Historical Biology
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713717695

Crocodilian behaviour: a window to dinosaur behaviour?

Peter Brazaitis[a]; Myrna E. Watanabe[b]
[a] Yale Peabody Museum of Natural History, New Haven, CT, USA [b] Naugatuck Valley Community College, Waterbury, CT, USA

To cite this Article Brazaitis, Peter and Watanabe, Myrna E.(2011) 'Crocodilian behaviour: a window to dinosaur behaviour?', Historical Biology, 23: 1, 73 — 90
To link to this Article: DOI: 10.1080/08912963.2011.560723
URL: http://dx.doi.org/10.1080/08912963.2011.560723

Historical Biology
Vol. 23, No. 1, March 2011, 73–90

Crocodilian behaviour: a window to dinosaur behaviour?

Peter Brazaitis[a]* and Myrna E. Watanabe[b]

[a]*Yale Peabody Museum of Natural History, 170 Whitney Ave., P.O. Box 208118, New Haven, CT 06520-8118, USA;* [b]*Naugatuck Valley Community College, 750 Chase Pkwy, Waterbury, CT 06708, USA*

(*Received 16 August 2010; final version received 18 August 2010*)

Modern crocodilians and birds are the only living representatives of the Archosauria, a group that also includes non-avian dinosaurs and pterosaurs. Modern crocodilians originated during the early Cretaceous period and dispersed globally. Examples of physiological similarities between living crocodilians and birds include similar amino acids in β-keratins among crocodiles, turtles and birds; oviduct homologies between crocodilians and birds; similar forelimb structures in crocodiles and other archosaurs and similarities in gene expression in limb development in alligators and chickens. While individual crocodilian species have adapted their behaviours to meet specific strategies for survival in specific habitats, core reproductive behaviours are universal among modern crocodilians and transcend speciation, morphology and geographic distribution. Hard-wired core behaviours include social signals that incorporate chemosensory, auditory and mechanoreception modalities; construction of a temperature-stabilising nest chamber to incubate eggs; and parental care of their young. Parental care may reflect a primitive character for archosaurs, including dinosaurs. Crocodilians use integumentary sense organs (ISOs) during courtship and in parental care, and similar structures may have had similar functions in dinosaurs. The presence of numerous foramina (possible ISOs) in the skulls of saurischians, along with the findings of fossilised nests with adults, may indicate similar complex behaviours, including parental care, in dinosaurs.

Keywords: dinosaurs; crocodilians; behaviour; temperature; reproduction; integumentary sense organs

Introduction

Palaeontologist Dodson (2003) wrote that crocodilians, ‘As the closest living reptilian relatives of the dinosaurs . . . support one branch of the extant phylogenetic bracket (EPB) for the Dinosauria (the other branch being birds [Aves]). Crocodilians thus necessarily play a role in elucidating the biology of dinosaurs.’

This was not accepted as a scientific fact in the mid-1970s. At that time, one of us (MEW) was a graduate student studying alligator reproductive behaviour. She would stand in front of Roy Chapman Andrews’s misidentified *Oviraptor* nest in a display case at the American Museum of Natural History and would think ‘This is a crocodilian nest.’ Our current knowledge supports the phylogenetic relationship noted by Dodson and at least a commonality of some behavioural characteristics. But back then, the question was how to make the leap from crocodilians to dinosaurs. A few miles away at the Bronx Zoo, the other co-author of this paper (PB) was experiencing a living lesson. Crocodilians in the zoo collections displayed universally shared behaviours that appeared to be common among all of the species, regardless of morphology or origin. At the time, these shared, seemingly ‘hard-wired’ behaviours, particularly reproductive behaviours, suggested to us a common ancestry. However, individual crocodilian species also adopt unique behavioural strategies, allowing them to live in different habitats and environments. More astonishing, crocodilians display behaviours that appear to parallel many avian behaviours.

Our goal in this paper is to call attention to the distribution, reproductive behaviours and key morphological structures that facilitate reproductive behaviours in modern crocodilians. This may provide a starting point for the discussion of the behaviour of ancestral forms.

The origin of crocodilians

We now view modern crocodilians as a continuum of their ancestral phylogeny (Brochu 2003). Crocodilians have their evolutionary beginnings more than 250 million years ago (mya) (Figure 1) in the early Triassic (Seymour et al. 2004). The proterosuchid–erythrosuchid line of evolution led to *Euparkeria*, a mid-Triassic, small archosaur that appears to be a species that is close to the crocodilian–dinosaur common ancestor (Seymour et al. 2004). From this poorly known organism, the line of descent split in the mid-Triassic, leaving the Crurotarsi, which led to crocodilians, and the Ornithodira, which led to dinosaurs, birds and pterosaurs (Seymour et al. 2004). The oldest known modern crocodilian fossil is from about 125 mya.

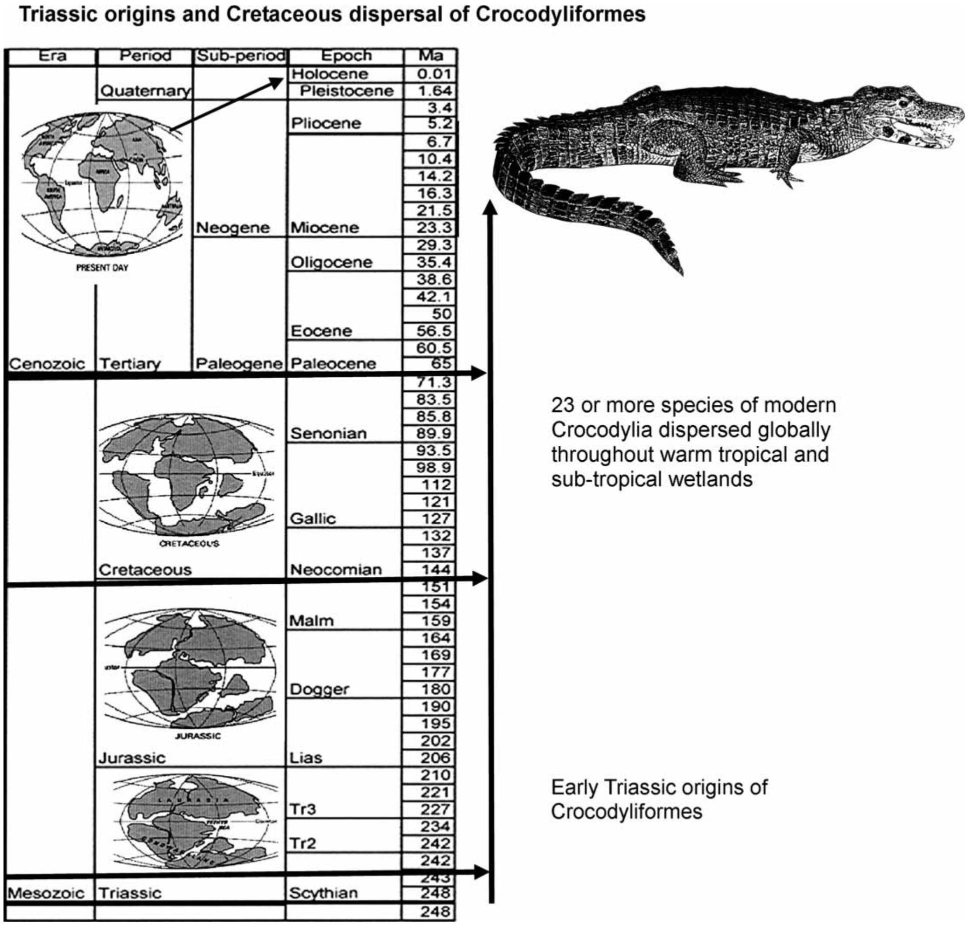
Donoghue et al. (1989) argued for the importance of fossils in phylogenic reconstruction. Salisbury et al. (2006)

---

*Corresponding author. Email: crocone@99main.com

ISSN 0891-2963 print/ISSN 1029-2381 online

DOI: 10.1080/08912963.2011.560723
http://www.informaworld.com



Triassic origins and Cretaceous dispersal of Crocodyliformes

23 or more species of modern Crocodylia dispersed globally throughout warm tropical and sub-tropical wetlands

Early Triassic origins of Crocodyliformes

Figure 1. Cretaceous dispersal of Crocodyliformes. The column to the left provides an evolutionary timeline in millions of years, with the global tectonics associated with the dispersal of crocodyliformes leading to modern crocodilians (adapted from Poling 1995/1997).

discussed the anatomical and osteological changes associated with the emergence of the Eusuchia, the only surviving crocodyliform suborder that now includes the three modern families of crocodilians, and presented a phylogenetic tree of morphological transformations from basal eusuchians to modern crocodilians (*Crocodylus porosus*). He called attention, however, to the difficulty in establishing the precise points of phylogenic transition from Neosuchia to Eusuchia and from Eusuchia to Crocodylia. Salisbury et al. (2006) supported a Laurasian origin for all three superfamilies of crocodilians.

Global dispersal of modern crocodilians

Modern crocodilians are distributed geographically throughout the tropical, sub-tropical and warmer temperate wetland regions of the world (Table 1), not only primarily inhabiting warm lowland grassland and forest habitats, but also taking advantage of upland forest habitats. For physiological reasons based on temperature requirements, or ecological reasons related to nesting strategies, prevailing and mean climatic, geographic or altitudinal temperatures may define the limits where modern crocodilians can exist (Shepard and Burbrink 2009). Modern crocodilians are not found in climates beyond about 35°–36° N and S latitudes (Lance 2003), and altitudes above about 600 m. However, Gorzula and Paolillo (1986) report evidence of *Paleosuchus trigonatus*, an Amazonian forest-dwelling species, at 1300 m.

The success of crocodilian dispersal throughout the Cretaceous period may have been favoured by a warm tropical ocean surface and climate (Savin 1977; Wilson and Norris 2001; Scott 2008). Many of the most widely dispersed crocodilians, the Crocodylidae, are also inextricably linked to the survival of warm climate mangrove forests found throughout coastal and river regions. Further, these unique ecosystems occur in six biogeographical regions that include nearly all tropical and sub-tropical coastal areas of the world. Today, consistent with the climatic limits for crocodilians, mangrove forests occur only within 30° of the Equator. Wherever mangrove forests and crocodilians occur, young immature crocodilians take advantage of the sanctuary that mangrove thickets provide to escape from predators. Mangrove

Table 1. Modern crocodilian species and their global distributions.

