The Neurocranium of *Anasinopa leakeyi* (Hyaenodonta, Mammalia) – a First Insight into Teratodontine Brain Morphology

Hjärnan hos *Anasinopa leakeyi* (Hyaenodonta, Mammalia) – ett neurokranium rekonstruerat genom datortomografi

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The work for this thesis was carried in cooperation with the Swedish Museum of Natural History.

Title page: Illustration of the neurocranium of *Anasinopa leakeyi* with endocast, in anterodorsolateral view.

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Abstract

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Therese Flink

The Hyaenodonta include a wide variety of carnivorous mammals ranging in age from late Palaeocene to middle Miocene. Although they reached a nearly global distribution, little remains of them today. Many of the taxa are based only on teeth and jaw fragments. If we are to understand how these animals lived and evolved, we must therefore make the most out of the material we have. Herein, I report on the first nearly complete skull of *Anasinopa leakeyi* (Teratodontinae), which was recently found in Northern Kenya. The skull is dorsoventrally compressed, but otherwise relatively undamaged. The aim of this study was to provide a first glimpse of teratodontine brain morphology by reconstructing the neurocranial of this skull and creating a digital endocast. The result was one of the most well preserved endocasts of any hyaenodont known to date, with many of the cranial nerves and blood vessels visible. The size of the optic foramen relative to the size of the brain is similar to that of the extant wolf, *Canis lupus*, suggesting that *A. leakeyi* may have had a similar visual acuity. The body mass of *A. leakeyi* was estimated to up to 25 kg, meaning that it may have hunted small or large animals, perhaps having the ability to shift to larger prey when needed, as do extant, similarly sized, Felidae and Canidae.

Endocasts are known from only a handful hyaenodont species, many of which were described by Radinsky in 1977. However, little work has been done on hyaenodont brains since then. The second aim of this study, therefore, was to place these hyaenodont brains, and particularly that of *A. leakeyi*, in the most recent phylogenetic framework, to better understand how the brain evolved in this group. This suggests that the evolution of a larger, more convoluted neocortex occurred convergently in several clades of Hyaenodonta. Furthermore, the presence of only a single neocortical sulcus in the earliest hyaenodonts calls into question the previous hypothesis of an ancestral pattern with two sulci for Artiodactyla, Perissodactyla and Carnivora. This study provides a basis for future research on brain evolution in Hyaenodonta, as well as showcases the possibilities offered by 3D technology.

Key words: Africa, Hyaenodonta, Miocene, neurocranium, palaeoneurology, Teratodontinae

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Therese Flink


Nyckelord: Afrika, Hyaenodonta, Miocene, neurokranium, palaeoneurologi, Teratodontinae

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1. Introduction

The extinct order Hyaenodonta (Van Valen 1967) encompasses a wide range of carnivorous mammals that roamed Europe, Africa, Asia and North America from the late Palaeocene to the middle Miocene. The clade was originally grouped with Oxyaenidae within the order Creodonta, coined by Cope (1875). However, Creodonta has been suggested to be diphyletic (e.g. Gheerbrant et al. 2006; Gingerich 1980; Morlo, Gunnell & Polly 2009; Polly 1994; Solé 2013; Solé et al. 2009) and is therefore now commonly split into the two orders Hyaenodonta and Oxyaenida (e.g. Solé et al. 2015; see Borths, Holroyd & Seiffert 2016 for a detailed history of Hyaenodonta as a taxon). The hyaenodons (Fig. 1) were in many ways similar to the Carnivora, an order that evolved somewhat later and includes the extant cats and dogs and their relatives. Large canines and a shearing cheek dentition are features of both orders. However, the shearing dentition is made up of developmentally different teeth in Hyaenodonta (Van Valkenburgh 1999), suggesting that the feature evolved separately in the two groups. Although hyaenodons and carnivorans filled many similar niches, they co-existed for tens of millions of years, before the hyaenodons finally went extinct at the end of the middle Miocene.

