Visualization of Comparative Anatomy: Jaw muscles of Theropod Dinosaurs and their extant relatives; Illustrating the story of functional morphology and evolution

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by
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Visualization of Comparative Anatomy:
Jaw muscles of Theropod Dinosaurs and their extant relatives;
Illustrating the story of functional morphology and evolution

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Abstract

Dinosaur anatomy is a largely unexplored subject in medical and scientific illustration. While paleo-artists produce fantastic artwork of colorful beasts in conceptualized habitats and inspire the design of fictional creatures and movie monsters, accurate research and referential materials are often limited to flat, diagrammatic and simple drawings. Using critical research, and physical evidence, more accurately rendered diagrammatic illustrations of dinosaur reconstructions are possible through the lens of modern medical and scientific illustration techniques for educational purposes. Specifically, I identify the evolutionary relationships of theropod dinosaurs with their extant relatives (bird and crocodilians), study the skulls of a series of theropod dinosaurs and define their physical features and perceived ecological niches in order to create renderings of their jaw musculature and possible reconstructed appearances. Rather than fantastic illustration, the series of 24 skull, muscle and reconstruction illustrations are meant to serve as clear, referential material that outline the homologous jaw muscles of several groups of theropods and draw visual similarity to their modern relatives.
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**Introduction**

In the summer of 2015, I attended the Association of Medical Illustrators conference in Cleveland, Ohio and was inspired by a presentation given by Ali Nabavizadeh, PhD, and Christopher Smith, MA. The primary subject was about comparative anatomy of vertebrates and the surprisingly relatively limited representation and documentation of anything outside of standard farm animals. I instantly knew that I wanted to contribute to their project and even extend its horizons. I have always been interested in the biodiversity of vertebrates, both modern and extinct, and their evolution. In fact, it was the time spent sketching my dissections in a vertebrate anatomy class during my undergraduate years that instigated my involvement with medical illustration and going back to these roots felt fitting for my independent research.

Coming from a natural sciences background, I knew that, I too, would like to see more updated anatomical illustrations of different vertebrates and as a medical illustrator, see the educational value that they can communicate to their audiences. Comparative anatomy is an important science for understanding the biodiversity and evolution of animals and can easily be supplemented by visual representations that communicate both the subtle and dramatic differences and similarities apparent in related organisms.

I have always been interested in dinosaurs in particular. However, current visualizations of exotic animal anatomy and biology, especially that of extinct life, is limited in terms of detail, volume and understanding. This is especially true for dinosaurs. As more is uncovered about these creatures, paleo-artists are producing a glut of fanciful illustrations of colorful feathered dinosaurs in conceptualized environments and circumstances. On the other hand, research and referential materials are often limited to purely flat, diagrammatic and simplistic drawings. It is important to strive for a marriage of these two approaches, thereby creating clear and accurate anatomical representations of dinosaurs while also incorporating the textures, color and volume that are the hallmarks of favored referential and educational anatomy material similar to that of Frank Netter’s approach. As a medical Illustrator, I understand that it is our role to not only provide accurate visuals, but also visuals that will actively engage the viewer. In the words of James Gurney, “Artists are the eyes of paleontology...Paleoart helps shape the way the public imagines dinosaurs” (2009). With that in mind, I feel that imagery that is both accurate, and informationally rich, is crucial to the field of study and how it is presented. Illustrations of
dinosaur hard and soft-tissue anatomy from a medical illustrator’s approach would benefit the paleontological community and those wanting to learn about these amazing creatures as a whole.

Specifically, my research and goal has been to explore and artistically represent the jaw muscles of different theropod dinosaurs and their extant relatives and to visually describe the morphological differences and similarities in this family tree. One of the most distinctive structures of any vertebrate is the skull. Ultimately, the shapes and structures of the skull can not only be used to deduce evolutionary relationships, but it can also be used to interpret function and offer a great deal of insight into an animal’s behavior, adaptations, diet and lifestyle in general. Comparative anatomical studies help us to understand how, and why, evolution in vertebrate design might have occurred (De Iuliis et. al., 2007). Naturally, the bony structures of the skull can also indicate osteological correlates of unfossilized tissues (e.g., muscles, ligaments, etc.) and can be used to imagine the faces of long extinct organisms (Holliday, 2009). The jaw muscles are what power vertebrate organism feeding and are crucial to their success as an important adaptive character that can be used to interpret the feeding function in birds, crocodilians, and other extinct taxa (Holliday et. al., 2007).

Additionally, it is my goal to further a lay audience’s understanding of what these dinosaurs’ relationships with extant animals (archosaurs including modern birds and crocodilians) are with visual representation.
Section I: Scientific Background

I-a: Project Description

After extensive research the project began by creating illustrations that were drawn from observation of specific theropod dinosaur skull specimens, including:

*Erlikosaurus andrewsi* – IGM 100/111 (Geological Institute of the Mongolian Academy of Sciences, Ulaan Bataar, Mongolia)

*Tyrannosaurus rex* – FMNH PR2081 (Field Museum of Natural History, Chicago, IL)

*Velociraptor mongoliensis* – AMNH 6515 (American Museum of Natural History, New York City, NY)

*Ornithomimus edmontonicus* - RTMP 95.110.1 (Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada)

*Ceratosaurus magnicornis* - MWC 1 (Museum of Western Colorado, Grand Junction, Colorado)

*Incisivosaurus gauthieri* – IVPP V 13326 (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China)

I also illustrated the skulls of a chicken (*Gallus gallus domesticus*) and the American alligator (*Alligator mississippiensis*) as the extant living archosaurs for comparison.