Species	Common name	Modern distribution
Family: Alligatoridae		
Genus: *Alligator*		
A. mississippiensis	American alligator	North America: southeastern USA
A. sinensis	Chinese alligator	Asia: middle Yangtse river – Wuhu, Anhui Province
Genus: *Caiman*		
C. crocodilus	Caiman	Central and South America
C. c. crocodilus	Common caiman	South America: Amazon River drainage basin
C. c. apaporiensis[a]	Rio Apaporis caiman	South America: east of the Andes; middle Rio Apaporis
C. c. fuscus	Rio Magdalena caiman	South America: northern Andes: Rio Magdalena, atlantic drainage; northwest Venezuela
C. c. chiapasius	Central American caiman	Mexico, Central America and South America: west of the Andes
C. latirostris	Broad-snouted caiman	South America
C. l. latirostris	Broad-snouted caiman	South America: west and south atlantic drainages of Brazil, Paraguay, Uruguay, north Argentina
C. l. chocoensis[a]	Argentine broad-snouted caiman	South America: north Argentina; Paraguay, Parana river drainages
C. yacare	Yacare caiman	South-central South America: Paraguay, Parana, Guapore river drainages, not Amazon
Genus: *Melanosuchus*		
M. niger	Black caiman	South America: Amazon River basin and drainages
Genus: *Paleosuchus*		
P. palpebrosus	Dwarf caiman	South America: tropical south America
P. trigonatus	Smooth-fronted caiman	South America: Amazon (forest) basin
Family: Crocodylidae		
Genus: *Crocodylus*		
C. acutus	American crocodile	North and South America; neotropical: Mexico, Central America; west coast South America, Peru to Venezuela; Caribbean Islands
C. intermedius	Orinoco crocodile	South America: Orinoco river and drainages
C. johnsoni	Johnston's crocodile	Australia: Northern territories
C. mindorensis	Philippine crocodile	Western Pacific: Philippine Islands
C. moreletii	Morelet's crocodile	Central America: Atlantic drainages; Mexico, Belize, Guatamala
C. niloticus	Nile crocodile	Africa: Sub-Sahara, historical to Israel and Jordan; Madagascar
C. novaeguineae	New Guinea crocodile	Western Pacific: Indonesia and Papua New Guinea
C. palustris	Mugger or marsh crocodile	South Asia, Indian sub-continent
C. p. palustris	Indian marsh crocodile	South Asia, Indian sub-continent: lowland India, Pakistan
C. p. kimbula[a]	Ceylon marsh crocodile	South Asia: Sri Lanka
C. porosus	Saltwater crocodile	North Australia, southeast Asia, India, Western Pacific, Palau, Solomon Islands, Vanuatu
C. rhombifer	Cuban crocodile	Caribbean: Zapata swamp, Isle of Pines
C. siamensis	Siamese crocodile	Southeast Asia and Malaysia (historical): recent Laos, Cambodia
Genus: *Mesistops*		
M. cataphractus	African slender-snouted crocodile	Central West Africa: mostly tropical forest
Genus: *Osteolaemus*		
O. tetraspis	Dwarf crocodile	Central West Africa
O. t. tetraspis	W. African dwarf crocodile	Central West Africa: mostly tropical forest
O. t. osborni	Congo dwarf crocodile	Central West Africa: Congo Basin
Family: Gavialidae		
Genus: *Gavialis*		
G. gangeticus	Indian gharial	India, Indian sub-continent: rivers of northern India and eastern Pakistan
Genus: *Tomistoma*		
T. schlegelii	Malayan false-gharial	Southeast Asia: lowlands of Thailand, Malaysia, Indonesia

Note: [a]May not be a valid sub-species. Source: Brazaitis (1973a, 1973b), King and Burke (1989) and Thorbjarnarson (1992).

ecosystems harbour an abundance of wildlife and produce an abundance of marine organisms, the sources of food for crocodilians (Brazaitis and Abene 2008; Luther and Greenberg 2009).

Modern crocodyliformes dispersed during the Cretaceous period, about 100 mya (Figure 1). Dixon (1979), Duellman (1979) and Turner (2004) provided a basis for the Gondwanan distribution of crocodyliforms (Figure 1). There are only two modern species of the genus *Alligator* (family: Alligatoridae), the American alligator, *Alligator mississippiensis*, of the southeastern and south-central USA and the Chinese alligator, *A. sinensis*, of southeastern China. Both species evolved separately at distant ends of the earth, and the fossil record reinforces Gondwanan crocodilian dispersal.

It is reasonable to believe that if the distribution and morphology (Brochu 2001) of modern crocodilians reflect the genetic evolution and dispersal of their Cretaceous ancestors, then why should we not believe that the ancestors of these ancient reptiles also shared their behaviours? This is likely if modern crocodilians also share physical structures that are an integral part of their evolutionary arsenal for survival, and these may facilitate the performance of their basic universal behaviours.

Structural and physiological similarities

Evidence of the biochemical relationship between crocodilians and birds (Dodson 2003) includes the following: (1) similarities in amino acid structure in β-keratins in Nile crocodile, *Crocodylus niloticus*, scalation and the scales of chicks' claws (Dalla Valle et al. 2009a) and (2) studies on turtle keratin showing it to be similar to that of the scales of crocodilians and scales of bird claws (Dalla Valle et al. 2009b). In fact, Prum and Brush (2002), citing Schweitzer et al. (1999), noted that immunological testing of feather-like epidermal appendages from an alvarezsaurid specimen, *Shuvuuia deserti*, showed the presence of β-keratin, an epidermal protein found only in birds and reptiles. Alibardi and Toni (2008) noted that the small proteins that compose feathers are modifications of ancestral proteins found in the evolutionary line from archosaurs to birds.

A study on seasonal changes in the oviduct of the American alligator, *A. mississippiensis*, notes structural homologies shared with birds (Bagwill et al. 2009). Because crocodilians and birds form the extant phylogenetic bracket of dinosaurs, this may hint at similarities in the structure and function of the oviducts of some dinosaurs.

Similarities in forelimb structure between crocodilians and other archosaurs – extant and extinct – were also noted (Meers 1999). Vargas et al. (2008) found that *HOXD-11* expression was absent during late developmental stages of the first digit in alligators, chicken and mice.

Harris et al. (2006), noting development of archosaurian tooth pattern in a mutant chicken, hypothesised that epigenetic changes influence loss of tooth development in birds, while maintaining the genetic potential to develop teeth. Again, this shows a line of descent between non-avian archosaurs – dinosaurs – and birds. Crocodilians shed and replace their teeth and regenerate teeth and jawbone that are lost (Brazaitis 1981; Erickson 1996). Erickson (1996) further noted similarities in incremental lines in the dentine of dinosaur teeth and those in both living and prehistoric crocodilians. He hypothesised tooth replacement rates in *Tyrannosaurus rex* based on those for *A. mississippiensis* (Erickson 1996).

Dodson (2003) looked at crocodilian ectothermy as a conundrum, separating crocodilians from some unknown endothermic dinosaurs on a direct line of ancestry to birds. Modern crocodilians have to meet physiological requirements that are dependent on body temperature and, in turn, the environmental temperatures to which they are exposed. However, crocodilians have retained a four-chambered heart, a condition absent in other ectotherms, suggesting that their archosaurian ancestry may have been endothermic (Seymour et al. 2004; Watanabe 2005). Seymour et al. (2004) hypothesised that modern crocodilian ancestors, with their four-chambered hearts and efficient circulatory systems, were, in fact, endothermic, with ectothermy being secondarily derived. Hillenius and Ruben (2004) questioned Seymour et al.'s (2004) conclusion, indicating that every piece of evidence they cite can be refuted. Farmer (2001) listed many attributes that are evidence of homeothermy in a species, including parental care. Gillooly et al. (2006), however, predicted inertial homeothermy for large dinosaurs and illustrated that this is what occurs in large crocodilians. Nevertheless, Hillenius and Ruben (2004) pointed out that within the archosaurs there must have been evolution of an increase of basal metabolic rate from 'near-ancestral levels to avian levels'. This still leaves the existence of the crocodilian four-chambered heart and inter-aortic foramen of Panizza, which shunts blood away from the pulmonary circulation and is present *only* in crocodilians, as a puzzle.

Another interesting similarity that may have physiological implications is the presence of gastroliths of various types in the stomachs of extant crocodilians (Cott 1961; Brazaitis 1969b) and fossil taxa, including fossilised alligatorids and dinosaurs (Wings 2007). Gastroliths are defined as stones within the stomach (Wings 2007). The purpose of these ingestions and the function of the stones remain unresolved (Brazaitis 1969b; Wings 2007).

Phylogeny of modern crocodilians

Crocodilian phylogenetic studies continue to evolve. Table 1 gives the taxonomy (after King and Burke 1989) and distribution of modern crocodilian species (Thorbjarnarson 1992). The new and powerful tools of molecular genetics continue to shed new light on modern and ancestral crocodilian relationships. These molecular genetics results often are a surprise to traditional taxonomists (Densmore 1983, 1989; Amato et al. 1994; Gatesy et al. 2003; McAliley et al. 2006; Willis et al. 2007; Gatesy and Amato 2008), sometimes compete for precedence with physical morphology (Poe 1996; Harshman et al. 2003; Janke et al. 2005) and sometimes expose broader species divergence (Schmitz et al. 2003; Eaton et al. 2009). Most exciting is the ability to utilise molecular tools to link modern crocodilians to their ancestors (Densmore and White 1991; Eaton et al. 2009).

Behavioural relationships

Molecular, morphological and cladistic insights may aid in developing an hypothesis linking modern crocodilian behaviours to those of their extinct archosaurian cousins. However, in the absence of hard paleontological evidence, much of this is conjecture. Nevertheless, probing of crocodilian behaviours may be important to a discussion of putative dinosaur behaviours.

Social signals and communication

Crocodilians can communicate with other members of their species by vocalisations. These social signals (Figure 2), some of which involve some form of percussion, produce water-borne vibrations and olfactory messages. Social signals include body posture or direct interactions between animals. For example, some of the social signals include a head emergent (some call it ‘head oblique’, e.g. Wang et al. 2007) and tail arched position, head slapping, jaw clapping, inflated posture, tail wagging or undulating (Vliet 1989), yawning and bumping or nosing an adjacent animal, as is seen in courtship (Garrick et al. 1978; Vliet 1989). These behaviours communicate specific information to animals nearby. For example, a head slap may be seen when a dominant animal returns to his usual territory, perhaps after hunting, and finds another adult animal present. The head emergent, tail arched position, along with either audible (to us) or inaudible bellowing, is an announcement that includes information on the bellower’s location, size and gender.

Sound plays an important role in crocodilian social behaviour. Numerous researchers have catalogued crocodilian vocalisations from ‘interest’ noises, such as simple grunts and growls, to distress calls of the young to grunts from young still in their eggs at hatching time (Campbell 1973; Garrick and Lang 1977; Herzog and Burghardt 1977; Garrick et al. 1978; Watanabe 1980; Hunt and Watanabe 1982; Vliet 1989; Vergne et al. 2007; Wang et al. 2007; Vergne and Mathevon 2008). When Watanabe (1980) analysed tapes of crocodilian vocalisations (Figure 3(A)–(D)) at the Smithsonian Institution 30 years ago, she used what was then the latest computerised technology much better than the old rolling drum sound spectrographs. With assistance from ornithologist Morton (1977), it was apparent that the crocodilian sounds fit well into his descriptions of avian and mammalian sounds. The vocalisations were in three major categories: harsh, low-frequency threatening sounds, such as a hiss; high frequency, pure tone fright or distress calls, typical of the distress grunt of a threatened hatchling or yearling; and calls between these two extremes, which may be classified as ‘interest’ calls. An interest noise may be in a lower frequency, but it is of moderately long duration and includes harmonics. Distress calls are chevron shaped, beginning at a higher frequency and ending, quite rapidly, at a lower frequency. They, too, have harmonics. But there is little in a crocodilian distress call to differentiate it from the distress call of a human. These are the sharp, rapid, high-pitched sounds of distress we make when we are suddenly hurt or frightened, sounds immediately understandable to other mammals. Bellows can be an interest sound, whereas hissing is a threat; both are low pitched, relatively long lasting and also may have harmonics. It would be logical to expect that if crocodilian vocalisations are similar in structure and meaning to those of birds and mammals, extinct archosaurs may well have made use of similar types of calls.