Hyaenodonta is currently placed together with Carnivora and Pholidota (pangolins), in Ferae (Fig. 2A; Flynn & Wesley-Hunt 2005; Friscia & Van Valkenburgh 2010; Solé et al. 2015). Ferae in turn is nested within Scrotifera together with the chiropterans (bats) and ungulates like horses, cows, deer, rhinos, pigs and whales (Fig. 2A; Benton 2015). However, the systematic affinities of Hyaenodonta are still widely debated (e.g. Borths, Holroyd & Seiffert 2016; Halliday, Upchurch & Goswami 2015; Spaulding, O’Leary & Gatesy 2009), as are the phylogenetic relationships within the order (e.g. Borths, Holroyd & Seiffert 2016; Borths & Stevens 2019; Rana et al. 2015).
Borths, Holroyd and Seiffert (2016) used parsimony analysis, standard Bayesian inference and Bayesian tip-dating on a large sample of hyaenodont taxa in an attempt to resolve the phylogeny within the order. In their study, as in many others, not all subfamilies were placed in a family, which is why the following summary mixes these taxonomic levels. All clades mentioned in this summary were found to be monophyletic unless otherwise specified. All of the analyses in Borths, Holroyd and Seiffert (2016) suggested that the African clade Teratodontinae is closely related to Hyainailouridae, a clade that, in turn, includes Hyainailourinae and Apterodontinae. These three subfamilies are united, together with a number of smaller taxa, in Hyainailouroidea, which includes the majority of the African hyaenodonts. Hyaenodontidae, which includes Hyaenodontinae and thus the famous *Hyaenodon* (the best known hyaenodont), was consistently placed separately from all the Afro-Arabian taxa. A previous study by Rana et al. (2015) recovered a monophyletic, European Proviverrinae as the sister group to Hyaenodontinae. Borths, Holroyd and Seiffert (2016), however, did not recover a monophyletic Proviverrinae. Instead, they found some proviverrines placed basally in Hyaenodonta and others placed within Hyaenodontidae as stem groups to Hyaenodontinae.
The most recent phylogeny by Borths and Stevens (2019) still recovers a Hyainailouroidea consisting of the three subfamilies Hyainailourinae, Apterodontinae and Teratodontinae (Fig. 2B). However, taxa previously included in Hyainailouroidea, but excluded from the three subfamilies, are in this new study in some cases, such as *Tritemnodon*, excluded from Hyainailouroidea, whereas others, such as *Kyawdawia*, are included in Teratodontinae, so that Hyainailouroidea exclusively consists of the three subfamilies. Their study also found a monophyletic Proviverrinae as the basal-most branch of the hyaenodont tree. Hyaenodontidae is placed further up the tree, and the Limnoceyoninae further down the tree than in Borths, Holroyd and Seiffert (2016).

The present study will focus on *Anasinopa leakeyi*, in the light of a newly found, damaged but nearly complete skull from the early Miocene of Kenya. This species, and indeed the genus, has previously been described based only on dentition and damaged or fragmented dentaries and maxillae (Morales, Brewer & Pickford 2010; Savage 1965; Tchernov et al. 1987). *Anasinopa* was originally described as a proviverrine, most similar to *Tritemnodon* and *Sinopa* (Savage 1965). The recent studies mentioned above consistently place it as a relatively derived teratodontine (e.g. Borths, Holroyd & Seiffert 2016; Borths & Stevens 2019), often as the sister genus to *Dissopsalis* (e.g. Fig. 19 and 22 in Borths, Holroyd & Seiffert 2016). However, it has also been placed as the sister taxon of *Furodon* (e.g. Fig. 17, 18, 20 and 21 in Borths, Holroyd & Seiffert 2016) or *Teratodon* (Borths & Stevens 2019). The genus includes three species, the type species *A. leakeyi* (Savage 1965) and the slightly smaller *A. haasi* from Israel (Tchernov et al. 1987) and *A. libyca* from Libya (Morales, Brewer & Pickford 2010).

The difficulty in resolving the systematics of Hyaenodonta in large part owes to the fact that many of the taxa, like *Anasinopa*, are based on very limited material, generally teeth and dentary fragments. These remains can be highly informative because they provide information on the animal’s diet, age and size, as well as its phylogenetic affinities. Nevertheless, there is much the teeth can’t tell us, but that may be revealed by the skull or post-cranial skeleton. Complete hyaenodont skulls are very rare, and thus, destructive sampling is generally out of the question. Advances in 3D tomography, however, allow us to reconstruct damaged skulls and to investigate their internal structure without causing any damage to the specimen.

Studies of the neurocranium can yield considerable information regarding both the ecology of the animal (e.g. Edinger 1962; Radinsky 1968) and about how brains in general evolve through time (e.g. Edinger 1962; Lyras 2009; Orliac & Gilissen 2012; Radinsky 1977, 1978). Previous studies on hyaenodont neurocrania are few in number, and almost exclusively based on physical casts, natural or man-made (Filhol 1877; Gaudry 1878; Gervais 1870; Klinghardt 1934; Lange-Badré 1979; Piveteau 1961; Radinsky 1977; Savage 1973; Scott 1886). The aim of this study is to digitally reconstruct the neurocranium of *Anasinopa leakeyi*, providing the first description of teratodontine brain morphology. Since the focus of this study is the neurocranium, only the posterior half of the skull was reconstructed. A reconstruction and description of the entire skull is beyond the scope of this study and will follow.
1.1 Fossil brains

In trying to understand the evolution of the brain solely by looking at living animals there is a great risk of misinterpretation. Indeed, the application of this approach has led to several misconceptions in the past. Most notably, it has been argued that brains follow a linear evolution towards larger size, that larger brains equal higher intelligence, and that intelligence is the recipe for success. Confirming or falsifying such deductions is impossible without looking at fossils. Using fossils provides a greater diversity of animals, and perhaps even more importantly, introduces the dimension of time to our understanding of evolution (Edinger 1962). Most mammal endocasts reproduce the majority of major features of the external morphology of the brain. The cerebrum, cerebellum and olfactory bulbs, as well as the major gyri and sulci (Fig. 3) are readily identifiable.

