

Crocodylians as Living Fossils

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Introduction

Nile crocodiles and American alligators belong to a group of reptiles called broad-nosed crocodylians. In the warmer parts of the world, broad-nosed crocodylians are the largest predators to walk on land. They are living fossils in the sense that they resemble ancient forms in the shapes and the ruggedness of their heads and bodies.

Their ecology and evolution is far better understood today than a few years ago. It is now possible to show which natural history patterns are universal and which are confined to one species, and to test explanations as to why certain crocodylians are living fossils. In this chapter I will outline their natural history and point out where new information has caused major changes in perspective.

It is now clear that only one group of crocodylians, the broad-nosed group, is at all stable. Species change, predators and prey change, but the common broad-nosed shape is perpetually renewed. The question arises: What processes make them living fossils?

Phyletic constraints (inability to produce major new forms) are an unlikely explanation in view of new fossil evidence. The broad-nosed group has given rise to many offshoots, including forms with delicate narrow snouts, forms with duckbills, and forms with strange tall snouts. Some tall snouted species were so ter-

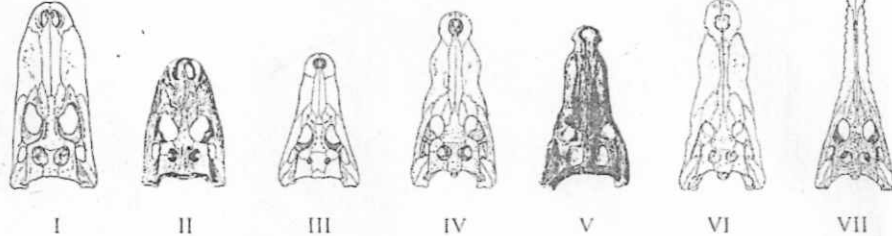
restrial that they had hooves! The broad-nosed group now appears as a central core in crocodylian evolution, able to innovate on many levels.

An ecological explanation for the stability of the core group is that the ancient design is selected by combat and by dispersal in avoidance of combat. Combat and dispersal are important in three processes: predation of small crocodylian species by larger species, cannibalism of subadults by adults, and sexual competition. Because these three conflicts are interactions among members of the group, the shape of individuals is partly insulated from extrinsic selective pressures from other groups, such as predators and prey.

Divergence from the core group can occur when a population gives up one or more conflicts. It can then replace the combat-ready design with a design better suited to catching small aquatic prey or to catching terrestrial prey. The divergent population may change further when it contacts broad-nosed crocodylians which eat or drive the new specialist from habitats where it can be caught.

Analogous conflicts between life stages within a species, between species of similar shape, and sexual competition may stabilize shape in other groups of animals and in plants.

I outline below the ecology, geography, relationships, variation, fossil record, and diversity of crocodylians, arranged in sections so that the reader may follow his or her own interests. The



	I	II	III	IV	V	VI	VII
RECENT	●		●	●		●	
PLEISTOCENE	●			● ₁			
PLIOCENE	●	● ₃		● ₁			
MIOCENE, MID LOWER		● ●	●				
OLIGOCENE		●					
EOCENE, UPPER			● ₄				
Bridger Fm.		●	● ₁	●		●	
Washakie Fm.				●		●	
Green R. fm.	● ₁				● ₅		●
Wasatch Beds		●		●			
PALEOCENE, UP.		● ₂					● ₁
Tongue R. Fm.		●					●
Nacimiento Fm. Torrejonian Puercan			●				● ₁
URavenscrag Fm.						●	
CRETACEOUS, UPPER							
Lance Fm.				●			
Hell Creek Beds		● _{1/2}		●			
Judith R. Fm.	●				●		
Kirtland Shale					●		
(six formations)				● ₇			
JURASSIC, UPPER					●	●	

data consist of my observations of American alligators in natural habitats and the primary literature. Generalizations are built around examples from the continent and time; and to avoid oversimplification brief note is made whether exceptions are known from other continents and times. We begin with the age of the broad-nosed shape and its common traits.

Relative Constancy of Shape

Many living broad-nosed crocodylians are so similar to extinct species that if they were exhibited side-by-side in zoos, the public and many herpetologists would be hard pressed to distinguish them. Examples of the first known forms are *Goniopholis lucasii* of North America and *G. simus* of Europe (shown as outline V in Table 1). Although they lived in the Upper Jurassic, more than 140 million years ago, their skulls had only a small difference in outline from several living crocodiles: The notches in the snout that receive the large canine teeth of the lower jaw are somewhat deeper in the Jurassic forms. The external similarity may not reflect direct ancestry of the living species, because the vertebrae and the position of the major air passages in the skulls of the ancient species show that they belong to an extinct suborder.

The common features of broad-nosed species are an amphibious head profile, a massive head in adulthood, a relatively wide snout, and a distinctive body shape described below. Some di-

versity is apparent in head outlines when viewed from above.

The amphibious head profile has nostrils, eyes, and ears higher than the rest of the head (Schmidt 1944; Cott 1975). Iordansky (1973:244) suggested that this profile makes a crocodile "inconspicuous to its terrestrial prey . . . when floating". This profile may be more important in concealment—crypsis—from other crocodylians in predation, sexual competition, and cannibalism. It may have little role in concealment from many underwater prey and predators.

The adult skull is massive, and the jaw gape is large in all species. The head is used with an unusual technique in combat, and in dismembering very large prey. The crocodylian seizes a limb or other convenient part in its jaws, then rolls over and over, tearing the part off (Schmidt 1944; Cott 1961; photos in Root and Root 1971). Broad-nosed species generally lack shearing teeth (Langston 1965; many others), and so cannot carve their meat, unlike the extinct terrestrial crocodylians and other terrestrial predators.

The external differences among broad-nosed species often seem minor because of the amphibious outline and sturdy construction of the head, and because head outline as seen from above changes during early growth. Good clean skulls can be assigned to species by the sizes and shapes of major bones, and aspects of their taxonomy based on anatomy have been confirmed by chromosome data in Cohen and Gans (1970). Some of the most useful traits in keys to

◁ • Head shapes are repeated from the Upper Cretaceous to the present, with little progression or divergence among amphibious forms.

• Shapes intermediate between categories occur repeatedly.

• Each dot represents a different species, except for two Recent species, as shown in Appendix 1.

^a Head profiles:

I *A. mississippiensis*

II *Alligator mcgrewi*

III *Caiman sclerops fuscus*

IV *Crocodylus moreleti*

V *Goniopholis simus*

VI *C. acutus*

VIII *C. johnstoni*; narrow-snouted, shown for comparison only.

Subscripts in the Table are:

1 Shape is inferred from partial material.

2 Snout has a constriction near the base deeper than in II.

3 Shape shares traits with I, II, and III.

4 Rear of skull is narrower than in III, resembling *Paleosuchus trigonatus*.

5 Shape is intermediate between V and III.

7 This giant skull has an unusual outline in Colbert and Bird's 1954 restoration, based on fragmentary material.

The head profiles of living species are for adults of moderate size for that species. The profiles are approximate because all change with growth and some change with geography (see text). Profile II is from Schmidt (1941), V is from Hulke (1878:Fig. 3) and may be distorted at the quadrates in preservation, and all others are from Wermuth and Mertens (1961). Species names and references are in Appendix 1.

scale arrangements (Brazaitis 1973; Wermuth and Mertens 1961).

Body shapes are quite similar throughout history in the broad-nosed group. Their major limb bones are short and almost slender, the feet are always plantigrade and are never paddles, and the tail is long and flat.

Habitats

With very few exceptions, the meeting place of land and water has always been home for the crocodilians.

(Minton and Minton 1973:15)

Alligator and crocodile habitats range from quite stable to very unstable. Their way of life or niche is broad as defined by habitat variety and by predators and prey.

The American alligator lives in almost every wetland category in eastern Georgia, from flooded forest to the Atlantic Ocean (Meyer 1975; in preparation). Its broad ecological tolerance is indicated by the large differences in available sunlight, temperature, and visibility between habitats such as flooded forests and flooded marshes. Tolerance is also known by alligator occurrence at seasonally dry sites and at manmade places such as canals and dammed ponds. Use of a wide range of habitats is also seen in Nile crocodiles (Cott 1961) and Australian estuarine crocodiles (Messel et al. 1981).

Use of water offers advantages in temperature regulation and energy savings, in addition to concealment. Spotila et al. (1972:1100) found that use of water "enables the alligator to survive a wide range of temperatures . . . Without water the alligator is severely restricted during the day and at night." Swimming is energetically less costly than walking for marine iguanas (Gleeson 1979) and I infer the same for amphibious crocodilians, for whom dispersal over long distances is important.

Subadult alligators use some sites where water is lacking for several months of the year. Subadults often live in marginal habitats lacking large adults. Habitat shift of subadults away from adult sites is best documented for American alligators at natural sites (Meyer 1975; in preparation). (*Natural* is defined in Appendix 2.) It may also occur in estuarine crocodiles and

simply disappear from sight, often not reappearing until they are approximately 1.5 m long (Messel et al. 1981; Cott 1961). Day/night shifts of subadult activity also may occur at some sites (Cott 1961; Watson et al. 1971). Cannibalism, discussed in the next section, appears to be the driving force of habitat shift.

Deep open ocean is rarely occupied by crocodilians at any lifestage today, although they often live on shorelines and in estuaries. They disperse across deep ocean, but rarely feed and never breed there (Meyer, in preparation). On warm continents there are few wet areas not occupied by crocodilians. These few have very rough water (Modha 1967; Messel et al. 1981; personal observation), or cold springs. They also include certain large African lakes after a local faunal extinction (Beadle 1974; many others), and a section of the Mekong River running in a very deep gorge (G. Davis, personal communication). Habitats and ecology are discussed further in three reliable introductions with citations: Minton and Minton (1973), Webb (1977), and the beautifully illustrated Cott (1975).

Prey and Predators

The prey and predators of broad-nosed crocodilians span an enormous range of sizes and orders, and vary with geography and time. The most universal predation on this group is cannibalism. Large adults are almost immune from predation.

Large prey is usually taken by drowning (Colbert 1962). Single Nile crocodiles have been seen seizing and drowning adult male giraffes, full-grown African buffalo bulls, and an adult male lion (Pienaar 1966, 1969). An American alligator was seen drowning a feral boar weighing more than 227 kg (over 500 lb) (McIlhenny 1935). Adult Nile crocodiles also seize mammals on land by waiting next to game trails (Cott 1961). In contrast, I find no record of crocodiles in Australia or caimans in South America taking large native mammals.

Diets differ radically from site to site, and small prey comprise almost the entire diet at some sites. Consider the contrast between the primary diets of Nile crocodiles at three locali-

ties: (1) snails, by crocodiles of many size classes, including the largest, up to 3.68 m (12 ft) long (Cott 1961); (2) insects, frogs, and cane rats (Cott 1961); and (3) a single species of fish, by crocodiles from less than 1 m to more than 4 m long, at a lake where available invertebrates are rare (Graham 1968). American alligator diets may diverge even more by locality: at one site, subadults take primarily apple snails (Fogarty and Albury 1967); at another, almost exclusively muskrats, while nearby alligators took snakes, fishes, and crabs (McIlhenny 1935); at a third site, a mixed primary diet of crayfish, turtles, and muskrats (Giles and Childs 1949); and finally, entirely vertebrates—herons, turtles, and garfish (McIlhenny 1935).

The idea that crocodylians are opportunists and generalists, eating the most locally abundant prey, is not supported by Chabreck's (1971) work with an alligator subadult population. In fresh water, they took primarily crayfish, birds, and a few fishes, but ignored abundant mammals and frogs. In nearby saline water, they took less food by volume, primarily crabs and crayfish, but no birds or mammals. The opportunist and generalist notion is supported by diets of some individuals, e.g., a wild estuarine crocodile eating crabs, an eel, a green sea turtle, and apparently pigs (Allen 1974), and occasionally by eating introduced species—livestock and humans.

Foraging goes beyond ambush predation to include search hunting. For example, American alligators repeatedly steal eggs from Canada goose nests at one site (Chabreck and Dupie 1976); juvenile alligators and Nile crocodiles act as terrestrial insectivores under some conditions (Cott 1961; Meyer, in preparation); and adults scavenge carcasses in water and on land.

