

## COMMENTARY

## Allure of El Lagarto—Why Do Dinosaur Paleontologists Love Alligators, Crocodiles, and Their Kin?

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With his elegant study of the forelimb musculature of crocodylians (“Crocodylian Forelimb Musculature and its Relevance to Archosauria,” this volume), Mason Meers addresses a glaring deficiency in the anatomical literature. This study will be of exceptional interest not only to herpetologists and anatomists, but also to dinosaur paleontologists, paleobiologists, and even dinosaur artists and illustrators who crave sound anatomical knowledge of the musculoskeletal system of crocodylians. El Lagarto (“the Lizard”), otherwise known as *Alligator mississippiensis*, has a long and distinguished pedigree. Its forebears date back to the beginning of the Age of Dinosaurs, in the Late Triassic, roughly 225 million years ago. Today, some 23 species of crocodylians populate tropical and warm temperate regions around the globe. The broad-snouted, wily swamp dweller of the southeastern United States has fascinated, and sometimes repelled, observers since Europeans invaded its territory five centuries ago (Spain claimed Florida in 1513, and established the city of St. Augustine in 1565). Europeans were smitten with the flora and fauna of the New World, and specimens were sent back for scientific description. So it was that the type specimen of alligator, the quintessential American citizen, the name-bearing alligator, came to reside in the Museum National d’Histoire Naturelle in Paris (Neill, 1971). But for a scientific error, it might actually have become a German citizen. In 1788, Johann F. Blumenbach of Göttingen applied the fatally flawed binomial *Lacerta alligator*. The Spanish epithet notwithstanding, this animal is no lizard. Botanist André Michaux sent another specimen to Paris, which A.F. Daudin described in 1802 as *Crocodylus mississippiensis*. (The French preferred the Latiniform *Crocodylus*, as do I, but the more recent preference has been for the Hellenic *Crocodylus*, which has priority.) Only a year later, the young United States purchased Louisiana from France, 3 years after France obtained the territory by treaty with Spain. In 1807, the great French anatomist and paleontologist Georges Cuvier provided the definitive generic name: *Alligator*. Regrettably, the aristocrat Cuvier haughtily disdained Citizen Daudin’s specific name, and designated it as *Alligator lucius*. In the fullness of time, it has come to be recognized as *Alligator mississippiensis* (Daudin).

Oblivious of these taxonomic niceties, the American alligator has seen its fortunes wax and wane throughout history. Alligators have been heavily exploited for leather,

and by the mid 20th century, population levels had fallen sharply. Fortunately for us dinosaur paleobiologists, state and federal protections have succeeded brilliantly, and today alligator populations in Florida, Louisiana, and other states are generally strong (estimated at over a million individuals). Obviously, habitat protection is the key to conservation, since all species of crocodylians require access to abundant water (i.e., swamps, ponds, and rivers).

Alligators are altogether impressive. Although females appear to finish growth by about 9 feet (2.7 m), males today reach 12–14 feet (3.7–4.3 m), and 18- and perhaps 19-footers (5.5–5.8 m) have been documented during the 20th century (McIlhenny, 1935; Meyer, 1984). Fortunately for us, as well as them, alligators are comparatively docile. Although they devour their share of family pets, attacks on humans are quite uncommon and fatalities are rare.

In addition to the American alligator, today there is also a Chinese alligator, *Alligator sinensis*. This animal presents an interesting biogeographic puzzle, which is resolved by understanding that alligators were more widely distributed in the past than they are today. The oldest known fossil alligator is *Alligator prenasalis* from the Oligocene of Nebraska. Other members of the family Alligatoridae are the caimans, which comprise six species that range from southern Mexico through Central America to Brazil and Paraguay. Caimans tend to be feistier than alligators, but fortunately they are generally smaller (7 feet (2.1 m) is typical). However, Neill (1971) noted that the black caiman (*Melanosuchus niger*) reaches a very respectable 13 feet (4 m). *Purussaurus* is a gigantic Miocene caiman from Brazil and Columbia that may have reached 12 m in length (Schwimmer, 2002). For a master-

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ful analysis of the osteology, paleontology, and phylogeny of the Alligatoroidea, see Brochu (1999).

Alligators and caimans are more familiar to inhabitants of the New World, but today crocodylids (members of the family Crocodylidae) are distributed worldwide, primarily in the tropics. How does one tell the difference between crocodylids and alligatorids? Crocodylids generally (but not always) have sharp snouts, and there is a notch behind the external nostrils through which an enlarged tooth on the jaw projects upward. More generally, both upper and lower teeth incline laterally and interdigitate, leaving a messy, toothy grin when the mouth is closed. Alligators and caimans tend to have broad snouts, and the enlarged tooth of the jaw is enclosed in a pit in the maxilla. The upper teeth are straight, and enclose the lower teeth, leaving a tidier appearance when the mouth is closed.

