *et al.*, 2006), marsupials (Macrini *et al.,* 2007a, c) and bats (Hutcheon *et al.,* 2002). Radinsky (1977, 1978) and Pérez-Barbería *et al.* (2007) were the main sources for relative brain sizes of carnivorans. Archaic ungulates studied by Radinsky (1978) and Schoch (1983) were also included, because these animals had some of the smallest relative brain sizes of all known mammals (Jerison, 1973; Radinsky, 1978). Cynodont data were obtained from various sources that include Olson (1944), Hopson (1980) and Quiroga (1980a). According to Radinsky (1978), an EQ value of approximately 0.2 appears to represent the lower limit of relative brain size (excluding the olfactory bulbs) in living and extinct mammals. Amongst living mammals, the lowest EQ values are found in didelphid opossums and placental insectivores (some soricids, erinaceids, and tenrecids). This criterion was therefore used to determine whether cynodont brain size closely corresponds with that of mammals.

CHAPTER FOUR
RESULTS

4.1 Computerized tomography scans

Out of the 44 fossil skulls originally scanned, only four specimens produced successful scans (see Appendix, Table 2). The scans of these specimens were reasonably clear and allowed measurements to be taken.

The scan of *Galesaurus* RC845 (Figure 4) has the clearest quality of all the scans. Internal cavities that include the cranial endocast has been revealed after the matrix was digitally removed. The scan clearly shows that the main part of the brain is presented by a long and narrow cerebrum. More posteriorly, the cranial endocast widens and deepens in the shorter cerebellar region. The olfactory bulbs are smaller than the rest of the brain and the foramen magnum appears dorsoventrally flattened.

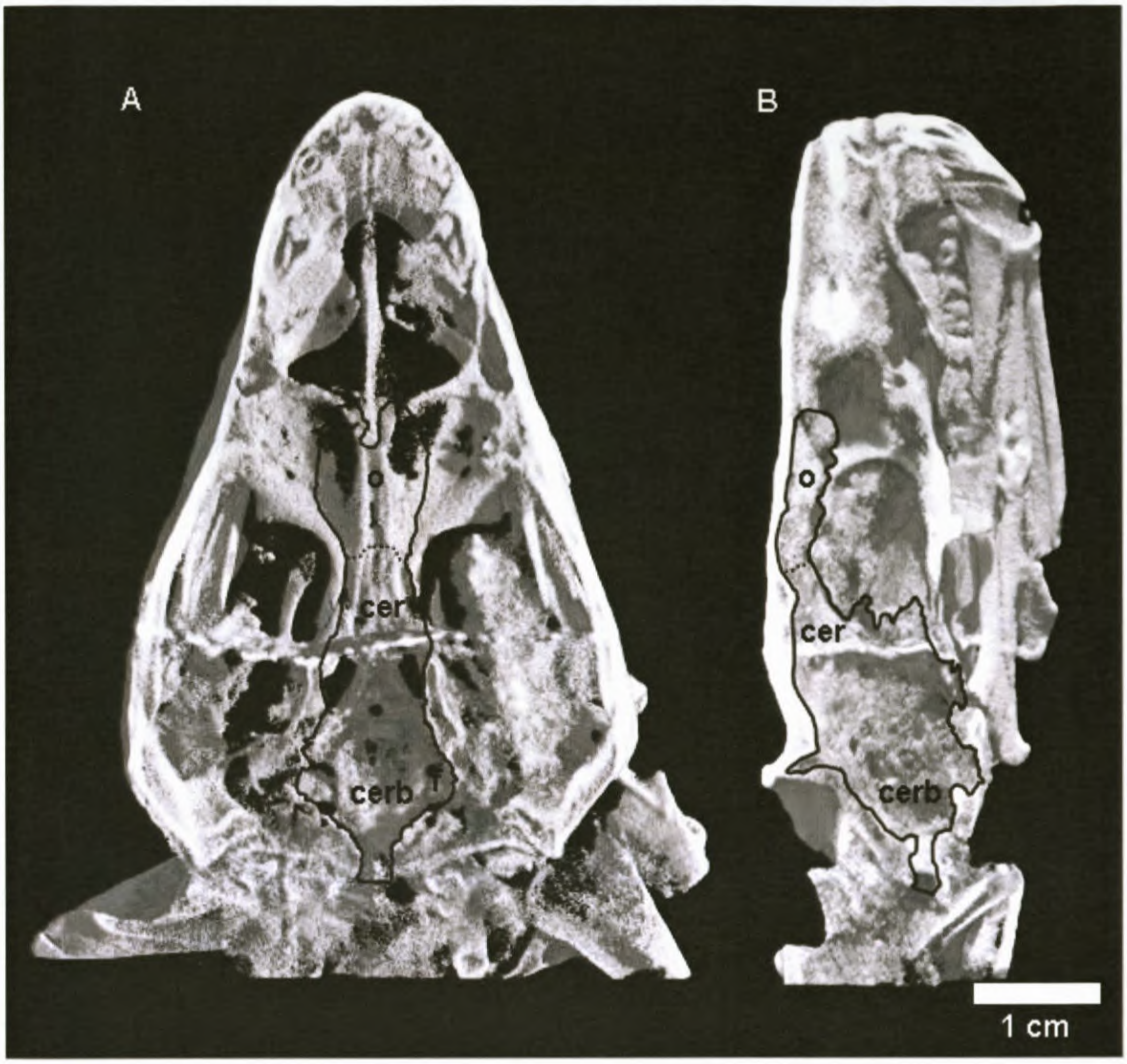


Figure 4. Stitched sagittal (A) and coronal (B) neutron computerized tomographic slices through the skull of *Galesaurus* RC845. The matrix has been digitally removed, and the outline of the cranial endocast is shown in black. The posterior ends of the olfactory bulbs are by a dotted line. Abbreviations: cer, cerebrum; cerb, cerebellum; f, flocculus; o, olfactory bulbs.

Most of the brittle skull fragments and adhesive in the posterior region of the *Platycraniellus* skull NMQR1632 (Figure 5) were digitally removed to reveal a fairly complete dorsal impression of the endocast on the ventral surface of the skull roof. The shape of the cranial endocast is similar to that of *Galesaurus* RC845, although the cerebellar region (especially the floculli) is better defined, and the olfactory bulbs are shorter, so that they appear circular in shape than those of *Galesaurus* RC845.

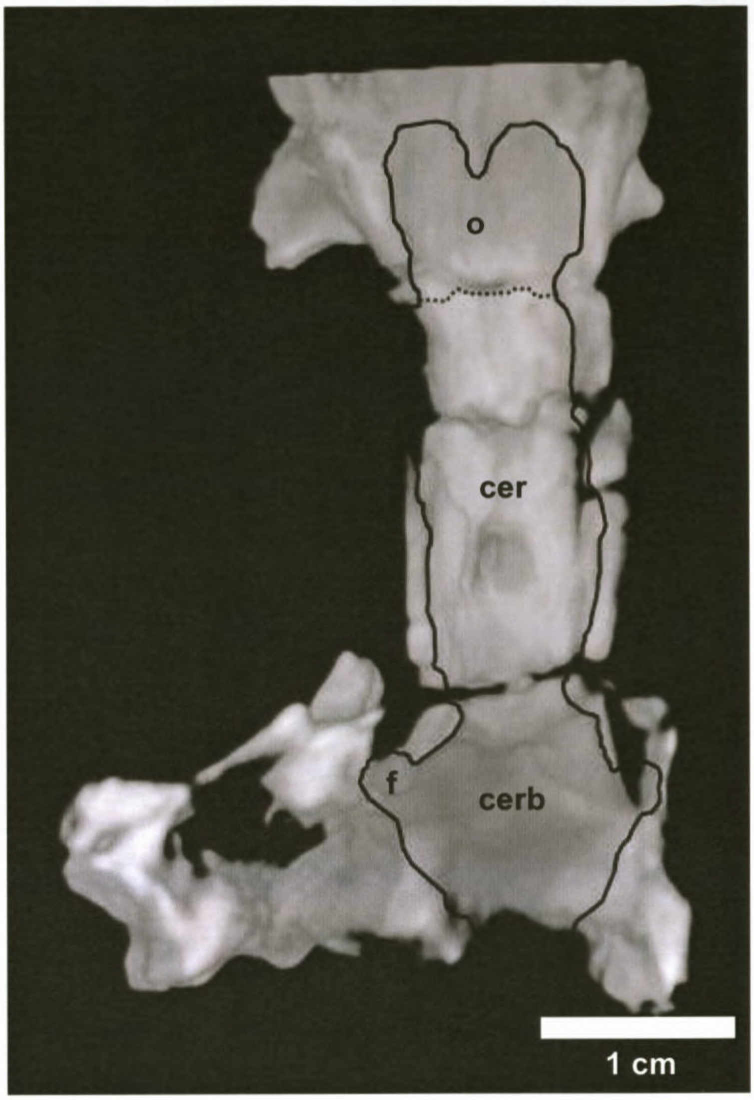


Figure 5. Digital rendering of a ventral view of the skull roof, showing the brain impression, of *Platycraniellus* NMQR1632. The outline of the cranial endocast is shown in black. The posterior ends of the olfactory bulbs are by a dotted line. Abbreviations: cer, cerebrum; cerb, cerebellum; f, flocculus; o, olfactory bulbs.

The scan of *Langbergia* NMQR3255 (Figure 6) is clearly different from the others. The olfactory bulbs are smaller than those of *Galesaurus* RC845 and *Platycraniellus* NMQR1632, and the foramen magnum is narrower and higher than that of *Galesaurus* RC845.

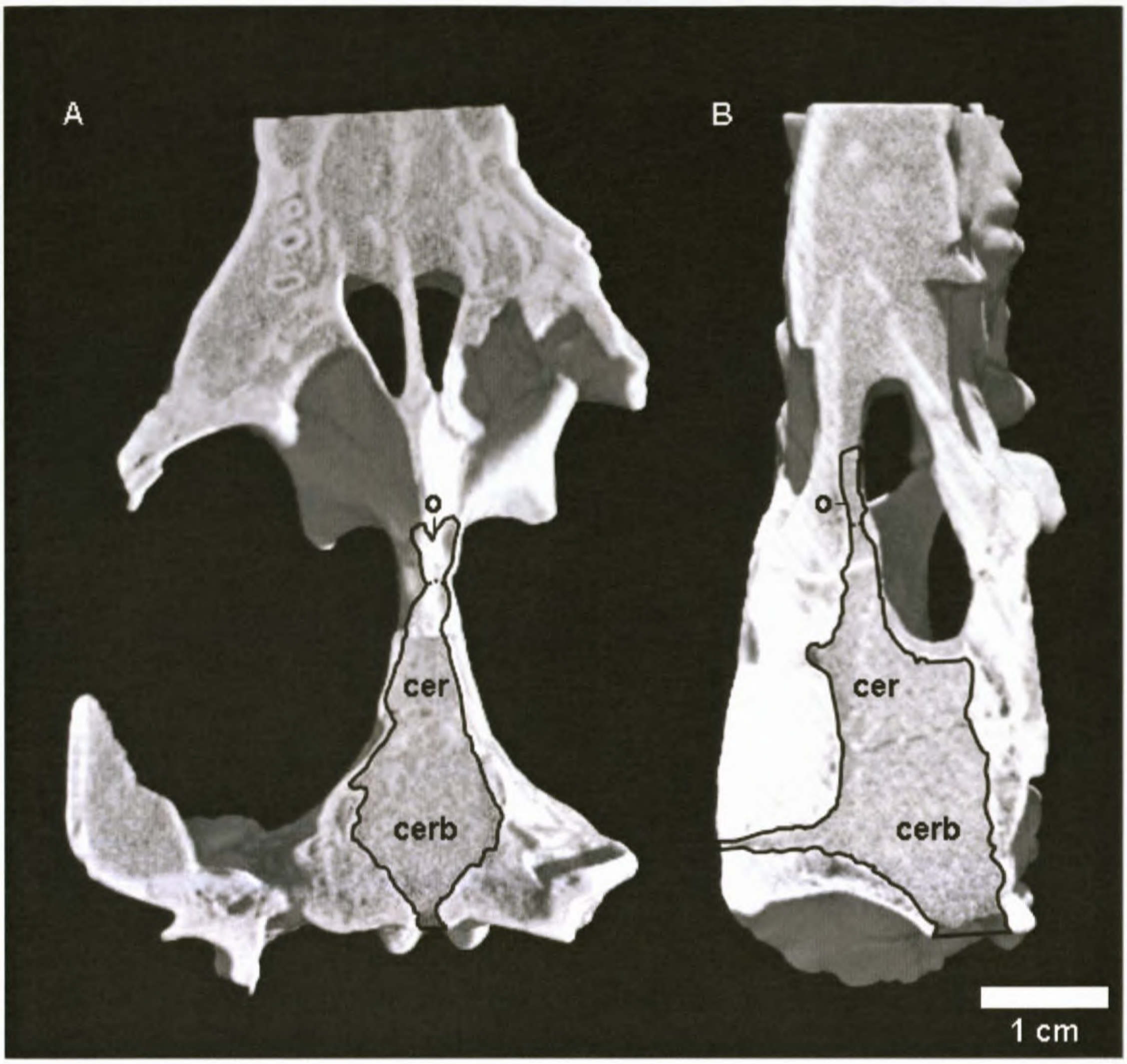


Figure 6. Stitched sagittal (A) and coronal (B) neutron computerized tomographic slices through the skull of *Langbergia* NMQR3255. The outline of the cranial endocast is shown in black. The posterior ends of the olfactory bulbs are by a dotted line. Abbreviations: cer, cerebrum; cerb, cerebellum; o, olfactory bulbs.

The basic shape of the endocast of *Tritylodon* BP/1/4265 (Figure 7) is similar to that of *Langbergia* NMQR3255, although it is more compressed, due to preservational dissortion. The cranial endocast is positioned more in the posterior portion of the skull when compared to the other cynodont taxa. The area anterior to the indicated endocast seems to represent the nasal cavities. There is an extension to the left of the hindbrain (see Figure 7) which may be an artefact, caused by either erosion or distortion during fossilization.