Predators on crocodylians vary greatly by continent, and except for cannibals many are modern in aspect. To emphasize crocodylian survival in the face of such diverse predation, I list the species involved. Black bears and raccoons often eat American alligator eggs, and otters and fishes take the young at times (Dietz and Hines 1980; Joanen 1969; Metzen 1977; others). In contrast, native rodents and varanid lizards eat Australian estuarine crocodile eggs (Webb 1977). Olive baboons often rob Nile crocodile nests, and a wide array of adaptive types take eggs at various sites, including:

varanid lizards, hyenas, jackals, mongooses, warthogs, and maribou storks (Cott 1961; P. Shipman, personal communication). Birds of six families, including eagles, take juveniles and lions kill the smaller adults (Cott 1961). Eggs are drowned when nests are flooded (Magnusson 1982); abiotic causes of mortality are not otherwise very important.

Cannibalism is the only predation common to all continents. Nile crocodiles are "much addicted to cannibalism" based on "(i) injured specimens, (ii) direct observation, and (iii) stomach contents" (Cott 1961). The larger a Nile crocodile is, the more likely it is to eat another (Cott 1961). Cannibalism is also known in estuarine crocodiles (Messel et al. 1981; Webb 1977) and the medium-sized spectacled caiman (Staton and Dixon 1975). Nichols et al. (1976) noted that "this mortality source is probably the major density dependent factor operating on Louisiana alligator populations."

Cannibalism is limited to conflicts where the prey is unlikely to inflict much damage on the predator. The cannibalism cited above involves adults eating subadults. I have circumstantial evidence that subadults eat unprotected juveniles: When a subadult moved into their burrow at a natural site during a drought, most juvenile alligators vanished, and a thorough search failed to find them. (Size classes are defined in Appendix 2.) At some sites, eggs are eaten by adults, including females who did not nest that season, cited under female competition below.

Where there are strong clues that cannibalism might interfere with an individual's genetic contribution to the next generation, cannibalism is not reported in crocodylians. I find no record of a male killing a nesting female of his own species at any natural site, even though males are often larger. I find no eyewitness report of adults cannibalizing juveniles in *natural* conditions in any species; instead, adult response to juvenile distress calls is well known (e.g. Romero 1983). At nursery sites in zoos or disturbed situations, subadults may be chased away or bitten gently, if they can then escape. This behavior has been reported for Nile crocodiles, (Pooley 1977), Morelet's crocodiles (Hunt 1977), American alligators (Hunt and Watanabe 1982) and marsh crocodiles (Whitaker 1974).

Very large crocodylians are almost immune from predation from any source (Dowling, per-

I accept for near-immunity (1) the maximum size known killed is much less than the maximum observed body size. (The largest individual reported killed by any predator was a lion-killed Nile crocodile 3.53 m (11 ft 7 in.) long, 0.5 m above minimum male breeding size in some populations [Cott 1961].) (2) A very long life is required to reach the great sizes documented even in the 20th century, because adult growth rates in nature (McIlhenny 1935; Cott 1961; Chabreck and Joanen 1979) are so low; and (3) many adult crocodylians are larger than their potential predators.

Comparing body sizes of predators walking on land indicates that at least one crocodylian species on every warm continent grows large enough to be almost free from predation. A wild alligator or crocodile 4.6 m (15 ft) long weighs more than 400 kg, heavier than any sympatric terrestrial predators: tigers, lions, bears of warm climates, and giant snakes. Lengths greater than 15 ft have been measured in the wild, although weights are rarely taken. American alligators have been measured at 5.84 m and 5.64 m (19 ft 2 in. and 18 ft 6 in., McIlhenny 1935), estuarine crocodiles at 6.1 m (20 ft) with larger estimates (Australia and India; Webb and Messel 1978a), Nile crocodiles at 5.5 m (18 ft) and a likely 6.4 m (21 ft) (Africa, see ref. in Cott 1961), and Orinoco crocodiles measured at 6.78 m (22 ft 3 in.) and estimated at 7.3 m (24 ft) (South America; Humboldt 1876).

Great size and probable near-immunity from predation also occurred in the past. The largest predators of all times to walk on land were the dinosaur *Tyrannosaurus* and the crocodile *Deinosuchus* (*Phobosuchus*) (Kurten 1978). Both lived in the Upper Cretaceous. Colbert and Bird (1954) estimate the giant crocodile's length in life as up to 50 ft (15.2 m). I estimate the likely boundaries of its size are 11 m (36 ft) and 6 metric tons, up to a less likely 15.2 m (50 ft) and 18.8 tons. This size range reflects the need to reevaluate its skull shape (W. Langston, personal communication) and the problems of size estimates suggested by Webb and Messel (1978a) for the estuarine crocodile. Based on co-occurrence of fossils in deposits in six states, Baird and Horner (1979) suggest that the giant crocodile, rather than *Tyrannosaurus*, was a major predator on duckbilled dinosaurs.

Broad-nosed crocodylians occur widely in tropical and warm temperate zones. They have unusual dispersal ability, moving easily to new river systems and to isolated wetlands. There is a clear pattern of endemism: The same species is not found in the interior of more than one continent.

Crocodylians live on every tropical continent and at least six species live in subtropical and temperate areas (Meyer, in preparation; Honneger 1975; see Dowling and Duellman 1978). The primary physical limit to ranges today is temperature, with all species limited to the zone between 40° north and 40° south of the equator (modified from limits of 35° north and south, suggested by Ostrom 1969). Cool climates have often set limits to distributions in the past (Sill 1968). The geography of the higher living taxa was thoughtfully reviewed by Dowling and Duellman (1978) and by Darlington (1957).

The Nile crocodile has the largest land distribution of any crocodylian. Its range includes all of Africa except the northwest, and even some oases in the Sahara desert in historical times (Minton and Minton 1973; others). An extinct African species also had a very large range (Tchernov 1976). Ranges of 200,000 sq km are moderate to small for most species in the interiors of continents.

Species with much smaller ranges are usually confined to islands or an isthmus by a very large crocodile. Examples are the Cuban crocodile (maximum length 3.7 m) and Morelet's crocodile (maximum approximately 2.9 m), both of which are confined by the American crocodile (maximum 6? m), (Schmidt 1924, 1932, 1944). This confinement presumably stems from direct predation, which Medem (1971) describes as the limit to sympatry. The small range of the Chinese alligator may result from elimination by humans (Honneger 1975; Wermuth and Mertens 1961). I find no indication that the range of any broad-nosed species is limited primarily by a mammal or bird group, e.g., by distinct allopatry with a warm-blooded predator.

Dispersal

Subadult and adult crocodylians have the unusual dual ability to travel easily overland and by water. This enables species to cross barriers

between drainage systems. It also allows crocodylians to occupy isolated wetlands, come into chronic conflict with each other, and to leave areas of intense conflict.

The most numerous dispersing groups are subadults and young adults. They are potentially abundant in species of large body size because clutches are large, and growth time to size of first reproduction is long (9 to 15 yr) (data in Cott 1961; McIlhenny 1935; Graham 1968; Chabreck and Joanen 1979). Subadult alligators are "consistently more active over a wider range of environmental conditions" than adult alligators (McNease and Joanen 1974:499). In view of Terpin et al.'s findings that "a very small alligator is more closely tied to the limits of its climate space" (1979:311), I suggest that they live closer to their physiological limits than adults do, especially when moving overland distant from water.

Overland travel is extensive for the Nile crocodile (Pienar 1966), American alligator (McIlhenny 1935; my observations), and three caiman species (Medem 1971; Gorzula 1978). My data indicate that the sizes walking on dry land range from subadult to large adult, because females from isolated sites are courted by adult males, and their progeny later disperse from those sites. The importance of overland travel is underscored by Zug's (1974) report that crocodylians are the only living reptiles to gallop.

The best documented long distance swimming records are for estuarine crocodiles. A radiotagged male 3.2 m (10.5 ft) long moved "at least 130 km, some 80 km being around the sea coast" of Australia (Webb and Messel 1978b). A 3.8 m (12.5 ft) male lived at Ponape Island, Eastern Caroline Islands, 1360 and 2400 km from the two nearest crocodile populations (Allen 1974). In Louisiana marshes, with their network of manmade canals, tagged bull alligators moved an average of 0.75 km each summer day. A large adult and a subadult each moved 52+ km in less than 9 months (Joanen and McNease 1972; McNease and Joanen 1974). These record distances were set where no other crocodylian species was present, and all were set by males.

Endemism

All fossil broad-nosed species from North America were endemic (compare Appendix 1 with taxa listed in Steel 1973; Meyer, in prepa-

ration). No broad-nosed crocodylian species occurs in the interior of more than one continent today or in history, even when the continents were closer together in the Late Jurassic and Early Cretaceous. Where a species occurs on two continents or on many islands, its populations seem restricted to within 300 km of the seacoast on the second land mass. Examples are the spectacled caiman and American crocodile (my interpretation of Central American maps of Smith and Smith 1977, C8 and C10), and estuarine crocodile (Australian maps and data in Messel et al. 1981). Exceptions to precise coastal limits may occur in major rivers. Endemism determines the minimum number of species worldwide.

Variation Within Species

There is substantial variation in anatomy and ecology in the few species carefully surveyed.

It is surprising to find, among a conservative group like the crocodiles, evidences of rapid evolutionary change and faunal discontinuities, as is demonstrated among Neogene and Quaternary taxa in eastern Africa.

(Tchernov 1976:370)

The Nile crocodile has changed substantially in time: A fossil jaw from Olduvai is more robust than that of the modern form (1.5 to 1.9 times as high, and broader). A related species shows little geographic variation in the Miocene, but underwent a "local adaptive radiation" into "four significantly different, readily distinguishable populations" in the Pliocene and Pleistocene (Tchernov 1976).

Several living species show considerable geographic variation. For example, one of Medem's subspecies of the living spectacled caiman is strikingly different in the taper of its snout from other *Caiman sclerops* (1955, 1960). In the Nile crocodile, living populations vary greatly from each other in head shape and in maximum body size (Kaelin 1933; Cott 1961). (Seven subspecies are suggested by Fuchs et al. (1974), but the adequacy of the material is doubted by Friar and Behler (1983).) The American alligator was not divisible into subspecies in a thorough study of scale patterns, but there was much variation in those patterns within populations (Ross 1979). Dodson (1975:350)

found that variation in a growth series of American alligator skeletons "compared favourably with values of V for taxonomically homogeneous samples of mammals."

Enzyme polymorphism data are published only for the American alligator. For three populations, Adams et al. (1980) found the proportion of polymorphic loci, $P = 0.15$, similar to values in other vertebrates. However, other work with single populations found $P = 0.06$ (Gartside et al. 1977), and $P = 0.045$ (Menzies et al. 1979). All three studies found heterozygosity low: respectively, $H = 0.022$, 0.021 , and 0.0086 . Adams et al. review possible causes of low H .

Lack of subspecies and low heterozygosity in the American alligator may be related to two peculiarities of its range: (1) It was probably reduced to the edges of its continent several times in the Pleistocene; and (2) it lacks inland sympatric species and the many isolated drainages found in Africa and South America (Meyer, in preparation).

Relationships and Origins

There is general agreement about evolutionary relationships among broad-nosed crocodylians, suggested by evidence from anatomy, geography (Meyer, in preparation), karyotypes (Cohen and Gans 1970), and biochemistry (Densmore and Dessauer 1979). There is much less agreement about relationships among narrow-nosed or terrestrial groups. One certainty emerges: Convergence and parallelism have been unusually important in crocodylian history (Langston 1973; Buffetaut 1979).

Crocodylians have strongly braced skulls, with complex sutures joining the bones (Langston 1973). The skulls are highly derived (S. B. McDowell, personal communication), and have sixteen ordinal skull traits (Langston 1973). Two groups are proposed as the first crocodylians. The Middle Triassic *Proterochampsa*, which clearly has an amphibious profile, is the first crocodile in Sill's view (1968, and others), but in Romer's (1971) view it is only a parallel form, and the first crocodylians are *Protosuchus*, *Orthosuchus*, and their Late Triassic relatives of perhaps more terrestrial habits. *Protosuchus* is discussed in detail by Colbert and Mook

(1951). Until ancestry is better known, statements about the nearest relatives and evolutionary rates of the earliest crocodylians will be quite speculative. Olson (1971) outlines five alternate classifications that differ primarily in which major groups are recognized as separate families and Mook (1962) adds a sixth.

Discovery of evolutionary paths to the modern crocodile suborder "furnished a stronger support to the hypothesis of evolution than even that of *Hipparion* and the Horse" (Duncan, in Huxley 1875). Modern crocodylians are called eusuchian. Compared with extinct mesosuchians, they have the internal nares (ends of the major air passage) placed further back on the palate, and have ball and socket rather than flat articulations between the vertebrae. Eusuchians were diverse by the Late Cretaceous, and several intermediate genera from the Early Cretaceous are known. The intermediate genera have small body sizes, fitting Cope's Rule as discussed by Stanley (1973). The new suborder apparently rose by mosaic evolution, and a key trait, placement of the internal nares, changed slowly (Joffe 1967; Buffetaut 1979).