Crocodyles entered recorded human history in the form of the Nile crocodile, first documented by the Greek writer Herodotus in the 5th century B.C. He introduced into the crocodylian literature two Egyptian words via the Greeks: *champsai* and *souchos*. Both of these root words are common in the pertinent scientific nomenclature. The mummified remains of Nile crocodyles are found in the pyramids—one such specimen is 15 feet long (4.6 m), just a little shy of the maximum recorded length for the species of 18 feet (5.5 m) (Cott, 1961; Meyer, 1984). Nile crocodyles are widespread throughout the freshwater rivers and lakes of Africa. These are aggressive predators that exact a fearsome toll of human flesh every year. Nile crocodyles participate in an interesting symbiosis with the hippopotamus. An adult hippo reportedly can bite a crocodile in half, but crocodyles have an irresistible fondness for baby hippo! Another memorable crocodile is *Crocodylus porosus*, the estuarine crocodile of Southeast Asia. Its distribution from India to the Philippines, from the Indian Ocean to the western Pacific, including the north coast of Australia, eloquently testifies to the prowess of this monster in saltwater, yet it swims up rivers well into freshwater. Documented specimens of this aggressive and dangerous predator reach 20 feet (6.1 m) (Meyer, 1984), and apocryphal accounts add 50% to this figure. A skull 1 m long adorns the Museum National d'Histoire Naturelle in Paris. Morphologically, the most divergent crocodylians are the gharials (*Gavialis gangeticus*), a needle-snouted fish-eater that ranges from the Indus River of Pakistan to the Irawaddy River of Myanmar (Burma). At 21.5 feet (6.4 m) in length, it is among the largest of living crocodylians; however, its specialized fish-catching snout renders it innocuous with respect to humans. Gharials are usually placed in their own family, the Gavialidae.

In a traditional Linnean classification (e.g., Carroll, 1988), the order Crocodylia of the reptilian subclass Archosauria is regarded as dating from the Late Triassic, but in the preferred modern cladistic rendering (e.g., Benton and Clark, 1988; Brochu, 1999; Sereno et al., 2001), the term Crocodylia indicates a crown group whose membership is restricted to descendants of the common ancestor of alligators, crocodyles, and gharials. Currently, the most inclusive term for the clade of archosaurs that includes Crocodylia is Crocodylomorpha. Basal crocodylomorphs from the Middle and Late Triassic to the Early Jurassic include small, hollow-boned, bipedal, possibly arboreal types such as *Terrestriusuchus* from Wales, *Gracilisuchus* from Argentina, *Sphenosuchus* from Argentina, and several Early Jurassic forms from China, including *Dibothro-*

*suchus* and *Phylloodontosuchus* (Harris et al., 2000). These animals diverge rather widely from stereotypic concepts of Crocodylia. More conventional Mesozoic forms derived in comparison to the sphenosuchians, but more basal than the crown group Crocodylia, are ascribed to the Crocodyliformes, of which the Crocodylia sensu stricto are but one clade. The Mesozoic fossil record is rich in crocodyliforms. Certain small terrestrial forms developed multicusped herbivorous teeth (Gomani, 1997; Barrett, 2000; Buckley et al., 2000). Large marine forms evolved repeatedly during the Mesozoic; many developed long, gharial-like snouts, and a few lost dermal armor and developed paddles and heterocercal tails (Buffetaut, 1979, 1982). Some truly immense crocodyliforms evolved, such as *Sarcosuchus* from the Early Cretaceous of Niger (Taquet, 1976; Sereno et al., 2001), with its skull of 1.6 m and body length estimated at 12 m, and *Deinosuchus* from the Late Cretaceous of the United States (Schwimmer, 2002)—also a 12-m monstrosity. Perhaps the prize-winner is *Stomatosuchus* from the early Late Cretaceous of Egypt, with its 2-m skull. Regrettably, the remains of this animal and its contemporaries, the theropod dinosaurs *Spinosaurus*, *Carcharodontosaurus*, and *Bahariasaurus* were destroyed in a Royal Air Force bombing raid over Munich in 1944 (Smith et al., 2001; Nothdurft, 2002).