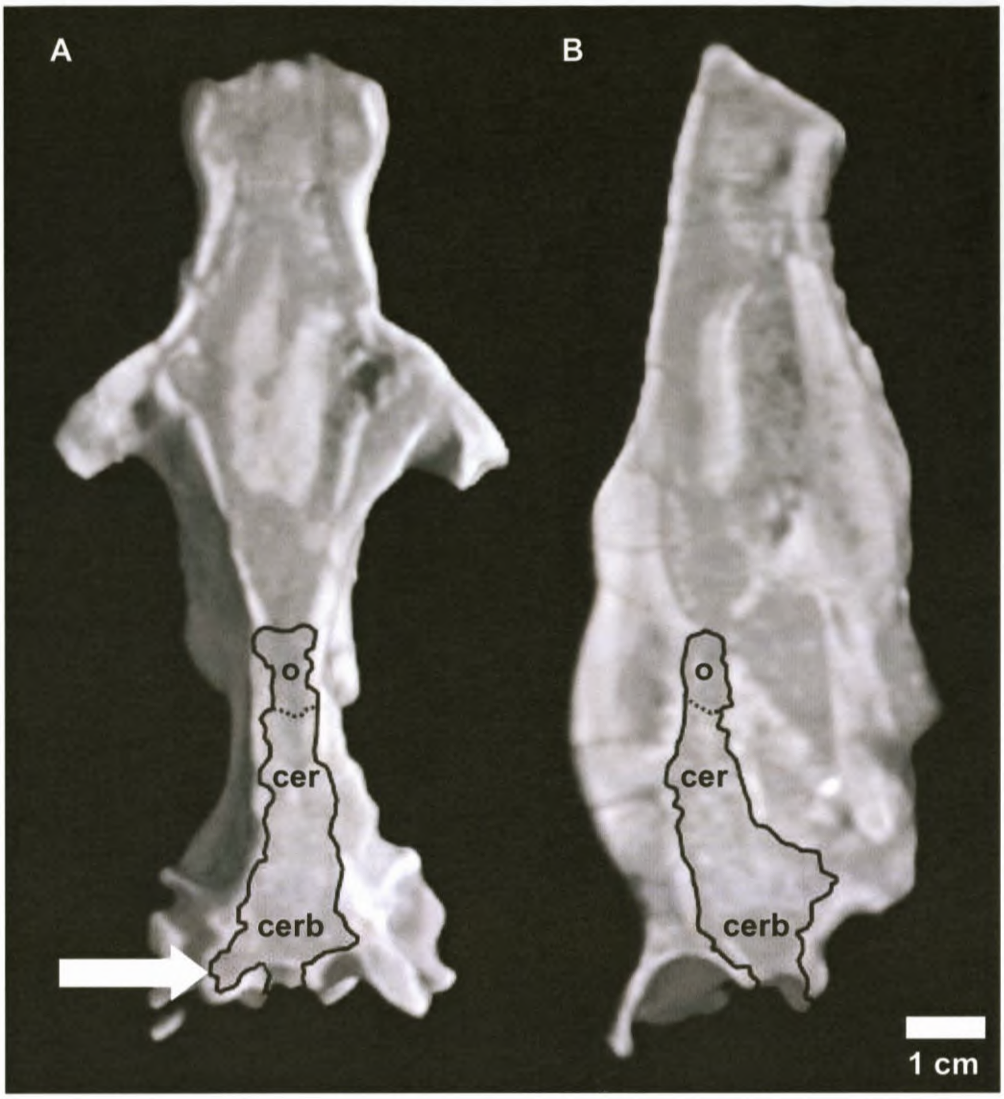


Figure 7. Sagittal (A) and coronal (B) neutron computerized tomographic slices through the skull of *Tritylodon* BP/1/4265. The outline of the cranial endocast is shown in black. The arrow indicates an anomaly to the left of the hindbrain. The olfactory bulbs are divided from the rest of the brain by a dotted line. Abbreviations: cer, cerebrum; cerb, cerebellum; o, olfactory bulbs.

Rotational animations of *Galesaurus* RC845 and *Thrinaxodon* BP/1/4942 were completed, because most of the matrix could be digitally removed from these fossils. In the case of BP/1/4942, a specimen identified as *Thrinaxodon* in the Karoo Fossil Collection of the Bernard Price Institute for Palaeontological Research, the sandstone matrix of the nodule (Figure 8) had been digitally removed and revealed a partial skull with no cranial endocast preserved (Figure 9). A ridge of glue used to reassemble the nodule and three small concentrations of grey siltstone situated anterior and posterior to the fossil (two to the back, seen in Figure 8, and another in the region of the snout, seen in Figure 9) were also revealed.

Figure 8. Photographs of the dorsal (A) and ventral (B) views of the nodule containing a skull of *Thrinaxodon* BP/1/4942.

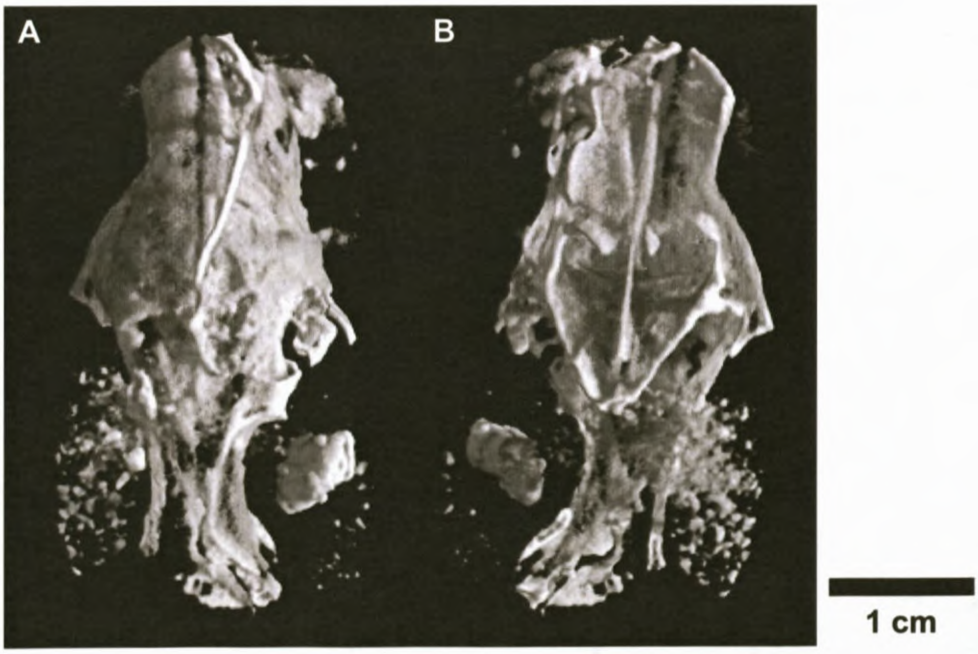


Figure 9. Digital renderings of the dorsal (A) and ventral (B) views of a *Thrinaxodon* skull (BP/1/4942), after sandstone matrix had been digitally removed.

4.2 X-ray diffraction

Background subtracted diffraction patterns of the tooth of *Trirachodon* BP/1/4200 revealed a mixture of the carbonate fluorapatite (inclusion of CO_3^- in the apatite structure) and stoichiometric fluorapatite phases. The diffraction pattern of the cranial bone showed that it is comprised predominantly of hydroxyapatite, with lesser non-stoichiometric and carbonated inclusions. The diffraction pattern of the matrix showed the presence of calcite, and an accessory mineral, carbonated calcium deficient hydroxyapatite, , identical in structure to that found in the skull.

The theoretical mass attenuation coefficient value for thermal neutrons in calcite (0.31 cm^{-1}) was very close to that of the fluorapatites found in the tooth (0.32-0.33 cm^{-1}) (Appendix, Table 3) Because hydroxyapatite has a higher attenuation value (0.42 cm^{-1}), it will absorb neutrons more readily than the other minerals and is seen more distinctly.

4.3 Endocast measurements

Most of the skulls were crushed and/or distorted and such fossils were not used for examination, as this would have influenced the measurements from the endocasts. Therefore endocast measurements were taken from four specimens that produced the clearest scans, namely *Galesaurus* RC845, *Platycraniellus* NMQR1632, *Langbergia* NMQR3255 and *Tritylodon* BP/1/4265. All the genera examined are relatively small cynodonts and range in skull length from 62.8 mm to 127.7 mm (Appendix, Table 4). Because *Platycraniellus* NMQR1632 consists of a partial dorsal portion of the skull, no height measurements could be taken for this specimen. It should be noted that the olfactory bulbs of the larger *Tritylodon* BP/1/4265 are smaller than either those of *Galesaurus* RC845 or those of *Platycraniellus* NMQR1632, that belong to smaller specimens. The endocast measurements were used to determine ratios.

The endocast width and height measurements of several cynodonts were compared to determine an endocast height to width ratio more accurate for cynodonts than Jerison's (1973) suggested ratio of 0.8 : 1 (Figure 10, data taken from Appendix, Table 5). No height measurements are available for *Thrinaxodon* BMNHR1713 (Watson, 1913), a situation that remains unchanged. Only the olfactory bulbs in *Procynosuchus* TSK34 (Kemp, 1979) and *Tritylodon* BP/1/4265 (0.78-0.8), and the brain of *Exaeretodon* MACN18114 (0.84) follow a height : width ratio (h/w) close to 0.8. *Galesaurus* RC845 and *Langbergia* NMQR3255 have an olfactory bulb height to width ratio (h_o/w_o) of 0.55-0.57, that reflects the flattened shape of the olfactory bulbs. The cynodont brain is as high as it is wide (h_b/w_b = 0.82-1.44), although its height exceeds its width in *Galesaurus* RC845, *Langbergia* NMQR3255, *Tritylodon* BP/1/4265 and the *Galesaurus* specimen examined by Olson (1944, Cynodont A).

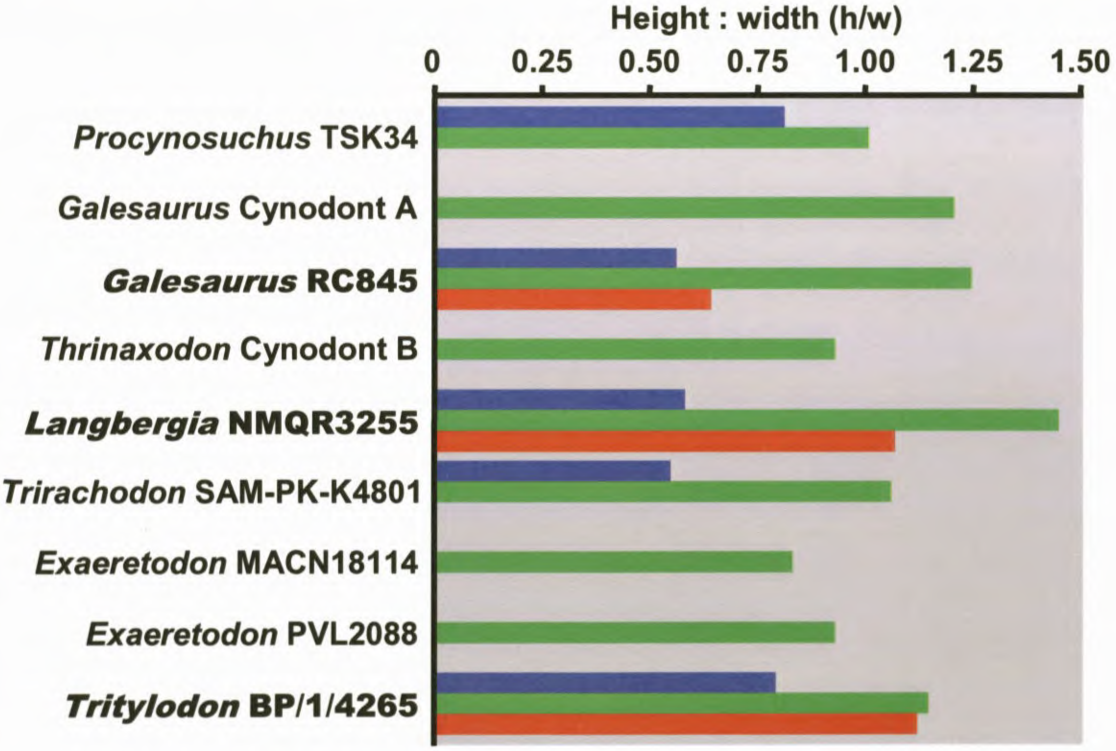


Figure 10. Height to width proportions of the olfactory bulbs (blue), brain (yellow) and foramen magnum (red) of the cynodonts examined in the present study (indicated in bold) and those documented in the literature.

Notable variation is present between *Langbergia* NMQR3255 and its closely related sister taxon, *Trirachodon* SAM-PK-K4801, with height to width of the brain (h_b/w_b) being larger in *Langbergia* NMQR3255. This implies that its brain may have been deeper than that of *Trirachodon* SAM-PK-K4801. *Galesaurus* specimens Cynodont A and RC845, and *Langbergia* NMQR3255 have deep cranial endocasts in comparison with other cynodonts, but those of both *Exaeretodon* specimens (MACN18114 and PVL2088) (Bonaparte, 1966) are relatively shallow.

No information is available in the literature about the average size of the foramen magnum in cynodonts. The results of the present study show a different ratio in *Galesaurus* RC845, and the derived *Langbergia* NMQR3255 and *Tritylodon* BP/1/4265. The latter genera apparently have a more circular opening. The average values for the height to width relationship for all specimens is 0.65 for the olfactory bulbs (h_o/w_o), 1.08 for the brain (h_b/w_b) and 0.93 for the foramen magnum (h_m/w_m). This indicates relatively flattened olfactory bulbs, and a deeper brain with an almost circular foramen magnum.