All living species and their extinct close relatives are placed here in one family for brevity, the Crocodylidae s.l. (sensu lato). In the Late Cretaceous the crocodylids appear with three fully formed subfamilies: Alligatorinae, Crocodylinae, and Tomistominae. The caimans may be a later group. Each of the major broad-nosed groups—alligators, crocodylines, and caimans—has had its own radiation into a variety of head shapes. Each has tended to form parallel morphological assemblies, leading to repeated treatments of each as a separate family. These radiations and parallelisms are another indication of evolutionary vigor.

The origins of one broad-nosed genus demonstrate an evolutionary pattern. One species is so intermediate between the living *Alligator* and the extinct *Allognathosuchus* that Patterson (1931) was "somewhat undecided" to which genus it should be assigned, finally designating it *Allognathosuchus riggsi*. Simpson (1933) implied it should be placed in *Alligator* with the earlier *Alligator prenasalis*, which he thought was closer to *Allognathosuchus* than to the living alligators. (Simpson also noted similarities of *A. prenasalis* with three South American caimans, but in view of their karyotypes (in Co-

hen and Gans 1970), those similarities now appear convergent.) This chain of intermediate forms is so subtle that experienced taxonomists disagree where one genus ends and the next begins.

Wide snouts (I and II in Table 1) appear first in the Upper Cretaceous. Their late appearance may be an advance made possible by the novelty of overlapping tooth rows, or it may be an artifact of the fossil record, because there are so few pre-Late Cretaceous skulls. (This paucity of pre-Late Cretaceous material is true of many other reptile groups [Ostrom 1969]). The only major dental change in the broad-nosed amphibious group since its origin is the periodic appearance and loss of bulbous rear crushing teeth. These were probably "independently acquired in several groups of small crocodylians . . ." (Buffetaut and Ford 1979).

Distribution in Time

The record of broad-nosed amphibious species in North America is shown in Table 1 as a range of head shapes, and in Appendix 1 as a list of species. North America's record covers the most time, has the longest well-sampled time interval, and has the most broad-nosed species of any continental record.

Species turnover is more rapid in the best sampled interval from the Uppermost Cretaceous through the Eocene than I had expected for a living fossil group (see Appendix 1). Most broad-nosed species are known from good diagnostic material from a single epoch or stage, counting Pleistocene/Recent appearances as one. This is also the rule in South America, which I interpret from Langston's (1965) accounts, and in the rest of the world, from Steel's (1973) summary, with a few exceptions below. Generic longevity is bimodal, another unexpected pattern.

Part of the restriction of species in time may result from a sampling problem, and part is real. The sampling problem is that only one good skull has been described in print for most species, even when several good skulls are known. As yet, teeth are often not identifiable to species. Few taxa have been carefully reviewed for change over time and in space (see Tchernov 1976 for such a review).

Three lines of evidence indicate that time restriction is real. (1) There are no published accounts of a broad-nosed species reappearing after a long absence, say 15 million years, from the record in any part of the world. (2) Change over time is substantial in two well-sampled African species (Tchernov 1976; variation). (3) There is little indication that a continent could have many similar species, each with a small range, so that ancient taxa could long persist undetected. In the interiors of continents, almost all species today have large to very large geographic ranges, even in complex drainages like the Amazon and the Orinoco.

Estimates of species turnover and faunal complexity depend on taxonomic reliability. Only species known from good comparative material are included in Table 1 and Appendix 1. Taxonomy of broad-faced taxa known from good skulls has been quite stable on the species level since 1910, despite the discovery of many new fossils and the naming of new species. Systematic practices in this group have improved greatly since the time of Cope and Marsh, in part owing to the examples set by occasional crocodylian contributions from C. W. Gilmore, B. Patterson, and G. G. Simpson.

There are a few apparently long-lived species: (1) the Nile crocodile, which was present but had more robust jaws in an early Pleistocene fossil from Olduvai, perhaps 1.8 million years ago (Tchernov 1976; Leakey 1971); (2) the living *Crocodylus porosus*, to which a partial snout is referred from the Pliocene of Australia, 4 to 4.5 million years ago (Molnar 1979); (3) the living marsh crocodile (*C. palustris*) of India, which is quite similar to the ?Pliocene *Crocodylus sivalensis* (Lydekker 1886); (4) the living *A. mississippiensis*, which occurs in the Late Pleistocene (Holman 1978), and which may be represented in Pliocene Florida skulls that have not been carefully studied; the Miocene Florida species is the extinct *A. olseni* (Auffenberg 1967).

Generic longevity is curiously bimodal. Genera commonly appear for either less than approximately 10 million years or for more than 20 million years. Genera of intermediate survival time are strikingly rare in North America (Appendix 1). This pattern is confirmed in South America (species accounts in Langston 1965), and in Europe (ranges in part from Russell et al.

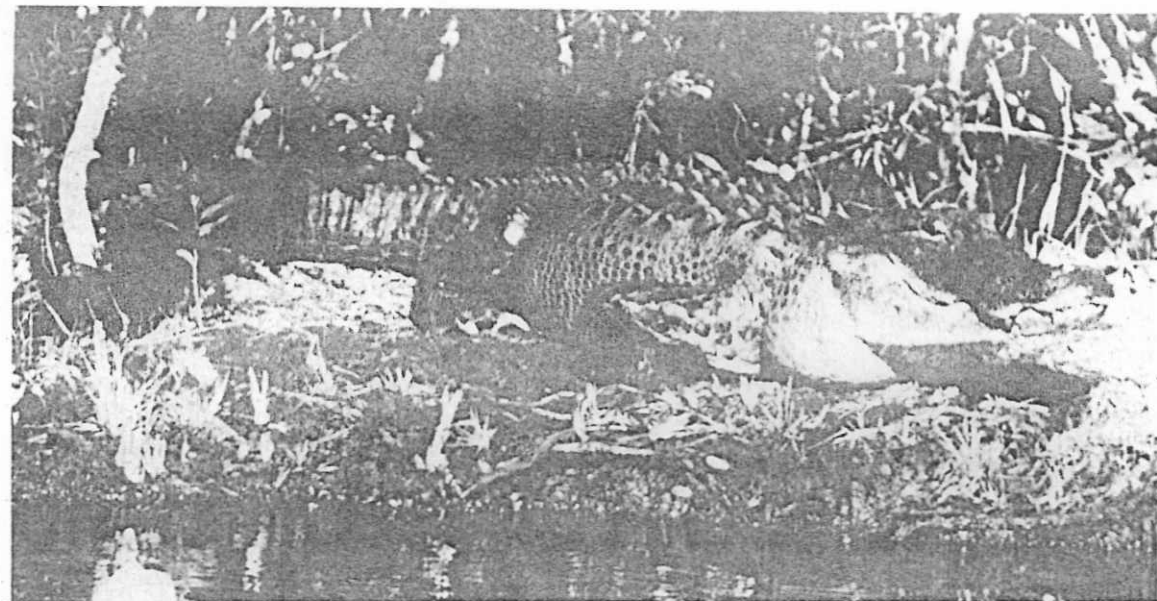


Fig. 1. Adult American alligator (*Alligator mississippiensis*) basking in the sun in the Okefenokee.

1982; and Steel 1973), and the rest of the world. It is as if those passing a stringent selective test persist for many millions of years. Perhaps only the Holarctic *Asiatosuchus* lasts an intermediate time, although taxonomic changes could produce others, e.g., by assigning *Allognathosuchus riggsi* and *Alligator*. This pattern is linked to the effect of two major extinctions (at the end of the Cretaceous and at the end of the Eocene). Each may be related to loss of many short-lived genera, but not to loss of many long-lived genera. It does not appear that the bimodal pattern of "generic longevity" has been demonstrated in other reptiles.

Diversity

I suggest here that diversity has been relatively stable for broad-nosed crocodylians since at least the Upper Cretaceous in three ways: (1) the number of species alive at the same time, (2) the presence of four or fewer species in each well-studied fauna, and (3) variety of head shapes.

There are 16 to 21 broad-nosed species alive today—the total varies with recognition of a few forms as species or subspecies. A count ranging from 10 to 30 species at any one time

may be typical of the group, after the time sequence of fossils becomes clear in the Late Cretaceous. This count is in accord with endemism patterns and geographic ranges discussed above, and with ecological processes and faunal structures, and the list of species known from good fossils in Appendix 1. (Species diversity before the mid-Cretaceous is difficult to analyze because the time relationships and taxonomy of earlier taxa are uncertain and the sample size is small.)

Each well-studied fauna has only one to four broad-nosed species—at any time since the origin of the broad-nosed group. Fauna here means all of the species in a drainage system at the same time. The presence of few species in particular faunas was recognized by Schmidt 1924, 1928; Patterson 1936; Langston 1965; and especially Medem 1971. Possible exceptions are discussed below. Even the faunas in South America today have few species, although it has the widest range of crocodylian morphology of any continent today.

Predation among crocodylian species maintains sympatry at low levels in the great drainage basins of South America, even in the vast Amazon Basin (Medem 1971). For example, large crocodiles eat the medium-sized spectacled caimans, which in turn feed on *Pa-*

leosuchus caimans in other habitats. After hide hunters eliminated the huge *Crocodylus* from the Atrato River, the spectacled caiman became abundant there for the first time. It had been confined to lagoons, creeks, and marshes previously by *Crocodylus* (Medem 1971). Similarly, in Central America the large American crocodile (*C. acutus*) displaces the smaller Morelet's crocodile into "small and vegetated bodies of water, and microsymbatry does not occur" (del Toro, in Smith and Smith 1977).

I have found several size classes of alligators together, but not the smallest and the largest in a few localities, usually large bodies of water disturbed by man. Because cannibalism between alligator size classes is similar to predation between crocodylian species, I suggest that two crocodylian species may cohabit where the smaller individuals can evade the larger.

Another proposed mechanism for low levels of sympatry is continuous growth with changes in diet, causing each crocodylian species to pass through a series of potential niches (Dodson 1975). Continuity of growth is a new insight, but current data show that diet does not predictably change from small subadults to large adults at some sites. A predictive model of faunal structure is described in the section on forces renewing an ancient shape.

In every fauna today, no two species share the same head shape and body size. Examples are South America today and the North American fossil record. Faunas are indicated in Appendix 1 as horizontal groups of species in the same state or physiographic province, excluding the Jurassic taxa whose time relationships are not understood. In contrast to the similarity of faunas and body shapes of broad-nosed crocodylians through time, large predatory mammals today have much different head and limb proportions than their counterparts in the Orellan (29–32.5 million years ago) (Van Valkenburgh 1982).

Diversity in physiology may correlate with patterns of body size in faunas, with smaller species having unusual capacities that may allow them to live in habitats free of larger species, or to escape pursuit by them. For example, the dwarf caiman survives exposure to low temperatures fatal to the sympatric, middle-sized spectacled caiman (Medem 1971). The latter, in turn, has a tidal lung volume seven times

greater than that of the larger allopatric Nile crocodile although values for baseline ventilation are similar (Glass and Johansen 1979). In another case, the two smaller crocodylians of the Congo Basin have broader nesting tolerances than the Nile crocodile (Lang, in Schmidt 1919). However, more data comparing species are needed (Smith 1979). A major study of American alligator metabolism (Coulson and Hernandez 1983) has laid the foundation for detailed comparative work.

Head-shape diversity is indicated in Table 1. Almost the entire historical range is shown, with each species represented on the continuum of adult shape. Diversity changes little from the Late Cretaceous to today; short-nosed species are now absent from North America, but remain in South America. Three unusual groups occurred, all offshoots of the broad-nosed group. The first group (*Brachychampsia* and *Ceratosuchus*) had more pinched snout bases than II; in addition, *Ceratosuchus* had small horn-like squamosals (Appendix 1). A more unusual shape group contains two duckbill clades with longer and more delicate snouts than I (*Mourasuchus* confined to the South American Miocene and ?Pliocene, Langston 1965, 1966; and two(?) genera confined to part of the Late Cretaceous of Africa, referenced in Steel 1973). The third unusual group is a miscellany comprised of species for which published plates show skulls difficult to interpret or terrestrial rather than broad-nosed amphibious in design.

Unusual head shapes appear in a very large fauna in the paleontologist's broadest sense, reviewed by Langston (1965). The Colombian La Venta fauna occurs in deposits some 700 m thick. It was resolved into four broad-nosed amphibious forms, an aberrant duckbill, two narrow-nosed species, and *Sebecus*, which many workers regard as highly terrestrial. The most complex lithologic unit, "the Monkey unit, with six crocodylian-producing localities" has probably no more than five species (Langston 1965), of which I believe only two are broad-faced amphibious forms. Further work on Central and South American fossils (Ferrusquia-Villafranca 1978) shows the same pattern of presence of few broad-nosed species in any local fauna.