Radinsky (1977) carried out a study of a large number of endocasts of early carnivores, including several hyaenodonts. He found that brain size tended to increase through time relative to body size in these animals, but he found no evidence for earlier assumptions that the ancestors of extant carnivores had larger brains than contemporaneous, now extinct, carnivores like hyaenodonts. He also found that the relative size of the neocortex increased through time in both hyaenodonts and miacids (a paraphyletic group of extinct carnivores forming part of the stem lineage of Carnivora). The neocortex in mammals is responsible for complex cognitive functions like spatial reasoning, sensory perception and voluntary movement. It is delimited anteriorly by the olfactory bulbs, laterally by the rhinal sulcus and posteriorly by the border between the cerebrum and the midbrain and cerebellum. Neocortical expansion is also seen in many other groups of mammals and is a great example of parallel evolution (e.g. Radinsky 1977, 1978).

As the neocortex expands, it becomes more convoluted, i.e., more sulci appear. In modern mammals, sulci have been shown to delimit different functional areas of the cortex, which means that enlargement of a certain gyrus may hint at a specific sensory specialization (e.g. Radinsky 1968; Welker & Campos 1963). However, similar sulcal patterns in distantly related taxa are not necessarily homologous. Lyras (2009) showed that three subfamilies of canids followed highly convergent paths of brain evolution, and that the cruciate sulcus appeared as many as four times independently within Canidae. In this study, the digital endocast of *Anasinopa*, as well as the hyaenodont endocasts previously discussed in Radinsky (1977) were placed in the latest phylogenetic framework, in order to better understand the evolution of the brain in the different hyaenodont lineages.

Figure 3. Illustration of the brain of *Thinocyon velox* to show the terminology of the main features of the mammalian brain. Based on Radinsky 1977.
2. Material and methods

2.1 Material

The specimen KNM-MO64199 of *Anasinopa leakeyi* consists of a nearly complete cranium (Fig. 5) from the early Miocene site Moruorot in Kenya (Fig. 4; see site information below). Parts of the postcranial skeleton were found in association with the skull but have yet to be excavated. It is clear from the postcranial skeleton, however, that the individual was an adult, as the growth plates are fused. The cranium is hitherto undescribed and belongs to the Department of Paleontology, Earth Sciences Division, National Museums of Kenya, Nairobi. It was discovered in 2016 during excavations by the West Turkana Miocene Project (PIs Susanne Cote, University of Calgary and James Rossie, Stony Brook University). This project forms part of the NSF-funded REACHE Project (https://www.reacheproject.com).

Comparative 3D surface renderings were generously provided by George A. Lyras and the FMNH (institutional abbreviations below). These included the hyaenodons *Megistotherium osteothlastes* (NHM-M26515), *Pterodon dasyuroides* (MNHN, Piveteau 1961), *Thinocyon velox* (cast: FMNH PM 57146, scan: AMNH 12631), and *Hyaenodon horridus* (cast: FMNH PM 57143, scan: AMNH 94760) and the carnivoramorph *Vulpavus palustris* (cast: FMNH PM 57174, scan: AMNH 19000).

2.2 Institutional abbreviations

Figure 5. Photographs of the fossil skull KNM-MO64199 of *Anasinopa leakeyi*, in A) dorsal, B) right lateral and C) ventral view. Photos: Lars Werdelin.
2.3 The site

Moruorot lies within the Lothidok Formation west of Lake Turkana in Northern Kenya (Fig. 4; for more detailed geological description and maps and stratigraphic sequence, see Arambourg 1944; Boschetto, Brown & McDougall 1992). It belongs to the Kalodirr Member, which has its base at around 17.5 Ma and its upper boundary at around 16.8 Ma (Boschetto, Brown & McDougall 1992). The member consists of tuffs overlain by a heterogenous assemblage of discontinuous layers of pyroclastic and clastic sedimentary rocks (Fig. 6). The uppermost tuffs have a red to yellow colour and contain vertebrate fossils as well as bird and ungulate tracks. Many of the tuffs are overlain by lahars which contain calcitic casts of logs, as well as imprints of grass and leaves and, less commonly, fossil fruit.