Based on these results (Appendix, Table 5), the estimated height of the olfactory bulbs, brain and foramen magnum of *Platycraniellus* NMQR1632 is 6.64 mm, 16.85 mm and 5.86 mm respectively, representing values higher than those of the cranial endocast in *Galesaurus* RC845. The entire cranial endocast is higher in *Tritylodon* BP/1/4265, and larger height measurements than those estimated for *Platycraniellus* NMQR1632 were also recorded in *Procynosuchus* TSK34 (olfactory bulbs (h_o)), *Langbergia* NMQR3255 (rest of the brain (h_b) and foramen magnum (h_m)) and *Exaeretodon* specimens MACN18114 and PVL2088 (h_b).

It is unlikely that any of the proportional differences (Appendix, Table 5) are due to allometry, because the skulls, with the exception of *Exaeretodon*, are all approximately similar in size. The possible influence of skull length on the widths and/or heights of the endocast was investigated. Little variation was found in the olfactory bulb height and width in relation to skull length (Appendix, Table 6). The basal cynodonts (*Procynosuchus* TSK34, *Galesaurus* RC845, *Platycraniellus* NMQR1632 and *Thrinaxodon* BMNHR1713) have ratios equal to or above the average ($w_o/S = 0.09$ and $h_o/S = 0.06$) (Appendix, Table 6), while the more derived taxa (*Langbergia* NMQR3255, *Trirachodon* SAM-PK-K4801 and *Tritylodon* BP/1/4265) have values below the average values, that suggest narrower, more laterally flattened olfactory bulbs in the latter genera. The maximum and minimum values for the length to width ratio of the olfactory bulbs vary by 0.49, while the maximum and minimum values for their length to height ratio vary by 0.84, suggesting that this part of the cranial endocast experienced more variation in depth than width. The maximum variation in the length to width ratio is between *Trirachodon* SAM-PK-K4801 and *Platycraniellus* NMQR1632, but in the case of the maximum length to height variation, it occurs between *Procynosuchus* TSK34 and *Galesaurus* RC845. The olfactory bulbs are flattened in the Triassic genera, in contrast those of the Late Permian *Procynosuchus* TSK34 and Early Jurassic *Tritylodon* BP/1/4265, that are relatively higher (Figure 11 and Appendix, Table 5). This part of the cranial endocast is also elongated, it being the longest in *Platycraniellus* NMQR1632.

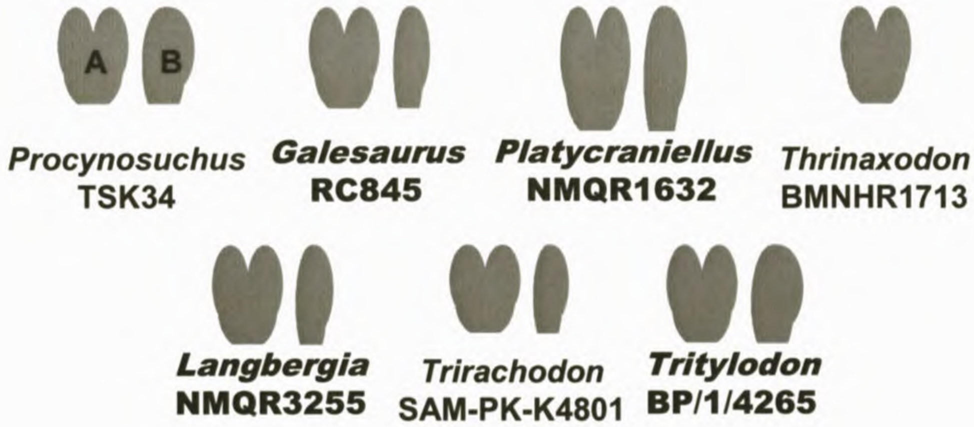
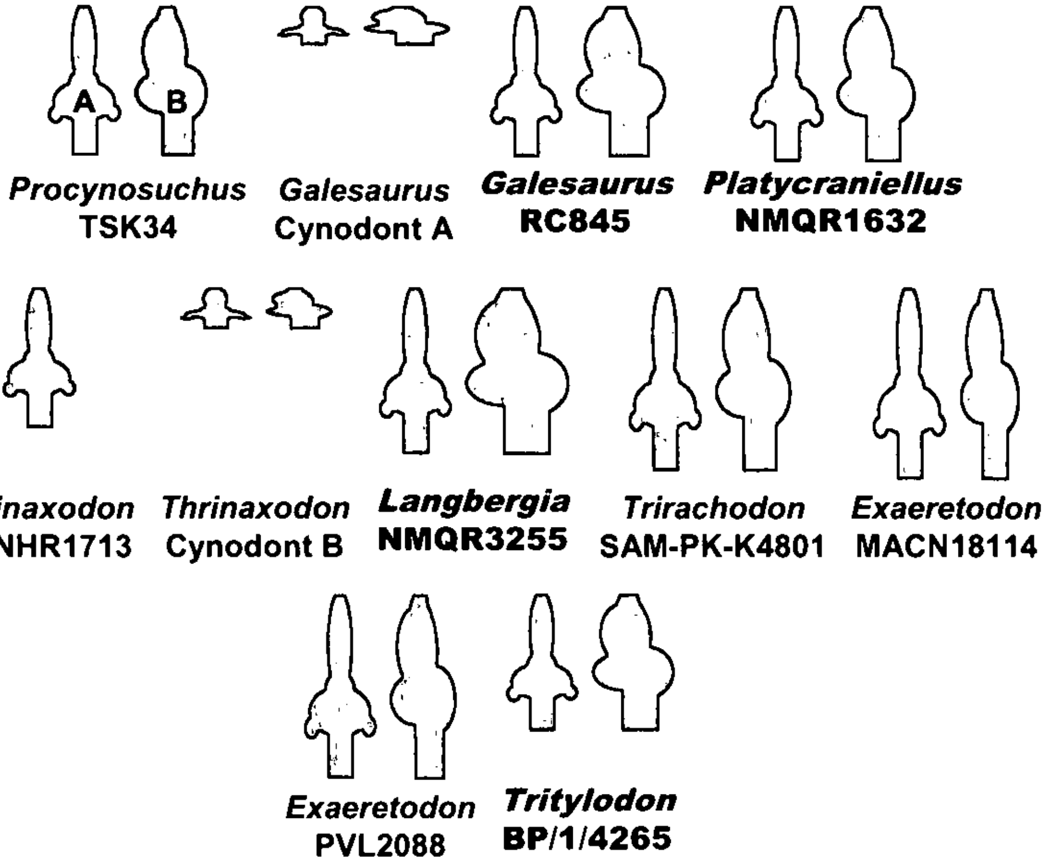


Figure 11. Schematic representations of the dorsal (A) and right lateral (B) views of the olfactory bulbs of the cynodonts examined in the present study (in bold) and those in literature, based on linear ratios. The proportional width measurements have been equaled to allow for comparison. The height measurements for *Platycraniellus* NMQR1632 were estimated, but no estimates are available for *Thrinaxodon* BMNHR1713 (see text).

Similar to the case of the olfactory bulbs, little variation is present in the proportions of the rest of the brain in cynodonts, with the minimum and maximum width to skull length varying by 0.13, and minimum and maximum height to skull length varying by 0.12 (Appendix, Table 6). *Galesaurus* Cynodont A, which had been examined by Olson (1944), has the widest and highest brain ratios. In contrast, *Exaeretodon* specimens MACN18114 and PVL2088 have the narrowest and laterally flattest brains.

Seven of the brains examined in the present study and the literature are tubular, i.e. elongated and almost as wide as they are high (Figure 12). The exceptions are: (1) *Galesaurus* Cynodont A and *Thrinaxodon* Cynodont B (Olson, 1944), that are unusually short when compared to specimens of the same genus, as well as other genera; and (2) relatively high cranial endocasts in *Galesaurus* RC845 and *Langbergia* NMQR3255 compared to other cynodonts. The basal genera have cranial endocasts of similar relative length, with the cranial endocast shape of *Platycraniellus* NMQR1632 corresponding to that of *Galesaurus* RC845. The cranial endocast of *Tritylodon* BP/1/4265 is shorter than those of other genera, such as the *Exaeretodon* specimens MACN18114 and PVL2088, which have particularly long cranial endocasts.



Procynosuchus TSK34
Galesaurus Cynodont A
***Galesaurus* RC845**
***Platycraniellus* NMQR1632**
Thrinaxodon BMNHR1713
Thrinaxodon Cynodont B
***Langbergia* NMQR3255**
Trirachodon SAM-PK-K4801
Exaeretodon MACN18114
Exaeretodon PVL2088
***Tritylodon* BP/1/4265**

Figure 12. Schematic representations of the dorsal (A) and right lateral (B) views of the brains excluding the olfactory bulbs of the cynodonts examined in the present study (in bold) and those in literature, based on linear ratios. The proportional width measurements of the brains are equaled to allow for comparison. It is possible that the representations for *Galesaurus* Cynodont A and *Thrinaxodon* Cynodont B are based on hindbrain proportions. The height measurements for *Platycraniellus* NMQR1632 were estimated, but no estimates are available for *Thrinaxodon* BMNHR1713 (see text).

To determine whether parts of the cranial endocast changed in size over geological time, the mean values of endocast length, width and height ratios for six geological zones were compared (Figure 13, data taken from Appendix, Table 7). No information is available regarding the olfactory bulbs of *Exaeretodon* MACN18114 and PVL2088 from the Ischigualasto Formation. The results suggest that cynodont olfactory bulbs were relatively flatter during the Triassic, with a slight reduction in length in the *Cynognathus* Assemblage Zone (represented by *Langbergia* NMQR3255 and *Trirachodon* SAM-PK-K4801). The length to width ratio of the olfactory bulbs (l_o/w_o) of *Procynosuchus* TSK34

(*Cistecephalus* or *Dicynodon* assemblage zones), *Cynognathus* Assemblage Zone taxa and *Tritylodon* BP/1/4265 (*Massospondylus* range zone) range from 1.26 to 1.33. Two taxa from the *Lystrosaurus* Assemblage Zone (*Galesaurus* RC845 and *Platycraniellus* NMQR1632) fall above the average of 1.33, suggesting relatively longer olfactory bulbs in those Early Triassic taxa.