Reproduction

Understanding modern crocodilian reproductive behaviour may provide insights into the reproductive behaviours and strategies of ancestral forms. The most basic of crocodilian behaviours are their very successful reproductive strategies. Varricchio et al. (2008) and Prum’s (2008) commentaries on theropod reproductive behaviour lead the authors of this paper to suggest that crocodilian behaviour may be similar to that hypothesised for theropod dinosaurs and known for birds, especially the more basal of the avian groups (Sekercioglu 1999). Although there are environmental adaptations, we can assume that reproductive behaviours are as hard-wired into an animal’s genetic make-up as is the shape of a forelimb, the structure of an oviduct or even the capacity to produce teeth.

Our ability to determine living species identity (Brazaitis 1971, 1973a, 1973b; King and Brazaitis 1971) and accurately sex crocodilians (Brazaitis 1969a) are central to the understanding of modern crocodilian

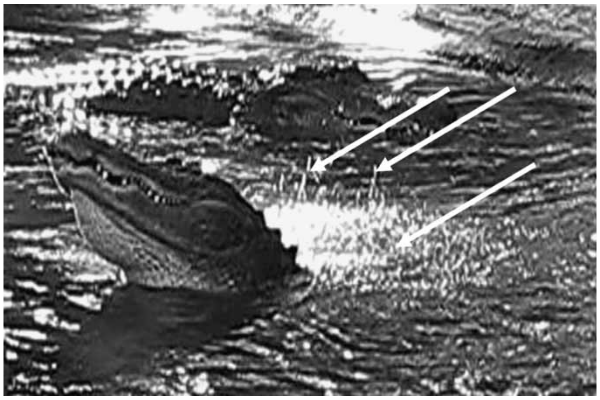


Figure 2. A large male American alligator, *A. mississippiensis*, raises his head in the bellowing posture. The expulsion of air from the inflated lungs, regulated at the throat, produces a roar-like bellow or coughing call. Water-borne vibrations accompany the call, causing droplets of water above the dorsal scalation (arrows) to leap vertically into the air. Musk is simultaneously emitted into the water from two throat glands located on the underside of the lower jaw. Crocodilian vocalisations are species and gender specific and vary in pattern, intensity, frequency, composition and range.

reproductive behaviours (Brazaitis and Abene 2008). Despite new technologies that improve field observation, there is little new in the scientific literature about behaviours of modern crocodilians (Higgs et al. 2002; Todd 2007; Vergne et al. 2007; Wang et al. 2007; Vergne and Mathevon 2008). During the past 30 years or so, the emphasis was placed on the husbandry and commercial development of crocodilians for products rather than studies of behavioural science.

All species of crocodilians practice universal reproductive behaviours (Thorbjarnarson 1996) that are programmed to occur at a time of the year when climatic conditions are most favourable for breeding, nesting and egg incubation, and for hatching to occur at a time when food of an appropriate size will be most abundant for offspring.

Crocodilian reproductive behaviours are highly consistent and conserved among individuals and species. Captive crocodilians experience different stimuli than wild crocodilians (Brazaitis and Abene 2008) – UV deprivation, differences in day/night lengths, unvarying ambient temperatures, interactions with other species, feeding behaviours, diets, etc. Nevertheless, their reproductive behaviours remain consistent with those of wild individuals. This is particularly true when nesting materials and conditions are provided that simulate wild environments. Breeding cycles in modern crocodilians are so closely programmed that a female will routinely breed during the same period each year, and subsequently build a nest and lay eggs in close proximity to or at the same site each year, in some cases virtually within the same calendar week (Thorbjarnarson 1992; Brazaitis and Abene 2008; Elsey et al. 2008). Equally fascinating is that offspring reared under artificial conditions from artificially incubated eggs, and deprived of parenting, mature and exhibit reproductive behaviours similar to those for wild animals. Furthermore, their annual reproductive cycles are similar to those of the species' native populations, suggesting a genetically hard-wired behaviour.

Thermoregulation to achieve optimum body temperature is an essential element needed to support metabolic functions, daily activity rhythms (Cott 1961; Brazaitis et al.

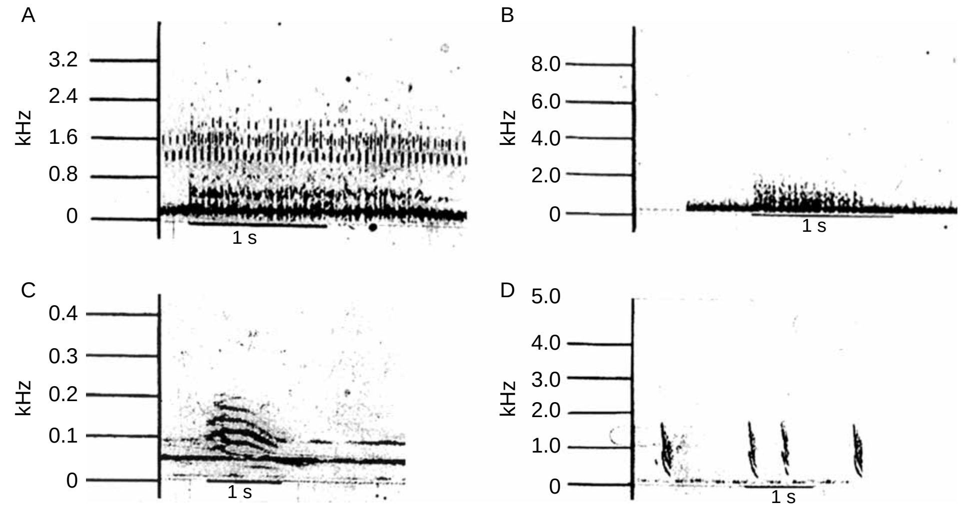


Figure 3. Sound spectrographs of American alligator, *A. mississippiensis*, vocalisations: (A) the bellow of an adult male, (B) bellow of an adult female, (C) female American alligator at her opened nest, facing new hatchling and (D) distress calls of hatchling American alligator.

1990) and reproductive behaviours of all modern crocodilians (Brandt and Mazzotti 1990). Crocodilians, as ectotherms, are critically dependent on exposure to narrow ranges of temperature. In the wild, temperature ranges usually are similar year to year. American alligators, for example, mate and build nests between certain weeks each year, depending upon the latitude. In captivity, to stimulate courtship and reproduction, the Chinese alligator was found to require exposure to a month or more of temperatures of approximately 8–10°C immediately before the breeding season of March to April, consistent with their breeding season in their home range in China.

Vocalisation and other social signals play an important role in crocodilian reproductive behaviour. Courtship is the initial activity that hails the beginning of the reproductive season for crocodilians. Animals need to advertise to make their locations known to each other. Their calls are species specific. For example, both sexes in both species of *Alligator* bellow (Figures 2 and 3(A) and (B)), although the Chinese alligator's (*A. sinensis*) sound is more cough-like. Some caiman (e.g. *Caiman yacaré*) make a sound that is more readily felt than heard by humans. Male gharials, *Gavialis gangeticus*, have a resonating chamber, called a ghara, at the distal end of the snout that surrounds the nares. This results in a horn-like sound (Brazaitis, personal observation; Whitaker and Basu 1983).

During this early courtship season, males may fight with other males or, in some species, females may fight with each other. These fights are for male territory, nesting territory and mates. Courtship results in an entire repertoire of new, stereotypical and highly programmed behaviours (Garrick and Lang 1977). The goal of courtship is to allow males and females of these rather pugnacious species to get close enough both to stimulate sexual behaviours and to allow for copulation. A male must be significantly larger than the female to be an acceptable mate (Figure 4). Behaviours are species specific and include approaching, head and/or neck rubbing, snout lifting, bubble blowing, splashing, sub-audible vibrations and circling, culminating in the male mounting the female. Mounting either results in the female breaking off the contact by swimming away or in copulation (Garrick and Lang 1977). Recent studies have shown that some female *A. mississippiensis* and Morelet's crocodile, *Crocodylus moreletii*, may mate with more than one male during mating season (Lisa et al. 2001; McVay et al. 2008; Lance et al. 2009). Despite this, Lance et al. (2009) showed that 70% of females in their study showed long-term mate fidelity, mating with the same male over a period of years.

Females are ready to lay eggs approximately 1 month post-copulation (Garrick and Lang 1977). Temperature and/or rainfall may affect the time of nesting, but it changes the time only by several weeks year to year (Garrick and Lang 1977; Lance 2003). For species that construct a mound nest of organic materials, nesting usually coincides with the rainy season, whereas hole-nesting species, such as *C. niloticus* (Cott 1961), generally nest during the dry season.

Figure 4. Cuban crocodiles, *Crocodylus rhombifer*, in copulatory position at the National Zoo, Washington, DC, USA (photo courtesy of John White). The female has assumed a 'head-up' submissive posture, signalling that the larger male is acceptable and will not be attacked. The male mounts the female from a dorsal position, wraps his body and tail laterally around the female until his tail crosses beneath the female with both cloacae aligned, to permit intromission. Intromission lasts only moments and may be repeated.

Table 2 assigns nesting strategies to 23 species of crocodilians, based on wild populations (Sill 1968; Joanen 1969; Brazaitis 1973a, 1973b; Thorbjarnarson 1992). Of these, seven species preferentially excavate a hole in sand beaches, river sandbars and banks, or gravel beds during the hot drier periods of the year. Hole-nesting species often encounter limited nesting sites and may practice colonial nesting strategies, particularly *Crocodylus johnstoni*, *C. niloticus* and *G. gangeticus*. The remaining species construct a significant mound nest composed of scraped together or mouth-carried organic, aquatic or forest debris materials, into which they excavate a chamber and deposit their eggs. Three species, *Crocodylus acutus*, *C. palustris* and *C. rhombifer*, are reported to hole nest and, on occasion, construct a mound nest in the wild (see Table 2).

Crocodilians deposit their eggs in a single event into a chamber, a 'nest', created by the female. The nest appears to protect temperature-sensitive eggs from extremes and variations in temperature. Stable incubation temperatures are a critical element for embryonic development, and range from about 29 to 36°C, depending on species and habitat environments (Magnusson et al. 1990). Ferguson (1985) provided extensive data on the incubation process. Ferguson and Joanen (1982) described the critical role that incubation temperature plays in determining the sex in *A. mississippiensis*, now found to be true for all crocodilians studied so far. The ability to detect and select a thermally appropriate site for the creation of a nest in which to

Table 2. Species size, nesting habitat and type of nest, egg clutch size and incubation.