Despite being discovered in the 1930s (Arambourg 1933), little work has been done at Moruorot until recent years. It is now, however, one of the main sites being excavated by the West Turkana Miocene Project. So far the site has yielded a wide variety of skeletal remains, including among others Prodeinotherium, a type of proboscidean; Cynelos macrodon, a species of bear-dog; Afrosmilus turkanae, a barbourofelid (sabre-toothed cat-like animal); Anasinopa leakeyi, the hyaenodont described herein; Paraphiomys pigotti, a rodent; Simiolus, a small hominoid ape; Turkanatherium acutirostratum, a rhinocerotid, and a large number of cetartiodactyls, such as Canthumeryx sirtensis. For full faunal list, see Leakey et al. 2011.

The skull of Anasinopa leakeyi was found in a fine-grained bed, associated with the skeleton of the primate Simiolus as well as two, currently unidentified carnivors, a snake and fragments of several smaller mammals. The fossils lay close to the top of a large flood deposit, which was exposed for a long time, likely millennia, before being covered by another flood deposit. Presumably the animals died in the flood as their bones were still associated.
2.4 Digital reconstruction

The specimen was scanned using a Nikon Metrology XTH 225/320 LC dual source industrial computed tomography scanner at the Evolutionary Studies Institute, University of the Witwatersrand, South Africa. The scan parameters were 80 kV and 130 μA, with a voxel size of 66.7 μm. The contrast between bone and sediment was good (Fig. 7), but because of the varying density of the bone and of the large amount of high-density crystals in the sediment, the contrast was insufficient for automatic segmentation. The bone was therefore segmented out manually in Avizo 9.5.0. Each fragment of bone was segmented as a separate material, resulting in 142 materials. The materials that were identifiable were rendered as surfaces and exported individually to allow the skull to be digitally reconstructed in Blender 2.79b. The bone was not plastically deformed, only fractured, and reconstruction thus consisted of reassembling the pieces. As the bone was not weathered, and most bone fragments were still in a near original position, it was possible to see how each piece fitted together with the rest. The medial and left parts of the skull were reconstructed using both fragments from those sides and mirrored fragments from the right side in order to make it as complete as possible. The composite left side was then mirrored, and the mirrored part fitted against the medial parts of the skull in order to make it complete. The reconstructed skull (Fig. 8) was again imported into Avizo, where it was converted into label format to allow segmentation of the cranial cavity. Due to the amount of missing bone, the cavity had to be manually segmented. Where bone was missing, segmentation followed the curvature of the surrounding bone; these areas are shown in darker grey in Fig. 9.

![Figure 7](image_url). Cross section of the scanned skull. The position of the cross section on the skull is indicated by a red line at the bottom of the figure, in ventral (left), dorsal (middle) and left lateral (right) view. Scale bar is 2 cm.
2.5 Body mass estimate

The body mass (BM, kilograms) of *Anasinopa leakeyi* was estimated using a method described by Morlo (1999) for Creodonta, using the average lower molar length (LML, millimeters; in the formula below). Since the specimen described herein included only the anterior-most part of the lower jaw, the average lower molar length was calculated based on the measurements of specimens M19081c and M19081d,e in Table 2 of the original description of *Anasinopa* by Savage (1965).

Morlo (1999): \[ \log_{10}(BM) = 3.5104 \times \log_{10}(LML) - 2.6469 \]

2.6 Phylogenetic comparison

Radinsky (1977) compared a large number of endocasts of early carnivores, including several hyaenodons and carnivoramorphs, and found that in both groups, brains showed a tendency to become more convoluted, with a larger neocortex, through time. He did not, however, look more closely at brain
evolution from a phylogenetic standpoint within Hyaenodonta. In this study, the hyaenodont brains described by Radinsky (1977) were placed in the latest phylogenetic framework (Borths, Holroyd & Seiffert 2016; Borths & Stevens 2019) together with the brain of *Anasinopa*, described for the first time herein. The aim was to place the brain morphology of *Anasinopa* in a phylogenetic perspective and to explore any patterns in brain evolution seen within this order of carnivores. The observations made herein regarding the patterns of brain evolution in Hyaenodonta simply provide a first glimpse, forming a base for further studies. They are based on the figures and descriptions by Radinsky (1977) as well as 3D surface renderings of several of the specimens described therein (for which, see Material above). Additionally, the estimated body masses of the various hyaenodont taxa were compared to their brain morphologies in order to explore any potential correlations between body mass of brain morphology that may provide suggestions for future research. The species included in the phylogenetic comparison, their body masses, and the references for those body mass estimates are listed in Table 1.

### 2.7 Systematic palaeontology

Superorder Ferae LINNAEUS, 1758  
Order Hyaenodonta, VAN VALEN, 1967  
Family Teratodontinae SAVAGE 1965  
**Genus Anasinopa, SAVAGE, 1965**  
**Type species.** *Anasinopa leakeyi* Savage, 1965 (type locality: Rusinga Island, Kenya).  
**Diagnosis.** See Savage (1965).  
**Other species.** *A. haasi* from Israel (Tchernov et al. 1987) Negev, Israel. *A. libyca* (Morales, Brewer & Pickford 2010), Gebel Zelten, Libya.