These eight skulls were digitally drawn and rendered in Adobe Photoshop and then were each given a set of jaw muscles, including the m. adductor mandibulae externus superficialis (mAMES), m. adductor mandibulae externus medialis (mAMEM), m. adductor mandibulae posterior (mAMP), m. pterygoideus ventralis (mPTv), m. pterygoideus dorsalis (mPTd) and m.
depressor mandibulae (mDM). Finally, the conceptualized skin of each animal was digitally painted over all of these structures and was given very careful consideration and advisory with respect to their perceived diets, behaviors and environments. With a total of 24 unique illustrations, they were not only intended for glossarial consumption but also to create an attractive exhibit that could engage, and clearly communicate information, to a lay audience. The detail and accuracy was meant to serve as a referential aid to comparative anatomists, biologists, paleontologists and artists in general. However I also aimed to appeal to a wider audience that may just be captivated to learn about and experience animals of a long gone era.

To reach this broad audience, the illustrations of the skulls, musculatures and faces were printed on a large scale (40 inches x 63 inches) in order to fully communicate the textures of bone, muscle, scales and feathers, grab the viewers’ attention, and allow for easy comparison to one another in consolidated arrangement (see Figure 27.). This poster was also accompanied by a short 2D animation that illustrated the muscle action on the mandible and the angle of gape on the tyrannosaur skull so that the viewer could also see the muscle’s action. Another supplement to the exhibit includes a painting of another dinosaur, a *Troodon* (see Figure 26.).

Not included in the anatomical set of drawings, this painting was meant to provide another point of context, and add another layer of interest to the viewer, by showing a dinosaur not as a fossil, not as a lumbering lizard in a swamp, but as a vibrant living animal in its environment. The *Troodon* was also included in the supplementary cladistics infographic that reveals it as the closest perceived theropod group to modern birds (see Figure 1.). The goal was to punctuate these birdlike qualities at a larger scale by also making a point of painting the animal at life size (3 feet by 6 feet) to immerse the viewer in what they were looking at. I want the viewer to think of dinosaurs not as mythical movie monsters but as living breathing animals that once existed and still have ties to those that live with us today. The painting was rendered in oil paints using traditional techniques and with careful consideration to both *Color and Light, A Guide for the Realist Painter* (2010), and *Imaginative Realism: How to Paint What Doesn’t Exist* (2009) by James Gurney - an author and artist known for his traditional painting expertise of dinosaurs and as the creator of the *Dinotopia* series (Gurney, 1992). This special consideration was given to ensure a sense of believable realism, motion and atmospheric lighting that could convince the viewer that it bore likeness to a naturally occurring animal. Gurney notes that carnivorous dinosaurs are nearly always depicted with their mouths forcibly agape (2009). While this may be
appropriate for a diagrammatical illustration to showcase the teeth, most creatures keep their mouths closed and, to convey a more naturalistic setting, it is best to communicate more with the body language and referencing contemporary wildlife.
Section I: Scientific Background

I-b: What is a Theropod?

Exploring the family tree and evolution of dinosaurs can be a daunting task; however, the focus of these illustrations explores a particular group known as the theropod dinosaurs. A theropod is a member of a suborder of dinosaurs called Theropoda, from the Greek “Wild beast foot” in reference to the classic three-toed footprints that they left behind. They first appeared in the late Triassic period 231.4 million years ago and were ancestrally carnivorous. Primarily recognized as bipedal super-predators, like tyrannosaurs, the family further diversified to fit herbivorous, omnivorous and insectivorous niches. From the small 47mm Microraptor to the gigantic 6 ton Tyrannosaurus rex, theropods all had relatively large eyes supported by an internal bone ring, teeth ranging from large, bladed, and serrated to absent, variable neck lengths usually in the classically described S-curve, and tails that could be long and flexible to short and stiff. Arms also varied in size from being long to severely reduced (as evident in the Tyrannosaurus rex) with four to one fingers on each hand (Paul, 2010). In all cases, the hind limbs were longer than the forelimbs and were especially long and powerfully built among the most cursorial (Benton, The Dinosauria, 2004).

What sets theropods apart from the rest is their living legacy. Recent evidence continually suggests that birds evolved from small theropods and are, in fact, the surviving descendants of the dinosaurs and as Gregory S. Paul so eloquently put it, “Birds are literally flying dinosaurs” (2010). In the mid-1990s complete specimens of small compsognathid theropods (Sinossauropteryx) were being discovered to be covered with dense coats of bristle-like protofeathers (Paul, 2010). The “missing link” known as Archaeopteryx was no longer a singular oddity, but one of many discoveries proving the rich lineage of feathered theropod dinosaurs that made a transition to modern day avian species. Over time these insulating protofeathers, derivatives of scales that were much like the down of a chick, developed into the accessories that enabled flight. Considering the body plan of birds however, this makes sense. Previously, birds had been thought to have developed flight as a primarily arboreal creature that would simply glide from tree to tree, similar to bats (Paul, 2010). However, this would suggest a semiquadrupedal posture with sprawling legs to form the connected airfoil (as in bats) but birds
are erect-legged bipeds whose legs are separate from the wings and achieve flight purely through independently strong forelimbs).