The "Bridger" crocodylians are a possible exception to the presence of few species in each

fauna (Appendix 1), but the vague locality descriptions in Cope (1883) and others do not allow definite assignment of many crocodylians to that formation, or to the Bridgerian land mammal age as defined by Berggren et al. (1978). The Bridger formation is 695 m thick (Bradley 1964), and I suggest that "Bridger" crocodylians include several successive faunas in the zoologist's sense of contemporary species in a drainage system. Their taxonomy is chaotic, with similar species named from isolated teeth and fragments, a practice long since abandoned by crocodylian workers.

Behavior and Mortality

Crocodylians have the most advanced behavior of any living reptile. Only two aspects of behavior are discussed here, both related to injury and mortality: sexual competition and parental defense. The reader interested primarily in evolutionary consequences of behavior may prefer to read the next section on forces renewing shape first.

One of Darwin's first examples of sexual selection was alligator "fighting, bellowing and whirling around" (1859:88). Injuries from sexual combat in male alligators and American crocodiles are described by McIlhenny (1935) and Hornaday (1875). C. B. Cory, Curator of Ornithology at the Field Museum, observed a fight between two male alligators in a Florida pond. The battle ended when the larger seized "his opponent by the upper jaw and immediately rolled over and over, breaking his opponent's jaw close to his head, killing him instantly" (Cory 1896:68).

Male Nile crocodiles patrol territories at breeding grounds and fight with other males (Modha 1967; Pitman 1941; Pooley 1977). Frequent deaths of male Nile crocodiles from fighting in the mating season were recorded in the 1930s (Pitman 1941). I find no indication that adult Nile crocodiles fight outside the seasons of courtship and nesting. Combat is rarely observed in nature today because the leather trade has decimated most populations and made the survivors wary of humans. In a popular book, Neill (1971) denies the existence of combat, cannibalism, and other natural history facts re-

ported by competent observers (Cott 1972; King 1972; and especially Fogarty 1972).

The injury rate increases with size to 63% in the largest male size class and 41% in the largest female size class in Nile crocodiles (Cott 1961), and with size in estuarine crocodiles and spectacled caimans of unstated sex (Webb and Messel 1977; Gorzula 1978). Crocodylians have great ability to recuperate from all but the most serious injuries (Gorzula 1978; Brazaitis 1981). At sites or in seasons where secondary factors increase the lethality of small injuries—such as the piranha attack of wounded caimans seen by Roosevelt (1924)—the risks of battle may be so high that disputes are settled with visual signals (Meyer, in preparation). Crocodylians of three continents do use a wide variety of visual signals, described by Modha (1967), Garrick, Lang, and Herzog (1978), Staton and Dixon (1977), and clearly illustrated by Cott (1975). Combat can uncover deception and poor judgment, inevitable when mere display controls important resources. Male narrow-nosed gharials may have a special organ of display, but unlike Darwin's (1859) other examples of sexual selection all broad-nosed species lack them.

Female Nile crocodiles fought to death at one nesting area (Pitman 1941) but communal nesting was documented at two other sites (Cott 1961, 1975). Nests of estuarine crocodiles are close to each other in some habitats in Australia (Magnusson 1980). American alligator females are not known to fight in the wild and their natural injury rate seems low today. Yet there does appear to be sexual competition and territoriality, as indicated by the following observations: (1) Only one adult with juveniles was resident at each *natural* isolated nesting and nursery site in Georgia (Meyer 1975, 1977); (2) nests and nurseries were generally well spaced in the vast Okefenokee marshes, and occurred in three different wetland categories, including apparently suboptimal breeding grounds, and at highly disturbed sites (in preparation; nest data in Metzen 1977); (3) alligator eggs or shells were found in 13% of stomachs of adult females, including those who had not nested that season (McNease and Joanen 1977), and eggs were found in stomachs of Nile crocodiles of unstated sex (Welman and Worthington 1943). I infer that nest protection from conspecifics can

be important. Here sexual competition and parental defense merge.

If an alligator can modify the topography of an isolated site in ways useful for hiding and defense, it may then have a great advantage over an intruder in choosing a place and time to fight. Alligators deepen and burrow in their wetlands extensively, and in isolated sites such changes in bottom contour are more extensive than those made by any other animal group (my data). Young females may either avoid small isolated nesting sites that are already occupied, or die in the attempt to invade. This adds to the obvious thermal advantages of deepening ponds and digging burrows and creates a perennial area of open water for combat. The need to defend ideal nesting sites could select for ability to modify sites, to make decisions quickly, and to learn local topography. Parental defense of nest and juveniles may also favor sturdiness, crypsis, and stealth (in preparation).

Selection for learning ability in defense of eggs and young by female alligators was suggested by Kushlan and Kushlan (1980). After ingenious experiments on defense, they concluded "alligators distinguish between types of potential predators . . . Such behavioral plasticity and attendant ability to learn quickly from experience is obviously highly adaptive." Dietz and Hines (1980:257) found that in response to human disturbance, female alligators "are able to modify an innate behavior such as nest defense without altering other behaviors such as nest maintenance or liberation of young." Alligators who protected their nests and juveniles most actively from human researchers had by far the lowest rates of nest loss to bears in Okefenokee (Metzen 1977 and my data). Nest defense is not common in some areas today, probably because hide hunters lured adults with juvenile calls (personal communication from hide hunters).

Parental attendance in natural habitats lasts up to two years in alligators at natural sites, comparable to care length in eagles and large predatory mammals (Meyer 1977). It depends on weather in some habitats (Chabreck 1965). Hatchling Australian estuarine crocodiles disperse within days after emergence in some habitats, but remain together in others (Webb and Messel 1978b). Parental behavior is complex in

all species investigated (e.g., Pooley 1977; Meyer 1978), and may even include provisioning the young by the adult female (McIlhenny 1935). Vocalizations are varied in character, frequency shift, and pulse rate shift (Herzog 1974; Herzog and Burghardt 1977; Meyer 1977). I see little indication that parental behavior is stereotyped.

Territoriality for food seems unlikely at first glance, since low energy requirements would not seem to require feeding territories at today's population densities. However, densities are artificially low now, and the concept should be re-examined. Spacing and group occurrence of alligators outside of reproduction are suggested by Meyer (1977; in preparation) and spacing of equal-sized estuarine crocodiles with tolerance of individuals in certain smaller size classes, by Messel et al. (1981).

Renewing an Ancient Shape

To inflict such terrible injuries on the armor plating of another crocodile, those jaws must be among the strongest in nature.

(Myers 1972:151)

I propose combat and its avoidance select for the classic shapes and construction of broad-nosed crocodylians. Combat and dispersal are common to three processes: predation between species, cannibalism, and sexual battle.

Combat would select for sturdy construction of the head and torso and for amphibious shapes offering concealment at the water's surface. Avoiding battle by hiding at a moment's notice would again select for amphibious head shapes. Avoidance by travel to isolated sites where large crocodylians are uncommon places a premium on walking overland and swimming long distances. The limbs and tail necessary for such dispersal are less ruggedly made than the head and torso, and are often severely injured in battle. The resulting compromise is the ancient design of broad-nosed crocodylians.

Based on data from five continents, the three processes suggested above could be more consistent in time and space than predator/prey relations. The data indicating that each conflict is a significant source of mortality are outlined in the relevant sections above. Other explanations

are outlined in the following section. For the sake of brevity, these processes are called *conflicts* within crocodilians—*competition* seems too vague a word when competing individuals are torn limb from limb.

I outline below how habitat shift and dispersal join the three conflicts, the evolutionary consequences of each conflict, the evolutionary result if a deme gives up cannibalism and sexual combat, and why these conflicts preserve shape in crocodilians more effectively than in some predatory mammals.

Habitat shift and dispersal intensify conflict in broad-nosed crocodilians. The most numerous dispersing groups are the subadults and young adults of large species, fleeing cannibalism and sexual competition. Habitat change and dispersal overland and by water cause each species to spread quickly in one drainage system, and to cross from one stream system to the next. This brings every broad-nosed species into prolonged conflict with other crocodilians in a large region.

Predation between species causes the habitat boundaries between species to be sharp, and sympatry to be low (a maximum of 4 species) (Medem 1971, discussed in Diversity above). Medem found that the larger species eat the smaller. The result inferred here is that any species or deme not fit for combat, e.g., having weak heads and teeth, will be eliminated from every habitat in which it cannot evade typical crocodilians.

The evolutionary consequences of predation and of habitat shifts can be predicted to be strong for small species. Even if they live in habitats quite different from those of adults of large species, they will be exposed to an influx of subadults and young adults of large species. Adults of smaller species would need to be better protected in battle and better equipped for avoidance of battle. They should be more robust, more terrestrial, or more agile than larger species, or they should be physiologically specialized for difficult environments avoided by larger species.

I believe this explains why several small living and fossil species have such formidable canine teeth and so much bony armor. They carry the broad-nosed morphotype almost to extremes. In performance, Medem (1958) notes the *Paleosuchus* caimans are agile jumpers and

fast swimmers compared with the larger caimans. In behavior, he notes their aggressiveness. In physiology, Medem (1971) notes the unusual temperature tolerance of the dwarf species.

Sexual combat and cannibalism may stabilize shape if only one broad-nosed species occupies a region. The frequency of injury and death from sexual combat at some sites (discussed in Behavior above), suggests that these conflicts are not trivial, and that the forces exerted on the skull in battle must be enormous. Busbey (1977) describes in detail the skull structures that resist maximum stress; Busbey (personal communication) and I have concluded independently that the skull design is well suited for maximum loads from rolling with an object between the jaws. I believe that the general source of maximum loads while rolling is another crocodilian, not prey, because large prey are not taken on several continents today and may have often been missing from local and continental faunas in the past.

Cannibalism of subadults and young adults may maintain skull sturdiness and dispersal ability. Cannibalism in crocodilians occurs when the predator is unlikely to be severely injured (as mentioned under Prey and Predators). A small increase in skull sturdiness, making a subadult more formidable as potential prey, would be rewarded by increased freedom from cannibalism.

If a deme gives up cannibalism and sexual combat to avoid injury, it can specialize in anatomy for a new diet. It risks losing ecological breadth and evolutionary longevity. For example, by evolving delicate feeding structures, a deme could improve feeding efficiency upon small abundant animals, especially fishes. It could gain in crucial aspects of life history theory: increased growth rates, clutch size, and hatchling size; decreased time to sexual maturity; and decreased feeding time with its exposure to predation.

At first, such a deme may survive if out of contact with other broad-nosed crocodilians, including typical demes of its own species. When contact with typical forms is resumed, such a deme will be confined to habitats in which it can escape being eaten by typical forms of the same body size—the fate of narrow-nosed crocodiles today. Confinement to

fewer habitats may reduce variety of selective pressures, setting the stage of further divergence in anatomy and further confinement in habitats.

Interactions among large crocodylians are different from those among large carnivorous mammals for four reasons: (1) Large crocodylians produce an order of magnitude more young annually per mother (20 to 80) than do large predatory mammals or birds. (2) Growth patterns are different. The young grow very slowly to *size* of first reproduction (9 to 15 yrs) in large species and even more slowly to maximum size (20 to 50 yrs). Hatchlings are tiny compared to adults: their weight ratio is 1:800 to 1:5000+ (Meyer, in preparation). Continuity of growth and niche change (Dodson 1975) are discussed under Diversity. (3) Almost all individuals return daily to shallow water near land, and thus can meet at a common setting. (4) Reptiles differ from mammals in biomass and feeding efficiency in ways that increase the frequency of encounters between individuals of similar shape.

Ectothermy (being cold blooded) allows potential crocodylian biomass to rise to a very high level, while allowing great bursts of activity. Recent reptiles and amphibians "are able to devote a very large portion of their ingested energy to producing new biomass". Their "net long-term conversion efficiencies . . . are many times greater than those of birds and mammals" (Plough 1980:102). Ability to survive long fasts and to fast rather than to feed actively when food is scarce also increases potential reptile biomass by reducing food competition at crucial times. The result I infer is that crocodylians become unusually abundant for top predators and can encounter each other frequently in many kinds of wet habitats. The capacities of small reptiles for burst activity are similar to those of small mammals, although varying with temperature and species (Bennett and Ruben 1979; Bennett 1980). High burst activity could be crucial in the relations of crocodylians with mammals and when crocodylians encounter each other.

The construction of the legs, feet, and the distal half of the tail is surprisingly light in broad-nosed crocodylians. The limbs and tail are often severely injured in fights (injury lists are in Cott 1961 and Webb and Messel 1977).