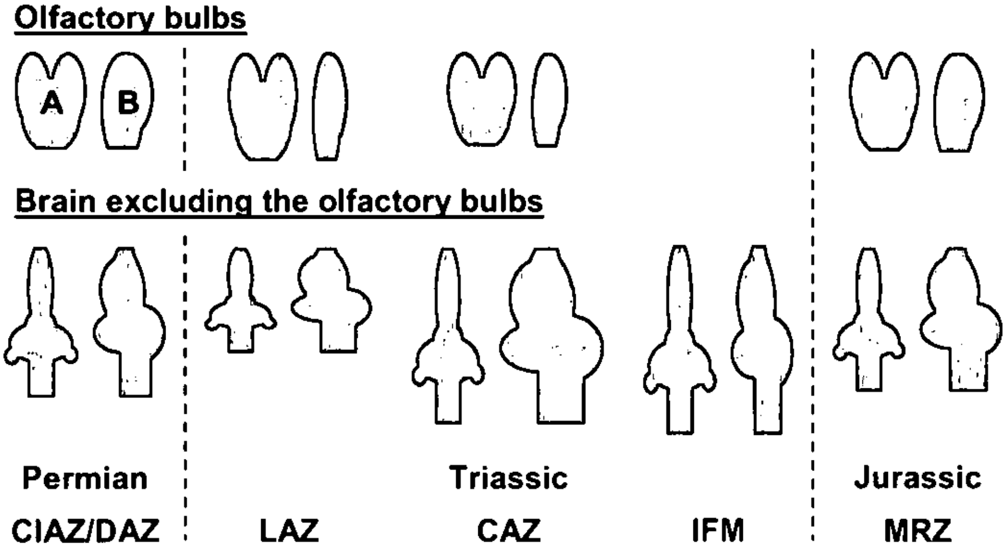


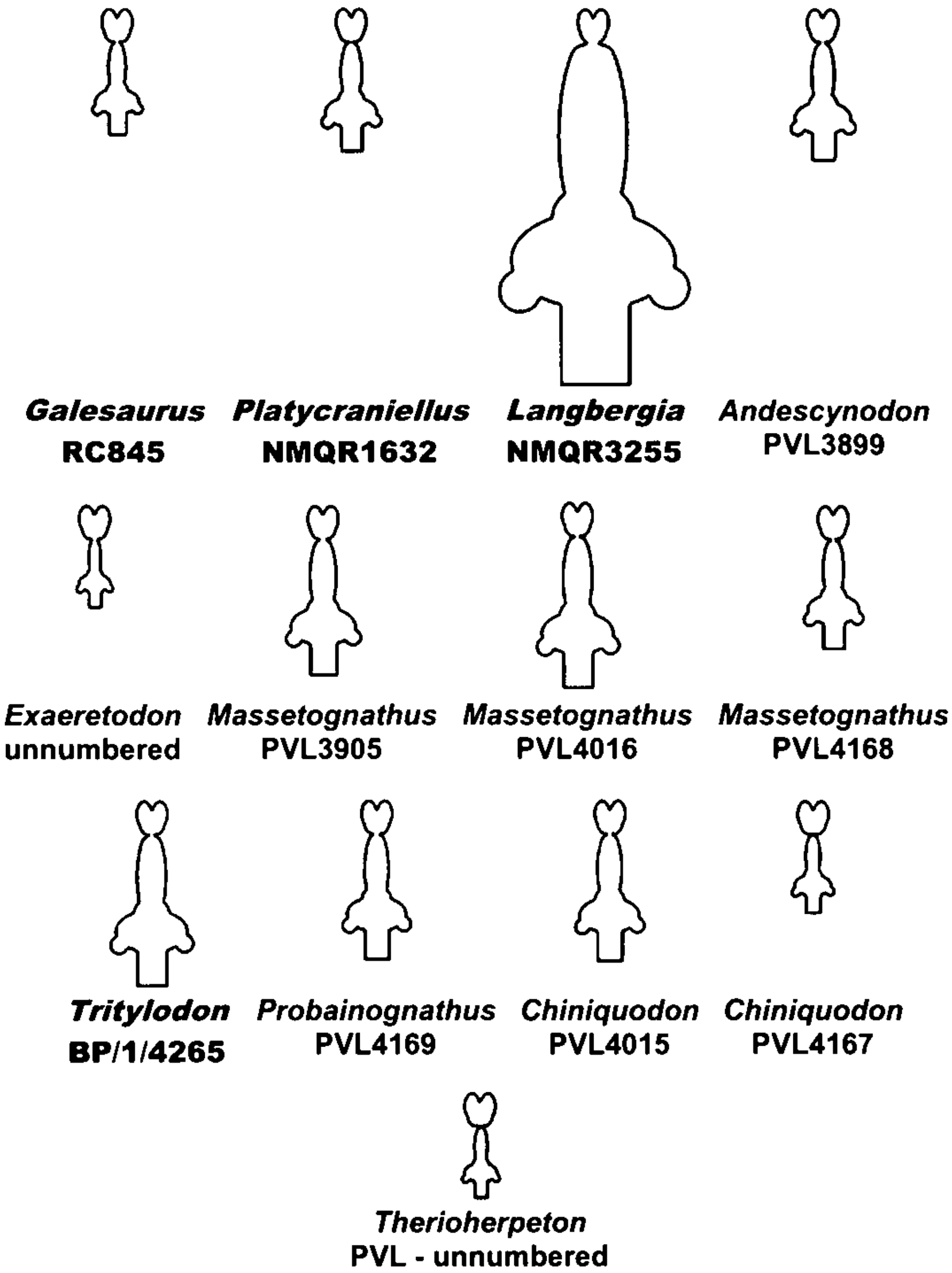
Figure 13. Dorsal (A) and right lateral (B) schematic representations of the cranial endocasts of the cynodonts examined in the present study and those in literature, based on average linear ratios, arranged according to stratigraphic position. The proportional width measurements have been equaled to allow for comparison. Abbreviations: CAZ, *Cynognathus* Assemblage Zone (Burgersdorp Formation); CIAZ/DAZ, *Cistecephalus* or *Dicynodon* assemblage zones (Teekloof Formation); IFM, Ischigualasto Formation; LAZ, *Lystrosaurus* Assemblage Zone (Katberg Formation); MRZ, *Massospondylus* range zone (Elliot Formation).

Height to width ratios of the cranial endocasts (h_b/w_b) are above average for taxa from the *Lystrosaurus* Assemblage Zone, the trirachodontids from the *Cynognathus* Assemblage Zone and *Tritylodon* BP/1/4265 from the *Massospondylus* range zone, that suggests that they had deep brains. The brain is deepest in taxa from the Early to Middle Triassic *Cynognathus* Assemblage Zone. The Middle Triassic taxa fall above the average value of 2.03 for the length to width ratio of the brain (l_b/w_b), with a maximum ratio of

2.52 in *Exaeretodon* from the Ischigualasto Formation, which suggests an elongation of the cranial endocast. The l_b/w_b ratios of the Late Permian, Early Triassic *Lystrosaurus* Assemblage Zone and Early Jurassic *Massospondylus* range zone taxa range below 2.03, that therefore indicate relatively shorter cranial endocasts compared with other cynodonts. A notable increase in the length to height brain ratio (l_b/h_b) is seen in the Triassic Period. The difference between the cranial endocast ratios of both the Early Triassic (*Lystrosaurus* Assemblage Zone) and Early Jurassic (*Massospondylus* range zone) taxa compared to other genera is notable, and one may speculate that the olfactory bulbs became relatively longer, and the rest of the brain deeper, narrower and shorter at the beginning of each period for some evolutionary reason.

Langbergia NMQR3255, *Platycraniellus* NMQR1632, *Probainognathus* PVL4169 and *Tritylodon* BP/1/4265, as well as the traversodontids (except *Exaeretodon*) have relatively small olfactory bulbs (1-10%) compared to the rest of the brain ($E_o : E_b$ = 0.01-0.1) (Figure 14, data taken from Appendix, Table 8), and with the smallest ratio present in *Langbergia* NMQR3255. In *Exaeretodon* and *Therioherpeton*, the olfactory bulbs formed 19-20% of the total endocast volume ($E_o : E_t$ = 0.19-0.2). The *Chiniquodon* endocasts reveal that this genus also had large olfactory bulbs ($E_o : E_b$ = 0.08-0.18), although less so in specimen PVL4015, which has a similar $E_o : E_b$ ratio of 0.08 to that of *Andescynodon* PVL3899 (Quiroga, 1980a). This trend is also seen in *Platycraniellus* NMQR1632 and *Tritylodon* BP/1/4265, with $E_o : E_b$ ratios identical to that of *Massetognathus* PVL3905 and PVL4168 (Quiroga, 1980a) ($E_o : E_b$ = 0.1 and 0.06 respectively).

Over geological time, the relative size of the olfactory bulbs compared to the rest of the brain appears to have increased in the carnivorous/insectivorous groups, particularly in the Probainognathia, except the Cynognathia. All of the cynodont genera examined in the present study have brains, the olfactory bulbs excluded, that take up 80% or more of the total cranial endocast volume ($E_b : E_t$ = 0.8-0.99). The estimated total endocast volume of *Platycraniellus* NMQR1632 (E_t = 5.09 cm^3) is larger than those of most cynodonts of similar body sizes, although it is comparable to that of *Chiniquodon* PVL4015 (4.82 cm^3) (Appendix, Table 8).



Galesaurus
RC845

Platycraniellus
NMQR1632

Langbergia
NMQR3255

Andescynodon
PVL3899

Exaeretodon
unnumbered

Massetognathus
PVL3905

Massetognathus
PVL4016

Massetognathus
PVL4168

Tritylodon
BP/1/4265

Probainognathus
PVL4169

Chiniquodon
PVL4015

Chiniquodon
PVL4167

Therioherpeton
PVL - unnumbered

Figure 14. Schematic representations of the cranial endocasts of the cynodonts examined in the present study (in bold) and those in literature in dorsal view, based on volumetric ratios. The proportional volumes of the olfactory bulbs have been equaled to allow for comparison. The proportional volumes for *Platycraniellus* NMQR1632 were estimated (see text).

4.4 Encephalization quotients

The EQ values of the cynodonts examined in the present study (Appendix, Table 9) were compared with those of fossil and living mammals from the literature (Figures 15, 16, 17 and Appendix, Table 10). Due to different methods of calculation used by the various authors, modifications were made to some of the values from the literature, in order to make the results comparable. It should be noted that the EQ of several Mesozoic mammals are based on single specimens.

It is clear from Figure 15, that the EQ_o values of cynodont olfactory bulbs range between 0.01 and 0.33 (average = 0.11). *Galesaurus, Exaeretodon* and *Therioherpeton* have relative large olfactory bulbs (EQ_o = 0.20-0.33) (Quiroga, 1980c; Quiroga, 1984). Other cynodonts have values ranging from 0.01 (*Langbergia*) to 0.12 (*Chiniquodon*) (Quiroga, 1978). The size of the olfactory bulbs of *Platycraniellus* falls between that of *Chiniquodon* and *Therioherpeton* (0.10-0.18). Despite individual variation of the relative brain size (EQ_b), EQ_o remains the same in all the *Massetognathus* specimens (0.06; n = 4) (Quiroga, 1978; Quiroga, 1980a; Rodrigues, 2005). It is notable that, even though some overlap of EQ_o values occurs, a division based upon differences in diet forms at approximately EQ_o = 0.06, with most of the carnivorous/insectivorous genera having values greater than 0.06 and the herbivores/omnivores (with the exception of *Exaeretodon*) less than 0.06.

The relative size of the olfactory bulbs in cynodonts is similar to those of most fossil and living mammals, with the exception of members of some mammalian groups, such as the afrosoricidans and carnivorans. *Langbergia*'s small olfactory bulbs (EQ_o = 0.01) are comparable in size to those found in the lower range of some living bats (0.01-0.43) (Baron *et al.*, 1996; Hutcheon *et al.*, 2002). The EQ_o values of the Traversodontidae (with the exception of *Exaeretodon*, which falls within the multituberculate range at 0.2) and *Tritylodon* come in below those of rodents and multituberculates, while the values of most other cynodonts fall within the lower range of monotremes (Figure 15).

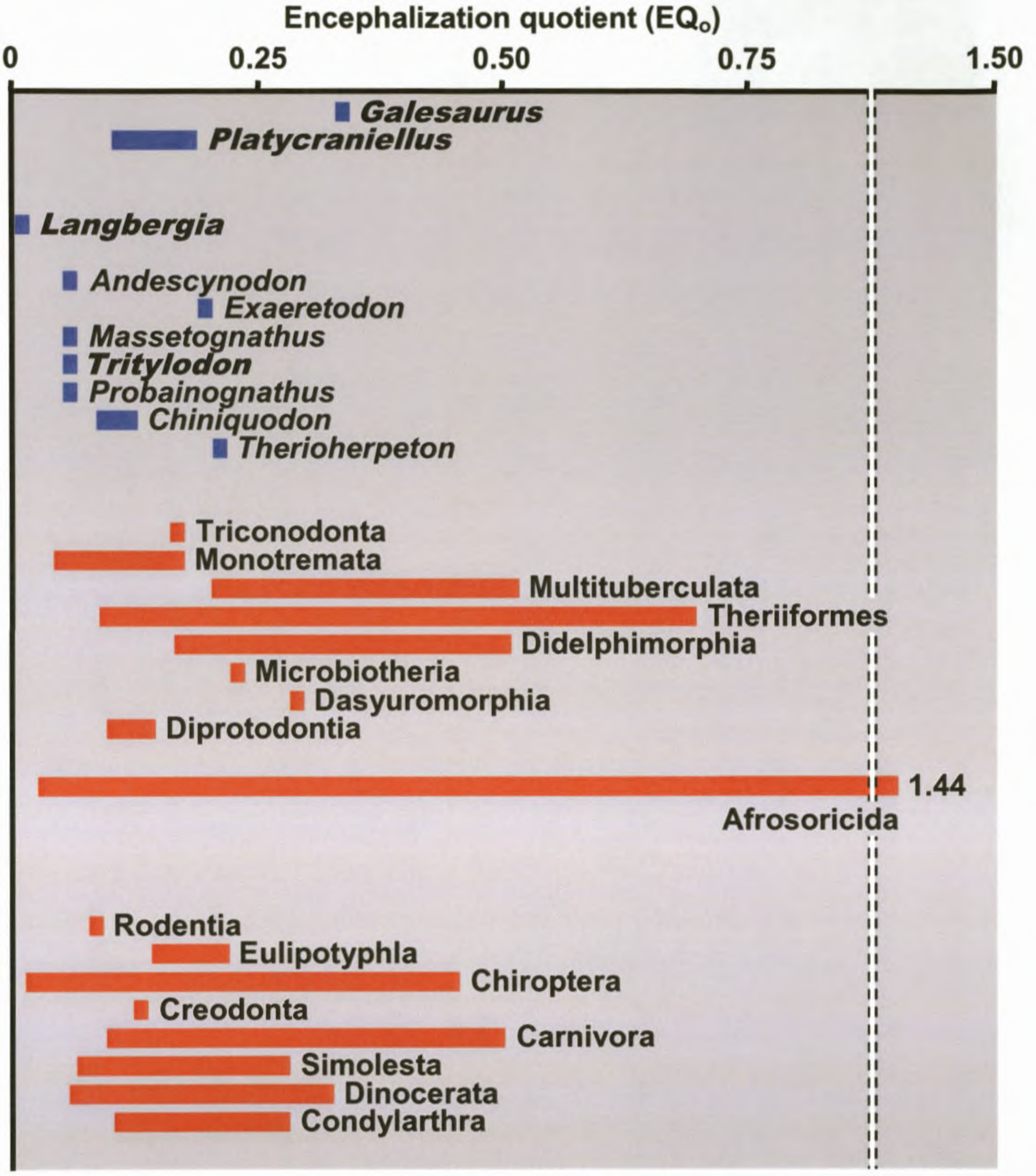


Figure 15. Ranges of encephalization quotients for the olfactory bulbs (EQ_o) of cynodonts (blue), and fossil and living mammals (red). The cynodonts examined in the present study are indicated in bold. The range for *Platycraniellus* is based on one cranial endocast and two body masses.

The relative size of the cranial endocast of *Massetognathus* PVL0968T, PVL3905 (EQ_b = 0.12), and PVL4016 (EQ_t = 0.14) are average in comparison with other cynodonts (Figure 16, 17). The relatively smallest total cranial endocasts are found in the traversodontids (EQ_t = 0.07-0.14), whereas many other Early and Early Middle Triassic genera, such as *Thrinaxodon,* *Diademodon* and *Langbergia*, have relatively small brains excluding the olfactory bulbs (EQ_b = 0.03-0.10).