Species	Species (size/m)	Preferred nesting habitat	Nest type	Range (no. eggs per clutch)	Approximate incubation days
Family: Alligatoridae					
Genus: *Alligator*					
A. mississippiensis	5.0	Inland freshwater wetland, coastal marsh	Organic mound	30–50	65–70
A. sinensis	2.0	Inland freshwater wetland	Organic mound	10–40	65–70
Genus: *Caiman*					
C. crocodilus		Inland freshwater wetland	Organic mound	15–30	80–82
C. c. crocodilus	2.8	Inland freshwater wetland	Organic mound		
C. c. apaporiensis[a]	2.0	Inland freshwater wetland	Organic mound		
C. c. fuscus	2.2	Inland freshwater wetland	Organic mound		
C. c. chiapasius		Inland freshwater wetland	Organic mound		
C. latirostris	2.5	Inland freshwater wetland	Organic mound	20–70	70
C. l. latirostris		Inland freshwater wetland	Organic mound		
C. l. chocoensis[a]		Inland freshwater wetland	Organic mound		
C. yacare	2.5	Inland freshwater wetland	Organic mound	21–38 30–60	75–80
Genus: *Melanosuchus*					
M. niger	5.0	Inland freshwater wetland	Organic mound	30–65	90
Genus: *Paleosuchus*					
P. palpebrosus	1.7	Inland freshwater wetland	Organic mound	10–15	90–100
P. trigonatus	2.3	Inland freshwater wetland	Organic mound, adopts termite nests	10–20	115
Family: Crocodylidae					
Genus: *Crocodylus*					
C. acutus	7.0	Inland freshwater and coastal wetlands	Hole, organic mound	30–60	90–100
C. intermedius	6.8	Freshwater wetland	Hole nesting	40–70	80–90
C. johnsoni	3.0	Freshwater wetland	Hole nesting	13 average	75–85
C. mindorensis	2.5	Freshwater wetland	Organic mound	10–20	85
C. moreletii	2.5	Inland freshwater and coastal wetlands	Organic mound	20–40	80
C. niloticus	7.0	Inland freshwater and coastal wetlands	Hole nesting	25–80	90–100
C. novaeguineae	3.4	Inland freshwater and coastal wetlands	Organic mound	22–45	80
C. palustris	4.0	Inland freshwater and coastal wetlands	Hole and mound	25–30	70–80
C. p. palustris		Freshwater wetland	Hole nesting	25–30	
C.p. kimbula[a]		Freshwater wetland	Mound nesting		
C. porosus	7.0	Inland freshwater and coastal wetlands	Organic mound	40–60	80–90
C. rhombifer	4.9	Inland freshwater and coastal wetlands	Hole and mound	30–40	60–75
C. siamensis	4.0	Freshwater wetland	Organic mound	20–50	80
Genus: *Mesistops*					
M. cataphractus	4.0	Inland freshwater wetland	Organic mound	16 average	110
Genus: *Osteolaemus*					
O. tetraspis	2.0	Inland freshwater wetland	Organic mound	10–20	85–105
O. t. tetraspis	2.0	Inland freshwater wetland	Organic mound		
O. t. osborni	1.5	Inland freshwater wetland	Organic mound		
Family: Gavialidae					
Genus: *Gavialis*					
G. gangeticus	7.0	Inland freshwater sandbars	Hole nesting	30–50	85–90
Genus: *Tomistoma*					
T. schlegelii	5.0	Inland freshwater wetlands	Organic mound	20–60	90

Note: [a]May not be a valid sub-species.
Source: Brazaitis (1973a, 1973b), King and Burke (1989), Sill (1968) and Thorbjarnarson (1992, 1996).

deposit and incubate eggs appears critical to the reproductive success of crocodilians.

The most productive nesting habitat for nearly all crocodilian species is freshwater wetlands/grasslands (Table 2). Saltwater crocodile, *C. porosus*, populations in the archipelago islands of Palau in the western Pacific, located 600 miles over open ocean from the nearest land mass, leave mangrove estuaries and forest habitats to seek the freshwater grasslands (Figure 5) of the islands' interior, in which they build their organic mound nests (Brazaitis et al. 2009). Some American alligators in Louisiana leave saline or brackish coastal marshes to build nests and rear young in inland freshwater-fed marshes. Others remain on levees, where there is fresh water, but that are surrounded by brackish water (Joanen 1969). Both the American alligator and the Chinese alligator build similar mound nests in freshwater grassland habitats.

Population size and distribution may well be dictated by the availability of appropriate nesting habitat. This habitat includes vegetation providing sufficient fuel to support fermentation and the resultant production of heat during the generally 70–90-day incubation period, to provide proper egg incubation temperatures. The greatest population density for *Caiman* in South America is in the prime nesting habitats of the Pantanal grasslands of Brazil (Brazaitis et al. 1996, 1998; Rebêlo and Lugli 2001) and the llanos of Venezuela (Thorbjarnarson 1991). *P. trigonatus*, an inhabitant of the Amazonian rainforest, lives in a habitat that is virtually devoid of direct warming sunlight. Its eggs require an incubation temperature of about 30°C. To compensate for the lack of heat-producing nesting material, *P. trigonatus* often builds its nest to incorporate active termite mounds. Thus, the nest is insulated from the cooling effects of direct contact with the forest floor, and 'borrows' the heat generated by the termite nest to augment the required incubation temperature (Magnusson et al. 1985, 1990).

Figure 5. Saltwater crocodile, *C. porosus*, nesting habitat in the freshwater grasslands of the interior highlands of the islands of Palau, Western Pacific. Lingual salt glands in adult and juvenile crocodilians (Grigg et al. 1980) are able to acclimate to changes in environmental salinity and excrete excess sodium and chloride ions (Cramp et al. 2008).

Observations at the Bronx Zoo of *A. sinensis*, *C. rhombifer*, *Crocodylus siamensis* and *Tomistoma schlegelii*, all organic mound-building species, showed that when deprived of organic nesting materials, females will excavate a hole in whatever substrate is available, deposit their eggs and then scrape over a mound of substrate covering. Under natural conditions, *A. sinensis* typically constructs a metre-high and equally wide organic mound nest similar to, but smaller than, that of the American alligator. However, under confined captive conditions and deprived of plant nesting materials, one Chinese alligator dug a hole for receiving her eggs that was virtually undetectable from the surrounding flat sand and bark substrate (Figure 6(A) and (B)).

The nest-building process may take several days to complete and does not commence until the female is ready to deposit her eggs. She will first select a suitable nesting site and may investigate a number of sites over several nights, even starting nests and then abandoning those she determines to be unsuitable. The availability of potential nesting sites may vary from year to year, depending on climatic conditions, such as sandbars that become exposed during dry seasons, or wetlands that may be flooded during particularly rainy years. Thus, nest sites are at a premium to all of the gravid females in a given population in any particular region. The availability of suitable nesting habitat is a limiting factor in crocodilian population expansion (Joanen 1969; Thorbjarnarson 1992; Brazaitis et al. 1996, 1998; Ryberg et al. 2002).

The first evidence of mound-type nest building may include the scratching together of surrounding vegetation, often called a 'pull', followed by successively more building activity over several days. Vegetation is generally heaped onto a mound by the female scratching material rearward with her hind feet, towards the centre of the nest site. American alligators are known to carry aquatic vegetation, mud, and sticks by mouth from the water and place them in the mound (Watanabe 1983).

Hole-type in-ground nests are dug by the female, who excavates material with her hind feet from beneath her, as she straddles the selected site. The depth of the excavation is generally determined by the reach of her hind limb. After a hole is dug into the nesting substrate, the female lays on top of the nest with her cloaca over the excavated egg chamber.

The deposition stance is somewhat tripod-like, the anterior body supported by the two front legs, and the extended tail providing the third support leg of the tripod, freeing the hind limbs. One of us (PB) has observed caiman laying their eggs into the soles of their two cupped hind feet, and gently releasing the eggs, one by one, into the nest cavity. The eggs usually are covered with a gelatinous material that appears to cushion the porcelainlike eggs as they drop onto one another. Eggs are laid in a stack from bottom to top. Once egg deposition is completed, the female climbs over and around the nest, covering it by scraping additional material over it with her hind legs until the eggs are completely buried in the egg chamber.

At the end of egg laying and nest building, female crocodilians appear to undergo an abrupt behavioural change towards heightened aggression at the slightest provocation and often remain at the nest site in attendance. Complete lack of attendance or diminishment of attendance as incubation progresses can result in nest predation. Watanabe's (1980) study of American alligator nesting behaviour in Georgia and Louisiana in the USA indicated great variability in female nest defence behaviour; this may not be the norm for all crocodilians. In the wild, American alligators may defend their nests vigorously throughout the approximately 2-month incubation period, may defend the nest on occasion or may not defend the nest at all. Nevertheless, females returned to the nests, crawled over them, leaving crawl marks on top of the nest and added additional vegetation. Nest predation can be fairly high. Although female American alligators may return to depredated nests to scrape together additional vegetation, predation was usually complete, leaving no intact, hatchable eggs. Eventually, the female abandons the depredated nest (Watanabe 1980).

Prior to egg hatching, even the most conscientious mother may leave the nest area to feed. But the advent of grunting from the young within the eggs prepares the female for nest excavation and probably also aids in hatching synchrony of the young (Vergne and Mathevon 2008; reviewed by Watanabe 1980). The female then crawls over the nest and, using forelimbs for digging and the snout apparently for sensing the egg chamber, she excavates the eggs. Eggs hatch serially, but within several hours the entire clutch hatches. Females carry newly hatched young to water, either singly (Figure 7, e.g. *A. mississippiensis*) or by the mouthful (e.g. *C. niloticus*), depending on species (Pooley 1977; Watanabe 1980). Unhatched eggs may also be carried, with the female gently cracking open the shell with her teeth (Pooley 1977; Watanabe 1980). The female also carries eggshells to clean up the nest site so that it does not attract predators (Pooley 1977; Watanabe 1980). During this time, females may communicate with the young (Figure 3(C); Watanabe 1980) or may be silent. Young may remain in proximity to the nest with the adult for several days or longer. Within weeks, the hatchlings may be moved. Different species or different populations of the same species may disperse at different times. Although some American alligators at the Okefenokee National Wildlife Refuge in Georgia, USA, remained with their mothers for two seasons, those in Louisiana began to disperse in weeks.

There is a high degree of parental care of young by the female parent. To a lesser degree, the male parent may also care for young. Females (and, in some cases, males) have been seen bringing food back to the young, serving as basking logs for the young and protecting young from predation (Brueggen 2002). In all species studied, crocodilians appear to pair bond in varying degrees. Experiments at the St. Augustine Alligator Farm, St. Augustine, FL, USA, with *C. siamensis*, found that not only did the female parent specifically allow her hatchling brood to feed from a piece of meat held firmly in her jaws, to the deliberate exclusion of her mate, but she also allowed an introduced hatchling American alligator to share in the feeding (Brueggen 2002).

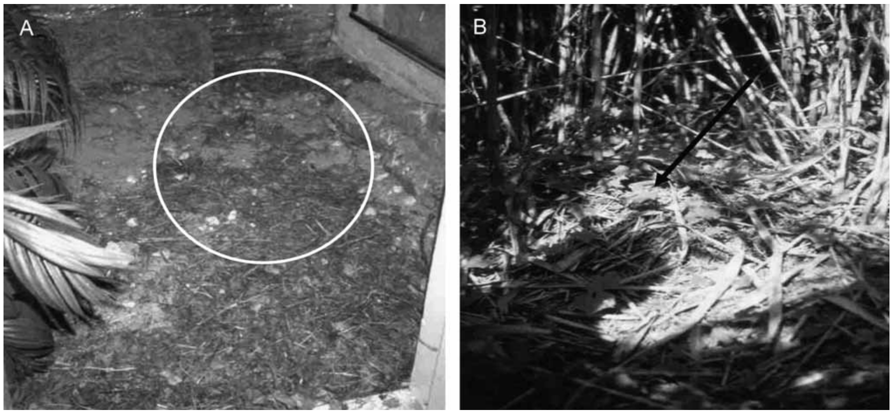


Figure 6. Crocodilians may alter nesting strategy. (A) Sand hole-nest of a captive Chinese alligator, *A. sinensis*, constructed by the female in the absence of organic nesting materials at the Bronx Zoo, Wildlife Conservation Society, NY, USA. Circle indicates nest site. (B) Organic mound-nest of cane grass, leaf debris and soil, constructed by *A. sinensis* in a natural 2-acre outdoor enclosure habitat at the Rockefeller Wildlife Refuge, Grand Chenier, LA, USA.