Their continued slender construction indicates that avoidance by dispersal may be quite important as a selective process, as indicated in *Distribution in Space*. After the hatchling stage, long distance travel is useful in reaching water and prey which vary with geography and seasonal rains, in avoiding cannibalism, interspecific predation, and sexual conflict, and in finding isolated mates.

The body plan of typical crocodylians may thus be shaped primarily by combat and by avoidance of combat. In ecological time these processes operate to structure faunas. In geological time, these processes may produce rapid convergence to basic crocodylian shapes and rugged construction, when a large slow-growing terrestrial predator enters the amphibious life.

Phyletic Constraints and Alternate Explanations

Other explanations for preservation of ancient shapes are simpler. They seem at first glance to be plausible, but are contradicted by the natural history data. Phyletic constraints— inability to produce major innovations—are discussed first, with an outline of the major divergent lines produced by the broad-nosed group. Following that are brief outlines of theories of large population sizes, unchanging environments, and the small area of the earth's fresh waters. These explanations have a common pattern: each is a simple, vague extension of an idea that is valid when limited to individuals or to parts of an ecosystem.

Phyletic constraints are a possible explanation for stasis. For example, the embryology of a group might be so integrated that major new features cannot appear. Thus failure to innovate can result from developmental constraints rather than from selection (Gould and Lewontin 1979). To test this idea, the record can be examined to see if members of a group have moved into entirely new ways of life, or have originated morphological oddities.

In fact, several new ways of life and odd morphologies have been produced by broad-nosed crocodylians, while the stable central shape group has always remained. They produced the following divergent forms, which share one

1. Highly terrestrial crocodiles appeared in several lineages. A lineage closely related to the living family Crocodylidae s.l., the pristichampsids, survived into the Eocene in North America and Europe. *P. vorax* had flattened serrated teeth, a high skull, and a round tail (Langston 1975; Busbey 1977, in preparation). The related *P. geiselalensis* of Europe (see Kuhn 1968) had hooves!
2. Duckbilled caimans with delicate snouts and many slender teeth appear in the South American Miocene (*Mourasuchus*, Langston 1965, 1966). They may have gathered algae or small animals by a straining technique, or grubbed in the mud. Their remains are scarce in sediments having remains of other eusuchians, suggesting habitat separation from them. The giant duckbilled crocodiles of Mid-Cretaceous Africa (*Stomatosuchus*) were "even more aberrant" and were independently derived (Langston 1965).
3. Narrow-faced crocodiles have arisen from broad-faced groups several times. There are two living *Crocodylus* of medium size with very slender snouts, one in Australia (*C. johnstoni*) and the other in Africa (*C. cataphractus*). Each is separately derived from typical *Crocodylus* (Longman 1925), and their karyotypes (in Cohen and Gans 1970) are different. Snout elongation occurred over time in populations of three African *Crocodylus* species but was never reversed (Tchernov 1976). Jurassic goniopholids also diversified into narrow-faced and broad-faced genera (Buffetaut and Ingavat 1980). (Habitat separations are outlined in the next section.)
4. Peculiar variants have appeared in body parts even of the broad-nosed species. For example, the keeled plates of bone that armor the backs of crocodiles and alligators have had strange forms, including unique spikes and blades on a Paleocene alligator (O'Neill et al. 1981), and smooth overlapping plates on a Paleocene crocodile (Erickson 1976). The scutes of some European Early Cretaceous goniopholids had lateral pegs projecting under adjacent scutes (Owen 1878). The scutes of a North American rela-

Thus predictions based on the hypothesis that phyletic constraints did not allow divergence by broad-nosed crocodilians, are contradicted by the record. New work in embryology indicates that alligator embryos do respond to experimental manipulation (Ferguson 1979). From this I infer that alligator development is not too canalized for change in one generation, and that phyletic constraints operating over many generations are unlikely from a biological point of view.

A second possible explanation is that some modes of speciation are prevented by large population sizes. I believe that modes of change occurring in small isolated populations can operate in some crocodilians, because dwarf caimans occur as small isolates in some areas (Medem 1971), and African dwarf crocodiles can be predicted from the few field data, and from the theory advanced here, often to live in small isolates. They could evolve in several of the transience modes described by Templeton (1981) or in the allopatric model of Mayr (1954, 1975). Chromosomal evolution is obvious in crocodilians (karyotypes in Cohen and Gans 1970). Thus the data do not support confinement of crocodilians to a few modes of evolution.

A third idea—that unchanging environments are linked with stasis—is supportable if stated as: The persistence of certain physical aspects of wetlands has permitted the persistence of conflicts stabilizing amphibious crocodilians. The chain of logic is: Most wetlands have some open water at some time of the year; the borders of open water with dry land and with air have distinct physical qualities, which are ageless as ideals but depend locally on the presence of vegetation; at open water the amphibious head shape of crocodilians is easily concealed, and at banks the typical body plan allows rapid entry and egress. The idea that selection by combat and its avoidance favor key traits in crocodilians rests on the occurrence of open water and open banks for at least part of each year.

However, the idea that wetlands are unchanging is incorrect if taken literally. Wetlands change quickly; many dry up seasonally. Wetlands are quite diverse, and their availability

changes over time. Wooded swamp, marsh, and river are quite different from each other in temperature, tree cover, and water flow. Their relative areas change with fluctuations in sea level, aridity, glaciation, topography, and plant evolution. The animals that live at the edges of wetlands—crocodylian predators and prey—also vary with time and geography. However, broad-nosed crocodylians on different continents (e.g., Africa/Australia) do not show major changes of shape with proven differences in their predators and prey. The unchanging environment idea is also incorrect if stated as: Living in wetlands guarantees success of amphibious groups. The fossil record shows that there have been many extinctions and radiations of amphibious predators, from labyrinthodont amphibians and phytosaurs to modern water snakes (e.g., *Natrix* s.l., *Nerodia*), and narrow-nosed crocodylians.

Finally, when Darwin coined the term *living fossils*, he suggested that the relatively small area of the earth's fresh waters has reduced rates of species origination, competition, and extinction (1859:107). Estes (1970) outlines the long history of many living freshwater lower vertebrates now in southeastern North America. However crocodylian ecology extends far beyond fresh water animals, to life and death interactions with terrestrial mammals. Also, at least seven Recent species including the American alligator occur in salt water (Meyer 1975; Messel et al. 1981; many others).

Narrow-Nosed Crocodylians

The fate of the narrow-nosed group supports the mechanism proposed for stasis of the broad-nosed group. Their snouts and teeth usually but not always lack the sturdiness needed for combat with broad-nosed crocodylians of the same body size. There are three very large species today. One, the tomistoma, is a living fossil in the sense that it is the last survivor of a subfamily. The second species is intermediate between narrow and broad nosed, the Orinoco crocodile, aptly named *Crocodylus intermedius*. It may cross a threshold during growth to reach sturdiness comparable to that of smaller broad-nosed species, becoming one of the dominant crocodylians in its fauna (see Medem's 1971 fau-

nal list). It is the last species in the New World to approach the narrow-nosed condition. The third large species, the gharial, is the last survivor of a once widespread rather young family. The two species of medium size are derived from broad-nosed *Crocodylus* (see above). They seem confined to regions in which large broad-nosed species are uncommon (my interpretation of Lang, in Schmidt 1919; Messel et al. 1981:459).

The upper jaw of a very large tomistoma or gharial is formidable in appearance, but large subadult heads seemed delicate in the museum specimens of tomistoma, gharial, and Orinoco crocodile that I examined. Ross (1974, in Whitaker and Rajamani 1974) observed gharial and marsh crocodiles together in a deep pool in a river, and cites aggression and avoidance but not biting. This is the only described instance of aggression without predation between any crocodylian species at a natural site. Gharials are highly derived, and as Buffetaut's (1978) family Gavialidae, may date only from the Eocene.

The narrow-nosed group has fluctuated in diversity and geographic range all through its history. Many adaptive types are extinct (teleosaurs, metriorhynchids, and dyrosaurids; see Buffetaut 1979, Romer 1966). Some adaptive types were so derived that they were not amphibious, but aquatic, e.g., the limbs were paddles and the tail had a reversed heterocercal bend in metriorhynchids. Convergence and parallelism led to taxonomic chaos in many narrow-nosed taxa, especially the dyrosaurids, until Buffetaut's recent work.

The Future

Crocodylians are now intensively killed for their skins to make vanity goods such as expensive purses. Most species are now threatened or endangered, as detailed by Honegger (1975). Crocodile farming was planned to reduce hide hunting in the wild, but instead it has worsened the conservation problem in Papua New Guinea by screening illegal killing of crocodiles in the wild, and it has failed to reduce captive juvenile mortality below levels in nature (Burgin 1980). The present partial bans on trade in skins are easily evaded—finished leather from endangered species is simply passed off as from le-

annually. The threat of extinction of many species will not abate, until international bans on trade in skins apply uniformly to all crocodilians.

Public opinion often favors conservation of crocodilians, even though they are correctly seen as dangerous to humans and livestock under some circumstances. The impact of crocodilians on human fisheries is beneficial in certain areas, by fertilization of low-nutrient waters in the Amazon (Fittkau 1973), and by removal of predators on valuable fishes in Africa (Cott 1961; Campbell, personal communication). The impact of alligators on wetlands is beneficial, because alligators dig holes that provide the last remaining water for many animal species during drought (Kushlan 1974; Meyer, in preparation; others). In Florida, a poll found that the American alligator is widely perceived as ecologically important, interesting, and sometimes hazardous to people, and respondents strongly favored its conservation (Hines and Scheaffer 1977).

Concluding Remarks

Darwin (1859) recognized that the young enter a world filled with older individuals, and that selection acts on all life stages during growth. Crocodilians illustrate how selection on all life stages can stabilize a group. Similar kinds of selection may stabilize shape in other animals and in plants when individuals encounter each other frequently under common conditions, and drive rapid divergence in small isolates.

Three stabilizing processes can be outlined in terms applicable to many groups. (1) Predation between species: Adults of dominant species (usually of large body size) select for survivors among several life stages of less dominant species. A more subtle interaction may be just as important: Subadults of dominant species interact with adults of less dominant species, and their selection is mutual. (2) Sexual competition: Within demes, sexual competition can stabilize anatomy, curtailing specializations that allow faster growth to adult size but reduce ability to compete at the time of reproduction. (3)

mine the conditions of their lives. Among the young, the older ones effectively select for survivors among the younger, and they select for aspects of parental treatment of the youngest.

This explanation for stability allows for variation within populations and within species of the stable group. It is compatible with a variety of genetic modes of evolution described by Templeton (1981), and the allopatric model of Mayr (1954, 1975). It does not rely on phyletic constraints or genetic stasis. There are certainly other causes of stability.

As a general hypothesis for conservation of shape, the degree to which these processes stabilize a species or a larger shape group is testable in some taxa and only inferable in others. For example, in eagles and arboreal mammals, it may be possible to estimate the ability of young to escape detection and chases by adults in ecological time, and to compare shapes and ways of life that are stable with those that are unstable in geological time. The inevitable gaps in the data base could be spanned by the judgment of field ecologists, and by noting differences in ecology and morphology on different continents, as done here for crocodilians. This theory may also account for the low diversity in general shape of the tyrannosaurs and other Cretaceous carnivorous dinosaurs, but lack of many kinds of data leaves the general hypothesis as but one of several possible explanations for a phenomenon that has received too little attention. For trees, testability is high. The majority of woody plant species in California are "15 to 50 million years" old (Stebbins 1982). Analogous processes could be evaluated as a means of stabilizing wood and leaf architecture within demes, for increasing physiological differences between species, and for founder and divergence effects.

These processes stabilize a "central" core, often while driving innovation into side groups. Neither stability nor innovation requires that each genetic species lasts a long time. One or more of the conflicts can be given up, and a deme can then change morphology and give rise to a specialized offshoot that lives in habitats free of the ancestral forms. Crocodilians have produced such specialists again and again.

Wilson (1980) describes the general origins of structured demes and of differences between demes.

These processes may cause divergence in small isolates. A divergent first generation could select for survivors among the next generations—an ecological founder effect. This could reinforce genetic mechanisms for change,

without requiring populations to remain so small that they undergo genetic founder effects. When the isolate again contacts the stable core group, it may diverge further if the core group excludes it from all but a few habitats. Thus the processes stabilizing anatomy, ecology, and physiology are inevitably linked to those driving divergence.

