Comparative, Functional Anatomy of Prey Acquisition and Feeding Adaptions in Non-Avian Theropods

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Abstract

Theropoda are a clade of saurischian dinosaurs that includes the most speciose extant clade of tetrapods, birds. Non-avian, carnivorous Theropoda, which dominated terrestrial predator niches during most of the Mesozoic, can be subdivided into generalist macropredators, small-prey-specialists and omnivores. The jaws tend to be the primary instruments of predation, the forelimbs are powerful, but limited in their range of motion so as to function as means of prey restraint. Some macrophages (Carnosauria) retained narrow heads and ziphodont teeth, which are ancestral traits of Theropoda, but evolved modifications of the skull and neck to allow advanced killing modes. In others, an increase in cranial robusticity correlates with greater aptitude at restraining prey (Abelisauridae) or crushing bone (Tyrannosauridae) and reduction of the forelimb. Dromaeosauridae had more flexible limbs and hypertrophied claws on both fore- and hindlimbs that may have replaced the jaws as the primary means of prey capture. Some lineages predominantly brought forth small-prey-specialists with jaws adapted to fulfill a gripping function, and in the case of Spinosauroidea this was accompanied by an amphibious lifestyle. A general, but not universal trend towards cursoriality and an increasingly bird-like mode of locomotion is also known in Cretaceous Theropoda.

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Preface

Birds are the most diverse extant tetrapods and have adapted to a multitude of different ecological roles, from apex predators to tiny insectivores and sizeable herbivores. Their usual volant nature and small body size should not, however, hide the fact that they form but the crown group of a lineage with an even longer and more varied evolutionary history. It is, of course, the theropods that are being referred to (or, to be precise, the stem-theropods) a taxon of dinosaurs that has captivated scientific and popular attention alike for almost two centuries. Since my childhood I have been one of those so-captivated, and theropods continue to be one of my main areas of interest.

During my last two years at high school, this long-held fascination with the topic paid off, when as part of my graduation I was tasked with completing a scientific work between 40,000-60,000 characters in length, on a subject of my own choice. It was immediately clear to me that I would write about theropods and so I did, choosing the topic as one about comparative and functional anatomy to accomodate for another one of my primary interests in science. It should at this point be noted that I feel a somewhat larger scale, or greater freedom regarding the scope, would have suited me better (as evident from the paper at hand exceeding the upper character limit significantly), though the organisational difficulties have to be considered. Nonetheless, I could learn important lessons before, during and after the writing process.
These ranged from formalities such as how to efficiently compose a list of references or acquire copies of paywalled publications to the stamina and focus it took to fit the admittedly massive amount of available and relevant information in such relatively short form.
The writing itself was mostly carried out during the months preceding the date of submittal, but the research that was finally condensed into the paper took a significantly longer time to complete; in fact it was the result of years of varying degrees of occupation with theropod anatomy and ecology.
The present work is the revised and improved version of the resulting matriculation thesis, which was finally handed in in February 2015 and presented in April of the same year.

I would like to thank my supervisor, Prof. Claudia Schneider, for her immense patience and enthusiasm, which she, as a newcomer to the field and despite her many other obligations, was remarkably able to muster up throughout the entire work and beyond.
Further thanks go to all those likeminded friends and colleagues who provided helpful discussions and aided me in improving my knowledge, helped me to find literature or to make corrections to the manuscript.

Introduction

Theropoda, a clade of chiefly carnivorous dinosaurs that first appeared during the Upper Triassic, are arguably among the most significant animal groups in the history of life, having dominated terrestrial ecosystems as apex predators for over 140 million years, and bringing forth some of the largest terrestrial predators of all time in the course of their evolution.

These creatures have captivated scientific and public attention since the early 19th century, when the first fossilised specimens were found and described as lizard-like creatures by early naturalists (e g. Buckland 1824). Since then, the understanding of their anatomy and lifestyles has changed drastically, as have the methods with which they have been studied, with technological advances during the last two decades radically increasing the amount of information that can be inferred from fossil specimens.

Throughout their entire evolution, Theropoda have included apex predators feeding on large animals (this even holds true for extant birds, but is most blatant in Non-Avian theropods such as the famous *Tyrannosaurus* and *Allosaurus*) but, as could be expected from such a long-lived taxon, many different lineages diverge from this ecology.

For example, Spinosauridae are generally agreed upon to have relied primarily on fish and other small animals (see for example Charig & Milner 1997: pp. 61 f., Holtz 1998, 2003, Kellner 2004), while some Abelisauroidea (Persons & Currie 2011a: pp. 4 f.) and Coelurosauria (Holtz 1994: pp. 480*f.*) were adapted for extreme cursoriality.

Even among Theropoda filling comparable niches, there are significant variations in anatomy as a result of evolutionary background and the ecology and functional anatomy of their prey.

Studies previously have (examples in parantheses) examined theropod palaeopathology (Rothschild et al. 2001), locomotory musculature (Bates *et al.* 2012, Carrano & Hutchinson 2002, Persons & Currie 2011a, b), forelimb function (Carpenter 2002, Senter & Robins 2005), neck musculature (Snively & Russell 2007) and craniodental mechanics (Abler 1992, Bates & Falkingham 2012, Rayfield 2004, 2005ab, Rayfield *et al.* 2001). The amount of data that has been collected is impressive, however a commonly occurring effect of the incomplete fossil record is to force research works to focus on a relatively small sample of well-known taxa, and often a specific body part, whose function is analysed in detail but also isolated from other aspects. Hence, only few taxa that are known from complete remains have been extensively studied, while many others remain at best incompletely known.

Inferences based on fossil taxa are limited and always lack confirmation from *in vivo* observations. Extant animals frequently employ behaviour that they are not anatomically adapted for, such as cursorial canids using their forelimbs for digging, volant gannets using their wings for swimming, and some populations of goats climbing trees (Conway *et al.* 2012). There are certain ambiguities in palaeontology, which might never be resolved, and features that we might never be able to make sense of, especially regarding behaviour, but also tissues that are not usually preserved in fossils but are critical to the appearance and function of the entire organism. Thus caution is advised when concluding about a fossil species' behaviour and ecology

based on their anatomy, meaning almost all inferences should be regarded as tentative. Therefore it is even more important to make use of as much of the available data as possible and try to see the entire picture.
Using the considerable body of published information at hand, a condensed survey and interpretation of literature relating to the anatomy of predatory theropods is attempted here. Findings are summarised in taxonomic rather than anatomical order. This way, I hope to contribute a slight degree of novelty to the subject by surveying and analysing a wide range of published data in an alternative form.

Where available, results will be discussed in the context of inferences that can be drawn from sources other than functional anatomy, such as palaeopathology, the study of bite marks and trace fossils and the observable behaviour of extant analogues.

In the conclusion, evolutionary developments and predatory ecotypes of non-avian theropods will be outlined, in an attempt to give reasons as to why Theropoda were the dominant carnivores in terrestrial ecosystems for much of the Mesozoic and to give an overview over their evolution throughout this time.

1. Materials and Methods

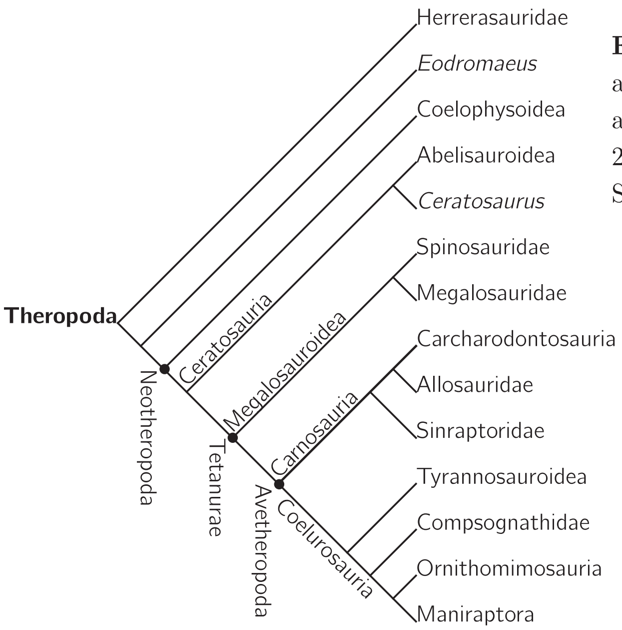

Figure 1: Simplified cladogram of theropod phylogeny as used in the present work. Phylogenetic relationships adapted from Carrano & Sampson 2008, Carrano *et al.* 2012, Makovicky *et al.* 2005, Martínez *et al.* 2011, Senter 2007.

1.1. Phylogeny and Nomenclature

Since the objective of the present work is not a phylogenetic or systematic revision of the non-avian Theropoda, phylogenetic relations consensually recovered by a number of relatively recent and comprehensive studies are used herein (see Fig. 1). The definition of Theropoda used is as the stem-based clade containing all Saurischians sharing a more recent common ancestor with Neoornithes than they do with Sauropoda. Those outside of Neotheropoda (sensu Martínez *et al.* 2011, p. 208), which is the clade containing the most recent common ancestor of *Coelophysis* and Neoornithes, are subsumed as "Ancestral Theropoda".

There is much debate concerning some aspects of theropod phylogeny. Notably, some studies have recovered Coelophysoidea as a subclade of Ceratosauria (e. g.: Tykoski & Rowe 2004), and the monophyly of Megalosauroidea and Coelophysoidea, as used here, is contested (e. g.: Holtz 1998a, Yates 2005). The particularly problematic phylogeny of Ancestral Theropoda is briefly discussed in section 2.1., but where both agree, the analyses of Sues *et al.* 2011 and Martínez *et al.* 2011 are followed.

The focus of this paper rests on predatory adaptions. In order to stay within reasonable limits, primarily herbivorous taxa are not discussed in detail here, neither are the almost 10 000 extant (Jetz *et al.* 2012: p. 1) and countless extinct species of birds, except where specific avian taxa are relevant as analogies to non-avian theropods.

1.2. Terminology

Where not stated differently, this is consistent with the cited literature. Where two or more are applicable, the most precise will be used (for example, labial and lingual will be preferred to lateral and medial when referring to the dentition).

1.3. Data Collection

The working basis and primary task of this thesis is to provide a literature survey of previously published information on Theropod

anatomy. Measurements were preferably quoted directly, and otherwise measured from images. Note that the total length of theropods is measured along the curves of the vertebral column. Where necessary, 2-dimensional measurements were taken using GIMP (http://www.gimp.org/) and the plugin "Measure Active Path" (http://registry.gimp.org/node/17235).
Since often the discussed clades of theropods show considerable size variation, categories (small≤3m<mid-sized≤7m<large) are used when referring to them.
Since this work focuses on carnivores, a number of unambiguously herbivorous theropoda (e.g. Ornithomimosauria, Therizinosauria) were omitted, and other probable herbivores (e.g. Oviraptorosauria, Troodontiodae) only touched on briefly to evaluate factors that could support carnivory.

2. Survey and Discussion of Functional Anatomy by Taxon

2.1. Ancestral Theropoda

A description of their evolutionary background and plesiomorphic characteristics facilitates further comparisons concerning theropod evolution. Hence this section mainly serves to outline a basis for analogies to more derived Theropoda.