*Anasinopa leakeyi* SAVAGE, 1965  
**Holotype.** Five fragments together comprising the maxillae and mandibles of one individual (M.19081a-e). M.19081a is a left maxilla with P4, M1 and alveoli of P2 and P3. M.19081b is a right maxilla with M1 and M2 and alveolus of M3. M.19081c is a right mandible with C, P1,4 and M1,3 and symphysis. M.19081d is a left mandibular fragment with M2 and M3. M.19081e is a left mandibular fragment with C and P4.  
**Type locality.** Rusinga Island in Lake Victoria, Kenya.  
**Diagnosis.** See Savage (1965).  
**Discussion.** *Anasinopa leakeyi* differs from *A. haasi* and *A. libyca* by is geographical location and noticeably larger size. *Anasinopa leakeyi* also has a less developed M3 talonid and P3 posterior cusp than *A. libyca* (Morales, Brewer & Pickford 2010). In *A. haasi*, the anterior crest of the P3 protoconid inclines more internally, and the mandibular ramus is higher than in *A. leakeyi* (Tchernov et al. 1987).
Figure 9. Digital endocast of *Anasinopa leakeyi*, in A) dorsal, B) lateral and C) ventral view. Areas where surrounding bone was missing are indicated in darker grey.
Figure 10. Drawings of the endocast of *Anasinopa leakeyi*, with several features indicated. The terminology used is based on Radinsky (1977), Lyras (2009) and Orliac and Gilisen (2012). Abbreviations: ama, accessory meningeal artery; lpn, lesser petrosal nerve; II-VIII refer to cranial nerves.
3. Results

3.1 Neurocranium

The cerebrum of *Anasinopa leakeyi* is drop-shaped in dorsal view whereas the cerebellum is square and noticeably narrower than the cerebrum, with relatively small hemispheres (Fig. 9A, 10A). In comparison with the hyaenodont endocasts described by Radinsky (1977), neocortical expansion in *A. leakeyi* appears fairly advanced. This is indicated by the relatively low position of the rhinal sulcus, compared with early hyaenodonts like *Tritemnodon* and *Thinacyon*. The position of the rhinal sulcus is similar to that of *Hyaenodon* and *Pterodon* but is not as low as in *Megistotherium*. The sulcus is straight and points clearly anterodorsally. There is one very prominent neocortical sulcus (Sulcus 1, Fig. 9A-B, 10A-B) parallel to the rhinal sulcus, as well as a smaller, more dorsal sulcus (Sulcus 2, Fig. 9A-B, 10A-B), consisting of two distinct dimples with a shallow furrow between them, which extends caudal of the posterior dimple. In dorsal aspect, both sulci appear to curve medially along their full length.

Unfortunately, as the anterior- and dorsal-most regions of the brain case were not possible to reconstruct, the morphology of the midline of the brain, as well as the olfactory bulbs, of *Anasinopa* remain unknown. It is therefore difficult to deduce the degree of anteroposterior expansion of the neocortex, as well as any features of the vermis.

On the ventral side of the endocast, several interesting features are preserved (Fig. 9C, 10C). On the cerebellum there are two small lateral extensions which are here interpreted to be for the vestibulocochlear nerve or cranial nerve (CN) VIII, as well as the facial nerve (CN VII), based on comparisons with extant carnivorans. Anterior to this is the cast of the oval foramen, which houses the mandibular nerve (CN V₃), accessory meningeal artery and lesser petrosal nerve. The maxillary nerve (CN V₂) runs along the ventral border of the piriform lobe. Parallel to this is the cast of the orbital fissure, which houses the oculomotor nerve (CN III), trochlear nerve (CN IV), ophthalmic nerve (CN V₁), abducens nerve (CN VI) and ophthalmic vein. Next to this, along the midline of the ventral side of the brain, runs the optic nerve (CN II) as indicated by the cast of the optic canal.

3.2 Body mass

The body mass of *Anasinopa leakeyi* was estimated using the mean length of the lower molars (Morlo 1999) based on measurements of the type specimen by Savage (1965). The type specimen was of a slightly greater size than the specimen described herein based on measurements of the upper dentition: 13.3 mm for P⁴ and 12.4-13.6 mm for M₁ of the type specimen (Savage 1965) and 9.3-10.0 mm for P⁴ and 12.0-12.3 mm for M₁ of the specimen herein. The measurements of the lower dentition used in the body mass calculations were 12.3 mm for M₁, 14.4 and 14.5 mm for M₂ (M19081c and d,e respectively) and 16.6 and 15.5 mm for M₃ (M19081c and d,e respectively) by Savage (1965). The mean length of each tooth was used to calculate the mean lower molar length. This resulted in a body mass of 25.42 kg.
However, because of the lack of close living relatives of Hyaenodonta, their body masses are estimated based on correlations in living animals such as carnivorans, which have a lower skull to body ratio. This means that the body mass is likely overestimated.