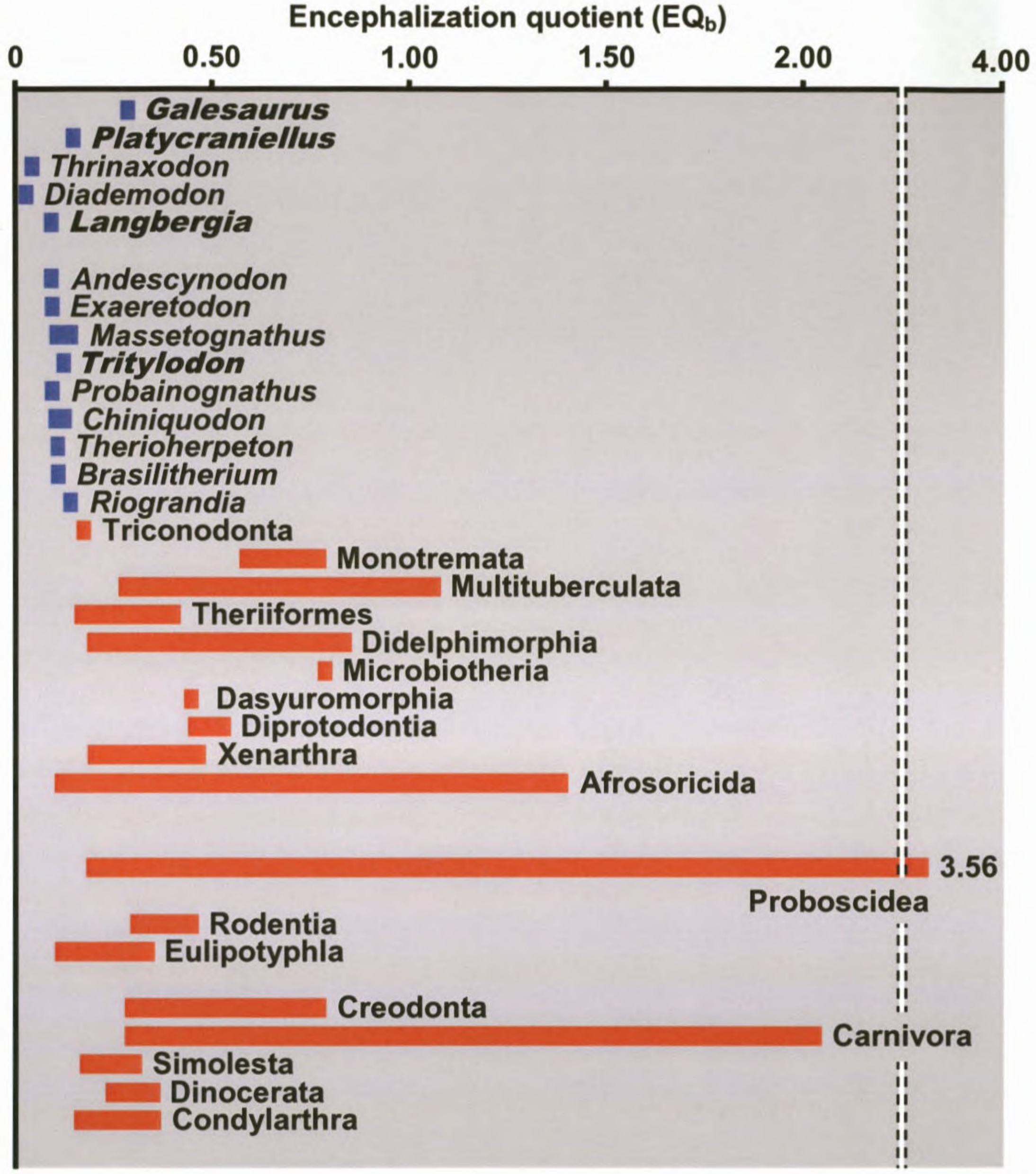


Figure 16. Ranges of encephalization quotients for the brain, the olfactory bulbs excluded (EQ_b), of cynodonts (blue), and fossil and living mammals (red). The cynodonts examined in the present study are indicated in bold.

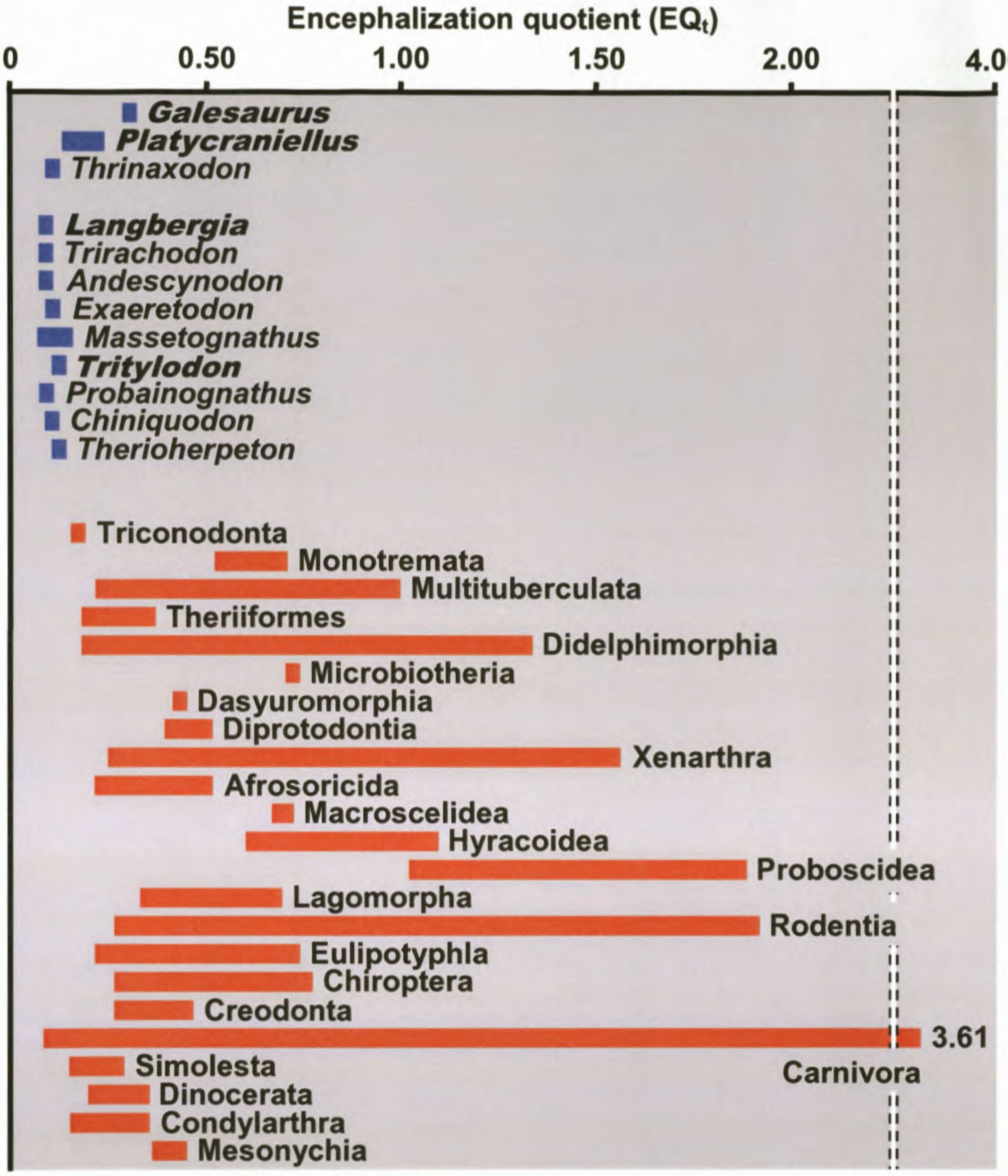


Figure 17. Ranges of encephalization quotients for the brain, the olfactory bulbs included (EQ_t), of cynodonts (blue), and fossil and living mammals (red). The cynodonts examined in the present study are indicated in bold. The range for *Platycraniellus* is based on one cranial endocast and two body masses.

Only *Galesaurus* (EQ_b = 0.29; EQ_t = 0.3) and *Platycraniellus* (EQ_b = 0.13-0.24; EQ_t = 0.13-0.23) have brain and total cranial endocast values higher than the supposedly minimum mammalian EQ of 0.2 (Radinsky, 1978). The Brazilian tritheledont *Riograndia* (EQ_b = 0.15, Figure 16) (Rodrigues, 2005) also groups close to the mammalian value. *Platycraniellus* and *Riograndia* have similar EQ values to those of early insectivorous mammals, such as *Triconodon*, and

Galesaurus also reaches the lower range of both creodonts and carnivorans. Some mammals have values below Radinsky's (1978) 'mammalian line' of 0.2. Of all the mammals, fossil or living, true insectivorans (Eulipotyphla) and tenrecs (Afrosoricida) have some of the smallest relative brain sizes (EQ_b = 0.10-0.34 and 0.10-1.39 respectively). The lowest mammalian EQ_t value is 0.08 (Carnivora) (Figure 17). Following this value, all eucynodonts, with the exception of *Diademodon* (EQ_t information not available), have cranial endocast EQ values that fall within the mammalian range ($EQ_b \geq 0.10$; $EQ_t \geq 0.08$). The basal epicynodont *Thrinaxodon* UCMZT42865 is the only cynodont specimen to have a smaller brain ($EQ_b = 0.05$) than those of the smallest-brained mammals.

To determine whether a change in relative brain size over geological time had occurred, the EQ values of cynodonts from nine geological biozones were compared in Figure 18 (data taken from Appendix, Table 11). Data of the traversodontid *Andescynodon* from the Argentinean Cerro de las Cabras Formation was included with those of the taxa from the *Cynognathus* Assemblage Zone, as these geological strata are considered to be time equivalents (Tucker & Benton, 1982). It is evident that a general reduction in EQ occurred during the Early Middle Triassic *Cynognathus* Assemblage Zone, but there was an increase of the EQ again during the Late Triassic. A reduction in the relative size of the olfactory bulbs occurred in the Early Jurassic. Above average cynodont cranial endocast sizes ($EQ_o \geq 0.11$; $EQ_b \geq 0.12$) are observed during the Early Triassic ($EQ_o = 0.2$; $EQ_b = 0.18$), Early Middle Triassic (only the olfactory bulbs, EQ_o = 0.2-0.21) and Late Triassic/ Early Jurassic (only the brain, EQ_b = 0.13-0.14).

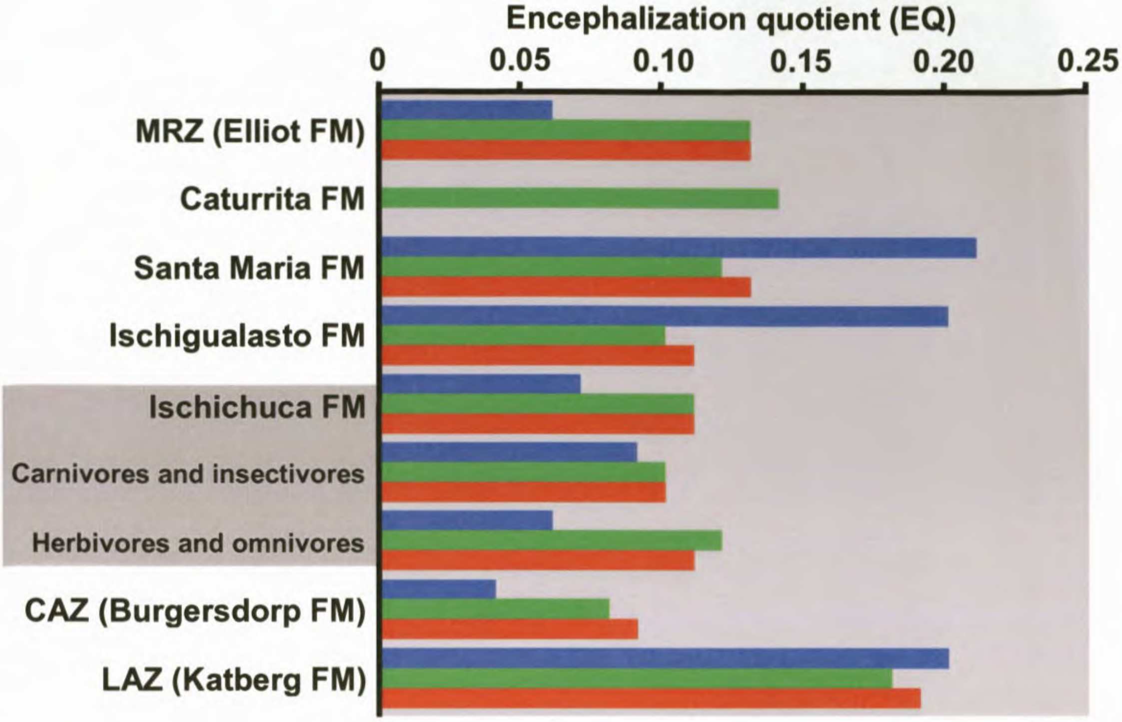


Figure 18. Ranges of encephalization quotients for the olfactory bulbs (blue), brain (yellow) and the entire cranial endocast (red) of the cynodonts examined in the present study and the literature, based on average values, arranged in stratigraphic order. Data on contemporaneous carnivores/insectivores and herbivores/omnivores are available from the Middle Triassic Chañares Formation (grey block). All formations range from Early to Late Triassic in age, apart from the *Massospondylus* range zone (Elliot Formation), which perhaps extends into the Early Jurassic. Abbreviations: CAZ, *Cynognathus* Assemblage Zone; FM, Formation; LAZ, *Lystrosaurus* Assemblage Zone; MRZ, *Massospondylus* range zone.

The Middle Triassic Chañares Formation in Argentina is the only zone that yieleded data for both carnivorous/insectivorous and herbivorous/omnivorous genera. Although the average relative brain size of the predatory probainognathians are slightly smaller than those of the herbivorous traversodontids (Appendix, Table 11), the olfactory bulbs are relatively larger in *Probainognathus* and *Chiniquodon* than those of *Massetognathus*. Similar tendencies are observed in the fossil and living mammals, which is thought to be diet-related. Amongst marsupials, the herbivorous Diprotodontia have relatively smaller olfactory bulbs (EQ_o = 0.09-0.14) compared to those of carnivorous and/or insectivorous orders (Didelphimorphia, Microbiotheria and Dasyuromorphia) (0.16-0.50) (Figure 15). Microbiotheria and certain Didelphimorphia, on the other hand, have relatively larger total endocasts (EQ_t = 0.39-0.43) (Figure 17). The total endocast size is relatively larger in the carnivorous Mesonychia (0.35-0.44) exceeds those of the herbivores (0.15-0.34) that belong to the orders Simolesta, Dinocerata and Condylarthra (collectively known as 'archaic ungulates'). Although overlap occurs between groups, the afrotherian herbivores (Hyracoidea and Proboscidea) have larger encephalization quotients (EQ_b = 0.17-3.56; EQ_t = 0.6-1.87) than the insectivores (Afrosoricida and Macroscelidea) (EQ_b = 0.1-1.39; EQ_t = 0.21-0.71) (Figure 16, 17).