Preeminent examples of basal Theropoda are the South American *Herrerasaurus ischigualastensis*, *Staurikosaurus pricei*, forming the clade Herrerasauridae (Langer *et al.* 2010: p. 72) that is usually recovered near the base of Theropoda as assumed here, and *Eodromaeus murphi* (Martínez *et al.* 2011). Other possible Non-neotheropod theropods include *Eoraptor lunensis*, *Guaibasaurus candelariensi*s (Langer 2004: p. 49), *Tawa hallae* (Nesbitt et al 2009), and *Daemonosaurus chauliodus* (Sues *et al.* 2011). However *Eoraptor* has recently been suggested to be a basal sauropodomorph (Martínez *et al.* 2011: p. 208*f.*, Sereno *et al.* 2013), *Guaibasaurus* has been variously interpreted as a basal saurischian or a sauropodomorph (Bonaparte *et al.* 1999: pp. 106*f.*, Novas *et al.* 2011: p. 341), and *Tawa* might be a basal Coelophysoid (Martínez *et al.* 2011, pp. 207*f.*). This discussion of phylogenetic relationships among basal theropoda may seem excessive, and indeed it is unrewarding because almost all the discussed taxa's affinities are controversial, but it is important to keep these uncertainties in mind. Most ancestral theropods were small, but some *Herrerasaurus* individuals seem to have exceeded 4m (Mortimer 2014c [online]).

In the purported basal theropod *Eoraptor*, a heterodont dentition including leaf-shaped teeth implies that it was not a specialized carnivore, but rather omnivorous (Sereno *et al.* 2013: p. 119), but in accordance with the hypothesis of this being their ancestral state, a number of basal theropods display traits consistent with hypercarnivory.
Basal theropods have ziphodont, i.e. labiolingually compressed, serrated and recurved teeth (Langer 2004: p. 30, Martínez *et al.* 2011: 206, Sues *et al.* 2011: p. 3462). An adaption for cutting flesh (D'amore 2009: p. 1294), this general tooth design is evidence of predatory habits in these animals. Skulls of *Herrerasaurus* and *Daemonosaurus* are narrow and deep (oreinirostral), and in the former elongated and relatively large

(longer than the neck, Sereno & Novas 1992: p. 1138). In *Staurikosaurus* it is unknown and the mandible poorly preserved, but its length and proportions (Bittencourt *et al.* 2009: p. 4) also suggest a relatively long cranium. The lower jaw has an intramandibular joint allowing for dorsoventral rotation of the dentary against the postdentary bones , a typical theropod trait that has been interpreted as a means to prevent prey escape by curling around the bitten portion (Sereno & Novas 1992, 1993: pp. 452*f.*, p. 472, Sues *et al.* 2011: p. 3461) or to absorb stresses (Holtz 2003: p. 331).

By contrast, *Tawa hallae* and *Eodromaeus murphi*, have proportionately small skulls , approximately 60-65% of neck length (Hartman 2014 [online], Martínez *et al.* 2011). While the majority of the dentition is ziphodont, in *Tawa* and *Daemonosaurus* the anterior teeth lack carinae and are separated from the rest of the tooth row by a diastema (Nesbitt *et al.* 2009: p. 1531, Sues *et al.* 2011: p. 3462). Ancestrally, theropods had an open, fenestrate skull lacking a well-developed bony palate, which suggests their skulls were poorly suited for withstanding torsional forces (Holtz 2003: p. 331).

Where known, cervical vertebrae of the sampled taxa were elongated, bearing short spinous processes and tall epipophyses, and the paroccipital processes point laterally (Langer 2004: pp. 28*f.*, Sereno & Novas 1993: pp. 458*f.*), suggesting an undifferentiated neck musculature not specialized for specific planes of movement as is the case in some derived theropods.

The forelimbs have functionally tridactyl, long hands, with vestigial 4th and 5th digits, and were less than half the length of the hindlimbs (Langer 2004: p. 33, Martínez *et al.* 2011: p. 207). *Herrerasaurus*' forearm was incapable of pronation or supination, constraining the palm in a transverse posture (Sereno 1993: p. 447), and the elbow was capable of attaining right-angled flexion as seen in lateral view. The robust built, prominent muscle attachments on the forelimb and scapulocoracoid (e. g.: olecranon, deltopectoral crest and acromion) and the presence of large, curved claws that (at least in *Herrerasaurus*) converged during flexion due to the angle of the metacarpophalangeal joints (Sereno 1993: p. 448). Raptorial forelimbs are consistent with the narrow skull and bladelike teeth, suggesting that the arms were used for prey restraint while the jaws caused fatal injuries, avoiding prolonged jaw-prey contact that could overstress the skull. However, it should be noted that as figured by Sereno and Novas (1992: p. 1139) the scapular blade of *Herrerasaurus* is shorter and less expanded distally than in more advanced theropoda, suggesting its associated musculature (Carpenter 2002: p. 72) was smaller.

Whilst their hindlimbs show a fully parasagittal, digitigrade posture, as is common to all theropods, the iliac blades of basal Theropoda were short (Langer 2004: p.33, Martínez *et al.* 2011, Nesbitt *et al.* 2009) compared to those of more derived taxa (e. g.:Madsen 1976: p. 42, Brochu 2003: p. 104*f.*), suggesting a smaller volume was occupied by the thigh musculature (primarily knee flexors and extensors) that originated there (Carrano & Hutchinson 2002: p. 210). This would result in a gait more driven by the hip joint than the knee, unlike in extant birds where the opposite is the case, fitting into an evolutionary trend of increasing the importance of knee movement in locomotion (Allen *et al.* 2013).

Because most basal Theropoda, including those most well-supported as such in recent studies, have these features, it seems most parsimonous to assume that the plesiomorphic state of Neotheropoda encompassed carnivorous specializations seen in *Herrerasauridae* and *Eodromaeus*, such as oreinirostral, lightly built skulls, ziphodont teeth and raptorial forelimbs. Due to phylogenetic inclarities it cannot be asserted whether dental modifications as seen in *T. hallae* and *D. chauliodus* are derived traits of Coelophysoidea or ancestral ones of Neotheropoda.

2.2. Coelophysoidea

The Coelophysoidea are a clade of small and mid-sized Theropoda from the Upper Triassic and Lower Jurassic (Carrano & Sampson 2004, Tykoski & Rowe 2004). They represent one of the first major diversifications of theropods. As noted previously, the phylogenetic placement of the group and some of its referred members is controversial. Some of the Coelophysoidea discussed here were among the largest predators in their respective ecosystems, likely making them apex predators.

Their fossils are often incomplete, however some (e. g. *Coelophysis*) are known from numerous well preserved specimens.

Coelophysoids followed a rather conservative body plan: A relatively small skull (Holtz 2003: p. 333), slender axis and elongated limbs. Larger coelophysoids had a more robust build and larger skulls than the small members (Welles 1984: p. 95), but Coelophysoidea in general were gracile by theropod standards (Paul 2010: pp. 71*f.*). Most recent biomechanical studies (Carpenter 2002, Rayfield 2005a) have focused on small members of the clade (especially *Coelophysis bauri*), due to their more complete fossils.

A peculiar feature of the clade is the loose attachment of the premaxilla to the rest of the skull, accompanied by a notched diastema and straight, unserrated premaxillary teeth (Tykoski & Rowe 2004: p. 52). Interpretations include a lever system used in biting, a snake-like swallowing apparatus or mechanical weakness of the skull that would preclude the acquisition of living prey (Bakker 1986, cited in Tykoski & Rowe 2004: p. 69, Welles 1984: p. 90).

However, there may not be a good reason to assume either; the flexibly attached premaxilla could have been useful in grappling small animals (Tykoski & Rowe 2004: p. 69), while the blade-like maxillary teeth (Smith *et al.* 2005: p. 722) were utilised for killing.

Sakamoto (2010: p. 3*f.*) found Coelophysoids to have an apomorphically low efficiency of transmitting bite force at the front of the tooth row, but conversely a very high one in the back. An inability to produce powerful bites at the front of the tooth row would remove the need for a strong attachment of the premaxilla, in favour of a flexible, hook-like arrangement that could secure a hold on prey (similar to the hooked teeth and kinetic skulls of many extant snakes). Prey would then be killed or devoured using a more powerful bite with the posterior teeth, if it was small enough to fit in the jaws. Larger prey might have been subdued with slashing bites.

Beam-theoretical analysis of its mandible found the dentary of *Dilophosaurus* to be reinforced near its anterior end, implying it commonly experienced strong loads (Therrien *et al.* 2005: p. 196). This strange combination of features might be explained by a mode of prey restraint in which the premaxilla served as a hook, securing the prey item against the lower jaw. Therrien *et al.* (2005) proposed that *Dilophosaurus* probably fed on animals

smaller than itself. 2D finite element analysis of a *Coelophysis* skull suggests that stresses during biting mainly accumulated in the posterior maxilla, jugal and frontoparietal region (Rayfield 2005a: p. 312).
In *Dilophosaurus* the paroccipital processes terminate dorsal to the occipital condyle, but the occiput is deep and the tuberosities near its base are prominent (Welles 1984: pp. 99*f.*), indicating a capacity for strong ventro- and lateroflexion. Coelophysoid necks were elongated, flexible and S-curved due pronounced opistocoely and thin cervical rib shafts (Tykoski & Rowe 2004: p. 55, Welles 1984: p. 91), resembling extant birds with a behaviour comprising strikes for small prey (e. g. Ardeidae and Ciconiidae, personal observation).
The forelimb is functionally tridactyl, with a vestigial fourth digit, and the manus is relatively short in proportion to the rest of the arm (Tykoski & Rowe 2004: p. 60). In *Coelophysis* maximum flexion of the elbow was limited to over 100° and the humerus remained posteriorly inclined even during protraction (Carpenter 2002: p. 72). Muscle attachment sites for pro- and retractors on the scapulocoracoid are weakly developed compared to other studied theropods (Carnosauria, Coelurosauria), these muscles were less powerful, which is consistent with the comparatively gracile forelimb structure and the small claws (Carpenter 2002: pp. 68*f.*). The forelimb of Dilophosaurus is notably more robust and adapted for grasping (Welles 1984: p. 177).

Compared to ancestral theropods, (derived?) Coelophysoidea tend to have longer ilia (Tykoski & Rowe 2004: p. 60) suggesting proportionately larger thighs and stronger knees. Coelophysoid tarsals and metatarsals are fused and elongated (Tykoski & Rowe 2004: p. 63), consistent with cursorial habits.

Small coelophysids were probably opportunistic predators of small animals (insects, small lepidosaurs, mammals etc.), built towards speed and agility rather than power. The predatory ecology of large-bodied coelophysoids (e.g. *Liliensternus*, *Dilophosaurus*) deserves further attention in the future. Larger, more robust skulls and proportions suggest proportionately larger prey, though possibly still smaller than themselves.

2.3. Ceratosauria

The Ceratosauria are another successful basal theropod radiation known from Early Jurassic to Upper Cretaceous strata of most continents (Allain *et al.* 2007, Carrano & Sampson 2008: p. 203). As compared to the Coelophysoidea, that are sometimes grouped within Ceratosauria (e. g.: Holtz 1998), Ceratosauria proper were much more diverse anatomically and morphologically.

All known Ceratosaurs appear to share the trait of an enlarged cnemial crest (Tykoski & Rowe 2004: p. 62) on the proximal tibia, which suggests the knee-extensor-musculature was particularly powerful. This trait is accompanied by prominent and sometimes very robust pre- and postacetabular processes of the ilium (e. g.: Bonaparte 1990: p. 29, Carrano *et al.* 2011: p. 28, Tykoski & Rowe 2004: p. 60).