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>BODY MASS (KG)</th>
<th>REFERENCE FOR BM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Megistotherium</td>
<td>Up to 800</td>
<td>Solé et al. 2015</td>
</tr>
<tr>
<td>Pterodon dasyuroides</td>
<td>~52</td>
<td>Solé et al. 2015</td>
</tr>
<tr>
<td>Apterodon macrognathus</td>
<td>10-45</td>
<td>Gagnon 1997</td>
</tr>
<tr>
<td>Anasinopa leakeyi</td>
<td>&lt;25</td>
<td>Present study</td>
</tr>
<tr>
<td>Tritemnodon</td>
<td>7.6-13</td>
<td>Egi 2003</td>
</tr>
<tr>
<td>Hyaenodon horridus</td>
<td>9-43</td>
<td>Egi 2003</td>
</tr>
<tr>
<td>Cynohyaenodon cayluxi</td>
<td>~1.7</td>
<td>Solé, Falconnet &amp; Yves 2014</td>
</tr>
<tr>
<td>Thinocyon</td>
<td>0.7-2.5</td>
<td>Egi 2003</td>
</tr>
</tbody>
</table>

Table 1. Body mass (BM) estimates for the hyaenodont species included in the phylogenetic comparison, with the source of each body mass estimate in the column to the right. The taxa are listed in the order they appear in the phylogeny, see Fig. 2B and 11.

### 3.3 Phylogenetic comparison

All members of the Hyainailouroidea included in this study have relatively large and convoluted neocortices compared to other hyaenodonts and are from the late Eocene or younger. The middle Eocene Tritemnodon however, the taxon most closely related to Hyainailouroidea, has a relatively small neocortex with only one neocortical sulcus. Anasinopa, the basal-most hyainailouroidean and only teratodontine in this study, has what appears to be the smallest and smoothest neocortex in this clade. That being said, the neocortex of Anasinopa is not much smaller than that of the hyainailourine Pterodon, and it is still fairly large compared to members of Hyaenodonta in general. The basal hyaenodont Thinocyon and the hyaenodontid Cynohyaenodon, from the middle and middle to late Eocene respectively, both have small neocortices with only one neocortical sulcus. The late Eocene to Oligocene Hyaenodon by comparison has a large and highly convoluted neocortex, similar to Anasinopa and Pterodon. The middle Eocene miacid Vulpavus was included to provide a comparison with an early carnivoramorph. It has a larger more convoluted neocortex than contemporaneous hyaenodonts, more similar to that of Anasinopa.

When comparing the brain morphology (Fig. 11, 12) to the estimated body masses (Table 1) of hyaenodonts, there appears to be a correlation between the degree of neocortical expansion and body mass. Indeed, the largest hyaenodont in this study, Megistotherium, weighing up to 800 kg (Solé et al. 2015), is also the species with the relatively largest neocortex. Similarly, the three smallest taxa
Thinocyon (0.7-2.5 kg, Egi 2003), Cynohyaenodon (1.7 kg, Solé, Falconnet & Yves 2014) and Tritemnodon (7.6-13 kg, Egi 2003) are also the taxa with the lowest degree of neocortical expansion. However, the differences in neocortical expansion between Pterodon, which weighed around 50 kg (Solé et al. 2015) and Megistotherium, which weighed several times as much, are fairly small.

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**Figure 11.** Phylogeny of hyaenodonts included in this study, with drawings of the endocasts for comparison. The nodes and ends of solid lines represent expected divergence date and age of the fossil endocast respectively. Where the age of the endocast is not exactly known, a time span is indicated in grey. Phylogeny and divergence dates follow Borths and Stevens (2019). The endocast of the miacid Vulpavus was included for comparison. Endocast drawings and ages, except that of Anasinopa which is described for the first time herein, are based on descriptions by Radinsky (1977), with the neocortex indicated in grey. Endocast drawings are not to scale.
Figure 12. Alternative phylogeny of hyaenodonts included in this study, with drawings of the endocasts for comparison. The nodes and ends of solid lines represent expected divergence date and age of the fossil endocast respectively. Where the age of the endocast is not exactly known, a time span is indicated in grey. Phylogeny and divergence dates follow Fig. 19 in Borths, Holroyd & Seiffert (2016) with the exception of Thinocyon (node indicated by grey circle) which is based on Fig. 18 in Borths, Holroyd & Seiffert (2016) where the divergence date was not estimated. The endocast of the miacid Vulpavus was included for comparison. Endocast drawings and ages, except that of Anasinopa which is described for the first time herein, are based on descriptions by Radinsky (1977), with the neocortex indicated in grey. Endocast drawings are not to scale.