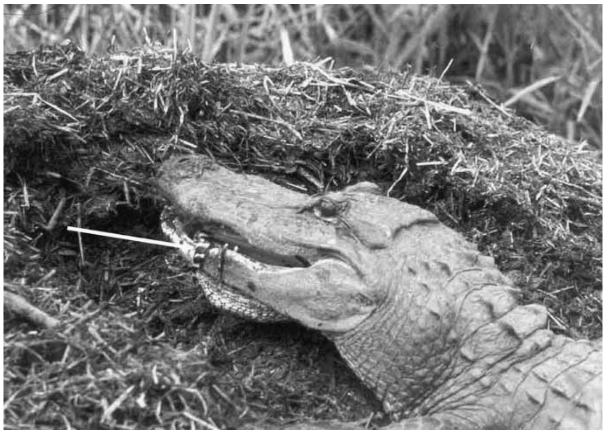


Figure 7. Female American alligator, *A. mississippiensis*, at excavated nest. She has opened nest and picked up a hatchling in her mouth. Bulge under lower jaw indicates a 'gular pouch,' in which the hatchling is carried to nearby water. Arrow indicates hatchling tail.

Learning

Only recently has the management of living zoological collections come to recognise the remarkable learning abilities of crocodilians. Drawing on basic crocodilian behaviours and sensory abilities, animal caregivers have developed crocodilian training programmes to enhance safe management, environmental enrichment and public education (Anon 2010). The limits of crocodilians' ability to respond to behavioural training are only beginning to be understood.

Omnivory

In captive situations, keepers have noted a broader range of feeding preferences among crocodilians than heretofore was expected. Caretakers at St. Augustine Alligator Farm in Florida, and at the Bronx Zoo, New York, USA, reported that when given the opportunity, *Alligator*, *Paleosuchus*, *Osteolaemus* and *Crocodylus* spp. will freely consume fruit and vegetables (Brueggen 2002). We do not know how this relates to diets in the wild, as we are accustomed to considering crocodilians as top predators. We do, however, know that they consume anything, including rocks (gastroliths), which they may harbour for prolonged periods (Cott 1961; Brazaitis 1969b), so fruit- and vegetable-eating behaviour may be more common than we think.

Colouration

Hatchling crocodilians are cryptically coloured and well camouflaged from predators. Juveniles are more vividly coloured than adults, but they basically retain their birth patterning to adulthood, when body colouration tends to fade to a uniform drab colour. However, two species of crocodilians undergo ontogenetic colour changes and have young that differ in colour and pattern from the adults, unlike the colour and pattern changes that birds exhibit as they mature. Hatchling Chinese alligators, *A. sinensis*, are predominantly black or dark brown with yellow-to-white markings and a conspicuous yellow-to-orange X on the snout (Figure 8(A)). By the end of the first year, the bright colouration fades and is replaced by overall grey and white body colouration with dark markings (Figure 8(B)). All

Figure 8. Ontogenetic colour and pattern changes occur in only two species of crocodilians: Chinese alligator, *A.sinensis*, and West African dwarf crocodile, *Ostolaemus tetraspis*. Both crocodilians are secretive dwarf species that utilise caves. (A) Hatchling *A. sinensis* are brightly coloured, with dark body bands and white and yellow markings. The dorsal aspect of the snout bears a conspicuous orange or yellow 'X'. (B) *A. sinensis* at 1 year, showing dark-mottled patterning on a white/grey body colour. (C) Mature *A. sinensis* in unicolour drab grey body colouration.

distinct colouration and markings are lost by maturity (Figure 8(C)). The African dwarf crocodile, *Osteolaemus tetraspis*, has dark brown-coloured young with yellow highlights and black markings on the head and body. The adult is uniformly coloured. Coincidentally, both Chinese alligators and African dwarf crocodiles are dwarf species that make use of burrows and, unlike other crocodilians, have large dark brown irises (Brazaitis 1973a). Chinese alligators build long, complex, many roomed burrows for year-round living including both winter hibernation and summer aestivation (Watanabe 1983). Similarly, *Osteolaemus* excavates burrows (Thorbjarnarson 1992) and may live communally in them and use them for aestivation in the hot summer (Waitkuwait 1989).

Integumentary sense organs (ISOs)

The presence of integumentary sense organs (ISOs; Brazaitis 1987) on crocodilians was described by Von Wettstein (1937) and, more recently, these were reported to be tactile and vibration sensing receptors (Necker 1974; Jackson et al. 1999; Soares 2002), with chemosensory and osmoregulatory functions (Jackson and Brooks 2007). Soares (2002) renamed ISOs as dome pressure receptors. She found them to be pressure sensitive and reported their occurrence in ancestral crocodyliforms. ISOs are restricted to the bony and soft tissue head regions of Alligatoridae species (Figure 9(A)), and are present on all body scalation of the Crocodylidae and Gavialidae (Figure 9(B)), with the possible exception of the mid-ventral caudal scalation that makes contact with the ground. Similarly, salt glands are also found on the tongue of Crocodylidae but not on the Alligatoridae (Grigg et al. 1980; Taplin et al. 1981; Cramp et al. 2008).

Observation of crocodilian behaviours at the Bronx Zoo (Brazaitis and Abene 2008) illustrated that body regions that bear ISOs are heavily used during courtship and for prey location, and may play a role in monitoring nest temperature. Many courtship behaviours involve sounds or water borne, vibration-producing social signals (mechanoreception) or rubbing profusely ISO-populated regions on the head and body regions of the other sex in pre-copulatory play (tactile stimulation; Figure 10(A)). The latter behaviours frequently result in what appears to be overstimulation, leading to scratching and rubbing. Territorial displays and courtship are often accompanied by the dispensing of musk (chemical release into the environment) from gular glands on the underside of the throat and at the cloaca.

As noted earlier, many vocalisations contain a subacoustic component. For example, in bellowing, as air is expelled from the inflated body, the thoracic regions of the body vibrate (Figure 2), producing lateral and dorsal vibrations. The water in contact with the body vibrates as well, in a pattern with the vocalisation. Droplets of water above the back may be forced vertically into the air in a display that sometimes is referred to as ‘dancing water’. Other crocodilians in the same body of water, both male and female, may respond to the vocalisations by orienting towards the sound source and moving in that direction (Brazaitis, personal observation; Watanabe 1980, 1983). We suggest that ISOs serve as vibratory receptors and are well developed during embryonic stages (Figure 10(B)).

ISOs appear to assist in nest site selection. All crocodilians have ISOs in the greatest profusion on the regions surrounding the anterior snout and jaws (Figure 10(B)). Gravid female crocodilians generally search for a nest site that is ‘warm’ relative to the general environment, and commence to dig ‘test’ holes. After digging a shallow hole, the female puts her snout into the hole before moving on or proceeding to excavate a nest (Brazaitis, personal observation; Watanabe 1983). The ability to use thermal detection in nest site selection may even be demonstrated in captivity, where water areas in crocodilian enclosures may be artificially heated to 25–30°C, while land substrates may remain at ambient lower temperatures. When water temperatures are elevated above substrate temperatures, crocodilians will often erroneously select for the warmer water as a ‘nest site’ in which to lay their eggs. If the substrate is then elevated above the water temperature, the female is redirected and then selects the substrate as an appropriate nest site.

Females attending a nest in the wild may thrust their ISO-bearing snouts into the substrate of the nest and remove or add materials, as needed, to maintain incubation temperatures. Lastly, crocodilians have massive snouts and are capable of exerting crushing power with their jaws. ISOs are particularly profuse on the lateral jaws, inside the mouth and around the base of the teeth (Figure 11(A)). Adult crocodilians are capable of picking up eggs and one or more neonates at a time in their jaws (tactile) unharmed, and carry them to safety (Ferguson 1979). Certainly, additional studies are needed to document how crocodilian sensory structures are utilised in reproduction and other behaviours. The presence of numerous foramina in bones that underlie regions where ISOs are particularly profuse (Figure 11(B)) may suggest a more complex crocodilian sensory capability.

Discussion

Information on crocodilians indicates the likely descent of dinosaurs and their relatives from a crocodilian-like ancestor. Thus, parallels between extant crocodilians and what we can hypothesise about the lives of some of the dinosaurs are not just tempting, but they are likely.

There is some evidence that some dinosaurs produced sounds. The lambeosaurines, for example, had crests that

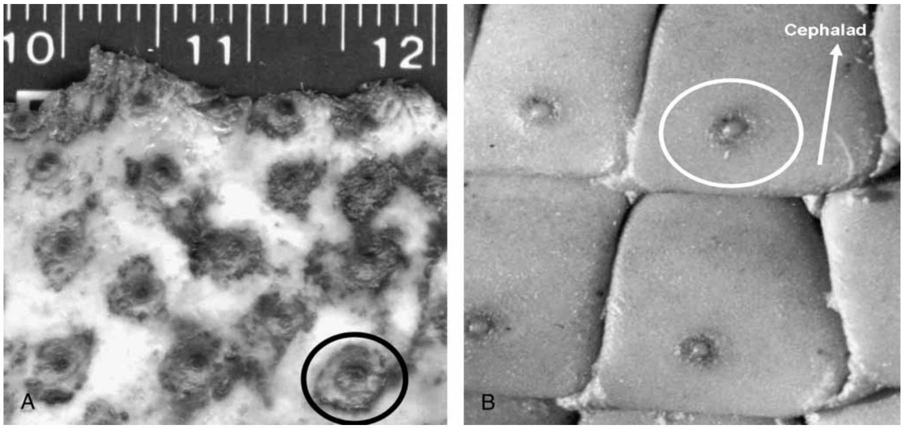


Figure 9. ISOs occur on the head and body scalation of members of the family Crocodylidae and Gavialidae, but are only present on the head in Alligatoridae: (A) circle indicates a single ISO on a skin fragment from the anterior mandible of a 2.5-m long adult male *A. mississippiensis*; (B) ISOs on the posterior region of the ventral scales of *C. niloticus*. A single ISO is generally found on each scale, although a single row of several ISOs may be found on ventral scalation in some species.