The most basal known Ceratosaurs are small to mid-sized, slenderly built animals such as *Limusaurus*, for which the presence of a toothless beak, long neck and gastric mill suggests it was herbivorous (Naish 2009 [online], Xu *et al.* 2009), and *Elaphrosaurus* (Carrano & Sampson 2008: p. 193).

On the other hand, the much larger (up to 6.7m long) and powerfully built *Ceratosaurus* (Hartman 2013c [online]) was clearly a macrophagous predator, known for its huge skull and extremely long, knife-like maxillary teeth (Madsen & Welles 2000: pp. 52*f.*, Smith *et al.* 2005: p. 722).
Studies of its neck musculature reveal that it lacked the specialization seen in Carnosauria and Tyrannosauridae (see section 2.5. and 2.6.1.), but was well-developed overall, as was the musculature adducting the jaw, suggesting a relatively powerful bite (Snively & Russell 2007: p. 955).
Ceratosaurus probably relied primarily on the puncturing and cutting ability of its teeth in conjunction with large jaws that had a high mechanical advantage (Sakamoto 2010: p. 4) to place powerful, high-efficiency bites and predate on large prey. However the long teeth might have been at risk of fracture, indicating that the animal preferred fleshy regions, and the mandible was primarily adapted for dorsoventral loads (Therrien *et al.* 2005: p. 197) making it unlikely that it held onto prey for long periods of time. An interesting theory was put forth by Bakker and Bir, finding that *Ceratosaurus* had a long, flexible body, well suited for an aquatic lifestyle, which they corroborated with data on the distribution of isolated teeth (Bakker & Bir 2004: pp. 302*f.*).

The Abelisauroidea are a highly derived clade of Ceratosauria that evolved during the Jurassic, but radiated and rose to dominance during the second half of the Cretaceous. These can be subdivided into two major clades, the Abelisauridae and the Noasauridae (Carrano & Sampson 2008).

Abelisauridae are a group of mid- to large-sized theropods particularly common on the southern continents of the latter half of the Cretaceous (Carrano & Sampson 2008: p. 203).
In stark contrast to *Ceratosaurus*, they typically sported shortened, but robustly constructed skulls, frequently bearing extensive cranial ornamentation and rugosities, and short teeth (Sampson & Witmer 2007: p. 97, Carrano & Sampson 2008: p. 211). Abelisauridae had robust necks with hyperossified, interlocking cervical ribs, low cervical neural spines and hyperelongated epipophyses, and the caudal transverse processes were deflected dorsally, suggesting an unusual muscular arrangement[1] (Bonaparte 1990: pp. 16*f.*, Méndez 2014b: pp. 578*f.*, O'Connor 2007: pp. 127*f.*). These traits are developed in varying degrees within the Abelisauridae, for example they are less marked in *Majungasaurus* than in *Carnotaurus* (Méndez 2014b: p. 579).
Among their most striking features is extreme shortening of the forelimb. In derived Abelisauridae the forearm is only about a quarter as long as the humerus, and the manus and digits are more or less reduced as well (Burch & Carrano 2012: pp. 7*f.*). While its overall robusticity and that of the muscle attachment sites on the scapulocoracoid suggest the forelimb was powerful, and the ball-shaped humeral head could have allowed for an extensive range of motion (Burch & Car-

[1] The epipophyses are the origination site of the *Musculus complexus*, which serves to dorsi- and/or lateroflex the neck in other theropods (e.g. Snively et al. 2007). An increased dorsal projection of these processes suggests increased emphasis on dorsiflexive leverage, compensating for the smaller leverage of the *M. transversospinalis* that originates from the neural spines. The region below the caudal transverse processes primarily houses the *M. caudofemoralis longus*, which is the main femoral retractor (Persons & Currie 2011a: p. 1). A dorsally angled transverse process increases its volume at the expense of epaxial musculature (*M. spinalis* and *M. longissimus*).

rano 2012: p. 15, Tykoski & Rowe 2004: p. 58), it is unlikely that the arms were used for prey capture.

Carnotaurus sastrei is suggested to have slammed its tooth rows into prey to kill it (Bakker 1998: p. 156). This conflicts with several lines of evidence such as the fact that muscle-insertions on the skull of *C. sastrei* lack an important adaption for head depression, ventral deflection of the paroccipital processes (Bonaparte *et al.* 1990; p. 6, Snively *et al.* 2013: p. 1). Furthermore, adaptions for maximising velocity reached by the upper tooth row during a strike would presumably include a long, flexible neck and a longer skull.
By contrast, Abelisauridae have relatively wide, robust necks and skulls and are extremely brevirostrine (Bonaparte *et al.* 1990: pp. 3*f.*, Méndez 2014b: 578, O'Connor 2007: p. 130), features that seem more suitable for gripping and controlling prey than for slashing or striking. The short skulls result in high biting efficiency (Sakamoto 2010: p. 4), that in combination with extensive cranial and mandibular kinesis (Mazzetta *et al.* 1998: pp. 188*f.*), could help maintain a grasp on prey items with little effort or risk of injuries. *Majungasaurus* by contrast has an akinetic, strongly co-ossified, very robust skull roof with fused nasals, implying reliance on prolonged and powerful bites (Sampson & Witmer 2012: p. 97). Therrien *et al.* (2005: pp. 197*f.*) found the mandibles primarily adapted for slashing bites, analogous to extant varanids. The teeth are short and compressed (Smith *et al.* 2005: p. 722), which corroborates both hypotheses in that Abelisauridae could have held onto prey with a powerful bite or pull, to either tear flesh or prevent prey escape.

Some abelisaurids, such as *Carnotaurus* and *Aucasaurus*, display traits linked to exceptional cursorial ability (Persons & Currie 2011b): a rigid vertebral collumn, enlarged attachment areas for the primary femoral retractor, *M. caudofemoralis longus*, (Méndez 2014a: p. 106) a strong femur (Mazzetta *et al.* 1998: p. 187) and long hindlimbs (Bonaparte 1990: p. 30, Hartman 2011, 2012b [online]). Conversely, others, such as *Majungasaurus*, had very short, stout legs and a low-slung, elongated body (Hartman 2012c [online]), suggesting they were slower, but possibly more suitable for tackling large prey.

Abelisauridae apparently filled a diverse range of predatory niches. While cursorial members could have functioned as pursuit predators of fast prey, short-legged Abelisaurids likely relied on ambush and quick acceleration, making them generalist macropredators. At least some abelisaurs had adaptions suggesting prolonged prey-contact, such as is present when shaking or restraining a struggling animal in the jaws. This could have served to compensate for their forelimbs' lack of functionality in predation.

The Noasauridae contain a number of small to mid-sized Abelisauroidea (*e. g.: Masiakasaurus knopfleri* at up to 2.3m long, some isolated remains are roughly twice this size, Carrano *et al.* 2011: p. 36, Lee & O'Connor 2013: p. 865) from the Cretaceous of the Southern Continents. The clade mostly compromises enigmatic and fragmentary taxa, but the comparatively well-known *Masiakasaurus* from Madagascar provides some insights into their anatomy.
This animal is peculiar in the morphology of its jaws, possessing a ventrally bent anterior

dentary and procumbent dentition, but the axial skeleton is largely consistent with other abelisauroids (Carrano *et al.* 2011: p. 38). Unlike Abelisauridae, Noasauridae retained plesiomorphic arms, which at least sometimes bore raptorial claws (Agnolin & Chiarelli 2009: p. 293). Noasaurids generally had elongated limbs (Carrano *et al.* 2011: p. 38), and in *Velocisaurus* the middle metatarsal had increased robusticity relative to the others (Holtz 1994: p. 496), indicating cursoriality.

Unlike for some other theropods in their size class (e. g.: section 2.6.2.), the functional anatomy of Noasauridae has not received a lot of attention. Despite a number of peculiarities clearly present in the group, and which could be linked to a very specialized diet (as claimed by Barret & Rayfield 2006: p. 221), the available material necessitates caution when making conclusions. Noasauridae were small, cursorial predators, filling niches, but the lack of conclusive correlates for some of their apomorphies make their purpose remain enigmatic.

Finally, the much larger (>11m, Mortimer 2014a [online]) *Deltadromaeus* and *Bahariasaurus* from the Cretaceous of Africa include remains of a robust shoulder girdle, moderately large forelimb and slender hindlimb, but are otherwise too incomplete to allow for conclusions (Carrano & Sampson 2008: pp. 192*f.*, Sereno *et al.* 1996: p. 989).

2.4. Megalosauroidea

Megalosauroidea, which are known from the Middle Jurassic to Late Cretaceous, are among the most diverse of all non-avian theropods. As a whole, the taxon contains two major clades, Megalosauridae and Spinosauridae (Carrano *et al.* 2012: p. 270), whose ecomorphology diverges heavily, especially in the skull.

Megalosauridae were mid-sized (Benson 2010: p. 139) to large (Hendrickx & Mateus 2014: p. 19) theropods with an almost worldwide distribution in Middle and Upper Jurassic ecosystems (Carrano *et al.* 2012).

Exemplified by *Torvosaurus tanneri* from the Upper Jurassic of North America, they typically had very large, strongly elongated (Allain 2002: p. 549[2]) skulls, stout legs, powerful forelimbs and long bodies (Hartman 2013a [online]).

Megalosaurid skulls and teeth were unusually long, similar to those of *Ceratosaurus* (cf. Benson 2010: p. 133: Fig. 1, Hartman 2013a [online], Hendrickx & Mateus 2014: p. 14). Furthermore, in *Torvosaurus* the jugal and dentary are both unusually deep and robust bones (Britt 1991: pp. 19*f.*) compared to other contemporaneous theropods.

These are both centres of stress concentration during biting (Rayfield 2005a: p. 312, Therrien *et al.* 2005: p. 181), so that increased robusticity indicates a powerful bite for *T. tanneri* and megalosaurids with similar anatomy (e. g.: Sereno *et al.* 1994, Benson 2010: p. 133: Fig. 1).

This is consistent with a large skull and bite marks on an *Allosaurus* pubis (Chure *et al.* 1998: p. 229) that are probably attributable to *Torvosaurus* due to their size. On the other hand, megalosaurid teeth were relatively thin and blade-like (Bakker 1998: p. 155), making them efficient cutting tools, but limiting their ability to process bone.

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[2] Allain (2002) reports extremely low cranial depth/length ratios for two megalosaurids. At least one of the specimens in question shows signs of coming from an immature individual (Allain 2005: p. 852), possibly exaggerating this feature. As exemplified by larger, adult Megalosauridae (for example *Torvosaurus spp.*, Britt 1991: pp. 11 f.), in general megalosaurid skulls were probably long and shallow, but markedly less than in these extreme cases.

Spinosauridae, were among the most specialized non-avian theropods known.

Characterized by large body size (e. g.:Dal Sasso *et al.* 2005, Kellner *et al.* 2011), very elongate skulls, large forelimbs bearing extremely large claws and often a more or less marked increase in the height of the neural spines, they have been described as "crocodile mimics" (Holtz 1998), on the basis of likely behavioural and dietary parallels.

Spinosauridae were probably amphibious, as shown by an extremely dense bone structure and atrophied hindlimbs in some spinosaurids, as well as isotope ratios of their teeth (Amiot *et al.* 2009, Ibrahim *et al.* 2014: p. 2, Stromer 1915: pp. 14*f.*).