4. Discussion

4.1 Anasinopa

The brain morphology of Anasinopa is rather typical of known hyaenodonts. The degree of neocortical expansion and convolution is intermediate to fairly advanced. Those nerves and blood vessels that are preserved on the ventral side of the endocast of Anasinopa are typical for the mammalian brain and comparable to those of many other mammals, e.g., the archaic ungulate Hyopsodus (Orliac, Argot &
Gilissen 2012), the artiodactyl Diacodexis (Orliac & Gilissen 2012), the notoungulate Mesotherium (Fernández-Monescillo et al. 2019), the primate Ignacius (Silcox et al. 2009) and the extant wolf Canis lupus. A study by Kirk (2006) showed that the amount of visual input, as indicated by the size of the optic foramen, is correlated with neurocranial volume in primates and carnivorns. He found that nocturnal species such as the primate Daubentonia had a smaller optic foramen in relation to brain size than did diurnal species, which supposedly receive more visual information. Because of the absence of the olfactory bulbs and the uncertain extent of dorsal expansion of the cerebellum in Anasinopa, the neurocranial volume is difficult to estimate. By simple visual comparison, however, the relative size of the optic foramen appears roughly similar to that of the wolf, and noticeably larger than that of Mesotherium, a rodent-like burrowing notoungulate (Fernández-Monescillo et al. 2019). As the wolf is a predominantly nocturnal animal with high visual acuity, this may suggest a similar life style for Anasinopa, although this needs to be more thoroughly tested in the future.

Savage (1965) originally described Anasinopa leakeyi as similar in size to the wolf, Canis lupus. Based on the body mass calculation performed herein, I suggest a somewhat lower body mass of up to 25 kg. This puts Anasinopa at the lower end of the hyaenodontan size range, as some hyaenodons, like the recently described Simbakubwa, may have reached body mass upwards of 1000 kg (Borths & Stevens 2019). Carbone et al. (1999) showed that carnivorns weighing more than 25 kg tend to hunt large vertebrate prey, that is, prey with a body mass similar to or larger than the predator itself. Smaller carnivorns weighing less than 21.5 kg, however, were found to mainly hunt prey (vertebrates and invertebrates) that weighed half or less of their own weight. All species of both canids and felids that weighed more than 21.5 kg were vertebrate feeders. Among the smaller species of canids and felids they found that 53% were vertebrate feeders, 29% omnivores, 16% vertebrate and invertebrate feeders and 2% purely invertebrate feeders. Assuming a similar correlation between body mass and prey choice in hyaenodons, Anasinopa may have preyed on either vertebrates or invertebrates. However, as pointed out by Carbone, Teacher and Rowcliffe (2007), several carnivorns in the transitional weight range 15-20 kg, like lynxes and jackals, can switch between hunting small and large prey. It is plausible that Anasinopa, lying close to that weight range, did the same.

4.2 Hyaenodonta

There appears to be a correlation between body mass and neocortical expansion within hyaenodonta (Table 1, Fig. 11, 12). A similar pattern has been found in primates by Schillaci (2008), who argued that this correlation had a confounding effect on potential correlations between neocortex ratio and behavioural complexity. To my knowledge, however, no correlation between neocortex ratio and body mass has been found, or indeed tested, in either Carnivora, nor any other group related to the Hyaenodonta. It may in part be a result of the correlation between neocortical expansion and geological age found by Radinsky (1977), as the largest hyaenodons in this study are also the geologically
youngest. Additionally, this potential correlation in Hyaenodonta is based simply on visual quantification of the neocortex. Taking actual measurements of the neocortical surface and statistically testing for a correlation with body mass is beyond the scope of this study and is encouraged in future research on both Hyaenodonta and Carnivora.

As pointed out by Radinsky (1977), the expansion and increased convolution of the neocortex through time is striking within the Hyaenodonta. When put into a phylogenetic context, however, it appears that this pattern occurred independently in the Hyainailouroidea and the Hyaenodontidae. The simplest brain morphologies are those of Thinocyon and Tritemnodon, both of which had only one neocortical sulcus. Based on their phylogenetic positions (Borths & Stevens 2019), that would suggest that the first hyaenodontids, as well as the first hyainailourines, also had relatively small neocortices with only one sulcus. This is further supported by the fact that Cynohyaenodon, a taxon that is consistently placed basally within Hyaenodontidae by Borths, Holroyd and Seiffert (2016) and Borths and Stevens (2019), also had only one prominent neocortical sulcus. Using both parsimony and Bayesian analysis, Borths, Holroyd & Seiffert recovered Limnocyoninae, and thus Thinocyon, higher up the tree, as the sister group of the clade containing Tritemnodon and Hyainailouroidea (Fig. 12; Fig. 17, 18, 20, 21 in Borths, Holroyd & Seiffert 2016). Using this phylogeny has little impact on the results herein, as the endocast of Cynohyaenodon still points towards a simple brain morphology of the early hyaenodontids, and thus the first hyaenodonts.