This realization suggests that the ancestors of birds had originally evolved as strong runners that would have learned how to fly from the ground up. As previously defined, theropod dinosaurs share the universal trait as powerfully legged bipeds so it can be surmised that the running theropods developed long feathers as a way to enhance turning while running and the ability to fly as a way to enhance their ability to escape up trees or capture arboreal prey.

This evolutionary model proposes that bird ancestors ran along the ground and leaped into the air, using their forelimbs first for balance and eventually for propulsion, by assisted flapping, as the surface area of feathers increased (Padian, *The Dinosauria*, 2004). Over time, short, running glides would have become flight when the forearms turned wings had gotten large enough to accommodate flapping and the furcula bone (fused clavicles) had increased in size to accommodate flapping muscles, as well ossified sternal ribs and shortened tails. Padian (2004) also notes that the forward thrust of the “hand” at the wrist is an action that is not found in typical tetrapods and is currently only present in birds and bats (Benton, *The Dinosauria*, 2004). That is what makes the sideways flexure of the wrist in maniraptorans, such as *Velociraptor*, an interesting key to the ability to evolve true flight. The presence of this wrist construction and the furcula, or wishbone, are both highly specific features that links theropods to birds. Similarly, they also both have air-filled bones, and documented evidence of similar nesting behaviors and rearing of young. Though not all theropods are proven to have had feathers by means of fossilized imprints, it can be inferred that many of them did, especially the coelurosaur, a group directly linked to birds that even included *Tyrannosaurus rex* (see Figure 1.).

In fact, flight feathers may have evolved so early on in theropod evolution that they had actually been lost during further dinosaur evolution. “Dinobirds” with only modest flight abilities and clawed hands, which could be used for other purposes, were more susceptible to losing this ability and several families of non-flying theropods have evidence of this loss with flight features including large sternal plates, bony uncinated processes on the supporting ribs, folding arms, and stiffened, shortened tails (Paul, 2010). Dromeaeosaurus (the raptors), and short-tailed oviraptors and therizinosaurs all show signs that some level of flight ability was present in their early evolution but was since lost as the niches they filled no longer needed that ability.
Section I: Scientific Background

I-c: How is the Alligator Different?

Unlike birds, the crocodilians are not direct descendants of the dinosaurs but are, in fact, related to the common ancestor of dinosaurs. The family that would become the crocodilians branched off from their shared ancestor before the first dinosaurs ever appeared (over 250 million years ago during the Triassic period). After a massive extinction at the end of the Permian period, 50%-60% of tetrapod organisms went extinct and left the predatory niches wide open for the smaller diapsids (ancient reptiles) that survived (Benton, *The Dinosauria*, 2004). The overarching group of diapsids that was the largest, and most successful was aptly named Archosauria (Greek for “ruling lizards”) and includes the crocodilians, pterosaurs, dinosaurs and birds (see Figure 1.). Skeletal features that are characteristic to the archosaurs include an antorbital fenestra, an antorbital fossa, a laterosphenoid bone, and an external mandibular fenestra that all shape the way the jaw muscles interact with the skull (De Iuliis et al., 2007).

Like the early theropods, some crocodylomorphs had bipedal body plans, such as *Ornithosuchus*, but, by the late Triassic, were largely outcompeted by the dinosaurs that were considered competitively superior animals with advanced locomotor adaptations (an erect gait) and physiological advantages such as homeothermy (“warm-bloodedness”) (Benton, *The Dinosauria*, 2004). As a result, dinosaurs rapidly diversified to available niches that they could outcompete for while the crocodylomorphs were limited to their familiar aquatic environments where they had evolved to be massive in comparison to their terrestrial forms. In fact, the ancient phytosaurs superficially resembled modern crocodilians (save for their placement of nostrils between the eyes) and had convergently evolved their most successful body plan that survives to modern times (Benton, *The Dinosauria*, 2004). Today, the only surviving Archosaurs are avian dinosaurs (the birds) and the true crocodilians. Though not a direct descendant, their familial connection still provides an alternative look at the origins of dinosaur and reptile morphology in contrast to birds being the most evolved derivative and the alligator being the most ancient iteration.
Section I: Scientific Background

I-d: How Did You Know What Colors to Make Them?

I didn’t! Because we cannot directly observe extinct animals, a responsible paleoartists job is to make educated guesses about representational choices like this. Even something like color selection of the skin, scales and plumage of the animal can carry huge implications about their lifestyle and cannot be purely chosen for aesthetic appeal. When making these decisions it is best to consider their habitats, lifestyles and what animals in the present day best fit the niches they might have occupied. For example, *Tyrannosaurus rex* was the top predator of its environment, much like a bear or a lion and probably had more muted, earthy tones while *Velociraptor* individuals were found in the Gobi Desert of Mongolia and, as ambush predators, would have blended into the sandy and rocky environments with a more mottled appearance to break up their outline from unsuspecting prey. Another consistent pattern of coloration that turns up in nature is countershading. Many animals are lighter on the belly than they are on back as a means of camouflage that disguises prey animals by offsetting the effects of shadowing on the bottom surfaces. Countershading also appears in aquatic predators like crocodilians and sharks (Gurney, 2009). I applied this to the speculatively furtive oviraptorosaur, *Incisivosaurus gauthieri*, and to the ferocious *Ceratosaurus magnicornis* that is even speculated to have been semi-aquatic in its hunting habits.