CHAPTER FIVE
DISCUSSION

5.1 Sample size

It is realised that the data resulting from the small sample size in the present study and sparse information from the literature limits the conclusions drawn here. Some of the conclusions appears contradictory and depends on the cause of the variation within the observed results. However, some general patterns emerged from this study that can serve as basis for further research.

5.2 Endocast characteristics

Size

The relatively small cranial endocast size (EQ_b and EQ_t) of the basal epicynodont *Thrinaxodon* (Simpson, 1927; Jerison, 1973; Hopson, 1979; Hopson, 1980) in comparison with those of the closely related *Galesaurus* RC845 and *Platycraniellus* NMQR1632 represents an artefact that probably results from the usage of two different *Thrinaxodon* specimens to calculate the EQ: UCMZT42865 (Jerison, 1973) was used to determine the relative brain size ($EQ_b = 0.05$), and BMNHR1713 (Simpson, 1927) was used to estimate the total cranial endocast size ($EQ_t = 0.11$). BMNHR1713 has an EQ_t value only slightly less than the lowest value of *Platycraniellus* NMQR1632 (EQt = 0.13-0.23; S = 8.6 cm (TM25), 11.4 cm (NMQR860)), that suggests that the much smaller value of UCMZT42865 (S = 6 cm) may be due to either sexual dimorphism or ontogenetic/individual variation. *Galesaurus* RC845 and *Platycraniellus* NMQR1632 have the largest cranial endocasts of all the cynodonts examined in the present study. This is surprising because it would be expected that the more derived cynodonts in other respects would also have larger cranial endocasts than *Galesaurus* and *Platycraniellus*. This paradoxical result needs to be confirmed with further testing by using a larger sample size in order to rule out the possibility of individual variation.

The olfactory bulbs of *Langbergia* NMQR3255 are notably smaller than those of all the other taxa and should be compared with other diademodontoids in future, once a larger sample becomes available. All other cynodonts have EQ_o values that are similar to those of fossil and living mammals. *Therioherpeton* has the largest olfactory bulbs, which fall within the lower size range of multituberculate mammals. In general, the relative size of the olfactory bulbs appears to increase slightly during cynodont evolution, particularly in the probainognathian lineage.

The brains, the olfactory bulbs excluded, of most cynodonts fall within the lower range of fossil and living mammals, i.e. above an EQ_b value of 0.1. However, some Middle Triassic cynodonts (*Andescynodon* PVL2894, *Massetognathus* PVL4168 and *Chiniquodon* PVL4167) have values (EQ_b = 0.08) less than 0.1. *Thrinaxodon* UCMZT42865 and *Diademodon* BMNR3767 have particularly small relative brain sizes (EQ_b = 0.03-0.05). A slight increase is seen in both diademodontoid and probainognathian cynodonts above the value of 0.1, with EQ_b values of *Tritylodon* and *Riograndia* only slightly less than those of the triconodont mammals.

The total cranial endocast sizes increase slightly in the more derived cynodonts, with all the eucynodonts (except perhaps *Diademodon*, for which data is unavailable, and *Massetognathus* PVL4168) that fall within the lowest range of mammals.

Shape

The structure of the cranial endocasts of all the cynodonts examined at first hand compare well with those described in the literature (Kemp, 1979; Quiroga, 1978; Quiroga, 1970; Quiroga, 1980c). Kielan-Jaworowska (1986) described a generalized cynodont cranial endocast and a similar shape was found in the forms investigated in the present study. Typically, large olfactory bulbs, and a narrow, tubular brain that widens posteriorly to form the cerebellum and associated parts are present.

The main reason why the cynodonts (*Galesaurus* Cynodont A and *Thrinaxodon* Cynodont B) in Olson's study (1944) appear to have such small (and shortened) brains (olfactory bulbs excluded) in comparison with other cynodont specimens, may be that Olson (1944) measured only the hindbrain, without taking into account the rest of the endocranial cavity. This probably explains why *Galesaurus* RC845 and *Platycraniellus* NMQR1632 in the present study have relatively longer cranial endocasts than those included in Olson's (1944) study.

5.3 Phylogeny

The posterior position of the cranial endocast (Figure 7) and increase in relative brain size (indicated EQ values in Figures 15, 16 and 17) seen in *Tritylodon* and some probainognathians does not resolve the current controversy of their phylogenetic affinities with mammals, but both groups of derived cynodonts give supporting evidence for increasingly mammal-like morphological characteristics during their evolution (Hopson & Kitching, 1972; Kemp, 1982; Hopson, 1991; Martinez *et al.*,1996, Rubidge & Sidor, 2001; Luo *et al.*, 2002; Bonaparte *et al.*, 2005; Abdala, 2007). The diademodontoids, such as *Diademodon*, Trirachodontidae and Traversodontidae, show little change in their range of EQ.

5.4 Daily activity

The higher olfactory bulbs and by implication better smelling (Kermack & Kermack, 1984) of *Procynosuchus* and *Tritylodon* may be associated with nocturnal habits (McLoughlin, 1980). The other taxa examined in the present study have flattened olfactory bulbs.

Most of the large therapsid predators, including gorgonopsians and therocephalians, went extinct at the end of the Permian Period (Sidor & Smith, 2004). Terrestrial vertebrates were of small body size (less than 2 m) during the earliest Triassic (Kemp, 1982; Behrensmeyer *et al.*, 1992; Smith & Ward, 2001; Kemp, 2005) and the risk of terrestrial predation by large archosauromorphs and therocephalians was low (Niven, 2005). This allowed *Lystrosaurus* Assemblage Zone (and possibly some *Cynognathus* Assemblage

Zone) cynodonts to forage by day (as indicated by their relatively flattened olfactory bulbs), and large olfactory bulbs would therefore not have been as important. When the large cynodonts (*Cynognathus, Diademodon* and some traversodontids) of the Early and Middle Triassic disappeared (Kemp, 2005), possibly due to competition with and/or predation by archosauromorphs (Bertoni-Machado & Holz, 2006) during the later part of the period, the Cynodontia was largely represented by the tritylodontids and tritheledonts (Kemp, 1982). They may have been nocturnal in order to escape predation and/or competition, and would therefore have relied largely on their sense of smell (Jerison, 1973; Hopson, 1979; Kermack & Kermack, 1984). Consequently they would have had larger olfactory bulbs and this is evident in *Tritylodon*.

5.5 Sociality

Hopson (1977) proposed that dinosaur brain size may be correlated with sociality. Pérez-Barbería *et al.* (2005) found evidence that changes in relative brain size and sociality are closely correlated over evolutionary time for several mammalian orders. This could mean that the small EQ_b values seen in some herbivorous Cynognathia may be related to asocial behaviour, and that *Diademodon* in particular was solitary, although it should be noted that *Diademodon* skeletons have been recovered from bone beds, which may indicate social behaviour. As *Galesaurus*, *Thrinaxodon* (E. Butler, *pers. comm.* 2010[3]), and several adult and juvenile *Langbergia* (Groenewald *et al.*, 2001; Abdala *et al.*, 2006) aggregations have been found, it was concluded that some form of parental care had developed (McCarthy & Rubidge, 2005). This evidence of gregarious behaviour of the basal epicynodonts and trirachodontids implies that they have been social animals. Because the EQ_b values of *Platycraniellus, Massetognathus, Tritylodon, Chiniquodon* and the tritheledonts are higher than those of *Thrinaxodon, Langbergia* and *Trirachodon*, these taxa may also have shown a degree of social behaviour, a typical characteristic of mammals.

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5.6 Habitat preferences

Although Triassic and Early Jurassic terrestrial ecosystems of Pangaea are characterized by widespread aridity as a wide generalization (Robinson, 1973; Tucker & Benton, 1982; Anderson & Anderson, 1983; Anderson & Anderson, 1985; Parrish *et al.*, 1986; Kutzbach & Gallimore, 1989; Smith *et al.*, 1993; McCarthy & Rubidge, 2005; Pires *et al.*, 2005; Smith & Botha, 2005), habitats that ranged from forest and open woodland to thicket and wetlands, were available that may have been inhabited by cynodonts (Anderson *et al.*, 1998).

Similar to a correlation between habitat complexity and relative brain size in predatory bats (Safi & Dechmann, 2005) and herbivorous ungulates (Schultz & Dunbar, 2006), it seems possible that *Platycraniellus,* the probainognathians and *Massetognathus* may have inhabited mixed habitats (e.g. open woodland). As is the case in bats, their large brains would have been advantageous in processing spatial information in such complex environments (Safi & Dechmann, 2005). Although stable isotope analysis suggests that *Diademodon* may have been nocturnal (the size of its olfactory bulbs are unknown to confirm this lifestyle) and/or preferred shady, damp micro-habitats (Botha *et al.*, 2005), this cynodont, as well as *Thrinaxodon*, may also have lived in more open habitats, based on their small EQ_t values (Figure 16). Similar to modern African herbivores such as hippopotamus, elephant, buffalo and black rhinoceros (Smithers, 1983; Estes, 1999; Apps, 2000), *Diademodon* may have ventured onto more open terrain at night to forage, seeking cover during the hottest hours of the day. On the basis of its small olfactory bulbs, *Langbergia* may also have inhabited more open habitats such as floodplains (Groenewald *et al.*, 2001).

Cynodonts with small cranial endocasts may also have inhabited habitats where resources were limited (Niven, 2005). Anderson *et al.* (1998) found that the South African traversodontid *Scalenodontoides* lived in a wide spectrum of terrestrial habitats, preferring those with small shrubs less than 50 cm high, and avoiding marshes dominated by unpalatable *Equisetum* horsetails. Dietary specificity and the absence of permanent water sources, for instance, would be a limiting factor for cynodonts (Botha *et al.*, 2005) especially during the harsh, arid Triassic Period.

Anderson *et al.* (1998) suggested that *Tritylodon* may have inhabited mainly riparian forests. This taxon, as well as *Galesaurus* and most traversodontids (especially *Exaeretodon*), may have inhabitated densely wooded habitats, where their large olfactory bulbs would have played an important role in orientation and locating food (Möhres & Kulzer, 1956; Luft *et al.*, 2003). Southern African tritheledontids are thought to have inhabited open woodland to forests (Anderson *et al.*, 1998). *Therioherpeton*'s large olfactory bulbs may therefore indicate that it preferred dense woodland or the edges of forests.

It has been suggested by Pérez-Barbería *et al.* (2005) and Finarelli and Flynn (2009) that a preference for closed habitats in carnivorans, inferred from relative brain size, may also be indicative of fossorial behaviour, for which fossil evidence exists in *Galesaurus* (E. Butler, *pers. comm.* 2010), *Thrinaxodon* (Damiani *et al.*, 2003) and *Langbergia* (Groenewald *et al.*, 2001).

5.7 Diet

Carnivory and insectivory

Hopson (1980) found that some herbivorous dinosaurs fall within the EQ range of contemporary predators, and Radinsky (1978) also found similarities in relative brain size between contemporary carnivores and ungulates. The overlap observed in the EQ values of the mammalian Afrotheria (herbivorous Hyracoidea and Proboscidea versus insectivorous Afrosoricida and Macroscelidea) indicates that it would probably be difficult to differentiate between herbivorous/omnivorous and insectivorous cynodonts based on the relative size of the total endocranial cavity alone. However, the results of the present study suggest that carnivorous and insectivorous cynodonts from the Middle Triassic Chañares Formation had larger olfactory bulbs than their contemporary herbivores. The insectivorous cynodonts investigated in the present study are characterized by their above average EQ_o values (0.08-0.33) that indicate an increased relying on smell.

In several vertebrate groups, active predators tend to have large EQ values (Platel, 1974; Platel, 1975; Jerison, 1973), and this is confirmed by the relative total cranial endocast size (EQ_t) of Mesonychia and certain marsupials (Radinsky, 1976, 1977, 1978; Macrini *et al.*, 2007a). Kemp (2007) suggested that among therapsids there was a progressive speciation bias for small carnivores, which was possibly influenced by their ecology. It is possible that *Galesaurus*, with its relatively larger cranial endocast and olfactory bulbs compared to other predatory taxa (McLoughlin, 1980) from the *Lystrosaurus* Assemblage Zone, may have been an obligate insectivore, similar to extant small carnivorans (Smithers, 1983). This observation is supported by its dentition, which was adapted for processing robust invertebrates such as insects (Kemp, 2005).

Herbivory and omnivory

Schultz and Dunbar (2006) found that browsing ungulates have relatively larger brain sizes than either frugivores/omnivores and grazers. Because their EQ_o values are less than those of other herbivorous cynodonts, it is thought that adult trirachodontids may have fed on low-growing plants. Although *Diademodon*'s relative brain (excluding the olfactory bulbs) size seems to suggest that it fed on low-growing plants, such as those growing in water (Botha *et al.*, 2005), it has also been described previously as being a bear-like omnivore (Grine, 1978; Kermack & Kermack, 1984; Anderson & Anderson, 1985; Anderson *et al.*, 1998). The results in the present study, based on limited information, therefore do not clarify the dietary status of this genus.