Living crocodylians generate great intrinsic interest as successful large-bodied ectotherms that thrive in a world dominated by endotherms, having ignored the cacophony and strife of the terminal Cretaceous extinctions that wiped out their more glamorous cousins, the dinosaurs. Crocodylians carry an additional burden. As the closest living reptilian relatives of the dinosaurs, they support one branch of the extant phylogenetic bracket (EPB) for the Dinosauria (the other branch being birds (Aves)), as articulated by Witmer (1995). Crocodylians thus necessarily play a role in elucidating the biology of dinosaurs. The EPB is a very useful technique for inferring the existence of various unpreserved soft-tissue structures or physiological states among fossils. How does the EPB work? As a simple example, crocodylians have a four-chambered heart, and birds have a four-chambered heart. It is a level I inference (i.e., a no-brainer!) that descendants of their common ancestor, for example the dinosaurs, had four-chambered hearts, unlike the majority of living ectotherms. What about dinosaurian endothermy? This is a much-debated question. Endothermy is lacking in Crocodylia but present in Aves, so it obviously evolved somewhere along the line between dinosaurs and modern birds. To infer endothermy for any given dinosaur is a level II inference (not a sure thing, but not exactly a wild guess either). A third problem is how to interpret structures that are observed in dinosaurs but are not found in living crocodylians or birds. Sauropods, the long-necked, plant-eating dinosaurs, are replete with enigmatic structures. Examples include the long cervical spines of *Amargasaurus*, or the inferred existence of a proboscis in sauropods, or auxiliary carotid "hearts" in the necks (Choy and Altman, 1992). Unique structures are interpreted in sauropods (see Witmer, 2001), but these are level III inferences (decidedly less secure). One of the things that the EPB underscores is the inappropriateness of using mammals as a basis for reconstructing the musculature of dinosaurs. Granted that short-limbed, sprawling, ectothermic crocodylians are not dinosaurs and have never been mistaken for dinosaurs (okay, rarely have been (Lamanna et al.,

unpublished results)), dinosaur paleontologists have nonetheless found the study of crocodylians, beginning with the common and accessible American alligator, to be extremely fruitful. Alfred Sherwood Romer, one of the great anatomists and paleontologists of the 20th century (though no fan of dinosaurs!) set the tone early in the century with a seminal study of crocodylian pelvic muscles, which he then used to reconstruct dinosaurian pelvic muscles (Romer, 1922). It has become almost (but not quite) a rite of passage for paleontologists to study crocodylians early in their careers. Whether they continue to do so depends on what they choose to specialize in. For me, the study of *Alligator* osteology (Dodson, 1975) was the necessary prelude for a career in dinosaur paleontology, and many of my students continue in a similar vein (Tumarkin-Deratzian, unpublished results; Lamanna et al., unpublished results), as do students of my students (e.g., Witmer, 1997; Meers, 2003).

The crocodylian hindlimb has been studied by various paleontologists, including Brinkman (1980), Rowe (1986), and Gatesy (1991); however, studies of the crocodylian forelimb are much less common. Fürbringer (1876) began the study of crocodylian forelimb muscles with a valuable presentation of the shoulder and brachium of *Crocodylus acutus*, the American crocodile. In the intervening century and a quarter, the forelimb has received only sporadic attention (that is, until now—in the definitive study by Meers (2003)). This contrasts with the crucially important role that forelimbs play in the biology of archosaurs. Consider the range of variation encountered in the forelimb of archosaurs. One of the earliest crocodylomorphs, *Terrestriuchus*, was bipedal, with shortened pentadactyl forelimbs. In typical crocodylians, the forelimbs have lengthened from this basal condition to more closely approximate the length of the hindlimbs, but both are short relative to body length. Some Mesozoic marine crocodylomorphs modified their forelimbs into paddles for swimming (Buffetaut, 1979; Benton, 1997). Pterosaurs are phylogenetically interpolated between crocodylomorphs and dinosaurs (Wellnhofer, 1991). These precocious (Late Triassic) tetradactyl fliers developed a unique wing predicated upon a greatly elongated fourth finger (*Pterodactylus* = “flying finger”). In early dinosaurs, the hindlimbs are lengthened and drawn underneath the body. Forelimbs in bipedal dinosaurs are generally shortened, with loss of digits initiated from the outside (fifth digit) inward (Sereno, 1997). The culmination of this trend in theropod (meat-eating) dinosaurs is seen in the great *Tyrannosaurus*, with its remarkable two-fingered, extremely shortened forelimbs. On the other hand, a lineage of smaller-bodied theropods, the maniraptorans, emphasized the forelimb to the extent that this limb, equipped with trenchant predatory claws (Ostrom, 1969, 1990), eventually was transformed into the tridactyl avian wing (Gauthier and Gall, 2001; Chiappe and Witmer, 2002). Within Aves, secondary flightlessness has evolved many times, leading to a reduction in wing size and the loss of skeletal elements. Archosaur forelimbs thus were certainly used for slow, ponderous walking, swift running, climbing, flying, swimming, and capturing and wounding prey, and were likely used for digging, nesting, courtship, as an accessory to copulation, and other functions about which we can only speculate. That such activities have evolved multiple times (e.g., at least twice for flight, and three or four times

for marine swimming) ensures that the Archosauria will continue to provide rich material for evolutionary studies.

A prerequisite for functional studies of archosaurs is a muscular template for the credible restoration of locomotor muscles. A major deficiency in the literature has now been addressed by Meers (2003), forming a fundamental baseline for evolutionary studies of the Archosauria. As a result, the study of archosaur forelimbs is expected to change in the coming years. With access to this modern anatomical work, new homologies are currently being delineated (Meers et al., unpublished results), and functional and artistic restorations of forelimbs of dinosaurs and other archosaurs will take on a more rigorous tenor.

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