However, it was recently discovered that it is possible to determine the color of preserved dinosaur feathers. The pigment containing organelles of feathers preserve surprisingly well and, even more fortunately, their shape varies according to color (Paul, 2010). This is what allows the restoration of the dinosaur feathers we’ve been lucky enough to find preserved in such good shape. A recent example is *Microraptor*, a sickle-clawed predator of maniraptorora that was covered head to toe in thick glossy black plumage and sported four wings 120 million years ago (Li, 2012). Surprisingly, the pigmentation found in *Microraptor*’s feathers would be described as iridescent blue-black and the perched, flying dinosaur would resemble something like modern day “grackles or a magpie or of indeed a crow.” Other dinosaurs such as *Anchiornis* and *Archaeopteryx* also were predominantly black. It is not known why this color scheme is common amongst them, but suggests that bird-like behaviors, such as display, evolved early in their dinosaur ancestors (Switek, 2012).
The same cannot be said about determining the colors of scales. While some researchers hypothesize that colorations could differ with scale patterns, some reptiles are uniform in color regardless of variation in scale pattern and no real correlation can be made (Paul, 2010). However, Paul speculates that, because dinosaur scales are arranged in rosette patterns, it is thought that they were better suited to carry bold and colorful patterns like those of some reptiles, birds, tigers and giraffes rather than uniformly gray skin of large mammals like elephants and rhinos.

Similarly, their color vision would have also encouraged the evolution of colors for display and camouflage (Paul, 2010). Dinosaur eyes were also more bird-like, rather than mammal-like, and while also sporting color vision, lacked a white surrounding the iris and were either fully colorful themselves or solid black as in seen in modern reptiles and birds. I hoped to represent these qualities as accurately as possible when designing the conceptualized faces of the selected specimens.

Another special consideration when designing the fully realized faces was the subject of “shrink wrapping”. “Shrink wrapping” is a term used to describe an inaccurate reconstruction of extinct animals wherein the skin is tightly compressed to the bony structures of the skull with no thought to the soft underlying tissues of the animal (i.e. the muscle), hence the term “shrink wrapped”. This is a very heated topic in the paleo-art community that often calls into question the credibility of a reconstruction. However, there is a correct way of doing what is often criticized. Unlike mammals, dinosaurs did not have any type of extensive facial musculature (necessary for making facial expressions) so the skin would be directly appressed to the skull. This is similar to the construction of modern reptiles and bird skulls and actually improves the ability with which they can be restored. However, that does not mean the muscles that the dinosaur skulls do have can be ignored. As can be noted from the pictured illustrations (see Figure 27.) dinosaurs generally had well developed jaw muscles regardless of how delicately or robustly built (Holliday, 2009). These powerful muscles would definitely impact the shape of the head as well as the orbital muscles (not pictured) that would cause the skin covering the large fenestra, near the orbit, to gently bulge outward (Paul, 2010). These large “holes” in the skull are called fenestrae and are especially pronounced in Theropod dinosaurs as a means of lightening their large skulls. Especially relevant to large carnivorous theropods, the pressures of a predatory lifestyle, increased size and a bipedal gate would call for reduced weight to an increasingly large
skull and also give further similarity to the hollow bones of birds that needed to lighten their weight to take to the skies.
Section II: The Body of Work

II-a: Cladistics

A cladogram is a diagram used to illustrate the evolutionary relationships among organisms. While it does not scale according to the chronology of these evolutionary events, the cladogram serves to link groups of organisms to their last common ancestor and give the viewer information about how closely or distantly related one group is to another. The pictured cladogram (see Figure 1.) traces the ancestry and evolution of the illustrated theropods in a different color from the groups that are not pictured in order to highlight the progression and guide the viewer. Similarly, a simpler cladogram is also included to provide a visual representation of the distinction between dinosaurs and the pictured alligator. It was my goal to simultaneously make the cladogram easy to understand, follow, and connect with the primary illustration while also including a comprehensive amount of information regarding the evolution of theropods and other auxiliary groups. This way, the curious viewer may be able to draw conclusions about the similarities and relationships among the different groups.

In the following paragraphs, I will provide more contextual information on each pictured dinosaur and their respective cladistics group. This includes analysis of the skull and jaw morphology and how that relates to an interpretation of their niche, diet and behavior. These descriptions will proceed from the most basal (earliest) dinosaur on the cladogram to the most recently developed groups.
Section II: The Body of Work

II-b: Ceratosauridae

By no means the earliest of the theropods, Ceratosaurus magnicornis of Ceratosauridae is the most basal dinosaur I’ve illustrated. It was a large, predatory theropod of the late Jurassic period reaching 20 feet in length and named for its characteristic nasal horn, and spade-like horns over the eyes, which are thought to have functioned for display or for head butting with others of the species, similar to modern day cassowaries (Paul, 2010). Though not the largest member of its group (that being Ceratosaurus nasicornis) analysis of the nearly complete C. magnicornis specimen (MWC 1) reveals a proportionately larger nasal horncore, that is responsible for its naming, as well as a longer and lower skull with a more robust quadrate (Madsen et. al., 2000). If these horns were used for display, or intimidation, it is likely that these horns would be brightly colored or sport some kind of pattern (see Figure 4.). In addition to these spikes, ceratosaurs also have been found to possess a row of short spikes, or osteoderms, along their back that may have served as armor to ward of thick brush or protect during confrontation.