All four representatives of the Hyainailouroidea, including Anasinopa which as a teratodontine holds a basal position in this clade, show at least two neocortical sulci. This may suggest an early development of the second sulcus within this clade. As already shown above and in many previous studies (e.g. Lyras 2009, Radinsky 1977), however, the development of sulci often occurs by convergent evolution. Since the teratodontines are thought to have diverged from the hyainailourids in the early Eocene (Borths & Stevens 2019), and the only teratodontine in this study, Anasinopa, lived more than 30 Myr later, I believe it premature to draw any conclusions regarding the hypothesized brain morphology of their common ancestor. Additionally, the sulcal shapes and patterns differ greatly between these four hyainailouroidean genera. None of the hyainailourids show the distinct dimples in the dorsal-most sulcus that are seen in Anasinopa and the sulci in Apterodon are clearly curved, a feature not seen in any other hyaenodont.

Most phylogenies in Borths, Holroyd & Seiffert (2016) and the one in Borths and Stevens (2019) place Tritemnodon as the sister group of Hyainailouroidea. However, Borths, Holroyd & Seiffert (2016) placed Tritemnodon within Hyainailouroidea, as the sister group of Hyainailouridae, when using Bayesian tip-dating (Fig. 12; Fig. 19 and 22 in Borths, Holroyd & Seiffert 2016). This phylogeny suggests that the second neocortical sulcus seen in Anasinopa either developed in parallel with the ones seen in members of Hyainailouridae or was lost in the branch leading to Tritemnodon. New findings of endocasts or crania of early teratodontines are therefore of the highest importance for our understanding of the evolution of the brain in this clade.
The oldest miacid endocast depicted in Radinsky (1977) is of *Vulpavus* (Fig. 11, 12) which had a relatively expanded neocortex with two sulci. Two neocortical sulci are also found in the earliest canids (Lyras 2009) and artiodactyls (Orliac & Gilissen 2012). It has been suggested that Artiodactyla, Perissodactyla and Carnivora are all derived from the same ancestral sulcal pattern with two neocortical sulci (Jerison 1973; Nieuwenhuys, Ten Donkelaar & Nicholson 1998). This was criticized by Orliac and Gilissen who pointed out that the orientation of these sulci differed among the early members of the three clades. The results herein bring further doubt to this hypothesis, since the earliest hyaenodonts appear to have had only a single neocortical sulcus. This suggests that either the common ancestor of the three orders had just a single neocortical sulcus, or the second sulcus was lost in the branch leading to Hyaenodonta. It is clear from the many convergent occurrences of additional sulci, such as the cruciate sulcus in canids, that there is a selective pressure towards a more convoluted neocortex. However, I have yet to find any definitive evidence for the loss of such a sulcus once it has developed. Certainly, the loss of a sulcus would require selective pressure. That kind of selective pressure is unlikely to appear unless the animal is living under severe energy constraints. As nerve tissue consumes a lot of energy, a simpler brain may be an advantage under such conditions, unless the advanced brain can make up for this increased consumption of energy by increasing the animal’s success in hunting or foraging.

Although it appears more likely that the ancestral condition within Scrotiferia is a neocortex with a single sulcus, this hypothesis is very sensitive to changes in the phylogeny of its members. The position of Hyaenodonta within Ferae is still debated, as are the relationships between the other members of Scrotiferia. Additionally, the endocast fossil record is extremely limited. This hypothesis, therefore, must be further and more thoroughly explored in future research.

**5. Conclusions**

The results of this study suggest that the expansion and increased convolution of the neocortex is likely to have occurred at least twice independently within Hyaenodonta: in the Hyaenodontidae and in the Hyainailourouidea. This highlights the importance of finding more material of hyaenodonts, especially early basal Hyainailourouidea, in order to truly understand how brains evolved in these animals. The simple brain morphology of the earliest hyaenodonts also points to a simpler ancestral sulcal pattern within Scrotiferia than previously suggested, unless sulci were lost in the branch leading to Hyaenodonta before eventually being regained in the later lineages. However, this hypothesis is very sensitive to changes in the phylogeny of Scrotiferia and needs to be further tested in future studies.

Like many previous studies on the evolution of the brain, this thesis shows that there is much we still do not know about how and why brains evolve in a certain way. This project shows the possibilities offered by 3D technology, which allow us to learn much more from damaged fossil materials than we ever have before. It encourages us to go back to old collections in search of material that has previously not been considered informative in studies of brain evolution and gives fresh hope of a better understanding of the evolution of the mammalian brain.
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7. References