Two subtaxa, the Baryonychinae and Spinosaurinae are set apart by that the former retained ziphodont, albeit thickened and extremely numerous teeth, while those of the latter were large, straight cones (cf. Charig & Milner 1997: pp. 28*f.*, Stromer 1915: pp. 8*f.*).

Jaw apparata of both these groups, however, suggest a diet primarily composed of fish, and other relatively small prey. Gracile snouts, as known for *Suchomimus* (Sereno *et al.* 1998: p. 1299), *Baryonyx* (Charig & Milner 1997: pp. 14*f.*) and *Spinosaurus* (Da Sasso *et al.* 2005: pp. 889*f.*) are favourable for reducing drag while catching prey in water, and were hence acquired convergently by piscivorous crocodilians and birds, and both spinosaurine and baryonychine teeth have broadened crowns (and in the case of Spinosaurinae, lack carinae) as an adaption for gripping prey at the likely expense of cutting efficiency. Mechanical analysis of Spinosaurid snouts and mandibles further supports the analogy to crocodilians: Cuff & Rayfield (2013: p. 9) found their rostral torsional and bending resistance to overlap that of extant, primarily piscivorous species like the *Gavialis gangeticus* and *Mecistops cataphractus*. The mandible of *Suchomimus* was strengthened in the anterior part (Therrien *et al.* 2005: pp. 198*f.*), opposing a notch in the upper tooth row, which could have served to grasp prey, and the *Spinosaurus* was morphologically similar (Stromer 1915: pp. 4*f.*).

Direct evidence, such as stomach contents (Charig & Milner 1997: p. 61), lost teeth (Kellner 2004) and remains of prey embedded in jawbones (Dal Sasso *et al.* 2005: p. 888), resulting from spinosaurid feeding or predation on fish, pterosaurs and small dinosaurs provide further confirmation.

The elongated neural spines typical for many spinosaurids (e. g.: Stromer 1915: pp. 14*f.*, Sereno *et al.* 1998: pp. 1298*f.*, Allain *et al.* 2012: p. 3) probably anchored ligaments helpful for stalking prey from above, but a purpose as a display structure must also be considered.

Megalosauroid forelimbs are massive and proportionately large, bearing robust, curved claws (Charig & Milner 1997: pp. 43*f.*, Holtz *et al.* 2004: pp. 88*f.*). These features are strongly indicative of a role in predation, likely as a secondary means of engaging prey after placing a bite, for example to stabilise its position relative to the prey item while subduing it, prevent its escape, or, at least in the case of Spinosauridae, to help pull aquatic prey onto land.

Their mechanics have not been studied in detail, but being bracketed phylogenetically by Avetheropoda and other theropods for which such data are available, its likely that the forelimb lacked an extensive anterior range of motion at the shoulder or elbow, but was well-suited for powerful clutching

(see sections 2.1.-2.6.).
It has been repeatedly suggested (Bailey 1997: p. 1134: Fig. 5, Ibrahim *et al.* 2014: p. 2) that at least some Spinosauridae were quadrupeds. However this strongly conflicts with known functional anatomy of theropod forelimbs and has yet to be supported by direct evidence pertaining to the forelimb itself (Headden 2013 [online]).

Megalosauridae and Baryonychinae, being closer to the plesiomorphic state of the clade, had proportionately large, robust ilia comparable to basal ceratosaurs' and stocky, albeit short hindlimbs (e. g.: Britt 1991: pp. 37*f.*, Hartman 2013a [online], Sereno *et al.* 1998: p. 1300). By contrast, the Spinosaurine *Spinosaurus* shows an apomorphic reduction of the entire hindlimb and pelvic girdle (Ibrahim *et al.* 2014: p. 1).

Spinosauridae were at least partially aquatic and incorporated fish and other moderately-sized prey into their diets, a specialization allowing them to avoid direct competition with other sympatric large-bodied theropods (Farlow & Holtz 2002: 259, Holtz 2003: pp. 335*f.*).
Other Megalosauroidea likely had a more varied diet, as reflected by less specialized anatomy, but there is evidence in the form of preserved stomach contents that at least sometimes they also fed on fish (Allain 2005: pp. 856), which could explain their body shapes as adaptions for swimming. A similar inference was drawn by Bakker & Bir (2004: p. 302), suggesting that megalosaurids from the Upper Jurassic Morrison Formation were adapted for life in fluvial habitats and predation on aquatic prey. Indeed opistocoelous dorsal vertebrae, indicative of great flexibility, have been reported in both Megalosauridae (Britt 1991: p. 25) and Spinosauridae (Stromer 1915: pp. 14*f.*).
If this hypothesis is correct, Megalosauroidea in general had a tendency towards such lifestyles. However, it is worth consideration that the anatomy of non-spinosaurid Megalosauroidea appears equally well suited for predation on large herbivorous dinosaurs by means of placing powerful, deep bites and possibly using their flexible bodies to faciliate forelimb use, and this behaviour is not ruled out by other evidence.

2.5. Carnosauria

Carnosauria (mostly represented by the similarly comprehensive but node-based Allosauroidea) form one of the most successful and dominant clades of theropods. They are known from the Middle Jurassic to Latest Cretaceous and probably had an almost global distribution (Carrano *et al.* 2012: pp. 271*f.*, Azevedo *et al.* 2013).
All known carnosaurs were mid- to large-sized predators, with some of them ranking among the largest terrestrial carnivores known (e. g. Brusatte *et al.* 2010: p. 37, Coria & Calvo 1998, Ortega *et al.* 2010, Sereno *et al.* 1996). The predominantly Cretaceous Carcharodontosauridae are the most speciose subclade, while the more basal, Jurassic Allosauridae are better studied due to their good fossil record.
Carnosaur skulls are oreinirostral, fenestrate and contain narrow, ziphodont teeth (Holtz *et al.* 2004: p. 84, Madsen 1976: pp. 54*f.* Smith *et al.* 2005: pp. 722-724). They are proportionately large (e. g. Madsen 1976: p. 13).
Finite element analysis of *Allosaurus*' cranium found it to be capable of resisting vertical loads exceeding 18kN despite a lightweight construction, with fenestrae (Rayfield *et al.*

2001: p. 1035). Stresses accumulate in the thick, fused frontoparietal region of the skull, while other elements (e. g. quadrate) are kinetic and may have been involved in absorbing stresses (Rayfield 2005b: pp. 357*f.*).
Muscle insertions on the base of the skull comprise reinforced basitubera and ventrally deflected paroccipital processes (Antón *et al.* 2003: p. 314), imparting ventroflexive moment arms for a powerful *m. rectus capitis*, *longissimus capitis* and *iliocostalis longus* and large insertions on the parietals suggest the presence of large dorsal neck muscles (Snively & Russell 2007: p. 955). By contrast, lateroflexive muscles are smaller or transformed into primarily ventroflexive ones (Snively & Russelll 2007: p. 955). Low, long spinous processes and the presence of opistocoelous joints in the neck made it very flexible (Snively & Russell 2007: p. 955, Snively *et al.* 2013: pp. 10*f.*). Its jaw joint and adductor chamber suggest a capacity for opening the jaws at an angle of ~90°, but in exchange for relatively weak jaw muscles (Bakker 1998, pp. 147*f.*), even though estimates for bite force have varied considerably (cf. Bates & Falkingham 2012: p. 4, Rayfield *et al.* 2001: p. 1035).
These traits allowed rapid, forceful strikes (Bakker 1998: pp. 152*f.*, Rayfield *et al.* 2001: p. 1036), or alternatively utilization of the neck to augment traditional biting by ventroflexion (Antón *et al.* 2003: p. 317). Both hypotheses were possibly within the living animal's capabilities (Snively *et al.* 2013: p. 14) and it should be mentioned that the dangers of tooth loss and dislocation of the mandible are relativized by polyphyodonty, extreme gape and cranial kinesis. The cervical flexibility and high angular accelerations (Snively *et al.* 2013: p. 14) corroborates striking or slashing movements. In either case, the bite produced large forces despite weak jaw adductors. While the narrow skull shape and lack of a solid palate presumably reduced lateral and torsional strength (Holtz 2003: p. 331), this would have been beneficial for increasing pressure by focusing this force on a small area (Henderson 1998[3]: p. 223).
Although a comparable degree of study has not been devoted to other Carnosauria, there are certain functional similarities. All Carnosaur teeth (and skulls) are compressed (with maxillary CBR[4] averaging between 0.36 and 0.55), indicating an adaption for cutting flesh. However, the tooth crowns of *Allosaurus* and *Sinraptor* are proportionally shorter (Smith *et al.* 2005: pp. 722*f.*, Snively *et al.* 2006: p. 448), and in other carnosaurs, especially derived Carcharodontosauridae, the paroccipital processes are not deflected as far as in Allosauridae (being intermediate between them and plesiomorphic Theropoda, Bakker 1998: pp. 156*f.*, Coria & Currie 2002: p. 805, Brusatte & Sereno 2007: pp. 908*f.*, Eddy & Clarke 2011, p. 15).
Some carcharodontosaurids also bear tall neural spines on or near the neck (e. g.: Hartman 2013b [online], Stovall & Langston 1950: pp. 706*f.*), relevant to myology and flexibility of these regions and contrasting with *Allosaurus*.

Based on neck and jaw anatomy, carnosaurs used drawing motions of their teeth, as exemplified by the pulling employed by monitor

[3] Note that some inferences from this paper and Therrien et al. 2005 are being disregarded here because they were influenced by an inaccurately restored skull referred to a taxon now regarded a synonym of *Allosaurus* (Chure 2000: p. 173 f.) and because the impact of head crests on cranial strength has been called into question (Rayfield 2011: p. 246), possibly applying to the horn of *Ceratosaurus*.

[4] The Crown Base Ratio (CBR) *sensu* Smith et al. 2005 is the ratio between the labiolingual width of the crown and its mesiodistal length.

lizards, the only extant ziphodont animals (D'Amore *et al.* 2011: p. 5). Derived Carcharodontosauridae had enlarged skulls (Coria & Salgado 1995, Hartman 2012a, 2013b [online]), which correlate with longer tooth rows and greater bite force. Carnosaurs in general, especially *Carcharodontosaurus*, had high mechanical advantages (Sakamoto 2009: p. 4), partly compensating for relatively small jaw muscles.

Mandible strength in Allosauridae was found to be consistent with slashing or slicing bites, but some members had thickened symphyses for prey restraint (Therrien *et al.* 2005: pp. 202*f.*). Premaxillary teeth of Carnosaurs are less blade-like than those of the maxilla (Smith *et al.* 2005: pp. 722*f.*), and could have been involved in gripping.