Though smaller and squatter than the tetanuran Allosaurus, that it shared its habitat with, ceratosaurs had proportionately larger, bladelike, upper teeth as well as larger lower teeth to match (Tykoski, The Dinosauria, 2004). These teeth, paired with its proportionately large and robustly built skull and large mAMES and mPV muscles (see Figure 3.), could have been used to deliver a powerful bite and inflict deep slashing wounds and trauma to ambushed large prey. Similarly, ceratosaurs could have also acted as aquatic ambush predators, if outcompeted by larger predators like Allosaurus on land, much like a crocodilian. This has been suggested because of its flexible, powerfully built tail, which has high vertebral spines and is half of the total body length that could serve as the sculling organ while swimming (Paul, 2010). Similarly, their highly developed teeth and jaws could also hint at this aquatic predation, allowing them to firmly grab and hold on to surprised prey in the water as a crocodilian would. These characteristics all came into play when given the Ceratosaurus its earthy tones and countershaded appearance despite the contrast to the ornate head gear. The lack of developed feathers is also a suggestion of how primitive it is in relation to other theropods with only minute inclusion of bristle like protofeathers.
Section II: The Body of Work

II-c: Tyrannosauroidea

Tyrannosaurid dinosaurs are among the most well recognized and distinctive theropods characterized by large skulls, steak-knife like teeth, long hindlimbs and severely reduced forelimbs; all seen in the most popularized *Tyrannosaurus rex*. However, recent findings have revealed the humbler beginnings of these titanic predators of the late Cretaceous wherein earlier tyrannosaurids of the Jurassic were much smaller (but with proportionately longer arms) and far from being the dominant predators (Hotlz, *The Dinosauria*, 2004). *Timburlengia eutoica*, a tyrannosaur discovered in Uzbekistan, was only about the size of a horse, but had a proportionately large braincase, like *T. rex*, suggesting intelligence and advanced senses of smell and hearing (Achenbach, 2016). Smithsonian paleontologist, Hans-Dieter Sues comments that “The skill set was the key qualification to apply for the job of top predator” and suggests that tyrannosaurs got smart before they got large (Achenbach, 2016). Because it is recognized as a true tyrannosaur, it acted as missing-link between even smaller tyrannosaur-like coelurosaurs and solidified the suspicions that tyrannosarids were truly basal coelurosaurs. This relationship could suggest the presence of feathers on later tyrannosaurs and is why I included them on my illustration of *T. rex* (see Figure 7.).

The famed *T. rex* is the largest identified species of the family, reaching 40 feet in length, 6 tons, with large and robust skulls exceeding 1 m in length (Holtz, *The Dinosauria*, 2004). Heavily built, the skull also housed increasingly forward facing eyes capable of stereovision, a larger brain, compared to other theropods, large olfactory bulbs, and serrated teeth. Compared with other theropods, it also had a shorter tail. The reduction of the tail and forelimbs was exchanged for a highly developed skull and enlarged and elongated legs that indicate capabilities for greater speed to theropods of comparable size (Paul, 2010). With its long legs, long skull full of teeth, sharp eyes and keen sense of smell, it is perceived that adult *T. rex* were fearsome hunters. This reputation is supported with additional evidence of healed tyrannosaurid inflicted wounds on elephant sized hadrosaurs and cerotopsids (Paul, 2010).

A well-developed skull also is inferred to have had well developed jaw muscles. In a study estimating the musculoskeletal constraints of theropod dinosaur jaws, it was found that *T. rex* had a maximum gape angle limit of 63.5 ° - 80 ° and an optimal tension limit at gape angles
of 28° and 32.5° to allow for high muscle efficiency, on a narrow trajectory, that suggests a homogenous muscle performance for a sustained bite force, as necessary to crush bone and dismember its prey (Lautenschlager, 2015). Their large size and their need for substantial amounts of flesh suggest their need to inhabit seasonally well-populated and well-watered forests rather than arid climates (Holtz, *The Dinosauria*, 2004). This environment, their role as a large, dominant, and sensory tracking ambush predator, all factored in to how I chose to color the *T. rex* in drab browns.
Section II: The Body of Work

II-d: Ornithomimosauria

Named as the “ostrich mimic”, ornithomimids were moderately sized theropods (from 10 to 20 feet in length) with small heads, and long slender necks, limbs and tails. Though they were not the most closely related to modern day birds, they convergently evolved many similar characteristics such as a lightweight skull, relatively large orbits and jaw margins that bear a rhamphotheca; a beak (Cuff et. al., 2015). Ornithomimids are also viewed as the most cursorial of theropod groups because of their long hind limbs (Makovicky et. al., 2004). With exceptionally well developed leg muscles, long, and strongly compressed feet, and no hallux bone, their speed potential is perceived to have been very high (Paul, 2010) and also suggests their niche as a prey animal that would need to escape quick predators. The most primitive ornithomimids had tiny teeth in their premaxillae, maxillae and mandibles. However, more derived members, such as the pictured *Ornithomimus edmontonicus*, have completely lost their dentition in the place of a beak that is inferred from the presence of foramina on the lateral surfaces of the premaxilla, maxilla and mandible as well as preserved remnants of keratinous rhamphotheca in two specimens. (Cuff et. al., 2015). This inclusion of a beak has led to much speculation on the dietary habits of ornithomimids and they have been looked at carnivores of small prey, insectivores as well as herbivores (Makovicky et. al., 2004). It should also be noted that in a study of Ornithomimid crania and musculature, by Cuff and Rayfield it was found that *Ornithomimus* possessed even the weakest bite force among ornithomimids and had very reduced jaw muscles relative to other theropods (see Figure 9) (Cuff et. al., 2015).