The size of the olfactory bulbs of the large *Exaeretodon*, which fall well within the range of carnivorous/insectivorous cynodonts, suggests dedicated omnivory in this genus that corresponds with the indication by its atypical (herbivorous) traversodontid teeth (Kemp, 1982). Some other traversodontids and tritylodontids are also considered to be omnivorous (Kemp, 1980; Abdala &

Malabarba, 2007; Hu *et al.*, 2009). The size of the olfactory bulbs of *Andescynodon, Massetognathus* and *Tritylodon* are similar to that of the insectivorous *Probainognathus*. The analogous rodents, especially squirrels, dormice, rats and mice, consume some insects and other live food on occasion (Smithers, 1983), whereas porcupines that eat carrion have been recorded (Roth, 1964). It is therefore possible that, although their dentitions suggest herbivory (Hopson & Kitching, 1972), *Andescynodon, Massetognathus* and *Tritylodon* may have supplemented their diet with alternative sources of protein.

5.8 Thermoregulatory status

The relative brain size (the olfactory bulbs excluded) of Chañares Formation cynodonts (with the exception of two specimens, *Massetognathus* PVL4168 and *Chiniquodon* PVL4167) supports McNab's (1978) suggestion that a basic form of endothermy may already have existed by the Middle Triassic, because their EQ_b values are above 0.1 (although still below 0.2) and within the range of living placental mammals. Furthermore, many other cynodonts (with the exception of *Thrinaxodon* and *Diademodon*) are on or above the mammalian defining line of 0.1, suggesting the possibility of endothermy (Rodrigues, 2005), at a lower body temperature than most living mammals (McNab, 1978). The results suggest that only *Galesaurus* and *Platycraniellus* bridge Radinsky's (1978) line of 0.2. When the relative total brain size of living lizards is determined using mammalian standards, the most encephalized species fall between EQ_t = 0.15-0.21 (Hopson, 1980). The correlation between large brains and endothermy in vertebrates is therefore dubious (Bennett & Ruben, 1986) and thus the precise thermoregulatory status of cynodonts remains speculative. It is likely that the relatively high EQs seen in *Galesaurus* and *Platycraniellus* are due to some factor other than temperature physiology.

5.9 Assessments

Body mass

Kemp (2009) thinks that expressing relative brain size as an encephalization quotient remains speculative. The standard equation for EQ relies in part on body mass (Jerison, 1973), which cannot be calculated with complete confidence for extinct animals (Kemp, 2009). The correlation between body mass and measurements from various parts of the skeleton needs to be investigated more thoroughly in a wide range of living mammals (Macrini *et al.*, 2007) to enable better mass extrapolation. By using more than one allometric equation to calculate body mass, an estimated body mass range can be determined for non-mammalian cynodonts, although the mean value will probably be, as in the case for the Mesozoic mammal *Kryptobataar* (Kielan-Jaworowska & Lancaster, 2004), similar to the resulting body mass derived from Jerison's (1973) equation.

Endocast volume

The methods of water displacement (Jerison, 1973; Radinsky, 1978), double integration (Jerison, 1969; Jerison, 1973) or cranial endocast modelling on an elliptical cylinder (Jerison, 1973; Kielan-Jaworowska & Lancaster, 2004) can lead to over- or underestimating the actual volume of the endocranium, and digital measurement of this space may thus be a more accurate method. However, most cranial endocast volumes from the literature are based mainly on the impressions of the brain on the skull roof (Kemp, 2009), because the floor of the braincase is not completely ossified (Jerison, 1979; Kemp, 2006). In the past, it has been assumed that the height proportions of the brain were reptilian, whereas certain authors (Watson, 1913; Olson, 1944; Rodrigues, 2005) focused only on the hindbrain, excluding the olfactory bulbs and/or forebrain from reconstructions of the cranial endocast. Available height measurements, however, suggest that therapsid cranial endocasts are deeper than those of reptiles (Kemp, 1969b; Kemp, 1979). More work is needed to determine more precise endocast proportions, especially with regard to height.

Brain size

There are various opinions about the percentage of the endocranial cavity (75-100%) that had in fact been filled by nervous tissue (Hopson, 1980; Quiroga, 1980c), and about what the precise density of the brain was (0.9-1.087 g/cm^3) (Coria & Currie, 2003; Witmer *et al.*, 2003; Saveliev & Alifanov, 2007). Assuming 90% of the endocranial cavity to represent of the brain volume, accepting a brain density of 1.0 g/cm^3 (Marino, 1999), and by standardizing information from the literature to these criteria, more reliable for absolute brain sizes of cynodonts and fossil mammals had been obtained in the present study.

Encephalization quotients

Jerison (1973) calculated the expected brain mass of non-mammalian therapsids with an equation for reptiles, which are an unrelated group. This resulted in therapsids not being comparable to mammals with regard to relative brain size. In contrast, the present study used the expected brain mass equation calculated from mammals. Based on empirical observation of the data for a range of mammals, the 'mammalian line' of 0.2 (Radinsky, 1978) was shifted to EQ_b = 0.1 and EQ_t = 0.08 (based on the EQ values for some mammals). Consequently, the relative brain and cranial encocast sizes of most cynodonts now fall into the lower range of mammals.

5.10 Future research

More cynodont genera, especially the medium-sized to large taxa, and in particular those from the Late Permian and Middle and Late Triassic Periods, as well as non-cynodont synapsids and Mesozoic mammals need to be examined more thoroughly to determine how brain evolution is interrelated to various factors in the development of the Therapsida, and the role brain evolution played in the appearance of true mammals. Examination of the specimens from the literature may reveal the accuracy of the techniques used to calculate the endocranial cavity in previous studies, while data about the cranial endocast measurements, size and shape of those fossils can supplement the limited information that is currently available. A larger sample size of well preserved skulls (without any adhesives) is needed before statistical analyses can be done in any detail. It may allow for more detailed research about the different parts of the complex hindbrain and phylogenetic characters to be identified from such cranial endocasts.

It may be necessary to rescan some of the skulls, and to use either high-energy X-rays (100 and 200 kV) in cases where thermal neutrons were unsuccessful, or to use thermal neutrons where X-rays did not adequately penetrate. Neutron computerized tomography, in combination with X-ray diffraction, has proven useful to determine the position, condition and chemical composition of fossils that are still contained within nodules of matrix, in this way aiding with the future preparation of such specimens. X-ray diffraction analyses of the skulls that produced unsatisfactory scans should be done, in order to determine how different materials within the fossils and matrix can influence the penetration of radiation beams, in particular thermal neutrons, and to make recommendations for future sample selection from such information. At present, however, it seems that matrix consisting of mainly sandstone allows for better thermal neutron penetration than mudstone.

Examination of a cranial endocast with computerized tomography creates the possibility of revealing information regarding various aspects of the lifestyle of cynodonts that has been investigated in other parts of the skeleton. Although it has been beyond the scope of the present study, computerized tomography as an analytical technique can also be used to investigate other internal features, for instance the size and shape of the nasal cavities, the absence/presence of maxilloturbinate bones, and the replacement of teeth. It is hoped that the present study will also open possibilities for the use of computerized tomography as an analytical technique for inferring the palaeobiology of various other fossil organisms as well.

CONCLUSIONS

Despite the small sample size and limited information from the literature, the present study has laid a solid foundation for future research in cynodont palaeoneurology. The results suggest that non-mammalian eucynodonts have acquired various increasingly mammal-like brain characteristics throughout their evolution. This is indicated by (1) the position of the brain to the posterior region of the skull in at least *Tritylodon*, when compared to less derived taxa; (2) changes in the proportions of different parts of the cranial endocast; and (3) increased relative brain size over time in several taxa, which fall into the lower range of mammals.

Radinsky's (1978) minimum mammalian EQ of 0.2 has been reassessed and found to be 0.1 for the brain, excluding the olfactory bulbs, and 0.08 for the total cranial endocast. All eucynodonts examined in this study (apart from *Diademodon*, for which data is unavailable) therefore have EQ_b and EQ_t values that fall within the mammalian range ($EQ_b \geq 0.1$; $EQ_t \geq 0.08$).

The relative size of the olfactory bulbs in most of the cynodonts studied (apart from *Langbergia*) falls within the lower range of fossil and living mammals. The relatively deep and large olfactory bulbs in *Procynosuchus, Galesaurus, Platycraniellus, Exaeretodon, Tritylodon, Chiniquodon* and *Therioherpeton* may be related to nocturnality, habitat or dietary preferences, such as omnivory, insectivory or carnivory.

Larger cranial endocasts (based on EQ_b falling into the lower range of known mammals) observed in *Galesaurus, Platycraniellus, Massetognathus, Tritylodon, Chiniquodon* and the tritheledonts may be related to a preference for mixed or dense habitat, or social behaviour.

APPENDIX

Table 1. Institutional abbreviations of cynodont specimens examined and noted in the present study.

Abbreviation	**Institution**
BMNHR	British Museum (Natural History), London
BP/1/	Karoo Fossil Collection, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires
NMQR	National Museum, Bloemfontein
PVL	Vertebrate Paleontological Section, Miguel Lillo Fundation, Universidad Nacional de Tucumán, Tucumán
RC	Rubidge Collection, Graaff-Reinet
SAM	South African Museum, Iziko Museums of Cape Town
TM	Transvaal Museum of Natural History, Pretoria
TSK	Oxford University Museum of Natural History, Oxford
UCMZT	Cambridge University, Cambridge

Table 2. Cynodont material used in neutron (NCT) and high-energy X-ray (HRXCT) computerized tomographic scanning. Those used for further study are indicated in bold.

	Scan results	
Genus and specimen	**NCT**	**HEXCT**
Procynosuchus		
BP/1/226		Unsuccessful
BP/1/1545		Unsuccessful
BP/1/2244		Unsuccessful
BP/1/2600		Unsuccessful
BP/1/5895	Unsuccessful	
NMQR280	Unsuccessful	
Cynosaurus		
BPI/1/47		Unsuccessful
Galesaurus		
NMQR135	Unsuccessful	
RC845	Successful	
SAM-PK-K9956	Unsuccessful	
SAM-PK-K10468	Unsuccessful	
Platycraniellus		
NMQR860	Unsuccessful	
NMQR1632		Successful
Thrinaxodon		
BP/1/4280		Unsuccessful
BP/1/4942	Unsuccessful	Unsuccessful
NMQR24	Unsuccessful	
NMQR810	Unsuccessful	
SAM-PK-K1468	Unsuccessful	
SAM-PK-K1498	Unsuccessful	
Cynognathus		
BP/1/1181	Unsuccessful	
NMQR1444	Unsuccessful	
SAM-PK-K10497	Unsuccessful	
SAM-PK-K11264	Unsuccessful	
SAM-PK-K11484	Unsuccessful	
Diademodon		
BP/1/990	Unsuccessful	
BP/1/3639	Unsuccessful	
BP/1/3754	Unsuccessful	
BP/1/3771		Unsuccessful
BP/1/3773	Unsuccessful	
Langbergia		
NMQR3255	Successful	

Table 2 (continued)

Genus and specimen	Scan results	
	NCT	HEXCT
Trirachodon		
BP/1/4200	Unsuccessful	Unsuccessful
BP/1/4201	Unsuccessful	
NMQR1298	Unsuccessful	
NMQR3256	Unsuccessful	
NMQR3280	Unsuccessful	
Luangwa		
BP/1/3731	Unsuccessful	
Massetognathus		
BP/1/4245	Unsuccessful	
Tritylodon		
BP/1/4265	Successful	
BP/1/4876	Unsuccessful	
BP/1/4965	Unsuccessful	
BP/1/5047	Unsuccessful	
BP/1/5089 a	Unsuccessful	
BP/1/5167	Unsuccessful	
Lumkuia		
BP/1/2669		Unsuccessful

Table 3. Chemical compounds measured from different areas of *Trirachodon* skull BP/1/4200, using X-ray diffraction (XRD), and their theoretical mass attenuation coefficient values for thermal neutrons.

Compound	Formula	Density (g/cm^3)	Attenuation coefficient (cm^{-1})
Canine tooth			
Carbonate fluorapatite	$Ca_{9.55}(PO_4)_{4.96}F_{1.96}(CO_3)_{1.283}$	3.12	0.32
Fluorapatite	$Ca_5(PO_4)_3F$	3.2	0.33
Skull bone			
Hydroxylapatite	$(Ca_{3.36}Na_{0.08})(Ca_{5.04}Na_{0.72})(PO_4)_{3.6}(CO_3)_{2.4}(OH)_2$	3.156	0.42
Matrix			
Calcite	$CaCO_3$	2.71	0.31
Hydroxylapatite	$(Ca_{3.36}Na_{0.08})(Ca_{5.04}Na_{0.72})(PO_4)_{3.6}(CO_3)_{2.4}(OH)_2$	3.156	0.42

Table 4. Linear skull and endocast measurements (in mm; see Figure 4, p. 43) of the cynodonts examined in the present study. The skull length of *Platycraniellus* is based on NMQR860 and TM25 (Abdala, 2007), because NMQR1632 is incomplete. Abbreviations: b, brain excluding olfactory bulbs; h, height; l, length; m, foramen magnum; o, olfactory bulbs; S, skull length; w, width.

		Endocast							
Genus and specimen	**S**	l_o	w_o	h_o	l_b	w_b	h_b	w_m	h_m
Galesaurus									
RC845	62.80	12.87	9.47	5.21	26.06	12.98	16.06	2.87	1.81
Platycraniellus									
NMQR1632		17.02	10.21	-	32.41	15.60	-	6.30	-
TM25	85.87								
NMQR860	114.16								
Langbergia									
NMQR3255	98.93	5.05	3.81	2.16	26.49	11.86	17.11	5.94	6.19
Tritylodon									
BP/1/4265	127.66	11.36	8.64	3.24	34.07	18.47	21.02	7.00	7.80

Table 5. Endocast height and width measurements (in mm; see Figure 3, p. 38) and ratios of cynodonts. The proportions were used to estimate endocast height measurements for *Platycraniellus* NMQR1632. The specimens CT scanned in the present study are indicated in bold. The rest of the specimens are from the literature (see Appendix, Table 12). Abbreviations: b, brain excluding olfactory bulbs; h, height; m, foramen magnum; o, olfactory bulbs; w, width.