Allosaurid forelimbs were tridactyl, moderate in size but powerful, bearing large, hooked claws and robust muscle attachments, and the scapular blade was long (Madsen 1976: pp. 37*f.*), indicating a powerful retractor musculature. By contrast, the coracoid was relatively short, indicating smaller origins of the protractor musculature (Carpenter 2002: p. 71), which makes it primarily adapted for posterior pulling, as would occur when preventing prey from fleeing. With size, the forelimbs become proportionately smaller but stockier, and the relative size of the coracoid and scapula increases (Canale *et al.* 2015: pp. 18*f.*, Senter & Robins 2005: p. 313). The humerus was unable to swing past the vertical and the elbow could not achieve right-angled flexion anteriorly (Senter & Robins 2005: pp. 313*f.*). While the forearm was incapable of rotation, the palm facing medially unless elevated laterally, the wrist and digits could be slightly adducted and abducted, extended and flexed significantly, some unguals being permanently flexed for impaling prey (Carpenter 2002: pp. 66*f.*: Fig. 7, Senter & Robins 2005: pp. 316*f.*). The limited range of motion might be linked to increased mechanical strength and leverage. Prey was likely apprehended with the jaws and then secured with the claws, for which alternatively utilisation for causing fatal penetration has been considered (Senter & Robins 2005: p. 314). The latter hypothesis is not tenable for most carnosaurs and on large prey animals, due to the insufficient size of their forelimbs and claws.

The hindlimbs are more elongated, and in combination with shorter, more rigid torsos indicate greater cursorial ability than those of basal Megalosauroidea or *Ceratosaurus* (Bakker & Bir 2004: p. 303). Both ilium and cnemial crest are well-developed (Holtz *et al.* 2004: pp. 90*f.*), indicating a powerful thigh musculature. However, they lack extreme adaptions for cursoriality, retaining more flexible tail-bases and feet with separate metatarsals (Holtz 1994: pp. 496*f.*, cf. sections 2.3 and 2.6). The giant carnosaur *Acrocanthosaurus* was found to have reduced cursorial abilities due to negative allometry in the size of hindlimb muscles (Bates *et al.* 2012: pp. 494*f.*).

Palaeopathological evidence points towards *Allosaurus* using its feet to restrain prey (Rothschild *et al.* 2001: p. 334), which would explain their metatarsals as adaptions for grasping. Carcharodontosauridae developed a dorsally displaced femoral head (e.g. Canale *et al.* 2015: p. 20, Coria & Currie 2006: p. 103, Stromer 1931: p. 16), hypothesized to have been advantageous for limb bone strength (Bates *et al.* 2012: p. 504). Increasing lateral ranges of motion, it might also have improved stability and maneuverability.

A peculiar case is represented by Megarap-

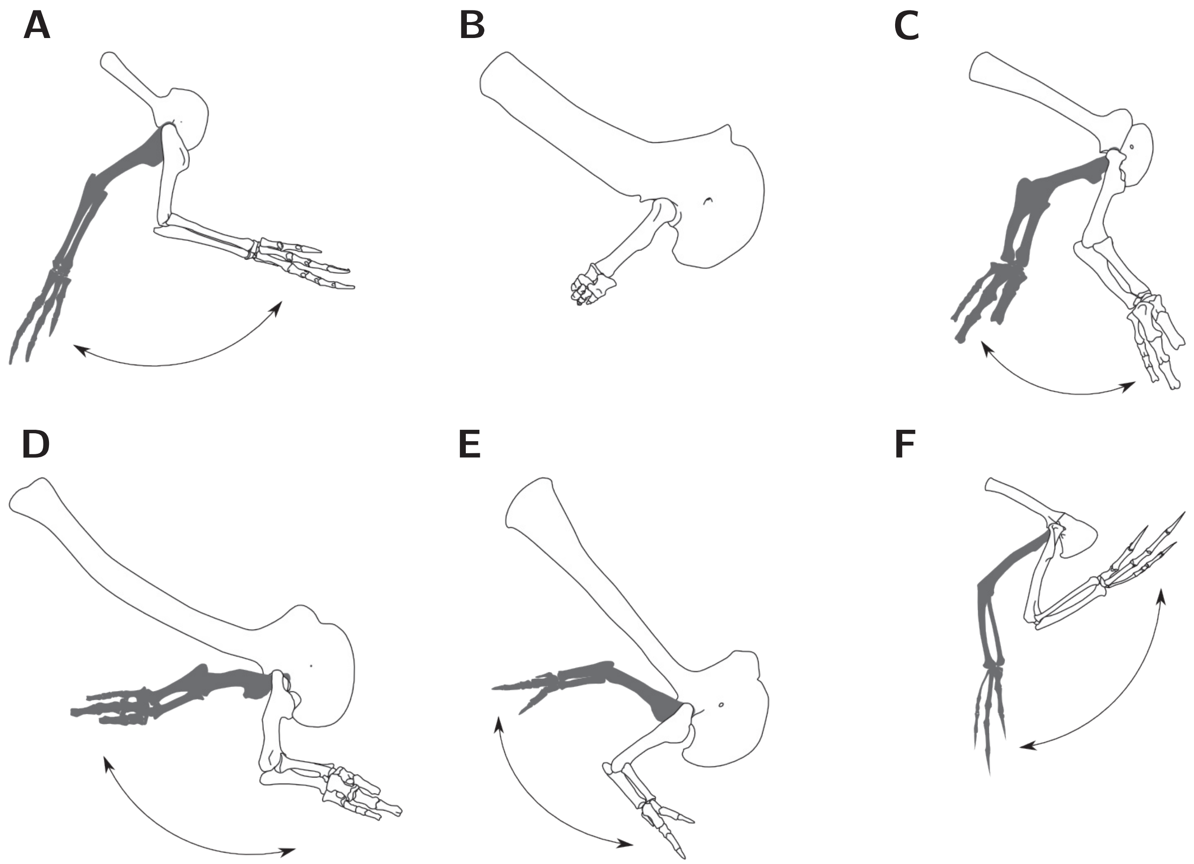

Figure 2: Selected theropod forelimbs and scapulocoracoids in lateral aspect, drawn to unit humeral length. **A:** *Herrerasaurus ischigualastensis* (Sereno 1993: pp. 426*f.*), **B:** *Majungasaurus crenantissimus* (Burch & Carrano 2012: pp. 3*f.*), **C:** *Allosaurus fragilis* (Gilmore 1920: pp. 58*f.*, Madsen 1976: pp. 137*f.*), **D:** *Acrocanthosaurus atokensis* (Currie & Carpenter 2000: pp. 221*f.*), **E:** *Tyrannosaurus rex* (Brochu 2003: pp. 94*f.*, Lipkin & Carpenter 2008: pp. 174*f.*, missing portions restored after Lambe 1917: pp. 49*f.*), **F:** *Deinonychus antirrhopus* (Ostrom 1969: pp. 91*f.*, 1974: pp. 3*f.*). Ranges of anteroposterior motion as indicated (Carpenter 2002: p. 72, Senter & Robins 2005: p. 315, Sereno 1993: pp. 444*f.*)

tora, recently classified as either derived carnosaurs or coelurosaurs (Benson *et al.* 2010: pp. 74*f.*, Carrano *et al.* 2012; Porfiri *et al.* 2014: pp. 48*f.*). Their cursorial hindlimb proportions and very long forelimbs (Benson *et al.* 2010: p. 76) would represent a case of convergence with coelurosaurs.

Carnosauria were probably generalist macropredators, with adaptions for brontophagy, the predation on extremely large animals, but not precluding reliance on smaller prey (Bakker 1998: pp. 145*f.*). This is supported by carnosaur bite marks on stegosaurs and sauropods (Hone & Rauhut 2009: p. 233*f.*). Their primary specializations are a powerful head depression or an increased skull size, supplemented by powerful clutching forelimbs.

2.6. Coelurosauria

Coelurosauria are known from Middle Jurassic to extant ecosystems, and include the smallest as well as some of the largest, birds themselves as well as the most birdlike nonavian Theropoda. Some coelurosaurs, such as Ornithomimosauria and many Maniraptora are regarded as herbivorous (Barrett 2005: p 354, Zanno & Makovicky 2011: pp. 235*f.*) and are thus not described in detail hereafter where this appears to hold true.

Coelurosaurs have a more laterally facing glenoid, allowing greater elevation but less protraction of the humerus, an elbow capable of more acute flexion and caudal transverse processes that are restricted to more anterior vertebrae (Carpenter 2002: p. 72, Senter 2006: p. 308, Holtz *et al.* 2004: p. 85).

Compsognathidae were small, Upper Jurassic and Lower Cretaceous coelurosaurs. Their dentitions were mostly ziphodont, but in at least some members the anterior teeth were conical (Hwang *et al.* 2004: p. 17), probably for prey restraint. Compsognathid forelimbs were only moderately long but unusually stocky and tridactyl, with a long manus and curved claws (Gishlick & Gauthier 2007: pp. 574*f.*, Hwang *et al.* 2004: pp. 20*f.*).
Some compsognathids seemingly had larger skulls (approximately neck length, Hwang *et al.* 2004: p. 15, Xing *et al.* 2012: p. 2) and more robust forelimbs with longer manus and claws than coelophysoids or ceratosaurs of their size, and might have been more generalist predators.
Fossilized stomach contents show that compsognathids fed on other coelurosaurs, ornithischians as well as lizards, mammals and fish, suggesting that they were ambush hunters (Xing *et al.* 2012: pp. 5*f.*).

2.6.1. Tyrannosauroidea

These small to large-sized Theropoda were present from the Middle Jurassic to latest Cretaceous (Holtz 2004: p. 111, Rauhut *et al.* 2010: p. 183). Ancestrally they resembled basal compsognathids in terms of size (although there were some very large basal tyrannosauroidea, Xu *et al.* 2012) and proportions, but members of the derived, Late Cretaceous Tyrannosauridae are notable for their widened skulls and ribcages (Hartman 2013d [online], Paul 2010: pp. 102*f.*).
Most Tyrannosauridae had broad skulls, especially postorbitally (Brochu 2003: pp. 6*f.*), containing enlarged jaw muscles, fused nasal bones, to which compressive and shear stresses were directed during biting[5], and solid bony palates formed by medially extensive maxillae and premaxillae, indicating greater strength, especially in torsional and lateral bending (Holtz 2003: p. 334, Snively *et al.* 2006: pp. 447*f.*). In *Tyrannosaurus*, kinesis of the maxilla-jugal suture absorbed tensile stress in this region (Rayfield 2004: p. 1451).
The mandible was adapted to resist torsion and bending loads in all planes (Therrien *et al.* 2005: p. 214) and narrower than the upper jaw (Meers 2003: p. 2), so that powerful jaw-adduction would impose additional shear stresses on bitten objects. A stiffened intramandibular joint and good leverage allowed for greater efficiency at transmitting bite force (Hurum & Currie 2000: p. 619, Sakamoto 2010: p. 4).
The teeth of many Tyrannosauridae are labiolingually thickened (Smith *et al.* 2005: pp. 726*f.*), and the serrations modified to function like dull, smooth edges, a loss of cutting ability linked to greater mechanical strength of the tooth (Abler 1992: pp. 178*f.*).
Tyrannosaurids were heterodont, with premaxillary teeth reduced in size and having both carinae shifted to the lingual side (Holtz 2004: p. 119).
Accordingly, the bite force of a specimen of *Tyrannosaurus* was recently estimated at over 57kN at the posterior teeth (Bates & Falkingham 2012: p. 4). The presence of tyrannosaurid puncture marks in large bones (Hone & Rauhut 2009: pp. 233*f.*) corroborates these results.

[5] An exception to this is *Tarbosaurus*, in which the nasals are bypassed by means of a reinforced maxilla-lacrimal articulation (Hurum & Sabath 2003: p. 187).