In 2012, hard evidence of feathers were found on three specimens of *Ornithomimus edmontonicus* in Canada; while the juveniles were mostly fuzzy, the arms of the adult had evidence of long feathers that would be similar to those on the wings of modern ostriches (Switek, 2015). However, this mimicry didn’t stop there. Fossilized skin was also preserved and revealed bare legs much like the plumage arrangement of ostriches, emus and their relatives that use this to dump excess heat (Switek, 2015). Similarly, I tried to capture the ostrich-like “eyelashes” that would shield the eyes from sun and improve the vision of the wide-eyed, fleet-footed *Ornithomimus*. (see Figure 10).
Section II: The Body of Work

II-e: Therizinosaurs

Therizinosaurids are a strange departure from previous theropods. They were small to gigantic theropods that had small heads and long necks (much like Ornithomimids) but instead of having long well developed legs, they had long arms with large claws on their hands. Therizinosaurids were also partially edentulous, with a series of blunt, leaf-shaped, peg-like teeth that were only absent from the premaxilla, and with their small gape and strong cheaks, suggest a highly, if not exclusively, herbivorous diet (Lautenschlager, 2015). This partial edentulism also suggests the presence of a rhamphotheca (Cuff et. al., 2015). Additional evidence of this beak comes from the heavy vascularization of the premaxilla that would have formed a heavier, and wider, horny sheath in contrast to the pointed and further reaching beak of *Ornithomimus* (Clark et. al., *The Dinosauria*, 2004). This combination of a wide beak, and rows of small teeth would have been ideal for stripping branches of leaves; a diet suggesting low energy levels and energy consumption.

The pictured *Erlikosaurus andrewsi*, (see Figures 11-13.) was a moderately sized therizinosaurid of 15 feet long and half a ton in weight with enlarged claws. Their short legs, and large, vegetation-digesting belly, suggest they would have been too slow to readily escape predators. Instead of defending themselves by becoming fast, therizinosaurs developed to be more imposing and used their long arms and hand claws to ward of predators though intimidation and threatening strikes (Paul, 2010). An animal with a similar niche would be the extinct giant sloth, *Megatherium*. Both were mostly likely, large, slow moving, leaf eating, animals whose primary defense was size and claws. Because they probably used intimidation rather than escape as a defense mechanism, it might not be unordinary for them to be colorful and without need for camouflage (see Figure 13.). The long feathers were also considered because of their classification under maniraptora (see Figure 1.) and that their ancestors have been suggested to have been gliders, or even to have evolved and lost the ability of flight (Paul, 2010).
Section II: The Body of Work

II-f: Oviraptorosauria

Oviraptorosaurs were a group of exclusively Cretaceous maniraptorans theropods that were misnamed “egg thief.” The first discovered fossils were near a clutch of eggs and it was thought to have been getting an easy meal. However, later discoveries revealed that more Oviraptor individuals were preserved over nests of their own eggs in avianlike brooding positions and were actually attentive parents (Osmolska et. al., The Dinosauria, 2004). They were small to large flying and flightless theropods, herbivorous or omnivorous, and with few to no teeth in later iterations in a shortened snout with thick, beak-like jaws (Paul, 2010). The illustrated Incisivosaurus gauthieri (see Figures 14-16) is known from a complete skull and is considered to be among the most basal of Oviraptors with four prominent teeth in the maxilla (Osmolska, et. al., The Dinosauria, 2004).

Incisivosaurus was as small Oviraptorosaur, of about 3 feet, with a short skull, large sternal plates, long necks, long arms, long claw hooked fingers, and long legs. Named for its enlarged incisor-like teeth, its jaws were also accompanied by a series of small, blunt teeth that were absent from the lower jaws tip. These teeth gave the animal a rodent like appearance and, in addition to its large jaw muscles that fit into a broad post orbital fenestra (see Figure 15.), is thought to have gnawed upon hard plant material (Paul, 2010). These animals were small and lightly built and were mostly likely a prey item for other theropods. Their primary defense would have been high speed running, climbing and biting (Paul, 2010). Their partially arboreal nature, and need to hide from predators in a warm forest environment, went into my decision to color Incisivosaurus in earthy tones of green and countershading for camouflage (see Figure 16).
Section II: The Body of Work

II-g: Dromaeosauridae

Unlike the movie monsters of *Jurassic Park*, dromaeosaurids (known as the raptors) were small to medium sized maniraptoran carnivores that, fossil evidence suggests, were entirely feathered and had long quill nodes for long feather arrays on their arms (Paul, 2010). Also exclusive to the Cretaceous period, these flying and flightless predators were characterized by relatively slender skulls filled with many small, single-edged, bladed teeth, large eyes and well developed olfactory bulbs. Despite having similarly strong sensory capabilities with the tyrannosaurs, the primary feature of the dromaeosaurs were their large arms and characteristic sickle-like claw on the hyper extendable second digit of each foot. With their slight build it is suggested that these claws were instrumental weapons for maiming prey that was chased down or ambushed and could also aid in climbing (Paul, 2010). Smaller species, such as *Microraptor*, are also known flyers and would have been primarily arboreal (Switek, 2012).