For Appendix see p. 124

Alligatorines

Crocodylines

Goniopholids: G

	Alligatorines		Crocodylines	Goniopholids: G
RECENT	<i>Alligator mississippiensis</i>	I	<i>Crocodylus acutus</i> = Amer. crocodile	VI
	Amer. alligator, southern U.S.			VI
	<i>Caiman sclerops fuscus</i>	III	Florida to Antilles and S. America	IV
	Brown caiman, Mexico to Colombia		<i>C. rhombifer</i> = Cuban crocodile	IV
			<i>C. moreleti</i> , Mexico & Cent. America	IV
PLEISTOCENE	<i>A. mississippiensis</i> , southern U.S.	I	<i>C. rhombifer</i> , <i>C. antillensis</i> , Cuba	IV
			<i>C. moreleti</i> subsp., Guatemala	I IV
PLIOCENE	<i>Alligator</i> sp., Florida	I	cf. <i>C. moreleti</i> , Baja Calif.	I IV
	<i>A. mefferdi</i> , Nebraska	×II×III		
MIOCENE, MID LOWER	<i>A. thomsoni</i> , Nebraska	I×II		
	<i>A. mcgrewi</i> , Nebraska	II		
	<i>A. olseni</i> , Florida	I×II		
OLIGOCENE: South Dakota	<i>A. (Caimanoidea) prenasalis</i>	I×II		
	<i>Caimanoidea visheri</i>	U		
Titanotherium Beds	<i>Allognathosuchus riggi</i>	NO		
EOCENE, UPPER	<i>Procaimanoidea utahensis</i>	4 III		Terrestrial Pristichampsine
Bridger? Fm. Wyoming	<i>Procaimanoidea kayi</i>	U I III	<i>C. affinis</i>	IV×III P. vorax UUU
	<i>Allognathosuchus polyodon</i>	II	<i>Brachyuranochampsia zangerli</i>	VI×V
	<i>Diplocynodon stuckeri</i>	ID NO	? <i>C. elliottii</i>	IV ?? <i>C. grinelli</i> NO
Washakie Fm. Wyoming			<i>C. clavis</i>	IV×III P. vorax UUU
			<i>B. eversolei</i>	VI
Green R. Fm.	<i>Alligator</i> ?n. sp., Wyoming of Grande 1980.	I×II	<i>Leidyosuchus wilsoni</i> , Wyoming	V×III
			<i>C. acer</i> , Utah	VI×VII
Wasatch Beds Wyoming	<i>Allog. heterodon</i>	U I?	<i>Orthogenysuchus olseni</i>	UU
	<i>Allog. wartheni</i>	NO		
PALEOCENE, UPPER	<i>Ceratosuchus burdoshi</i> , Colorado	2 II	<i>L. riggsi</i> , Colorado	I U VI×VII
Tongue R. Fm.	<i>Wannaganosuchus brachymanus</i> , N. Dakota	II	<i>L. formidabilis</i> , N. Dakota	VI×VII
Nacimiento Fm. Torrejonian Faunal Zone	<i>Akanthosuchus langstoni</i> , N. Mexico	? NO	<i>L. multidentatus</i> , N. Mexico	UVI×VII
			<i>Navajosuchus novomexicanus</i>	III
U Ravenscrag Fm. Puercan Zone			<i>L. acutidentatus</i> , Saskatchewan	VI
	<i>Allog. mooki</i>	II×III		
Lance Fm, near Cret./ Paleocene	<i>Prodiplocynodon langi</i> , Wyoming	III×IV boundary	<i>L. sternbergi</i> , Wyoming	IV×III
UPPER CRETACEOUS	<i>Brachychampsia montana</i>	1, 02 II	<i>L. sternbergi</i> , Montana	IV×III
			<i>Pinacosuchus mantiensis</i> ?crocodile	NO
Hell Cr. Beds North Horn Fm.				
Judith R. Fm. Alberta	<i>Albertochampsia langstoni</i>	I	<i>L. canadensis</i>	V
			<i>L. gilmorei</i>	V
Kirtland Shale			<i>Goniopholis kirtlandicus</i> , G N.Mex.	V
"Greensand" in six Fms.	<i>Bottosaurus harlani</i> , New Jersey	NO		
			<i>Deinosuchus</i> 7 U	?IV×III
Dakota Sandst. Mowrie Sh. Fm.?			(giant crocodiles in six states)	
			<i>Dakotasuchus kingi</i> , Kansas	NO
UPPER JURASSIC All Morrison Fm. in the broad sense			<i>Coelosuchus reedii</i> , Wyoming	NO
			<i>Amphicotylus (G.) lucasii</i> , G. Colorado	V
			<i>G. gilmorei</i> , G. Wyoming	V×VI
			<i>G. stovalli</i> , G. Oklahoma	V×VI
			<i>Goniopholis felix</i> , G. Colorado	V×VI
			<i>Eutretauranosuchus delfsi</i> , G. Colorado	U

Species references: *Akanthosuchus* (O'Neill et al. 1981)/*Albertochampsia* (Erickson 1972)/*Alligator* in Pliocene and Miocene Florida (Aufenberg 1967), *A. mississippiensis* in Pleistocene Florida (Holman 1978), assignment of Pleistocene midcontinent material uncertain to species (Preston 1979)/*A. mefferdi* head shape is closer to *M. niger* skull ca. 20 cm long, than to I×II./*Alligator* ?n. sp. is shown in oblique view in Grande 1980. The head shape assigned here is an approximation./*Allognathosuchus wartheni* (Bartels 1980 for formation)/*Botto-saurus* conten. and range (Gilmore 1911). *Caiman sclerops* = *Caiman crocodilus* following Medem (1955, 1971, etc.) as the acknowledged best taxonomy; its range in Central America and that of *C. acutus* (Smith and Smith 1977)/*Crocodylus*: assignment of Eocene species from North America to this genus is not certain, and *C. clavis* may be a junior synonym of *C. affinis* (Buffrenil and Buffetaut 1981, W. Bartels; personal communication 1983)/*C. acer* and *L. wilsoni* (Grande 1980 for formation)/cf. *C. moreleti* in late Pliocene (Miller 1980)/*C. johnstoni* rather than *C. johnsoni* is used by current workers on that species, (e.g., Messel et al. 1981)/*Dakotasuchus* (Vaughn 1956 for formation)/*Deinosuchus* treated as a genus here—the three named species are not well distinguished by their authors; Baird and Horner 1979 for presence in six states; W. Langston, personal communication that skull shape needs re-evaluation; D. Baird, personal communication that lateral profile of anterior snout is unusual/*Go-*

niopholis (Mateer 1981 that perhaps North American species should be placed in *Eutre-tauranosuchus*)/*Hyposaurus* (G.) *natator* excluded from this list because it was narrow snouted (Troxell 1925) although included in list of broad-snouted species in Steel 1973/*Leidy-osuchus* (Baird and Horner 1979 and D. Baird, personal communication of occurrence in the Late Cretaceous in North Carolina and Georgia)/*L. canadensis* and *L. gilmorei* (W. Langston, personal communication 1983, that designation of Judith River Fm. rather than Old Man Fm. is correct)/*L. formidabilis* (Erickson 1976)/*P. vorax* (Langston 1975; Busbey, in preparation)/*Wannaganosuchus* (Erickson 1982).

The times and formations listed are the most precisely known strata of good published material. Stratigraphic names prior to 1965 follow USGS practice in Keroher (1966) or the *Lexicon of Geologic Names in Alberta* (1954). There are three exceptions, where major changes in formation names make the location of described fossils uncertain: the Wasatch Beds, New Jersey Greensand, and Plateau Valley Beds. For all North and Central American species the primary literature was reviewed. For brevity, I refer the reader to Steel (1973) and Kuhn (1936) for the remaining citations, which are accurate. The taxonomy used throughout is the best published work. Assignments to subfamily are convenient but often problematical. Synonymizing of species names in two unpublished theses is not followed here, in accordance with Smith's (1981) rules of priority.

- Almost all species are restricted to one formation or time interval.
- Each potential fauna, a horizontal group in the same state or physiographic province, has very few species. Fauna is used in the zoologist's sense. (The apparent exception, the Bridger species, is discussed in the text. The time sequence and taxonomy of the Upper Jurassic species are uncertain.)

Head profiles are given in Table 1. The unusual profiles, marked U, are discussed in the text. Fm. = formation.

1 Shape is inferred from partial material.

2 Snout has a constriction near the base deeper than in II.

3 Shape shares traits with I, II, and III.

4 Rear of skull is narrower than in III, resembling *Pa-leosuchus trigonatus*.

5 Shape is intermediate between V and III.

7 This giant skull has an unusual outline in Bird's restoration, based on fragmentary material.

? Taxonomic distinctness is uncertain.

NO No skull has been figured.

ID Species not based on comparative material, but it is distinct in its fauna.

hatching, of size just emerged from egg.

Juvenile: potentially still in care of an adult, e.g., up to 80 cm for large species like the American alligator. Subadult: smaller than common size of first breeding, e.g., up to 180 cm for female American alligators, larger for males.

Adult: of breeding size.

Natural habitat; a working definition for crocodylians is: the site is not modified by canals, water pumping, or other human influences on the presence of open water and of dry banks. Exotic plants are rare or absent from the wetland, especially plants offering cover for crocodylians, and wetland forest structure has no major alterations by logging or fires related to logging. Overland egress to other sites is not artificially restricted. Motorboats and airboats are rarely present (less than one day each three months), and harassment of crocodylians by humans rarely occurs.

Broad-nosed and narrow-nosed: these are equivalent to the respective terms, short-nosed (brevirostrine, often used as synonymous with alligators or broad-nosed crocodiles) and long-nosed (longirostrine, often used as synonymous with gharials and other narrow-nosed taxa). A glance at the head profiles in Fig. 1 shows the ambiguity in the short-nosed/long-nosed dichotomy, when used as descriptors of major shape groups.

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Literature

Adams, S. E., Smith, M. H., Baccus, R. 1980. Biochemical variation in the American alligator. *Herpetologica* 36(4):289-296.

- Allen, G. R. 1974. The marine crocodile, *Crocodylus porosus*, from Ponape, Eastern Caroline Islands, with notes on food habits of crocodiles from the Palau Archipelago. *Copeia* 1974(2):553.
- Auffenberg, W. 1967. Fossil crocodylians of Florida. Plaster Jacket, Florida State Mus., No. 5.
- Baird, D., Horner, J. R. 1979. Cretaceous dinosaurs of North Carolina. *Brimleyana* 2:1-28.
- Bartels, W. S. 1980. Early Cenozoic reptiles and birds from the Bighorn Basin, Wyoming, pp. 73-79. In: Gingerich, P. D. (ed.), *Early Cenozoic paleontology and stratigraphy of the Bighorn Basin, Wyoming*. U. Mich. Papers Paleont. No. 24.
- Beadle, L. C. 1974. *The inland waters of Tropical Africa*. London: Longman Group.
- Bennett, A. F. 1980. The metabolic foundations of vertebrate behavior. *BioScience* 30(7):452-456.
- Bennett, A. F., Ruben, J. A. 1979. Endothermy and activity in vertebrates. *Science* 206:649-654.
- Berggren, W. A., McKenna, M. C., Hardenbol, J., Obradovich, J. D. 1978. Revised Paleogene polarity time scale. *J. Geol.* 86:67-81.
- Bradley, W. H. 1964. *Geology of Green River Formation and associated Eocene rocks in southwestern Wyoming and adjacent parts of Colorado and Utah*. Geological Survey Prof. Paper 496-A, U.S. Gov't Printing Office.
- Brazaitis, P. The identification of living crocodylians. *Zoologica (NYZS)* 1973:59-101.
- Brazaitis, P. 1981. Maxillary regeneration in a marsh crocodile, *Crocodylus palustris*. *J. Herpetology* 15(3):360-362.
- Buffetaut, E. 1978. Sur l'histoire phylogenetique et biogeographie des Gavialidae (Crocodylia, Eusuchia). *C. R. Acad. Sc. Paris, t.287, Serie D, No. 10:911-914.*