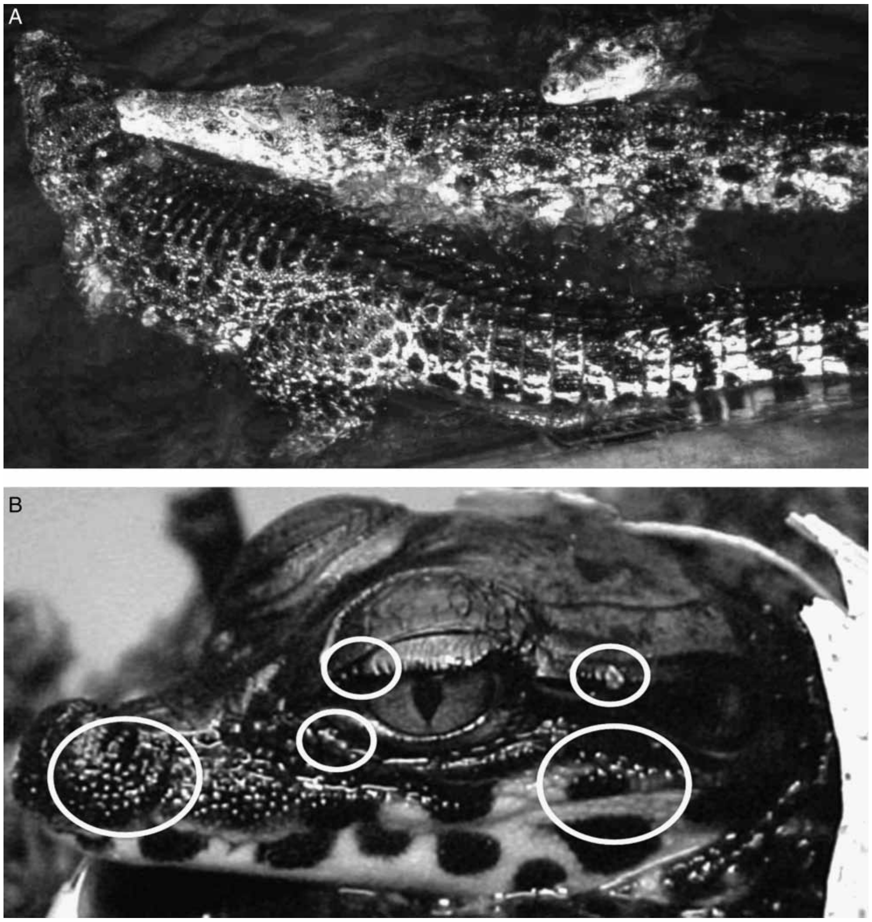


Figure 10. Body regions bearing ISOs are employed during courtship and reproduction: (A) two female Cuban crocodiles, *Crocodylus rhombifer*, engage in rubbing their ISO-bearing jaw regions on each other and the male (left), as a prelude to copulation with the male; (B) ISOs are well developed in hatchling crocodilians. Circles indicate ISOs on a hatchling West African dwarf crocodile, *O. tetraspis*, emerging from its egg.

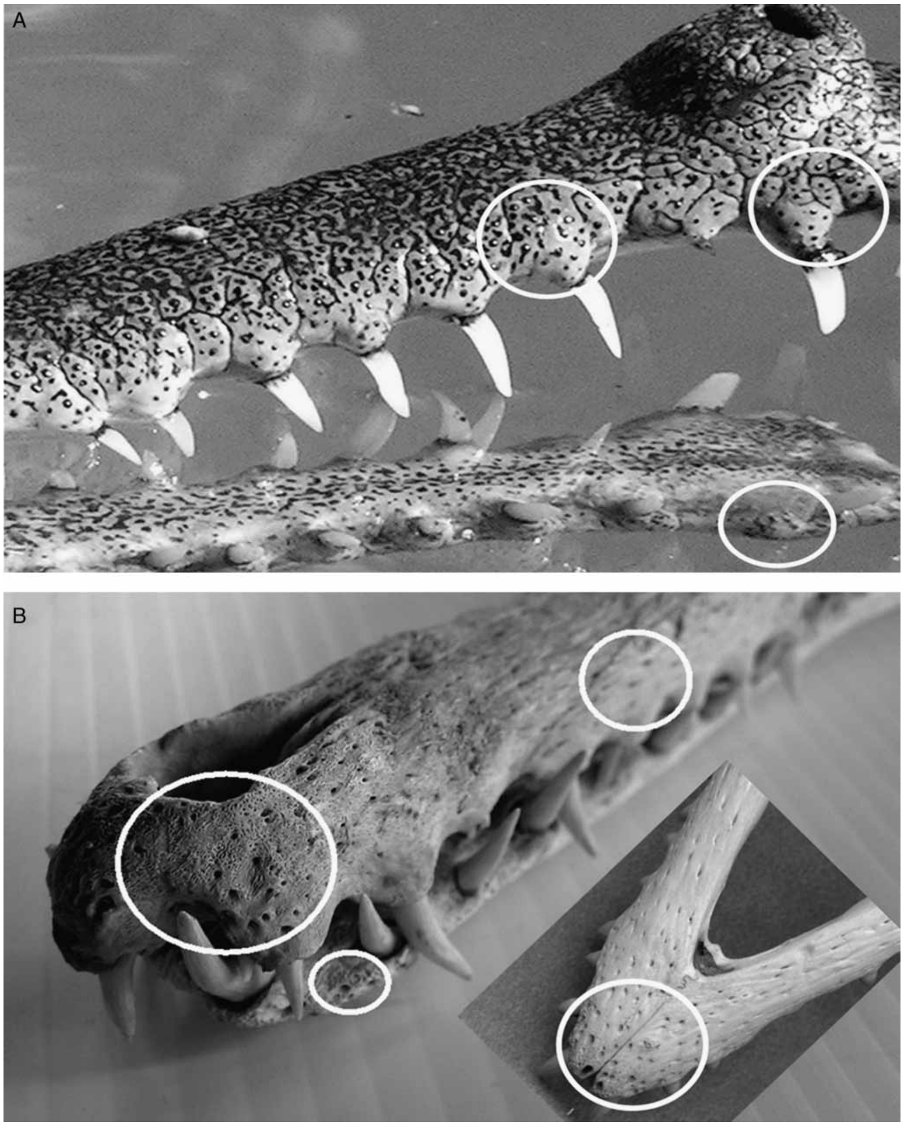


Figure 11. External ISOs are highly innervated (Von Wettstein 1937; Jackson and Brooks 2007) and appear to be closely associated with foramina in underlying bone: (A) ISOs on the maxilla, mandible and surrounding the teeth of an adult female gharial, *G. gangeticus*; (B) foramina underlying skin bearing ISOs on the maxilla of the Malayan false gavial, *T. schlegelii*, family Gavialidae. Insert: foramina on ventral mandible of a juvenile Nile crocodile, *C. niloticus.*

appeared to be resonating chambers (Weishampel 1981, 1997; Evans 2006). Weishampel (1981) assumed, based on an acoustic analysis of the nasal cavity structure, that adults made low-frequency sounds, while juveniles produced sounds in higher frequencies. He suggested that these hadrosaurs vocalised as a means of communication between parent and offspring. But hadrosaurs are on a different line of evolution from sauropod dinosaurs and theropods, thus leading to the following question: Did saurischians, who had less-complex apparati for vocal resonation, also communicate through vocalisations? There is no reason to assume they did not, especially in view of the highly vocal communicatory behaviours between crocodilian mothers and their young.

Varricchio et al. (2008) hypothesised that *Troodon*, *Oviraptor* and *Citipati*, troodontid and oviraptorid dinosaurs, respectively, were likely to have male-only parental care of the nest. They based their conclusion on comparison of egg and female body size in birds and crocodilians, and leg bone microscopic structure, indicating that there was no recent resorption within the long bones. Had the long bones shown resorption, it could be assumed that the specimen on the nest was a female that had recently laid eggs, and the resorption would be from the removal of calcium from the bone to produce the calcareous shells. The assumption that *Troodon* (Varricchio et al. 1997, 2008) and *Oviraptor* (Norell et al. 1995) would be brooding eggs like a bird is fascinating. But we do not know how attentive the animal was. Did it ever leave the nest to feed? That would be necessary if the brooding parent helped the young hatch, as crocodilians do, as that requires significant energy expenditure. Was the nest exposed to the elements or were the eggs buried under soil or vegetation, as occurs in mound nest building crocodilians? Although Jackson (personal communication) argues against a covered nest for *Troodon*, based on eggshell pore density and gas conductance, an exposed nest would assume constant parental care both for maintaining a constant incubation temperature and for protection of the eggs. An open nest with a brooding parent also implies that the species was endothermic or at least maintained a body temperature higher than ambient conditions. That a male was the brooding parent is not strange. Male crocodilians were seen to participate in parental behaviour (Brazaitis, personal observation; Blohm 1982; Watanabe 1983) and it would not be unexpected for male dinosaurs to also have participated in parental care.

As noted by Meng et al. (2004), the fossilised nest of 34 juvenile *Psittacosaurus* sp. along with an adult appears to illustrate post-hatching parental care in this species. Again, this may indicate behaviour homologous to that of ancient crocodilians, although it is possible that similar behaviours evolved numerous times during archosaurian evolution.

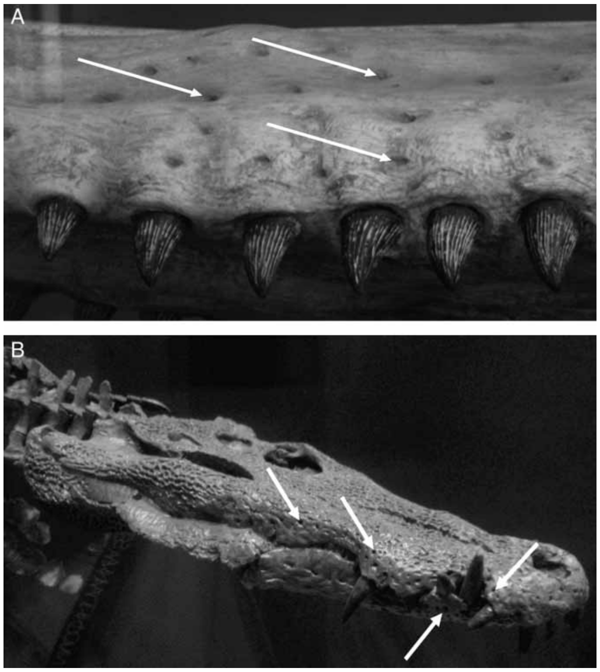


Figure 12. Similar foramina occur in fossil forms in regions corresponding to those on modern crocodilians: (A) arrows indicate foramina on the jaws of *Kronosaurus* from the early Cretaceous of Australia (Longman 1924; *Kronosaurus* in the collection of the Museum of Comparative Zoology, Boston, MA, USA); (B) arrows indicate foramina on the jaws of *Borealosuchus* (*Leidyosuchus*) (cast) Crocodyliformes, Eusuchia, from the late Cretaceous and Eocene of North America (Brochu 1997; Museum of the Rockies, Bozeman, MT, US).

Structures that appear to be ISOs are visible on some saurischian skulls, such as on *T. rex*, *Kronosaurus* and *Borealosuchus* (Figure 12(A) and (B)), and on the skin imprints of other dinosaurs. Does this mean that these sense organs, that appear to be also present in the skulls of crocodilian ancestors, somehow functioned similarly in ancient crocodiles, saurischian dinosaurs and modern crocodiles? Are such ISOs similar to the sensory organs found between the teeth of extant crocodilians that allow the adult to sense the presence of a hatchling in her mouth (Ferguson 1979)? These are questions to be pondered and to which there may never be answers.

Our point of view is purely of interest because it makes us realise that *Troodon*, whether it was a male or a female sitting on the nest, whether the nest was exposed or was covered with decomposing plant material or with the soil substrate, was carrying out parental behaviour, as were *Citipati*, *Oviraptor* and *Psittacosaurus*. If, indeed, that behaviour was similar to the parental behaviour of crocodilians and birds, the importance of the discovery is that this is possibly hard-wired, genetically predetermined behaviour, along with the physiological mechanisms that facilitate this behaviour, and was inherited from some of the earliest reptiles – and, dare we suggest, perhaps from even earlier species.