The illustrated *Velociraptor mongoliensis* is known to have inhabited arid, sandy climates and would have been primarily terrestrial (Norell *et. al.*, *The Dinosauria*, 2004). Up to 8 feet in length and only about the height of a dog, they were hardly imposing at first glance. However, it is suggested that they would have hunted in packs when several individuals, of a comparably sized dromaeosaur (*Deinonychus*), were discovered together with their prey. Predatory behavior was observed in the famous “fighting dinosaurs” specimen, in which a *Velociraptor* was fossilized in what appeared to be the act of combat with a *Protoceratops* (Norell *et. al.*, *The Dinosauria*, 2004).

These arch predators had a particularly lightly built skull (see Figure 17.) which suggests more prominent use of their large claws to inflict slashing wounds rather than delivering any powerful bite (Paul, 2010). Their slender jaws were most likely adapted to simply handle the food after the killing and the focus of the skull was mainly for prey detection. To highlight these features of the *Velociraptor*, I gave the animal hooded eyes, much like those of a hawk, that would help in spotting prey in an open, sunny environment, as well as earthy colors that would allow them to ambush in groups in their desert home (see Figure 19.).
Section II: The Body of Work

II-h: Troodontidae

Unlike the other pictured theropods, I chose to render the *Troodon* in an oil painting, at life size, full bodied, and in its environment rather than only focusing on the skull and jaw muscle structures (see Figure 26.). By applying both accurate inferences about their paleobiology, and using traditional techniques, my goal is to instill the viewer with a sense of recognition of the dinosaur as a living, breathing animal that shared ancestry with the birds we see every day. Troodontids were small to medium sized raptoran theropods of the late Jurassic to the Cretaceous period and, though similar in build to the dromaeosaurs, were more lightly built. (Paul, 2010). They shared the same signature sickle claw, though it was much less enlarged, had shorter arms, more slender skulls with smaller, serrated teeth, and larger, more forward facing eyes, exceptionally developed middle ears and one of the highest encephalization quotients among nonavian dinosaurs (Makovicky et. al., *The Dinosauria*, 2004). Their proportionately long hind limbs, and presence of the sickle claw, indicate a cursorial, agile, and predatory, lifestyle; while their weaker arms, lighter build and smaller teeth indicate reduced climbing ability and perhaps a more omnivorous diet consisting of only small prey items, eggs and plant matter (Paul, 2010).

Similarly, their large brains, large eyes, and sensitive hearing, could also indicate a nocturnal and opportunistic lifestyle in which Troodontids could find alternative food sources while avoiding competition and predation of larger predators during the day. Troodontids are named for their “wounding teeth”. The prominent serrations of their small teeth are morphologically more like the teeth of herbivorous reptiles (Holliday, 2009) and further suggest their omnivorous, opportunistic habits and similarly more furtive and nocturnal behaviors. With their nocturnal habits in mind, and their bird-like qualities and closeness, I decided to give the *Troodon* colorful plumage that would still allow them to blend in to the cool night forest. Following the discovery of iridescent black-blue plumage in *Microraptor* (Switek, 2012), it could be surmised that, like birds today, feathers could also be used for communication and display. However, these flashy dinosaurs were primarily arboreal and could escape into the trees; they could afford to be flashy. I tried to represent this display quality with a bright, blue head, though, because *Troodon* were flightless and terrestrial, gave the body cool greens as well.
Section II: The Body of Work

II-i: Extant Groups: Aves and Suchia

The skulls and jaw musculature of the chicken (*Gallus gallus domesticus*) and the American alligator (*Alligator mississippiensis*) share similarities to the skulls of theropod dinosaurs but all bear significant morphological features that indicate their divergent niches and evolution. Aves, or birds, have skulls that are characterized by complete loss of teeth in place of the rhamphotheca, or keratinous beaks, large orbits, and the loss of the upper temporal (post orbital) arch to form a round cranium with only a single opening for muscle attachment (DeIuliis *et. al.*, 2007) (see Figures 20-21.). Their large eyes, lighter skulls, and greatly reduced jaw muscles (reduced morphologically to fit into only the single opening) illustrate their departure from the role of the large predators since only the smallest dinobirds were able to survive the Cretaceous mass extinction 65 million years ago (Paul, 2010). Holliday and Witmer (2007) suggest that the reduction of the jaw muscles makes it difficult to sufficiently distinguish them and are often recognized under different names than their homologous counterparts in their more robust archosaurs such as the alligator and more basal theropods.

Similarly, Holliday (2013) notes that the alligator jaw musculature is also “three-dimensionally complex and difficult to illustrate in two-dimensional media” (Holliday *et. al.*, 2013). Using images of the 3D interactive model of the jaw musculature of a young *Alligator mississippiensis*, (Holliday, *et. al.*, 2013) I was able to illustrate the major superficial muscles of the jaw that correlate with the conceptualized musculature of the theropods (see Figure 24.). In strong contrast to the chicken, the elongated rostrum, formed by the frontal and maxilla, is greatly flattened, very solid and has a sculpted texture that is indicative of dermal ossification (osteoderms) that adhere to the dorsal regions of the skull (DeIuliis *et. al.*, 2007) (see Figure 23.). The socketed teeth are simple and conical, made to puncture and hold tightly onto prey rather that slice and process and the impressively broad depressor muscle is ideal to snap down quickly on ambushed prey that it would drag down into its watery home.
Conclusion