- Buffetaut, E. 1979. The evolution of the crocodylians. *Sci. Amer.* 1979:130-144.
- Buffetaut, E., Ford, R. L. E. 1979. The crocodylian *Bernissartia* in the Wealden of the Isle of Wight. *Paleontology* 22(4):905-912.
- Buffetaut, E., Ingavat, R. 1980. A new crocodylian from the Jurassic of Thailand, *Sunosuchus thailandicus* n. sp. (Mesosuchia, Goniopholidae) and the paleogeographic history of Southeast Asia in the Mesozoic. *Geobios* 13(6):879-889.
- Buffrenil, V. de, Buffetaut, E. 1981. Skeletal growth lines in an Eocene crocodylian skull from Wyoming as an indicator of ontogenetic age and paleoclimatic conditions. *J. Vert. Paleont.* 1(1):57-66.
- Burgin, S. 1980. Crocodyles and crocodile conservation in Papua New Guinea, pp. 295-300. In: Moura, L., Pernetta, J., Heaney, W. (eds.), *Traditional conservation in Papua New Guinea: Implications for today*. Inst. Applied Social and Economic Research, Boroko, Papua New Guinea.
- Busbey, A. B. 1977. Functional morphology of the head of *Pristichampsus vorax* (Crocodylia, Eusuchia) from the Eocene of North America. M.A. thesis, U. Texas, Austin. Unpublished, cited with author's permission.
- Chabreck, R. H. 1965. The movement of alligators in Louisiana. *Proc. SE. Assn. Game and Fish Comm.* 19:102-110.
- Chabreck, R. H. 1971. The foods and feeding habits of alligators from fresh and saline environments in Louisiana. *Proc. SE. Assn. Game and Fish Comm.* 25:117-124.
- Chabreck, R. H., Dupie, H. P. 1976. Alligator predation on Canada goose nests. *Copeia* 1976(2):404-405.
- Chabreck, R. H., Joanen, T. 1979. Growth rates of American alligators in Louisiana. *Herpetologica* 35(1):51-57.
- Cohen, M. M., Gans, C. 1970. The chromosomes of the order Crocodylia. *Cytogenetics* 9:81-105.
- Colbert, E. H. 1962. The weights of dinosaurs. *Amer. Mus. Novit.* 2076:1-16.
- Colbert, E. H., Bird, R. T. 1954. A gigantic crocodile from the Upper Cretaceous beds of Texas. *Amer. Mus. Novit.* 1688:1-22.
- Colbert, E. H., Mook, C. C. 1951. The ancestral crocodylian *Protosuchus*. *Bull. Amer. Mus. Nat. Hist.* 97(3):147-182.
- Cope, E. D. 1883/4. *The Vertebrata of the Tertiary Formations of the West*. Book 1. Washington, DC: U.S. Gov't Printing Office.
- Cory, C. B. 1896. *Hunting and fishing in Florida, including a key to the water birds*. 2nd ed. Boston: Estes and Lauriat.
- Cott, H. B. 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* 29:210-357.
- Cott, H. B. 1972. Review of: W. T. Neill (1971). *Nature* 237:468.
- Cott, H. B. 1975. *Looking at animals: a zoologist in Africa*. New York: Scribners.
- Coulson, R. A., Hernandez, T. 1983. Alligator metabolism: studies on chemical reactions *in vivo*. *Comp. Biochem. Physiol.* 74(1):1-182.
- Darlington, P. J. 1957. *Zoogeography: the geographical distribution of animals*. New York: Wiley.
- Darwin, C. R. 1859. *On the origin of species*. (Facsimile reprint of the first edition, 1964). Boston: Harvard U. Press.
- Dietz, D. C., Hines, T. C. 1980. Alligator nesting in North-Central Florida. *Copeia* 1980(2):249-258.
- Densmore, L. D., Dessauer, H. C. 1979. Preliminary molecular evidence on relationships within the Alligatoridae, p. 24. In: 26th Ann. Meeting of the Herpetologist's League, 21st Ann. Meeting of the SSAR.
- Dodson, P. 1975. Functional and ecological significance of relative growth in *Alligator*. *J. Zool. London* 175:315-335.
- Dowling, H. G., Duellman, W. E. 1974/78. *Systematic herpetology: a synopsis of families and higher categories*. New York: HISS Publications.
- Erickson, B. R. 1972. *Albertochampsia langstoni*, gen. et sp. nov., a new alligator from the Cretaceous of Alberta. *Sci. Publ. Sci. Mus. Minnesota* 2, No. 1:1-13.
- Erickson, B. R. 1976. Osteology of the early eusuchian crocodile *Leidyosuchus formidabilis*, sp. nov. *Sci. Mus. Minnesota Monogr.* 22:1-61.
- Erickson, B. R. 1982. *Wannaganosuchus*, a new alligator from the Paleocene of North America. *J. Paleont.* 56(2):492-506.
- Estes, R. 1970. Origin of the Recent North American lower vertebrate fauna: an inquiry into the fossil record. *Forma et Functio* 3:139-169.
- Ferguson, M. J. W. 1979. The American alligator (*Alligator mississippiensis*): a new model for investigating developmental mechanisms in normal and abnormal palate formation. *Medical Hypotheses* 5:1079-1090.
- Ferrusquia-Villafranca, I. 1978. Distribution of Cenozoic vertebrate faunas in middle America and problems of migration between North and Central America. *Bol. Inst. Geol. Univ. Nat. Auton. Mexico*, 101:193-321.
- Fittkau, E. J. 1973. Crocodyles and the nutrient metabolism of Amazonian waters. *Amazonia* 4(1):103-133.
- Fogarty, M. J. 1972. Review of W. T. Neill (1971). *J. Wild. Mgmt.* 36:1370-2.
- Fogarty, M. J., Albury, J. A. 1967. Late summer

- foods of young alligators in Florida. Proc. SE. Conf. Game and Fish Comm. 1967:220-222.
- Friar, W., Behler, J. L. 1983. Review of H. Wermuth und R. Mertens (1977). Liste der rezenten Amphibien und Reptilien. Testudines, Crocodylia, Rhynchocephalia. Das Tierreich, W. De Gruyter, New York. Herp. Rev. 14(1):23-25.
- Fuchs, K., Mertens, R., Wermuth, H. 1974. Die unterarten des Nilkrokodils, *Crocodylus niloticus*. Salamandra 10:107-114.
- Garrick, L. D., Lang, J. W., Herzog, H. A. 1978. Social signals of adult American alligators. Bull. Amer. Mus. Nat. Hist. 160(3):153-192.
- Gartside, D. F., Dessauer, H. C., Joanen, T. 1977. Genic homozygosity in an ancient reptile (*Alligator mississippiensis*). Biochem. Genet. 15(7/8): 655-663.
- Giles, L. W., Childs, V. L. 1949. Alligator management on the Sabine National Wildlife Refuge. J. Wild. Mgmt. 13:16-28.
- Gilmore, C. W. 1911. A new fossil alligator from the Hell Creek Beds of Montana. Proc. U.S. Natl. Mus. 41, No. 1860:297-302 + 2 pl.
- Glass, M. L., Johansen, K. 1979. Periodic breathing in the crocodile *Crocodylus niloticus*: consequences for the gas exchange ratio and control of breathing. J. Exp. Zool. 208(3):319-325.
- Gleeson, T. T. 1979. Foraging and transport costs in the Galapagos marine iguana, *Amblyrhynchus cristatus*. Physiol. Zool. 52(4):549-557.
- Goetz, S. J. 1978. An ecological study of *Caiman crocodilus crocodilus* inhabiting savanna lagoons in the Venezuelan Guayana. Oecologia 35:21-34.
- Gould, S. J., Lewontin, R. C. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proc. Roy. Soc. London 205:582-598.
- Graham, A. 1968. The Lake Rudolf crocodile (*Crocodylus niloticus*) population. Mimeo. report to the Kenya Game Dept.
- Grande, L. 1980. Paleontology of the Green River Formation with a review of the fish fauna. Geol. Surv. Wyoming, Bull. 63.
- Herzog, H. A. 1974. The vocal communication system and related behaviors of the American alligator. (*Alligator mississippiensis*) and other crocodylians. M.A. Thesis, U. Tennessee.
- Herzog, H. A., Burghardt, G. M. 1977. Vocal communication signals in juvenile crocodylians. Z. Tierpsych. 44:394-404.
- Hines, T. C., Scheaffer, R. C. 1977. Public opinion about alligators in Florida. Proc. Ann. Conf. SE. Assoc. Fish & Wildl. Agencies 31:84-89.
- Holman, J. A. 1978. The Late Pleistocene herpetofauna of Devil's Den sinkhole, Levy County, Florida. Herpetologica 34(2):228-237.
- Honegger, R. E. 1975. Red data book, Vol. 3: Amphibia and Reptilia. IUCN, Morges, Switzerland.
- Hornaday, W. T. 1875. The crocodile in Florida. Amer. Nat. 9:1-6.
- Hulke, J. W. 1878. Notes on two skulls from the Wealden and Purbeck Formations indicating a new subgroup of Crocodylia. Geol. Soc. London Quart. J. 34:377-383.
- von Humboldt, A. 1876. Personal narrative of travels to the equinoctial regions of America. Ross, T. (tr.), Vol. 2. London: Bell.
- Hunt, R. H. 1977. Aggressive behavior by adult Morelet's crocodiles *Crocodylus moreleti* toward young. Herpetologica 33:195-201.
- Hunt, R. H., Watanabe, M. E. 1982. Observations on maternal behavior of the American alligator, *Alligator mississippiensis*. J. Herp. 16:235-239.
- Huxley, T. H. 1875. On *Stagonolepis Robertsoni*, and on the evolution of the crocodylia. Geol. Soc. London Quart. J. 31:423-436. (Duncan's comments & discussion are on pp. 436-438.)
- Iordansky, N. N. 1973. The skull of the Crocodylia, pp. 256-284. In: Gans, C. (ed.), Biology of the Reptilia, New York: Academic.
- Joanen, T. 1969. Nesting ecology of alligators in Louisiana. Proc. SE. Assn. Game and Fish Comm. 19:141-151.
- Joanen, T., McNease, L. 1972. A telemetry study of adult male alligators on Rockefeller Refuge, Louisiana. Proc. SE. Assoc. Game and Fish Comm. 1972:252-275.
- Joffe, J. 1967. The "dwarf" crocodiles of the Purbeck Formation, Dorset: reappraisal. Paleontology 10(4):629-639.
- Kaellin, J. A. 1933. Beiträge zur vergleichenden Osteologie des Crocodylienschädels. Zool. Jahrbuch, Anatomie 57:535-714.
- Kerher, G. C., and others. 1966. Lexicon of geologic names of the U.S. U.S. Geol. Surv. Bull. No. 1200. 3 Vol.
- King, F. W. 1972. Review of W. T. Neill (1971). BioScience 22:119.
- Kuhn, O. 1936. Fossilium Catalogus. 1: Animalia, Pars 75: Crocodylia. Gravenhage: W. Junk.
- Kuhn, O. 1968. Die Vorzeitlichen Krokodile. München: Verlag Oeben.
- Kurten, B. 1978. The age of dinosaurs. New York: McGraw-Hill.
- Kushlan, J. 1974. Observations on the role of the American alligator (*Alligator mississippiensis*) in the southern Florida wetlands. Copeia 1974 (4): 993-996.
- Kushlan, J., Kushlan, M. S. 1980. Function of nest attendance in the American alligator. Herpetologica 36(1):27-32.