Acknowledgements

We wish to express our thanks to David Varricchio, Frankie Jackson, Montana State University, Bozeman, MT, and the National Science Foundation for travel funding to allow our attendance at the 4th International Symposium on Dinosaur Eggs and Babies, and for their hospitality. Special thanks to Frankie Jackson for her assistance in the preparation of the figures used in the manuscript. Thanks also to Gregory Watkins-Colwell and the Yale Peabody Museum of Natural History, Department of Vertebrate Zoology; John White for use of images; Bruce Foster and Bill Holmstrom, NY Wildlife Conservation Society; Joseph Martinez and Harvard University, Museum of Comparative Zoology, Cambridge, MA; Museum of Natural History, University of Kansas, Lawrence, KS; John Brueggen and the St. Augustine Alligator Farm, St. Augustine, FL; Bruce Shwedick and Dr. Kent Vliet.

References

Alibardi L, Toni M. 2008. Cytochemical and molecular characteristics of the process of cornification during feather morphogenesis. Prog Histochem Cytochem. 43(1):1–69.

Amato G, Gatesy J, Brazaitis P. 1994. PCR assays of variable nucleotide sites for identification of conservation units. In: Molecular ecology and evolution: approaches and applications. Basel, Switzerland: Birkhauser. p. 215–226.

Anon. 2010. Professional development program: crocodilian biology and captive management. St. Augustine Alligator Farm, May 21–28, 2010, St. Augustine, FL. Silver Springs, MD: Association of Zoos & Aquariums (unpagin).

Bagwill A, Sever DM, Elsey RM. 2009. Seasonal variation of the oviduct of the American alligator, *Alligator mississippiensis* (Reptilia: Crocodylia). J Morphol. 270:702–713.

Blohm T. 1982. Husbandry of Orinoco crocodiles (*Crocodylus intermedius*) in Venezuela. In: Crocodiles: Proceedings of the 5th Working Meeting of the Crocodile Specialist Group, IUCN – The World Conservation Union, Gland, Switzerland. p. 267–285.

Brandt LA, Mazzotti FJ. 1990. The behavior of juvenile *Alligator mississippiensis* and *Caiman crocodilus* exposed to low temperatures. Copeia. 1990(3):867–871.

Brazaitis P. 1969a. Determination of sex in living crocodilians. Br J Herpetol. 4:54–58.

Brazaitis P. 1969b. The occurrence and ingestion of gastroliths in two captive crocodilians. Herpetologica. 25:63–64.

Brazaitis P. 1971. *Crocodylus intermedius* a review of the recent literature. Zoologica. 56:71–75.

Brazaitis P. 1973a. The identification of living crocodilians. Zoologica. 58(3–4):59–101.

Brazaitis P. 1973b. The identification of *Crocodylus siamensis*. Zoologica. 58:43–45.

Brazaitis P. 1981. Maxillary regeneration in a marsh crocodile *Crocodylus palustris*. J Herpetol. 15(3):360–362.

Brazaitis P. 1987. Identification of crocodilian skins and products. In: Wildlife management: crocodiles and alligators. Chapter 38. Chipping Norton, NSW: Surrey Beatty & Sons. p. 374–386.

Brazaitis P, Abene J. 2008. A history of crocodilian science at the Bronx Zoo Wildlife Conservation Society. Herp Rev. 39(2):135–148.

Brazaitis P, Eberdong J, Brazaitis PJ, Watkins-Colwell GJ. 2009. Notes on the saltwater crocodile *Crocodylus porosus* in the Republic of Palau. Bull Peabody Mus Nat Hist. 50(1):27–48.

Brazaitis P, Rebêlo GH, Yamashita C. 1996. The status of *Caiman crocodilus* and *Melanosuchus niger* populations in the Amazonian regions of Brazil. Amphibia Reptilia. 17:377–385.

Brazaitis P, Rebêlo GH, Yamashita C. 1998. The distribution of *Caiman crocodilus crocodilus* and *Caiman yacare* populations in Brazil. Amphibia Reptilia. 19:193–201.

Brazaitis P, Yamashita C, Rebêlo GH. 1990. A summary report of the CITES central South American caiman study. Phase I: Brazil. In: Crocodiles. Proceedings of the 9th Working Meeting of the Crocodile Specialist Group. AQGland, Switzerland: IUCN. Vol. 1. p. 100–115.

Brochu CA. 1997. A review of *Leidyosuchus* (Crocodyliformes Eusuchia) from the Cretaceous through Eocene of North America. J Vert Paleontol. 17(4):679–697.

Brochu CA. 2001. Crocodylian snouts in space and time: Phylogenetic approaches toward adaptive radiation. Am Zool. 41:564–585.

Brochu CA. 2003. Phylogenetic approaches toward crocodilian history. Ann Rev Earth Planet Sci. 31:357–397.

Brueggen J. 2002. Crocodilians: fact vs. fiction. Proceedings of the 16th Working Meeting of the Crocodile Specialist Group; 2002 Oct 7–10; Gainesville, FL. p. 204–210.

Campbell HW. 1973. Observations on the acoustic behavior of crocodilians. Zoologica. 58:1–11.

Cott HB. 1961. Scientific results of an inquiry into the ecology and economic status of the Nile crocodile (*Crocodylus niloticus*) in Uganda and Northern Rhodesia. Trans Zool Soc London. 29(4):211–337.

Cramp RL, Meyer EA, Sparks N, Franklin CE. 2008. Functional and morphological plasticity of crocodile (*Crocodylus porosus*) salt glands. J Exp Biol. 211:1482–1489.

Dalla Valle L, Nardi A, Gelmi C, Toni M, Emera D, Alibardi L. 2009a. β-keratins of the crocodilian epidermis: composition structure and phylogenetic relationships. J Exp Zool B Mol Dev Evol. 312B:42–57.

Dalla Valle L, Nardi A, Toni M, Emera D, Alibardi L. 2009b. Beta-keratins of turtle shell are glycine–proline–tyrosine rich proteins similar to those of crocodilians and birds. J Anat. 214:284–300.

Densmore LD. 1983. Biochemical and immunological systematics of the order Crocodilia. In: Evolutionary biology. New York, NY: Plenum Press. p. 397–465.

Densmore LD, III. 1989. Molecular systematics of the order Crocodilia. Am Zool. 29:831–841.

Densmore LD, III, White PS. 1991. The systematics and evolution of the Crocodilia as suggested by restriction endonuclease analysis of mitochondrial and nuclear ribosomal DNA. Copeia (3):602–615.

Dixon JR. 1979. Origin and distribution of reptiles in lowland tropical rainforests of South America. In: Chapter 9: The South American herpetofauna: Its origin, evolution, and dispersal. Monograph No. 7. Lawrence, Kansas: Museum of Natural History, The University of Kansas. p. 217–240.

Dodson P. 2003. Allure of El Largato – Why do dinosaur palaeontologists love alligators, crocodiles, and their kin? Anat Rec. 274A:887–890.

Donoghue MJ, Doyle JA, Gauthier J, Kluge AG, Rowe T. 1989. The importance of fossils in phylogeny reconstruction. Annu Rev Ecol Syst. 20:431–460.

Duellman WE. 1979. The South American herpetofauna: a panoramic view. In: Chapter 1: The South American herpetofauna: Its origin, evolution, and dispersal. Monograph No. 7. Lawrence, Kansas: Museum of Natural History, The University of Kansas. p. 1–28.

Eaton M, Martin A, Thorbjarnarson J, Amato G. 2009. Species level diversification of African dwarf crocodiles (Genus *Osteolaemus*): a graphic and phylogenetic perspective. Mol Phylogenet Evol. 50(3):496–506.

Elsey RM, Trosclair PL III, Glenn TC. 2008. Nest-site fidelity in American alligators in a Louisiana coastal marsh. Southeast Nat. 7(4):737–743.

Erickson GM. 1996. Incremental lines of von Ebner in dinosaurs and the assessment of tooth replacement rates using growth line counts. Proc Natl Acad Sci USA. 93:14623–14627.

Evans DC. 2006. Nasal cavity homologies and cranial crest function in lambeosaurine dinosaurs. Paleobiology. 32(1):109–125.

Farmer CG. 2001. A new perspective on the origin of endothermy. In: New perspectives on the origin and early evolution of birds: Proceedings of the international symposium in honor of John H. Ostrom. New Haven, CT: Yale Peabody Museum of Natural History. p. 389–409.

Ferguson MWJ. 1979. The palatal histology of *Alligator mississippiensis*. IRC Med Sci: Resp Syst. 7:472.

Ferguson MWJ. 1985. Reproductive biology and embryology of the crocodilians. In: Biology of the Reptilia. Vol. 14:Development A. New York: John Wiley and Sons. p. 329–491.

Ferguson MWJ, Joanen T. 1982. Temperature of egg incubation determines sex in *Alligator mississippiensis*. Nature. 296(5860): 850–853.

Garrick LD, Lang JW. 1977. Social signals and behaviors of adult alligators and crocodiles. Am Zool. 17:225–239.

Garrick LD, Lang JW, Herzog HA, Jr. 1978. Social signals of adult American alligators. Bull Am Mus Nat Hist. 160:153–192.

Gatesy J, Amato G. 2008. The rapid accumulation of consistent molecular support for intergeneric crocodilian relationships. Mol Phylog Evol. 48:1232–1237.

Gatesy J, Amato G, Norell M, DeSalle R, Hayashi C. 2003. Combined support for wholesale taxic atavism in Gavialine crocodylians. Syst Biol. 52(3):403–422.

Gillooly JF, Allen AP, Charnov EL. 2006. Dinosaur fossils predict body temperature. PLoS Biol. 4(8):e248, doi:101371/journalpbio0040248.

Gorzula S, Paolillo A. 1986. La ecologia y estado actual de los aligatoridos de la Guyana Venezolana. In: Crocodiles. Proceedings of the 7th Meet IUCN/SSC Crocodile Specialist Group. Caracas, Venezuela. Gland, Switzerland: IUCN. p. 37–54.

Grigg GC, Taplin LE, Harlow P, Wright J. 1980. Survival and growth of hatchling *Crocodylus porosus* in saltwater without access to fresh drinking water. Oecologia. 47:264–266.

Harris MP, Hasso SH, Ferguson MW, Fallon JF. 2006. The development of archosaurian first-generation teeth in a chicken mutant. Cur Biol. 16:371–377.

Harshman J, Huddleston CJ, Bollback JP, Parsons TJ, Braun MJ. 2003. True and false gharials: a nuclear gene phylogeny of Crocodylia. Syst Biol. 52(3):386–402.

Herzog HA, Burghardt GM. 1977. Vocalization in juvenile crocodilians. Z Tierpsychol. 44:294–304.

Higgs DM, Brittan-Powell EF, Soares D, Souza MJ, Carr CE, Dooling RJ, Popper AN. 2002. Amphibious auditory responses of the American alligator (*Alligator mississippiensis*). J Comp Physiol A. 188: 217–223.

Hillenius WJ, Ruben JA. 2004. Getting warmer, getting colder: reconstructing crocodylomorph physiology. Physiol Biochem Zool. 77(6):1068–1072.