Though there are several other groups of unmentioned theropods (see Figure. 1) and numerous unexplored dinosaur groups among the Sauropodomorphs and Ornithischians, I hope that this series of illustrations offers a starting point for a more comprehensive anatomical and paleobiological look at extinct wildlife such as dinosaurs. The supplementary descriptions and analysis of each pictured specimen serve more as a brief introduction to further readings and research about these animals, to set a context for the primary attraction; the illustrations. Ultimately, I would one day like to see a glossary of these kinds of anatomical studies, and conceptualizations of prehistoric life, that could be consumed by paleontologists, biologists, researchers, artists, and dinosaur fans alike.
Figure 1. Cladogram following the separation between dinosaurs and crocodilians (Suchia) and tracing the origins and diversification of theropod dinosaurs and the rise of modern day birds (Aves).
Figure 2. Skull of *Ceratosaurus magnicornis*. 
Figure 3. Jaw muscles of *Ceratosaurus magnicornis*; m. adductor mandibulae externus superficialis (mAMES), m. adductor mandibulae externus profundus (mAMEP), m. adductor mandibulae posterior (mAMP) (underlying the mAMES), m. pterygoideus ventralis (mPTv), m. pterygoideus dorsalis (mPTd) and the m. depressor mandibulae (mDM).
Figure 4. Face of *Ceratosaurus magnicornis*. 
Figure 5. Skull of *Tyrannosaurus rex.*
Figure 6. Jaw muscles of *Tyrannosaurus rex*; m. adductor mandibulae externus superficialis (mAMES), m. adductor mandibulae externus profundus (mAMEP), m. adductor mandibulae posterior (mAMP) (underlying the mAMES), m. pterygoideus ventralis (mPTv), m. pterygoideus dorsalis (mPTd) and the m. depressor mandibulae (mDM).
Figure 7. Face of *Tyrannosaurus rex*. 
Figure 8. Skull of *Ornithomimus edmontonicus*. 
Illustrations

Figure 9. Jaw muscles of *Ornithomimus edmontonicus*; m. adductor mandibulae externus superficialis (mAMES), m. adductor mandibulae externus profundus (mAMEP), m. adductor mandibulae posterior (mAMP) (underlying the mAMES), m. pterygoideus ventralis (mPTv), m. pterygoideus dorsalis (mPTd) and the m. depressor mandibulae (mDM).
Illustrations

Figure 10. Face of *Ornithomimus edmontonicus*.
Figure 11. Skull of *Erlikosaurus andrewsi*. 
Illustrations

Figure 12. Jaw muscles of *Erlikosaurus andrewsi*: m. adductor mandibulae externus superficialis (mAMES), m. adductor mandibulae externus profundus (mAMEP), m. adductor mandibulae posterior (mAMP) (underlying the mAMES), m. pterygoideus ventralis (mPTv), m. pterygoideus dorsalis (mPTd) and the m. depressor mandibulae (mDM).
Illustrations

Figure 13. Face of *Erlikosaurus andrewsi*. 
Illustrations

Figure 14. Skull of *Incisivosaurus gauthieri*. 
Illustrations

Figure 15. Jaw muscles of *Incisivosaurus gauthieri*; m. adductor mandibulae externus superficialis (mAMES), m. adductor mandibulae externus profundus (mAMEP), m. adductor mandibulae posterior (mAMP) (underlying the mAMES), m. pterygoideus ventralis (mPTv), m. pterygoideus dorsalis (mPTd) and the m. depressor mandibulae (mDM).
Illustrations

Figure 16. Face of *Incisivosaurus gauthieri*. 
Illustrations

Figure 17. Skull of *Velociraptor mongoliensis*. 
Figure 18. Jaw muscles of *Velociraptor mongoliensis*; m. adductor mandibulae externus superficialis (mAMES), m. adductor mandibulae externus profundus (mAMEP), m. adductor mandibulae posterior (mAMP) (underlying the mAMES), m. pterygoideus ventralis (mPTv), m. pterygoideus dorsalis (mPTd) and the m. depressor mandibulae (mDM).
Illustrations

Figure 19. Face of *Velociraptor mongoliensis*. 
Figure 20. Skull of *Gallus gallus domesticus.*
Illustrations

Figure 21. Jaw muscles of *Gallus gallus domesticus*; m. adductor mandibulae externus profundus (mAMEP), the m. depressor mandibulae (mDM) are retained from dinosaur anatomy while other pictured muscles mAMCL, mAMCM, mAMEV. mAMER are homologous but renamed.
Illustrations

Figure 22. Face of *Gallus gallus domesticus*. 
Illustrations

Figure 23. Skull of *Alligator mississippiensis*. 
Illustrations

Figure 24. Jaw muscles of *Alligator mississippiensis*; m. adductor mandibulae externus superficialis (mAMES), m. adductor mandibulae externus profundus (mAMEP), m. adductor mandibulae posterior (mAMP) (underlying the mAMES), m. pterygoideus ventralis (mPTv), m. pterygoideus dorsalis (mPTd) and the m. depressor mandibulae (mDM).
Figure 25. Face of *Alligator mississippiensis*. 
Illustrations

Figure 26. *Troodon inequalis*. Oil on hardboard panels. 3 ft. by 6 ft.
Illustrations

Visualization of Comparative Anatomy
Jaw muscles of Theropod Dinosaurs and their extant relatives, illustrating the story of functional morphology and evolution

Figure 27. Comparative anatomy chart of all illustrations.
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