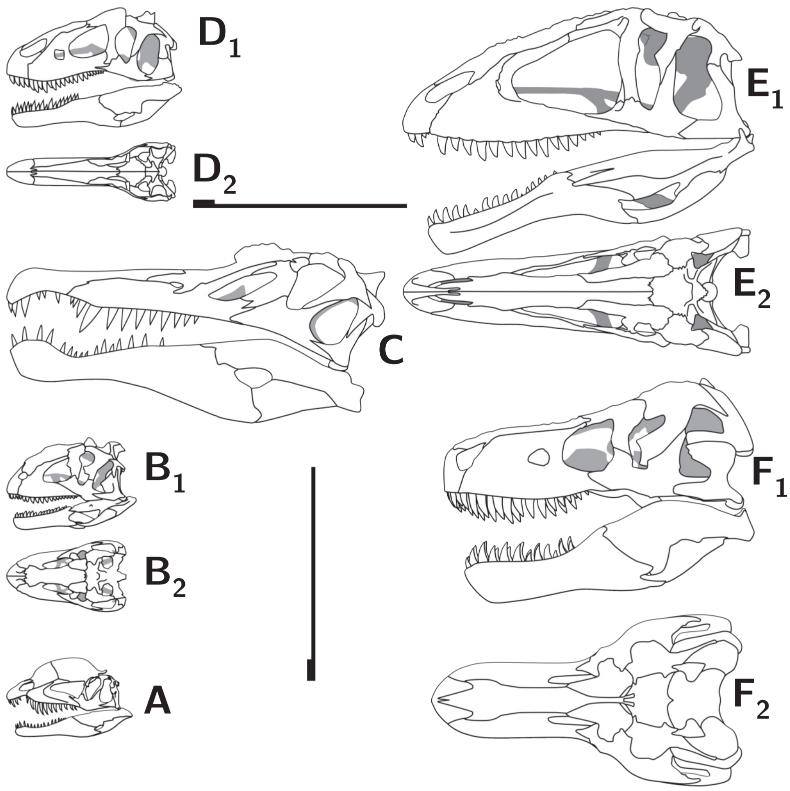

Figure 3: Selected theropod crania to the same scale **A:** *Dilophosaurus wetherilli* (Welles 1984: pp. 95*f.*), **B:** *Majungasaurus crenantissimus* (Sampson & Witmer: pp. 34*f.*), **C:** *Spinosaurus aegyptiacus* (Dal Sasso *et al.* 2005: pp. 888*f.*, Stromer 1915: pp. 4*f.* restored after Sues et al. 2002: p. 544), **D:** *Allosaurus sp.* (Rayfield *et al.* 2001: pp. 1034*f.*, Snively *et al.* 2006: p. 448, Snively *et al.* 2013: pp. 3f.), **F:** *Tyrannosaurus rex* (Brochu 2003: pp. 6*f.*, restored after Hurum & Sabath 2003: p. 166), **E:** *Carcharodontosaurus saharicus* (Sereno *et al.* 1996: p. 988, restored after Eddy & Clarke 2011: p. 4).

Tyrannosaurid necks are short and robust, with relatively flat centra and tall spinous processes, and their opistotics are broad, with muscle insertions optimised for dorsi- and lateroflexion (Holtz 2004: p. 121, Snively & Russell 2007: pp. 938*f.*). Hence, tyrannosaurids had the capacity for powerful shaking, twisting and pulling movements, to aid in breaking bones, but at the expense of acceleration and flexibility (Snively *et al.* 2013: p. 14).

Tyrannosauroid arms were ancestrally long and tridactyl, but the Tyrannosaurid forelimb is reduced (Holtz 2004: pp. 122*f.*). While some features, including an atrophied brachial plexus, less prominent muscle insertions on the limb bones, and the reduction of the manus (Griffin 1995 cited in Holtz 2004: p. 135, Holtz 2004: pp. 123*f.*) indicate vestigialism, others, such as the large shoulder blade and robust bones indicate they were powerful despite major constraints to their anterior range of motion making them incapable of reaching forward much further than the shoulder (Carpenter 2002: pp. 71*f.*, Lipkin & Carpenter 2008, cf. section 2.5.). Whether the forelimb was used in predation remains contentious (cf. Lipkin & Carpenter 2008, Lockley *et al.* 2008), but alternatives, such as to aid in rearing up (Stevens *et al.* 2008: p. 201) should be considered.

Most tyrannosauroidea have unusually elongated hindlimbs for their size, and display an unusual anatomical feature of the foot called the arctometatarsus, in which the metatarsus was strongly elongated for animals of their size and composed of tightly articulated metapodials (Holz 1994: p. 497). Energy was transferred from the wedge-like middle metatarsal to the outer elements of the foot, where it was absorbed by ligaments, functionally unifying the metapodials and thus reducing loads on the middle metatarsal during locomotion (Snively & Russell 2002: p. 40).

The Tyrannosauroid ilium is very long, often exceeding the femur length (Holtz 2004: p. 124) and the thigh muscles were massive (Hutchinson *et al.* 2011: p. 14). A modeling approach found positive allometry in *M. caudofemoralis* sizes (Persons & Currie 2011b: pp. 127*f.*), however estimates from other studies match those of Carnosaurs, and the result could be the product of a bias in overall weight estimates (Bates *et al.* 2012: pp. 500*f.*).

Tyrannosauridae appear to have been unusually cursorial for their size. In advanced tyrannosaurs, the forelimb likely played a neglegible role in predation, with the jaws' increased aptitude at crushing bone and resisting torsion, making them the main instruments for prey capture, restraint and killing.

2.6.2. Maniraptora

Maniraptora are a global clade existing since the Middle Jurassic (Zhang *et al.* 2008).

The small Late Jurassic and Cretaceous Alvarezsauroidea were either birds (Padian 2004: p. 224) or basal maniraptorans (Choiniere *et al.* 2010: pp. 572*f.*) and have been hypothesized to have been either herbivorous, or insectivorous (Zanno & Makovicky 2011: p. 234).

Their skulls are kinetic and small, usually bearing many small, needle-like teeth, even tough they were ancestrally ziphodont, and the necks of derived members are markedly opistocoelous, indicating a high degree of flexibility (Choiniere *et al.* 2010: pp. 572*f.*).

The forelimb is robust and bears a prominent olecranon for powerful elbow extension, and in all but the basalmost member it is shortened and functionally monodactyl, although it sometimes retains vestigial digits (Choiniere *et al.* 2010: p. 572).

Their cursorial adaptions, encompass arctometatarsal and sometimes fused metatarsals, reinforced hip and knee joints, a reduced fibula and a stiffened torso, which could also serve to stabilize the body during other actions, such as digging, consistent with using the forelimbs for opening insect mounds (Hone *et al.* 2013: p. 456, Xu *et al.* 2010: p. 16).

Oviraptorosauria, Cretaceous Maniraptora from the northern hemisphere, are characterized by long necks, short tails and small skulls that often terminate in robust, toothless beaks (Osmólska *et al.* 2004: pp. 165*f.*). Usually small or mid-sized, but sometimes very large (e. g.: Xu *et al.* 2007), their diet is a matter of debate (Farlow & Holtz 2002: p. 251, Zanno & Makovicky 2011: p. 234). Their mandibles are remarkably similar to those of extant psittaciform birds (cf. Witmer & Rose 1992: p. 109), and their robust skulls (Farlow & Holtz 2002: p. 251) are suitable for producing potent bites. These could have been employed for various purposes, such as feeding on eggs, plants or small animals, but the presence of raptorial claws on their forelimbs (Osmólska *et al.* 2004: p. 176) is most consistent with an at least partially carnivorous diet. Some derived oviraptorosaurs had an arctometatarsalian pes, and many had strongly elongated hindlimbs, which made them quick runners (Osmólska *et al.* 2004: p. 183).

Deinonychosauria are known from the Upper Jurassic and the Cretaceous of almost all continents (Lubbe *et al.* 2009, Makovicky & Norell 2004: pp. 185*f.*, Norell & Makovicky

2004: pp. 197*f.*). Two distinct subclades are recognised; Troodontidae and Dromaeosauridae.
Troodontidae had small, coarsely serrated and basally constricted teeth, indicating herbivory, but in combination with raptorial claws, making it likely that they were omnivores (Fowler *et al.* 2011: p. 8, Holtz *et al.* 1998: pp. 160*f.*). Their cursorially proportioned hindlimbs have arctometatarsi, which are fused to the tarsus in some adults (Makovicky & Norell 2004: p. 192).

Dromaeosauridae on the other hand show pronounced hypercarnivorous adaptions, preeminently curved, greatly enlarged (in some cases ~25cm long) claws, especially those on the second digit of the foot (Kirkland *et al.* 1993: pp. 10*f.*).
An analogy can be drawn to accipitrid birds, which make use of similar claws for the grasping, pinning down and stabbing of small to very large prey (Fowler *et al.* 2011: p. 3, Mason 2000: pp 244*f.*, Olendorff 1976: pp. 131*f.*). Moreover, their pedal digits had ginglymoid articulations to resist torsional loads, and were capable of sufficient flexion to provide a firm grip (Senter 2009: p. 8).
Due to their curvature and strength properties, it was suggested that the claws were built for climbing (Manning 2009: p. 1404).
Others have proposed them to be slashing weapons, and indeed they show more or less pronounced degrees of mediolateral flattening (Kirkland *et al.* 1993: pp. 10*f.*, Ostrom 1969: p. 134). However there is no evidence that they were sharp enough to cut flesh, although the unguals' keratin sheath is an unknown (Carpenter 1998: p. 138), and experimental studies using a restored claw of *Velociraptor* found it incapable of doing so, but suitable for puncturing and hooking (Manning 2006: p. 111). The larger size of some dromaeosaurids (e. g.:Kirkland *et al.* 1993) might still also have enabled them to tear through flesh, due to greater body mass, the limiting factor to the force they could excert.
A unique piece of fossil evidence comes from a *Velociraptor* specimen preserved in what appears to be a fatal confrontation with a *Protoceratops*. The dromaeosaurid's pedal claw is preserved in the ceratopsian's throat region, indicating it was used to sever the carotid artery or jugular vein (Carpenter 1998: p. 136), and was possibly the main weapon of prey dispatch.

Dromaeosaurid skulls are long and narrow (Norell & Makovicky 2004: p. 197), with ziphodont teeth and enlarged, apically curved denticles on the distal carina that could have served to facilitate retaining a grip on living prey while tearing meat (Fowler *et al.* 2011: p. 8). Therrien *et al.* (2005: pp. 207*f.*) found their mandibles generally to be weak, which is consistent with low mechanical advantages found by Sakamoto (2010: p. 4), but remarked that those of *Dromaeosaurus* were stronger, indicating greater reliance on its jaws as opposed to the claws.
By contrast, estimates based on tooth marks suggested very powerful bites for *Deinonychus* (Gignac *et al.* 2010: p. 1169). In the light of its jaw morphology, these tooth marks might have been caused by a force other than jaw adduction.