Hunt RH, Watanabe ME. 1982. Observations on the maternal behavior of the American alligator *Alligator mississippiensis*. J Herpetol. 16(3):235–239.

Jackson K, Brooks DR. 2007. Do crocodiles co-opt their sense of “touch” to “taste”? A possible new type of vertebrate sensory organ. Amphibia Reptilia. 28:277–285.

Jackson K, Butler DG, Youson JH. 1999. Morphology and ultrastructure of possible integumentary sense organs in the estuarine crocodile (*Crocodylus porosus*). J Morphol. 229:315–324.

Janke A, Gullberg A, Hughes S, Aggarwal RK, Arnason U. 2005. Mitogenic analyses place the gharial (*Gavialis gangeticus*) on the crocodile tree and provide pre-K/T divergence times for most crocodilians. J Mol Evol. 61:620–626.

Joanen T. 1969. Nesting ecology of alligators in Louisiana. Proc SE Assoc Game Fish Commun. 23:141–151.

King FW, Brazaitis P. 1971. Identification of commercial crocodilian skins. Zoologica. 56:15–70.

King FW, Burke RL. 1989. Crocodilian, tuatara, and turtle species of the world: a taxonomic and geographic reference. Washington, DC: Association of Systematics Collections. p. 1–15.

Lance SL, Tuberville TD, Dueck L, Holz-Schietinger C, Trosclair PL, III, Elsey RM, Glenn TC. 2009. Multiyear multiple paternity and mate fidelity in the American alligator, *Alligator mississippiensis*. Mol Ecol. 18:4508–4520.

Lance VA. 2003. Alligator physiology and life history: the importance of temperature. Exp Gerontol. 38(7):801–805.

Lisa MD, Glenn TC, Elsey RM, Dessauer HC, Sawyer RH. 2001. Multiple paternity and mating patterns in the American alligator, *Alligator mississippiensis*. Mol Ecol. 10:1011–1024.

Longman HA. 1924. A new gigantic marine reptile from the Queensland Cretaceous. *Kronosaurus queenslandicus* new genus and species. Mem Queensl Mus. 8:26–28.

Luther DA, Greenberg R. 2009. Mangroves: a global perspective on the evolution and conservation of their terrestrial vertebrates. Bioscience. 59(7):602–612.

Magnusson WE, Lima AP, Hero J, Sanaiotti TM, Yamakoshi M. 1990. *Paleosuchus trigonatus* nests: Sources of heat and sex ratios. J Herpetol. 24(4):397–400.

Magnusson WE, Lima AP, Sampaio RM. 1985. Sources of heat for nests of *Paleosuchus trigonatus* and a review of crocodilian nest temperatures. J Herpetol. 19(2):199–207.

McAliley LR, Willis RE, Ray DA, White PS, Brochu CA, Densmore LD III. 2006. Are crocodiles really monophyletic? Evidence for subdivisions from sequence and morphological data. Mol Gen Evol. 39:16–32.

McVay JD, Rodriguez D, Rainwater TR, Dever JA, Platt SG, McMurry ST, Forstner MRJ, Densmore LD. 2008. Evidence of multiple paternity in Morelet’s crocodile (*Crocodylus moreletii*) in Belize, CA, inferred from microsatellite markers. J Exp Zool. 309A: 643–648.

Meers MB. 1999. Evolution of the crocodylian forelimb: anatomy biomechanics and functional morphology [doctoral thesis]. The John Hopkins University School of Medicine.

Meng Q, Liu J, Varricchio DJ, Huang T, Gao C. 2004. Parental care in an ornithischian dinosaur. Nature. 431:145–146.

Morton ES. 1977. On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. Am Nat. 111:855–869.

Necker R. 1974. Dependence of mechanoreceptor activity on skin temperature in Sauropsids: I Caiman. J Comp Phys. 92:65–73.

Norell MA, Clark JM, Chiappe LM, Dashzeveg D. 1995. A nesting dinosaur. Nature. 378:775–776.

Poe S. 1996. Data set incongruence and the phylogeny of crocodilians. Syst Biol. 45(4):393–414.

Poling J. 1995/1997. Geologic ages of earth history [citted 2009 May 20]. Available from: http://www.dinosauria.com/dml/history.htm.

Pooley AC. 1977. Nest opening response of the Nile crocodile *Crocodylus niloticus*. J Zool. 182:17–26.

Prum RO. 2008. Who’s your daddy? Science. 322:1799–1800.

Prum RO, Brush AH. 2002. The evolutionary origin and diversification of feathers. Quar Rev Biol. 77(3):261–295.

Rebêlo G, Lugli L. 2001. Distribution and abundance of four caiman species (Crocodylia: Alligatoridae) in Jaú National Park, Amazonas, Brazil. Rev Biol Trop. 49(3–4):1095–1109.

Ryberg WA, Fitzgerald LA, Honeycutt RL, Cathey JC. 2002. Genetic relationships of American alligator populations distributed across different ecological and geographic scales. J Exp Zool. (Mol Dev Evol). 294:325–333.

Salisbury SW, Molnar RE, Frey E, Willis PMA. 2006. The origin of modern crocodyliforms: new evidence from the Cretaceous of Australia. Proc Royal Soc. B. 273:2439–2448.

Savin SM. 1977. The history of the earth’s surface temperature during the past 100 million years. Annu Rev Earth Planet Sci. 5:319–355.

Schmitz A, Mausfeld P, Hekkala E, Shine T, Nickel H, Amato G, Böhme W. 2003. Molecular evidence for species level divergence in African Nile crocodiles *Crocodylus niloticus* (Laurenti 1786). Comptes Rendus Palevol. 2(2003):703–712.

Schweitzer MH, Watt JA, Avca R, Knapp L, Chiappi L, Norell M, Marshall M. 1999. Beta-keratin specific immunological reactivity in feather-like structures of the Cretaceous Alvarezsaurid, Shuvuuia desert. J Exp Zool B: Mol Dev Evol. 285(2):146–157.

Scott CR. 2008. Climate history. Available from: http://wwwscotesecom/climate.htm

Sekercioglu C. 1999. Megapodes: a fascinating incubation strategy. Harvard J Undergraduate Sci. 5(2):77–83.

Seymour RS, Bennett-Stamper C, Johnston SD, Carrier DR, Grigg GC. 2004. Evidence for endothermic ancestors of crocodiles at the stem of archosaurian evolution. Physiol Biochem Zool. 77(6):1051–1067.

Shepard DB, Burbrink FT. 2009. Phylogeographic and demographic effects of Pleistocene climatic fluctuations in a montane salamander *Plethodon fourchensis*. Mol Ecol. 18:2243–2262.

Sill WD. 1968. The zoogeography of the Crocodylia. Copeia. 1968:76–88.

Soares D. 2002. An ancient sensory organ in crocodilians. Nature. 417:241–242.

Taplin LE, Grigg GC, Harlow P, Ellis TM, Dunson WA. 1981. Lingual salt glands in *Crocodylus acutus* and *C. johnstoni* and their absence from *Alligator mississippiensis* and *Caiman crocodilus*. Science. 212:1045–1047.

Thorbjarnarson J. 1991. An analysis of the spectacled caiman (*Caiman crocodilus crocodilus*) harvest program in Venezuela. In: Tropical wildlife use and conservation. Chicago, IL: University of Chicago Press. p. 217–235.

Thorbjarnarson J. 1992. Crocodiles: An action plan for their conservation. Gland, Switzerland: IUCN. p. 1–136.

Thorbjarnarson JB. 1996. Reproductive characteristics of the order Crocodylia. Herpetologica. 52(1):8–24.

Todd NP. 2007. Estimated source intensity and active space of the American alligator (*Alligator mississippiensis*) vocal display. J Acoust Soc Am. 122:2906–2915.

Turner AH. 2004. Crocodyliform biogeography during the Cretaceous: evidence of Gondwanan vicariance from biogeographical analysis. Proc R Soc Lond B Biol Sci. 271:2003–2009.

Vargas AO, Kohlsdorf T, Fallon JF, Vandenbrooks J, Wagner GP. 2008. The evolution of HoxD-11 expression in the bird wing: insights from *Alligator mississippiensis*. PLoS One. 3(10):e3325. Available from: http://www.plosone.org.

Varricchio DJ, Jackson F, Borkowski J, Horner JR. 1997. Nest and egg clutches of the dinosaur *Troodon formosus* and the evolution of avian reproductive traits. Nature. 385:247–250.

Varricchio DJ, Moore JR, Erickson GM, Norell MA, Jackson FD, Borkowski JJ. 2008. Avian paternal care had dinosaur origin. Science. 322:1826–1828.

Vergne AL, Avril A, Martin S, Mathevon N. 2007. Parent-offspring communication in the Nile crocodile *Crocodylus niloticus*. Naturwissenschaften. 94:49–54.

Vergne AL, Mathevon N. 2008. Crocodile egg sounds signal hatching time. Curr Biol. 18:R513–R514.

Vliet K. 1989. Social displays of the American alligator (*Alligator mississippiensis*). Am Zool. 29:1019–1031.

Von Wettstein O. 1937. Ordnuung der Klasse Reptilia: Crocodilia. In: Handbuch Der Zoologie Eine Naturgeschichte der Stamme Destierreiches. Berlin and Leipzig: Walter de Gruyter & Co. p. 236–248.

Waitkuwait WE. 1989. Present knowledge on the west African slender snouted crocodile, *Crocodylus cataphractus* Cuvier 1824 and the west African dwarf crocodile, *Osteolaemus tetraspis* Cope 1861. In: Crocodiles. Their ecology, management and conservation. A special publication of the IUCN/SSC Crocodile Specialist Group. IUCN–The World Conservation Union, Publication N.S. Gland, Switzerland. p. 259–275.

Wang X, Wang D, Wu X, Wang R, Wang C. 2007. Acoustic signals of the Chinese alligator (*Alligator sinensis*): social communication. J Acoust Soc Am. 121:2984–2989.

Watanabe ME. 1980. The ethology of the American alligator with emphasis on vocalizations and response to vocalizations [doctoral dissertation]. New York, NY: Biology Department, New York University.

Watanabe ME. 1983. The Chinese alligator: is farming the last hope? Oryx. 17:176–181.

Watanabe ME. 2005. Generating heat: new twists in the evolution of endothermy. Bioscience. 55:470–475.

Weishampel DB. 1981. Acoustic analyses of potential vocalization in lambeosaurine dinosaurs (Reptilia: Ornithischia). Paleobiology. 7(2):252–261.

Weishampel DB. 1997. Dinosaurian cacophony: inferring function in extinct organisms. Bioscience. 47(3):150–159.

Whitaker R, Basu D. 1983. The gharial (*Gavialis gangeticus*): a review. J Bombay Nat Hist Soc. 79(3):531–548.

Willis RE, McAliley LR, Neeley ED, Densmore LD III. 2007. Evidence for placing the false gharial (*Tomistoma schlegelii*) into the family Gavialidae: inference from molecular gene sequences. Mol Phyloget Evol. 43(3):787–794.

Wilson PA, Norris RD. 2001. Warm tropical ocean surface and global anoxia during the mid-cretaceous period. Nature. 412:425–429.

Wings O. 2007. A review of gastrolith function with implications for fossil vertebrates and a revised classification. Acta Palaeontol Pol. 52(1):1–16.