AMER. ZOOL., 29:1051–1054 (1989)

Crocodilians in Perspective![1]

CARL GANS

Department of Biology, The University of Michigan, Ann Arbor, Michigan 48109-1048

SYNOPSIS. The prediction of the 1960s that crocodilians would soon be extinct has happily proven to be unduly pessimistic. The survival and recovery of substantial stocks provides us with the unexpected opportunity to learn about their adaptations, important not only because of their place as relicts of a major reptilian radiation, but also as giant animals, reptiles substantially larger than all but marine turtles.

Some twenty years ago, the talented Wilfred T. Neill published *The Last of the Ruling Reptiles.* This review of crocodilians noted some of the astonishing attributes of these fascinating animals, but concluded that they were clearly on the way out, because of hunting and the environmental destruction observed by him in Florida and other places. This was indeed sad! Not only did it seem that we were about to lose a group of animals of intrinsic interest to zoologists, but Professor Coulson, to whom this symposium is dedicated, was simultaneously demonstrating that crocodilians had many unique and previously misunderstood properties. His reevaluation of their comparative physiology disclosed that crocodilians were much more than scaled-up lizards or mice. Clearly, dogs and white rats were not the ideal organisms from which all useful physiology could be extrapolated.

Happily and quite unexpectedly, we are now able to reverse some of Neill's pessimistic predictions. A completely different group of biologists became involved with crocodilian biology, and their practical efforts have saved some crocodilians for the moment. Increasing public concern with environmental issues and the demand for the protection of natural areas suddenly made park management and wildlife protection more widely respectable and increased the resources therefor available. Parallel studies in Natal, Kenya, Australia, Louisiana, and Tel Aviv led to a new and global look at crocodilians, increasing our understanding of their reproductive patterns and leading to demands for their protection.

The several studies provided major gains in our comprehension of their biology, particularly their development and ecology. These projects provided the data for major propaganda efforts, generating public awareness about issues of conservation and endangered species. Such messages reached most homes via their television screens and gradually convinced the public that more than a few cuddly animals were fascinating, and that crocodilians were particularly interesting. They were large and of curious habits, hardly sluggish as often assumed after seeing one in an old-fashioned zoo. The public became aware of the idea that these reptiles might be as close as anything to the extinct giant reptiles that once roamed our planet; we benefitted from the increasing popularity of dinosaurs and their ilk, publicizing that crocodilians were important because they might provide clues to dinosaurian biology.

A most important product of the new activity was the demonstration that crocodilian reproduction was not an unplumbable mystery, so that numbers of animals could be raised with modest effort. If hunting and environmental destruction could be proscribed, this conclusion provided hope of once again having self-perpetuating populations of crocodilians.

Unfortunately the literature about this protectionist effort continues to be extremely scattered. Much consists of mimeographed and poorly duplicated reports, obviously unreviewed and unedited before publication. Some very signif-

[1] From the Symposium on *Biology of the Crocodilia* presented at the Annual Meeting of the American Society of Zoologists, 27–30 December 1987, at New Orleans, Louisiana.

icant results have been forced into proprietary journals with quite distinct and often limited forms of distribution. Many conferences occurred closer to the habitat of the residual crocodilians than to that of most zoologists, attendance was often limited (sometimes by invitation only) and the results there reported were published late or never.

At the very least, this diffusion and isolation has had the profound disadvantage that it contributed to a lack of a comparative base for reptilian studies. The term "reptiles" may be cladistically inappropriate as reptiles can only be defined by exclusion (*i.e.*, non-endothermal amniotes); however, there are many things to be gained by analyzing comparatively the adaptive corollaries of this grade of organisms (*cf.* Mazzotti and Dunson, this volume). Hence, I welcome the trend to more open symposia, such as the present one, and to a venue in which diverse specialists for other groups can listen and contribute.