Genus and specimen	h_o	w_o	h_o/w_o	h_b	w_b	h_b/w_b	h_m	w_m	h_m/w_m
Procynosuchus									
TSK34 [a]	8.00	10.00	0.80	15.00	15.00	1.00			
Galesaurus									
Cynodont A [b]				12.00	10.00	1.20			
RC845	5.21	9.47	0.55	16.06	12.98	1.24	1.80	2.90	0.63
Thrinaxodon									
Cynodont B [b]				12.00	13.00	0.92			
Langbergia									
NMQR3255	2.16	3.81	0.57	17.11	11.86	1.44	6.30	5.90	1.06
Trirachodon									
SAM-PK-K4801 [c]	4.30	7.90	0.54	15.00	14.3	1.05			
Exaeretodon									
MACN18114 [d]				28.00	34.00	0.82			
PVL2088 [d]				23.00	25.00	0.92			
Tritylodon									
BP/1/4265	6.78	8.64	0.78	21.02	18.47	1.14	7.80	7.00	1.11
Average	**4.52**	**6.54**	**0.65**	**18.88**	**17.18**	**1.08**	**5.30**	**5.30**	**0.93**

Table 6. Proportions of the cynodont endocasts examined at first hand and those from the literature. The specimens CT scanned in the present study are indicated in bold. Abbreviations: b, brain excluding olfactory bulbs; h, height; l, length; o, olfactory bulbs; S, skull length; w, width.

Genus and specimen	l_o/w_o	l_b/w_b	l_o/h_o	l_b/h_b	w_o/S	h_o/S	w_b/S	h_b/S
Procynosuchus								
TSK34	1.30	2.00	1.63	2.00	0.09	0.07	0.14	0.14
Galesaurus								
Cynodont A		0.54		0.45			0.16	0.19
RC845	1.36	2.01	2.47	1.62	0.15	0.08	0.21	0.26
Platycraniellus								
NMQR1632	1.67	2.08			0.09-0.12		0.14-0.18	
Thrinaxodon								
BMNHR1713	1.31	1.87						
Cynodont B		0.57		0.62			0.20	0.18
Langbergia								
NMQR3255	1.33	2.23	2.34	1.55	0.04	0.02	0.12	0.17
Trirachodon								
SAM-PK-K4801	1.18	2.45	2.16	2.33				
Exaeretodon								
MACN18114		2.56		2.78				
PVL2088		2.47		3.00				
Tritylodon								
BP/1/4265	1.31	1.84	1.68	1.62	0.07	0.05	0.14	0.16
Average	**1.35**	**1.88**	**2.06**	**1.77**	**0.09**	**0.06**	**0.16**	**0.19**

Table 7. The mean proportions of the cranial endocasts of the cynodonts examined in the present study, arranged in stratigraphic order. Abbreviations: b, brain excluding olfactory bulbs; h, height; l, length; o, olfactory bulbs; w, width.

Geological zone	h_o/w_o	h_b/w_b	l_o/w_o	l_b/w_b	l_o/h_o	l_b/h_b
Cistecephalus Assemblage Zone	0.80	1.00	1.30	2.00	1.63	2.00
Dicynodon Assemblage Zone	0.80	1.00	1.30	2.00	1.63	2.00
Lystrosaurus Assemblage Zone	0.55	1.12	1.45	1.41	2.47	0.90
Cynognathus Assemblage Zone	0.56	1.25	1.26	2.34	2.25	1.94
Ischigualasto Formation		0.87		2.52		2.89
Massospondylus range zone	0.78	1.14	1.33	1.91	1.77	1.65
Average	**0.70**	**1.06**	**1.33**	**2.03**	**1.95**	**1.90**

Table 8. Volumetric data (in cm³) derived from digital endocasts of the cynodonts examined in the present study (indicated in bold), compared to data from the literature (see Appendix, Table 12). Abbreviations: b, brain excluding olfactory bulbs; E, volume; o, olfactory bulbs; t, total endocast.

Genus and specimen	E_o	E_b	E_t	E_o/E_b	E_o/E_t	E_b/E_t
Galesaurus						
RC845	0.43	3.06	3.49	0.14	0.12	0.88
Platycraniellus						
NMQR1632	0.44	4.62	5.06	0.10	0.09	0.91
Langbergia						
NMQR3255	0.02	2.56	2.58	0.01	0.01	0.99
Andescynodon						
PVL3899 [e]	0.10	1.23	1.33	0.08	0.08	0.93
Exaeretodon						
unnumbered [f]	5.24	21.31	26.56	0.25	0.20	0.80
Massetognathus						
PVL3905 [e]	0.11	1.73	1.84	0.06	0.06	0.94
PVL4016 [g]	0.19	3.51	3.70	0.05	0.05	0.95
PVL4168 [e]	0.32	3.18	3.50	0.10	0.09	0.91
Tritylodon						
BP/1/4265	0.32	5.85	6.17	0.06	0.05	0.95
Probainognathus						
PVL4169 [h]	0.08	1.12	1.20	0.07	0.07	0.93
Chiniquodon						
PVL4015 [g]	0.36	4.47	4.82	0.08	0.07	0.93
PVL4167 [e]	0.53	2.89	3.42	0.18	0.16	0.84
Therioherpeton						
PVL - unnumbered [i]	0.07	0.29	0.36	0.23	0.19	0.81
			Average	**0.11**	**0.10**	**0.91**

Table 9. Brain and body mass estimates, and encephalization quotients of the cynodonts examined. The specimens CT scanned in the present study are indicated in bold. The rest of the specimens are from the literature (see Appendix, Table 12). Abbreviations: b, brain excluding the olfactory bulbs; E_i, estimated brain mass; EQ, encephalization quotient; L, body length; o, olfactory bulbs; P, body mass; t, total endocast.

Genus and specimen	E_{io} (g)	E_{ib} (g)	E_{it} (g)	L (cm)	P (g)	EQ_o	EQ_b	EQ_t
Galesaurus								
RC845	0.39	2.75	3.14	25.12	668.72	0.33	0.29	0.30
Platycraniellus								
NMQR1632	0.39	5.56	5.96					
NMQR860				45.66	4017.04	0.10	0.13	0.13
TM25				34.35	1709.57	0.18	0.24	0.23
Thrinaxodon								
BMNHR1713[j]			0.99		550.00			0.11
UCMZT42865[k]		0.36		24.30	500.02		0.05	
Diademodon								
BMNHR3767[l]		7.20		127.50	110871.79		0.03	
Langbergia								
NMQR3255	0.02	2.30	2.32	39.57	2614.25	0.01	0.10	0.09
Trirachodon								
SAM-PK-K4801[c]			1.35		1000.00			0.10
Andescynodon								
PVL3899[e]	0.09	1.11	1.20	28.00	926.00	0.06	0.10	0.09
PVL3894[e]		1.10		30.60	1209.00		0.08	
Exaeretodon								
unnumbered[f]	4.72	19.18	23.89	111.20	58009.37	0.20	0.10	0.11
Massetognathus								
PVL0968T[m]		4.14		47.60	4549.93		0.12	
PVL3905[e]	0.10	1.56	1.66	30.00	1140.00	0.06	0.12	0.11
PVL4016[g]	0.17	3.16	3.33	38.00	2314.91	0.06	0.15	0.14
PVL4168[e]	0.29	2.86	3.15	50.00	5273.00	0.06	0.08	0.07
Tritylodon								
BP/1/4265	0.29	5.27	5.56	51.06	5617.31	0.06	0.13	0.13
Probainognathus								
PVL4169[h]	0.07	1.01	1.08	26.00	741.49	0.06	0.10	0.10
Chiniquodon								
PVL4015[g]	0.32	4.02	4.33	48.00	4665.60	0.08	0.13	0.12
PVL4167[e]	0.48	2.60	3.08	46.00	4106.00	0.12	0.08	0.09
Therioherpeton								
PVL - unnumbered[i]	0.06	0.26	0.32	12.40	80.44	0.21	0.12	0.13
Brasilitherium								
PVL0760T[m]		0.15		9.18	32.59		0.12	
Riograndia								
PVL0601T[m]		0.25		10.40	47.46		0.15	
					Average	**0.11**	**0.12**	**0.14**

Table 10. Encephalization quotient range of cynodonts, and fossil and living mammals. The references are from Table 12. Abbreviations: b, brain excluding the olfactory bulbs; EQ, encephalization quotient; o, olfactory bulbs.

	EQ range			
Taxon	**o**	**b**	**Total**	**References**
CYNODONTIA				
Galesaurus	0.33	0.29	0.30	present work
Platycraniellus	0.10-0.18	0.13-0.24	0.13-0.23	present work
Thrinaxodon		0.05	0.11	c, j, k, n
Diademodon		0.03		k, l, f
Langbergia	0.01	0.10	0.09	present work
Trirachodon			0.10	c, n
Andescynodon	0.06	0.08-0.10	0.09	f
Exaeretodon	0.20	0.10	0.11	e, f
Massetognathus	0.06	0.08-0.15	0.07-0.14	e, f, g, m
Tritylodon	0.06	0.13	0.13	present work
Probainognathus	0.06	0.10	0.10	e, g, h
Chiniquodon	0.08-0.12	0.08-0.13	0.09-0.12	e, o
Therioherpeton	0.21	0.12	0.13	i
Brasilitherium		0.12		m
Riograndia		0.15		m
MAMMALIA				
Triconodonta	0.17	0.17	0.17	j, k, p
Monotremata	0.04-0.17	0.56-0.77	0.51-0.69	q, r, s
Multituberculata	0.20-0.51	0.26-1.07	0.21-0.98	j, k, t
Theriiformes	0.08-0.69	0.14-0.41	0.17-0.35	p, u, v, w
Didelphimorphia	0.16-0.50	0.17-0.84	0.17-1.32	k, x, y, z
Microbiotheria	0.23	0.79	0.73	y
Dasyuromorphia	0.29	0.45	0.43	y
Diprotodontia	0.09-0.14	0.43-0.54	0.39-0.49	y
Xenarthra		0.18-0.47	0.24-1.54	x
Afrosoricida	0.02-1.44	0.10-1.39	0.21-0.50	k, aa, ab
Macroscelidea			0.66-0.71	aa
Hyracoidea			0.60-1.08	x
Proboscidea		0.17-3.56	1.01-1.87	k, x, ac
Lagomorpha			0.32-0.68	x
Rodentia	0.08	0.29-0.45	0.26-1.89	k, x, ad, ae
Eulipotyphla	0.14-0.19	0.10-0.34	0.21-0.73	k, x, aa, ab, af
Chiroptera	0.01-0.43		0.25-0.76	ag, ah
Creodonta	0.13	0.28-0.77	0.26-0.45	k, ai, aj
Carnivora	0.09-0.47	0.28-2.04	0.08-3.61	k, x, ak, ai, al, am, an
Simolesta	0.06-0.25	0.16-0.30	0.15-0.28	f, k, aj, ao
Dinocerata	0.05-0.30	0.22-0.35	0.20-0.34	f, k, aj
Condylarthra	0.10-0.25	0.15-0.35	0.15-0.33	f, k, aj
Mesonychia			0.35-0.44	ai, aj, ap

Table 11. Mean values of encephalization quotients of the cynodonts examined in the present study, arranged in stratigraphic order. Data on contemporaneous carnivores/insectivores and herbivores/omnivores are available from the Chañares Formation. Abbreviations: b, brain excluding olfactory bulbs; h, height; l, length; o, olfactory bulbs; w, width.

Geological formation/biozone	**EQ_o**	**EQ_b**	**EQ_t**
Lystrosaurus Assemblage Zone	0.20	0.18	0.19
Cynognathus Assemblage Zone	0.04	0.08	0.09
Chañares Formation	0.07	0.11	0.11
Carnivores and insectivores	(0.09)	(0.10)	(0.10)
Herbivores and omnivores	(0.06)	(0.12)	(0.11)
Ischigualasto Formation	0.20	0.10	0.11
Santa Maria Formation	0.21	0.12	0.13
Caturrita Formation		0.14	
Massospondylus range zone	0.06	0.13	0.13
Average	**0.13**	**0.12**	**0.13**

Table 12. Literature sources of the data used in Appendix, Tables 5, 6 and 8 to 11.

Abbreviation	Reference	Tables
a	Kemp, 1979	5
b	Olson, 1944	5
c	Hopson, 1979	5, 10
d	Bonaparte, 1966	5
e	Quiroga, 1980a	8, 10
f	Quiroga, 1980c	8, 10
g	Quiroga, 1978	8
h	Quiroga, 1980b	8, 10
i	Quiroga, 1984	8
j	Simpson, 1927	9, 10
k	Jerison, 1973	9, 10
l	Watson, 1913	9, 10
m	Rodrigues, 2005	9, 10
n	Hopson, 1980	10
o	Quiroga, 1979	10
p	Edinger, 1964	10
q	Hines, 1929	10
r	Jerison, 1979	10
s	Macrini *et al.*, 2006	10
t	Kielan-Jaworowska & Lancaster, 2004	10
u	Kielan-Jaworowska & Trofimov, 1980	10
v	Kielan-Jaworowska, 1984	10
w	Macrini *et al.*, 2007b	10
x	Crile & Quiring, 1940	10
y	Macrini *et al.*, 2007a	10
z	Macrini et al., 2007c	10
aa	Bauchot & Stephan, 1966	10
ab	Bauchot & Stephan, 1970	10
ac	Sikes, 1971	10
ad	Mace & Eisenberg, 1982	10
ae	Mann *et al.*, 1988	10
af	Thewissen & Gingerich, 1989	10
ag	Baron *et al.*, 1996	10
ah	Hutcheon *et al.*, 2002	10
ai	Radinsky, 1977	10
aj	Radinsky, 1978	10
ak	Wirz, 1950	10
al	Weiler, 1992	10
am	Pérez-Barberia *et al.*, 2007	10
an	Dong, 2008	10
ao	Schoch, 1983	10
ap	Radinsky, 1976	10

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