- Langston, W. 1965. Fossil crocodylians from Colombia and the Cenozoic history of the Crocodylia in South America. U. Calif. Publ. Geol. Sci. 52:1-157 + 5 pl.
- Langston, W. 1966. *Mourasuchus* Price, *Nettosuchus* Langston, and the family Nettosuchidae (Reptilia: Crocodylia). Copeia 1966:882-885.
- Langston, W. 1973. The crocodylian skull in historical perspective, pp. 263-284. In: Gans, C. (ed.), Biology of the Reptilia, Vol. 4D. New York: Academic.
- Langston, W. 1975. Ziphodont crocodylians: *Pristichampsus vorax* (Troxell), new combination, from the Eocene of North America. Fieldiana Geol. 33(16):291-314.
- Leakey, M. D. 1971. Olduvai Gorge, p. 291. Vol. 3. Cambridge U. Press.
- Lexicon of geologic names in Alberta and adjacent portions of British Columbia and N.W. Territories. 1954. Alberta Soc. Petr. Geol., Calgary.
- Longman, H. A. 1925. *Crocodylus johnsoni* Krefft. Mem. Queensland Mus. 8(2):95-102.
- Lydekker, R. 1886. Palaeontologica Indica. Mem. Geol. Surv. India, ser. 10, V. 2:209-240.
- Magnusson, W. E. 1980. Habitat required for nesting by *Crocodylus porosus* (Reptilia: Crocodylidae) in Northern Australia. Aust. J. Wildl. Res. 7:149-156.
- Magnusson, W. E. 1982. Mortality of eggs of the crocodile *Crocodylus porosus* in northern Australia. J. Herp. 16(2):121-130.
- Mateer, N. J. 1981. The reptilian megafauna from the Kirtland Shale (Late Cretaceous) of the San Juan Basin, New Mexico. p. 59. In: Lucas, S. G., Rigby, J. K., Kues, B. S. (eds.), Advances in San Juan Basin paleontology. U. New Mexico Press.
- Mayr, E. 1954. Change of genetic environment and evolution, pp. 155-180. In: Huxley, J., Hardy, A. C., Ford, E. B. (eds.), Evolution as a process. London: Allen and Unwin.
- Mayr, E. 1975. The unity of the genotype. Biol. Zbl. 94:337-388.
- McIlhenny, E. A. 1935. The alligator's life history. Boston: Christopher Publ. (Also reprinted by the SSAR, 1976).
- McNease, L., Joanen, T. 1974. A study of immature alligators on Rockefeller Refuge, Louisiana. Proc. SE. Assn. Game and Fish Comm., 28:482-500.
- McNease, L., Joanen, T. 1977. Alligator diets in relation to marsh salinity. Proc. Ann. Conf. SE. Assn. Fish and Wildlife Agencies 31:36-40.
- Medem, F. 1955. A new subspecies of *Caiman sclerops* from Colombia. Fieldiana Zool. 37:339-343.
- Medem, F. 1958. The crocodylian genus *Paleosuchus*. Fieldiana Zool. 39:227-247.
- Medem, F. 1960. Notes on the Paraguay caiman, *Caiman yacare* Daudin. Mitt. Zool. Mus. Berlin 36(1):129-142.
- Medem, F. 1971. Biological isolation of sympatric species of South American crocodylia, pp. 152-158. In: Crocodyles. IUCN Publ. N.S. No. 52.
- Menzies, R. A., Kushlan, J., Dessauer, H. C. 1979. Low degree of genetic variability in the American alligator (*Alligator mississippiensis*). Isozyme Bulletin 12.
- Messel, H., Vorlicek, G. C., Wells, A. G., Green, W. J. 1981. The Blyth-Cadell rivers system study and the status of *Crocodylus porosus* in tidal waterways of Northern Australia. Vol. 1 of the series: Surveys of tidal river systems in the Northern Territory of Australia and their crocodile populations. Sydney: Pergamon.
- Metzen, W. D. 1977. Nesting ecology of alligators on the Okefenokee National Wildlife Refuge. Proc. SE. Assn. Fish and Wildl. Agencies, 31st Conf.
- Meyer, E. R. 1975. Alligator ecology and population structure on Georgia sea islands. Amer. Soc. Ichth. Herp. 55th Meeting: p. 54.
- Meyer, E. R. 1977. Alligator behavior, ecology, and populations in some Okefenokee marshes. Amer. Soc. Ichth. Herp. 57th Meeting Program Abstract.
- Meyer, E. R. 1978. Female alligator opening her nest and carrying hatchlings to water. Color motion picture footage in: Dragons of paradise, a one-hour documentary distributed to U.S. public television, 1978-1983.
- Miller, W. E. 1980. The late Pliocene Las Tunas local fauna from southernmost Baja California, Mexico. J. Paleont. 54:762-805.
- Minton, S. A., Minton, M. R. 1973. Giant reptiles. New York: Scribners.
- Modha, M. L. 1967. The ecology of the Nile crocodile (*Crocodylus niloticus* Laurent) on Central Island, Lake Rudolf. E. Afr. Wildl. J. 5:74-95.
- Molnar, R. E. 1979. *Crocodylus porosus* from the Pliocene Allingham formation of North Queensland, Australia: results of the Ray E. Lemley Expeditions, Part 5. Mem. Queensland Mus. 19(3):357-365.
- Mook, C. C. 1962. A new species of *Brachyuranochampsia* (Crocodylia) from the Bridger Beds of Wyoming. Amer. Mus. Novit., No. 2079:1-6.
- Myers, N. 1972. The long African day. New York: Macmillan.
- Neill, W. T. 1971. The last of the ruling reptiles, alligators, crocodyles, and their kin. New York: Columbia U. Press.
- Nichols, J. D., Viehman, L., Chabreck, R. H., Fenderson, B. 1976. Simulation of a commercially harvested alligator population in Louisiana. Louisiana State U. Agric. Exper. Station, Bulletin No. 691.

- Olsen, E. C. 1971. Vertebrate paleozoology. New York: Wiley.
- O'Neill, F. M., Lucas, S. G., Kues, B. S. 1981. *Akanthosuchus langstoni*, a new crocodylian from the Nacimiento formation (Paleocene, Torrejonian) of New Mexico. *J. Paleont.* 55(2):340-352.
- Ostrom, J. H. 1969. Terrestrial vertebrates as indicators of Mesozoic climates. *Proc. N. Amer. Paleont. Conv.* 347-376.
- Owen, R. 1878. Order. *Crocodylia*. Suppl. No. VIII to the: Monograph on the fossil Reptilia of the Wealden and Purbeck Formations. London: Palaeontographical Society.
- Patterson, B. 1931. Occurrence of the alligatoroid-genus *Allognathosuchus* in the Lower Oligocene. *Field Mus. Nat. Hist., Geol. Ser.* 4(6):223-226 + 1 pl.
- Patterson, B. 1936. *Caiman latirostris* from the Pleistocene of Argentina, and a summary of South American Cenozoic Crocodylia. *Herpetologica* 1:43-54.
- Pienaar, U. de V., FitzSimons, V. F. M. 1966. The reptiles of the Kruger National Park. *Koedoe* No. 1.
- Pienaar, U. de V. 1969. Predator-prey relationships amongst the larger mammals of the Kruger National Park. *Koedoe* 1969:108-176.
- Pitman, C. R. S. 1941. About crocodiles. *Uganda Journal* 9:89-114.
- Pooley, A. C. 1977. Nest opening response of the Nile crocodile *Crocodylus niloticus*. *J. Zool. London* 182:17-26.
- Pough, F. H. 1980. The advantages of ectothermy for tetrapods. *Amer. Nat.* 115(1):92-112.
- Preston, R. E. 1979. Late Pleistocene cold-blooded vertebrate fauna from the mid-continental United States. *U. Mich. Paper on Paleont.* No. 19:1-53.
- Romer, A. S. 1966. *Vertebrate paleontology*. (3rd ed.) U. Chicago Press.
- Romer, A. S. 1971. The Chanares (Argentina) Triassic reptile fauna XI. Two new long-snouted thecodonts, *Chanaresuchus* and *Gualosuchus*. *Breviora*, MCZ, No. 379.
- Romero, G. A. 1983. Distress call saves a *Caiman c. crocodilus* hatchling in the Venezuelan llanos. *Biotropica* 15(1):71.
- Roosevelt, T. R. 1924. *Through the Brazilian wilderness*. New York: Scribners.
- Root, J., Root, A. 1971. Mzima, Kenya's spring of life. *Natl. Geogr.* 140(3):350-373.
- Ross, C. A. 1979. Scalation of the American alligator. *U.S. Fish and Wildl. Serv., Special Sci. Rept.: Wildlife* No. 225:1-8.
- Ross, C. A. 1974. Gharial in Corbett National Park (U.P.), p. 8. In: Whitaker and Rajamani 1974.
- Russell, D. E. and 32 coauthors. 1982. *Tetrapods of the Northwest European Tertiary Basin*. Geologisches Jahrbuch, Reihe A, Heft 60.
- Schmidt, K. P. 1919. Contributions to the herpetology of the Belgian Congo based on the collection of the American Museum Congo Expedition, 1909-1915. *Bull. Amer. Mus. Nat. Hist.* 39:385-624.
- Schmidt, K. P. 1924. Notes on Central American crocodiles. *Field Mus. Nat. Hist., Zool. Ser.* 12(220):79-92.
- Schmidt, K. P. 1928. Notes on South American caimans. *Field Mus. Nat. Hist., Zool. Ser.* 12(252):203-231 + 6 pl.
- Schmidt, K. P. 1932. Notes on New Guinean crocodiles. *Field Mus. Nat. Hist., Zool. Ser.* 18(8):164-173.
- Schmidt, K. P. 1941. A new fossil alligator from Nebraska. *Field Mus. Nat. Hist. Geol. Ser.* 8(494):27-32.
- Schmidt, K. P. 1944. Crocodiles. *Fauna* 6(3):67-72.
- Sill, W. O. 1968. The zoogeography of the crocodylia. *Copeia* 1968:76-88.
- Simpson, G. G. 1933. A new crocodylian from the *Notostylops* beds of Patagonia. *Amer. Mus. Novitates*, No. 623.
- Smith, E. N. 1979. Behavioral and physiological thermoregulation of crocodylians. *Amer. Zool.* 19:239-247.
- Smith, H. M., Smith, R. B. 1977. Synopsis of the herpetofauna of Mexico, pp. 49-116. Vol. 5.
- Smith, H. M. 1981. A suggested protective declaration for taxonomic dissertations. *Herp. Rev.* 12:98.
- Spotila, J. R., Soule, O. H., Gates, D. M. 1972. The biophysical ecology of the alligator: heat energy budgets and climate spaces. *Ecology* 53(6):1094-1102.
- Stanley, S. M. 1973. An explanation for Cope's Rule. *Evolution* 27(1):1-26.
- Staton, M. A., Dixon, J. R. 1975. Studies on the dry season biology of *Caiman crocodilus crocodilus* from the Venezuelan llanos. *Memoria Cien. Nat., Caracas*, 35:237-265.
- Staton, M. A., Dixon, J. R. 1977. Breeding biology of the spectacled caiman, *Caiman crocodilus crocodilus*, in the Venezuelan llanos. *U.S. Fish and Wildl. Serv. Wildlife Res. Rept.* 5:1-21.
- Stebbins, G. L. 1982. Perspectives in evolutionary theory. *Evolution* 36(6):1109-1118.
- Steel, R. 1973. Crocodylia, pp. 1-116. In: *Encyclopedia of paleoherpetology*, Part 16. Stuttgart-Portland: Gustav Fischer Verlag.
- Tchernov, E. 1976. Crocodylians from the late Cenozoic of the Rudolf Basin, pp. 370-378. In: Coppen, Y. et al. (eds.), *Earliest man and environments in the Lake Rudolf Basin*. U. Chicago Press.

- Templeton, A. R. 1981. Mechanisms of speciation: a population genetic approach. *Ann. Rev. Ecol. Syst.* 12:23-48.
- Terpin, K. M., Spotila, J. R., Foley, R. E. 1979. Thermoregulatory adaptations and heat energy budget analyses of the American alligator, *Alligator mississippiensis*. *Physiol. Zool.* 52(3):296-312.
- Troxell, E. L. 1925. *Hyposaurus*, a marine crocodylian. *Amer. J. Sci.* 10:489-514.
- Van Valkenburgh, B. 1982. Evolutionary aspects of terrestrial large predator guilds. *Third North Amer. Paleont. Conv. Proc.* 2:557-562.
- Vaughn, P. P. 1956. A second specimen of the Cretaceous crocodile *Dakotasuchus* from Kansas. *Trans. Kansas Acad. Sci.* 59:379-381.
- Watson, R. M., Graham, A. D., Bell, R. H. V., Parker, I. S. C. 1971. A comparison of four East African crocodile (*Crocodylus niloticus*) populations. *E. Afr. Wildl. J.* 9:25-34.
- Webb, G. J. W. 1977. The natural history of *Crocodylus porosus*. In: Messel, H. and Butler, S. T. (eds.), *Australian animals and their environments*. Sydney: Shakespeare Head Press.
- Webb, G. J. W., Messel, H. 1977. Abnormalities and injuries in the estuarine crocodile, *Crocodylus porosus*. *Austr. Wildl. Res.* 4:311-319.
- Webb, G. J. W., Messel, H. 1978a. Morphometric analysis of *Crocodylus porosus* from the north coast of Arnhem Land, Northern Australia. *Austr. J. Zool.* 26:1-27.
- Webb, G. J. W., Messel, H. 1978b. Movement and dispersal patterns of *Crocodylus porosus* in some rivers of Arnhem Land, Northern Australia. *Austr. Wildl. Res.* 5:263-283.
- Welman, J. B., Worthington, E. B. 1943. The food of the crocodile (*Crocodylus niloticus* L.). *Proc. Zool. Soc. London* 113:108-112.
- Wermuth, H., Mertens, R. 1961. *Schildkröten-Krokodile-Brückenechsen*. Jena: Gustav Fischer Verlag.
- Whitaker, R. 1974. Notes on behaviour, ecology, and present status of the marsh crocodile (*Crocodylus palustris*) in south India. Madras Snake Park Trust and Conservation Center, India.
- Whitaker, R., Rajamani, V. C. 1974. Gharial survey report. Madras Snake Park Trust and Conservation Center, India.
- Wilson, D. S. 1980. The natural selection of populations and communities. Menlo Park: Benjamin/Cummings.
- Zug, G. R. 1974. Crocodylian galloping: an unique gait for reptiles. *Copeia* 1974:550-552.