The arm (especially the hand) is very long and slender, over 60% the length of the leg (Norell & Makovicky 2004: p. 204), and the elbows were able to flex at an acute angle (Carpenter 2002: p. 72). In *Deinonychus*, the scapula is short, but the coracoid enlarged,

indicating the presence of powerful protractor musculature, but smaller retractors (Carpenter 2002: p. 68). The manus was capable of pronation by means of rotation at the wrist, and large arks of flexion/hyperextension and abduction/adduction (Carpenter 2002: pp. 66*f.*). The resultant anterior range of motion and a large protractor musculature, would have facilitated grasping prey or branches in front of them.
The forelimbs bore feathers, forming wings that enabled small members of arboreal gliding flight (Dyke *et al.* 2013: p. 3) and may have served for increasing stability in larger, terrestrial forms (Fowler *et al.* 2011: p. 2). The tail base was flexible and the only area with distinct transverse processes, while the distal part was slender and stiffened by elongated bony projections of the chevrons and prezygapophyses (Ostrom 1969: pp. 60*f.*). The tail might have served as a dynamic stabilizer for balance and quick turns. Dromaeosaurid ilia have long postacetabular processes, the pubes are retroverted, and the femoral fourth trochanter is absent in most dromaeosaurs (Norell & Makovicky 2004: pp. 205*f.*), indicating the *M. caudofemoralis*, inserting there, had a reduced role in locomotion as opposed to thigh musculature. Derived dromaeosaurs have a broad, kinetic metatarsus, consistent with a grasping function, and the second toe was inferably carried off the ground to prevent blunting of the claw (Fowler *et al.* 2011: p. 6).

There are some exceptions to these traits such as *Austroraptor cabazai*'s small, conical teeth and shortened forelimbs (Novas *et al.* 2009: p. 1102), which could indicate a specialization for piscivory, and *Adasaurus mongoliensis*' reduced second pedal ungual (Norell & Makovicky 2004: p. 207).

The majority of Dromaeosauridae were generalist predators, that, unlike other Theropoda, probably relied primarily on their limbs, especially the feet, for pinning down prey and puncturing vital structures. Association of *Deinonychus* fossils with the ornithopod *Tenontosaurus* (Norell & Makovicky 2004: p. 209), and *Velociraptor* with *Protoceratops* (Hone *et al.* 2010) attest to macrophagous behaviour, while the presence of mammal, fish and bird remains in stomach cavities of *Microraptor* (Xing *et al.* 2013: p. 4) provides evidence of smaller prey.

3. Conclusion

Non-avian Theropoda have predominantly included predatory forms throughout their evolution.

Ancestrally they possessed parasagittal hindlimbs, oreinirostral skulls, ziphodont teeth and clawed forelimbs built for clutching. From this ancestral condition, functional anatomy in mesozoic theropods followed a number of predominant trends and acquired derived traits to adapt to different behaviour.

All Theropoda are digitigrade and have somewhat cursorial proportions, but in some an increased length of the metatarsus and lower leg, and functional unification within these limb segments further increases the stride length and decreases the distal limb mass. This development is probably linked to a specialization in faster prey. In Cretaceous ecosystems of the northern hemisphere, Hadrosauria and Ceratopsidae were the dominant large herbivores (Dodson et al. 2004: p. 494, Horner et al. 2004: p. 438), and they must have been significantly faster than fully graviportal animals (Paul & Christiansen 2000: p. 462), such as the Sauropods that thrived during the Jurassic (Farlow et al. 2010: p. 412), a plausible explanation for increased cursoriality in large theropods. Additionally a number of small theropoda with these adaptions (many coeophysoidea, Ceratosauria and Coelurosauria) could have benefited from them to escape predation by larger, sympatric predators, as well as for catching their probable small, nimble prey.

Adaptions for such prey is also evident in a number of theropods, the most notable examples of which are Coelophysoidea Spinosauridae and Alvarezsauroidea, with adaptions encompassing jaws, teeth and necks, designed to catch and grip small animals. In the case of Spinosauridae, this includes adaptions for an aquatic lifestyle, resembling that of crocodiles. Similar adaptions were present in some Megalosauridae and Ceratosauria, which were more conventional in other regards.

Conversely, generalists and large-prey-specialists tended to have large jaws, which were their primary weapons in most cases. Their sheer size and robusticity implies impressive bite forces, but some, especially Tyrannosauridae, show adaptions of skull, mandible and neck to increase them and improve their aptitude at processing bone, while others, especially Carnosauria, sacrificed it to increase gape angles and cervical mobility to aid in striking and tearing of flesh.

The role of theropod limbs in predation varied, being extremely reduced in some forms (e. g. Tyrannosauridae, Abelisauridae) and important in others (Megalosauroidea, Carnosauria, most coelurosaurs). A special case is represented by Dromaeosauridae, whose limbs were most likely their primary instrument of predation.

The only terrestrial predators of the Jurassic and Cretaceous rivalling large Theropoda in size were Crocodyliformes (e.g. Sereno et al. 2001: p. 1516), and even they were largely aquatic. The reason for which Theropoda were able to suppress other carnivores so successfully seems to be their ability to fill all these niches more efficiently than other taxa were able to by means of a plesiomorphic anatomy well-suited for carnivory. This also explains why most, though not all, Mesozoic Theropoda were predatory.

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List of Figures

Appendix: Supplementary Life Reconstructions

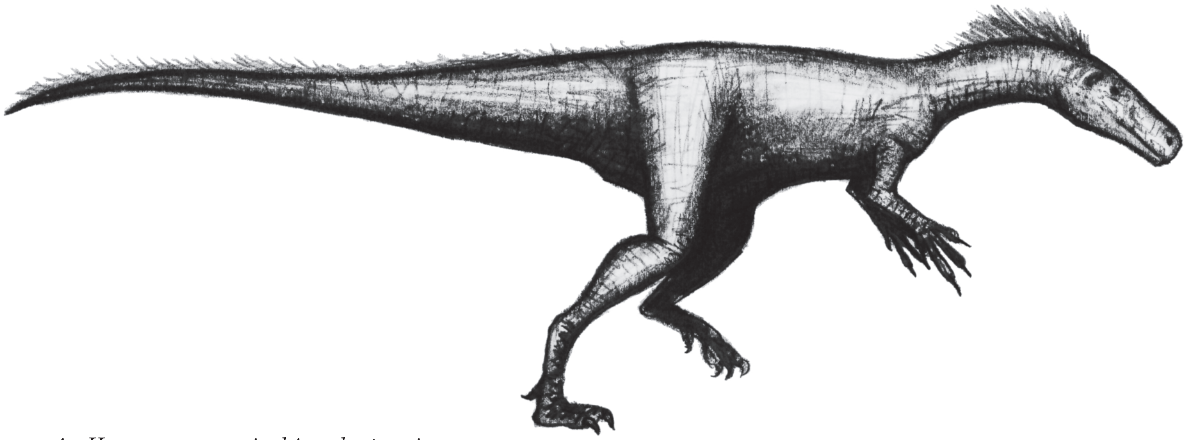

Figure 4: *Herrerasaurus ischigualastensis*

A

B

C

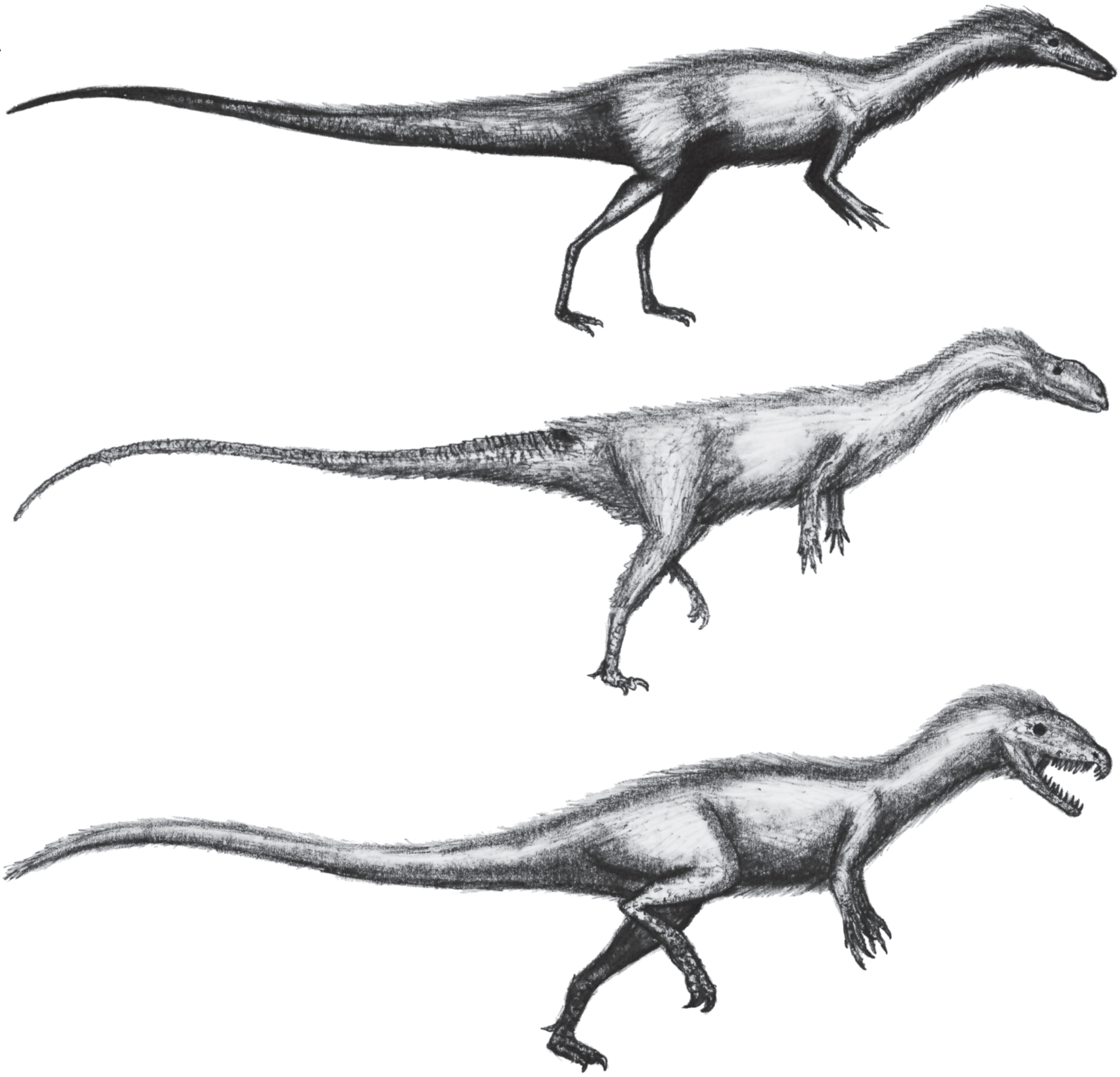

Figure 5: Coelophysoidea. **A:** *Coelophysis bauri*, **B:** *Liliensternus liliensterni*, **C:** *Dilophosaurus wetherilli*

Figure 6: *Ceratosaurus dentisulcatus* (Ceratosauria)

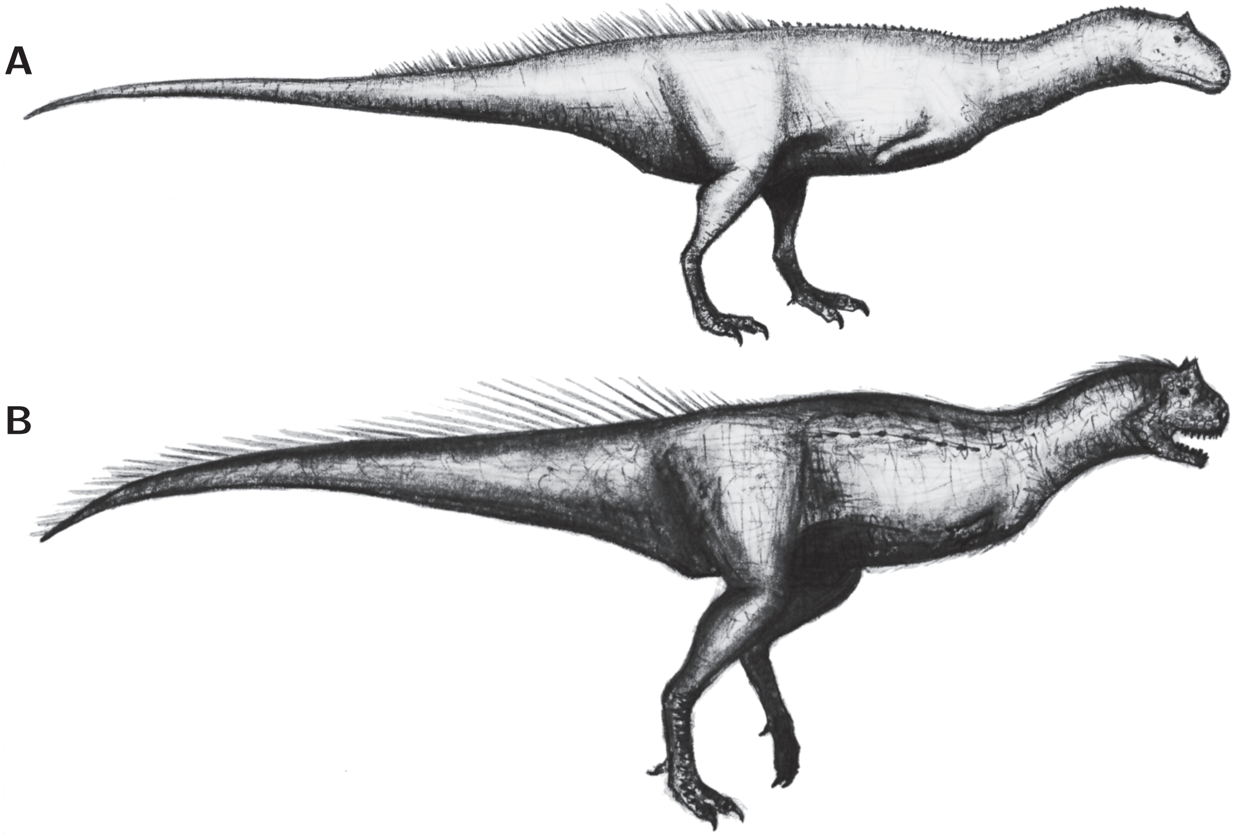

Figure 7: Abelisauridae. **A:** *Majungasaurus crenantissimus*, **B:** *Carnotaurus sastrei*

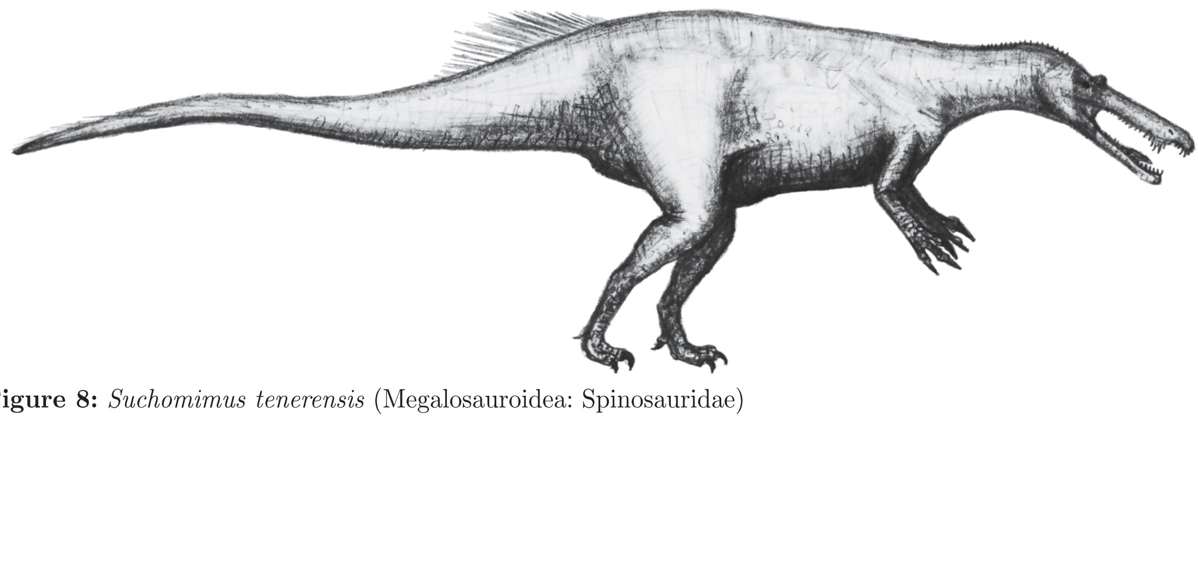

Figure 8: *Suchomimus tenerensis* (Megalosauroidea: Spinosauridae)

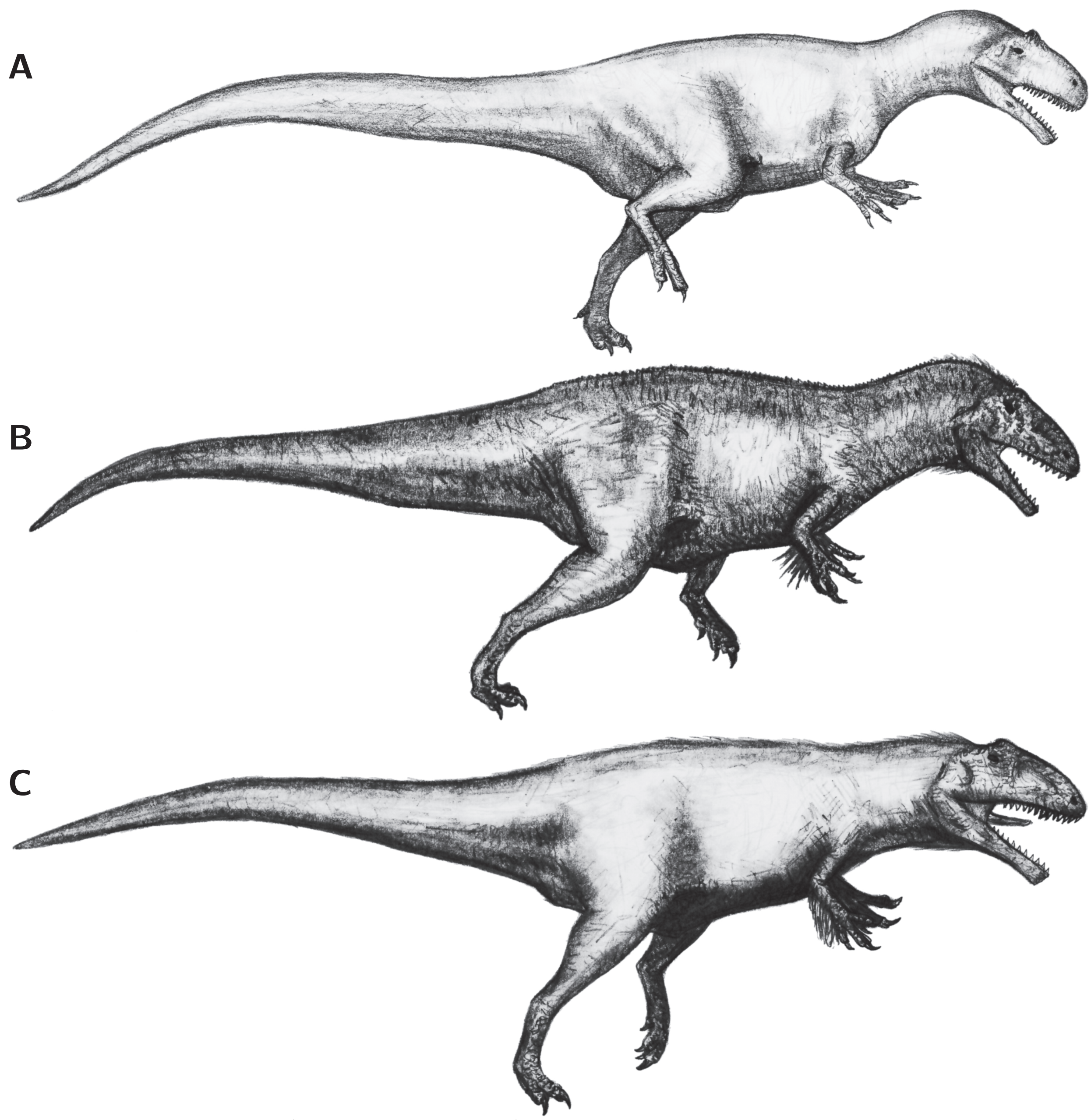

Figure 9: Carnosauria. **A:** *Allosaurus fragilis*, **B:** *Acrocanthosaurus atokensis*, **C***: Giganotosaurus carolinii*

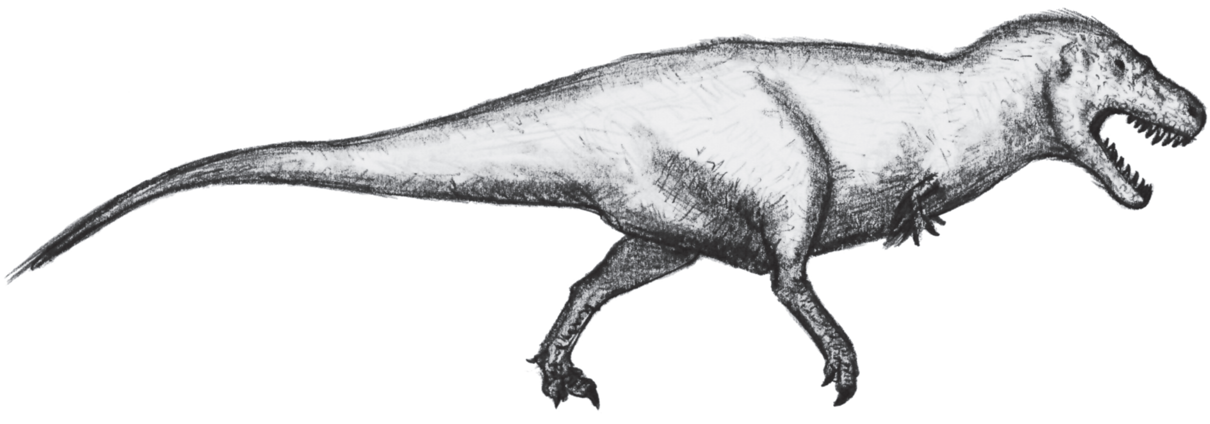

Figure 10: *Tyrannosaurus rex* (Tyrannosauroidea: Tyrannosauridae)

Figure 11: Maniraptora. **A:** *Jinfengopteryx elegans*, **B:** *Deinonychus antirrhopus*

The above set of life restorations is purely supplementary in purpose. All reconstructions are the work of the author, underlying anatomy is based on skeletal diagrams in Paul (2010) and/or sources given in "Survey and Discussion of Functional Anatomy by Taxon".

I hereby affirm:

- That I have authored the present thesis myself.
- That I have made content that is not of my own making visible as such and cited its source.
- That I have not made use of any form of illegal help.

Darius Nau

Höchst, 13th August 2015