It is quite clear from our program that we have been able to obtain new data on many aspects of crocodilians and to update ongoing projects. It is even more clear that the real crocodilians differ profoundly from those curious organisms referred to in textbooks as recently as two decades ago. For instance, growth of the real animals is very vagile; thus, nutrition and temperature play an enormous role in its rate and probably in size at sexual maturity and even absolute size of adults, as nicely documented in this volume (Coulson *et al.*, this volume). They have a complex series of social displays (Vliet, this volume), which to me seemed to represent a marvelous opportunity for test by methods of functional morphology. Crocodilian metabolism is that of ectotherms, but also incorporates variants due to the enormous size these animals may attain, an issue that expands on the studies of their thermal equilibrium pioneered decades ago by Cowles and his colleagues. Their sex and apparently many other important aspects, such as growth rate and final size (see Lang *et al.* and list in Webb and Cooper-Preston, this volume) are determined by the temperature at which the eggs are incubated. Crocodilians show responses to marine influences, some species and some ontogenetic stages being much more tolerant of salinity than others (see Taplin and Grigg, this volume). Also, crocodilian species seem to differ drastically in their ability to accommodate to situations of rapid water flow and terrestrial transit. For a few species, we now know much about physiology, about normal development and responses to developmental manipulations (Deeming and Ferguson, this volume). Beyond this, we have more specific data from local studies regarding their current status, movement patterns (Hutton, this volume), management (Joanen and McNease, this volume), reproductive cycles (Lance, this volume), and release patterns on different continents and countries.

No one seems now to argue about the specific status of crocodilians, and the immunological studies confirm the reality of the present taxonomic scheme. In contrast, this volume documents that the introduction of new characters has not generated an equivalent concurrence on the suprageneric levels. Evaluating this situation from the viewpoint of a taxonomist involved with other reptilian groups has led me to several observations, that may have a bearing on this issue. There is substantial evidence that the crocodilians share many details of structure and physiology. They may well be the remnants of a single major radiation with past extinctions, but these are unlikely to have been recent. The animals are large and tend to the capacity for occupancy of large ranges which show little overlap; indeed, the commonality of cannibalism among certain classes would limit coexistence. Hence, morphological and physiological adaptation to particular environments may be less obvious than behavioral differences and minor historical accident in explaining present distributions. Resolution of such a situation requires careful analysis of additional morphological and biochemical characteristics, not only in all extant species but in their ontogenetic stages as well. It also requires more effective outgroup comparison, both

of reptiles of other groups and specifically of reptiles that occupy environments ecologically similar to both those now occupied and those marginal to present crocodilian ranges.

Clearly, we now know much about encouraging reproduction in the wild, about raising organisms in captivity (with its success differing drastically and often unnecessarily), and about the possibilities for restocking. The potential for commercial utilization of crocodilians, hunted or farmed, has been established in some areas and for particular species; however, much argument remains about the influence of this commercial component on conservation efforts. Recovery of stocks of some species, such as *Alligator mississippiensis* and *Crocodylus johnstoni*, indicate the spectacular potential.

However, the latter forms may be relatively harmless and we still face queries about cohabitation with crocodilians. This may pose little problem for the smaller forms, and even for *Alligator mississippiensis*. This species now seems to predate only an occasional pet, with only the very largest individuals posing a danger to adult humans. However, what about other species, such as *Crocodylus niloticus* and *C. porosus*, which have proven records for predation on large vertebrates including *Homo sapiens*? Do the claims that animals in intensively hunted regions avoid man reflect learning or the selective removal of a genetically distinct subgroup from their population? Also problematic are situations in which crocodilians may affect commercially valuable stocks of other organisms or are said to interfere with their harvest (such as by destroying nets). Issues such as this transcend academic zoology and involve sociological and management concerns. However, ecological and behavioral studies on crocodilians are fundamental, as they have to provide the data base that may help resolve such issues.

Other unsolved questions keep coming to mind as one listens to reports of successful propagation. After all, crocodilians are the largest of the Recent reptiles. They represent one end of the volumetric scale, with their mean mass being very much greater than that of even the large marine turtles, which represent a quite different and distinct adaptive peak. It seems important to utilize the continuing availability of crocodilians in order to increase our understanding of many biological processes.

One specific set of issues that deserves more attention is that of microgeographical differences among populations. Do polymorphic and similar differences relate to environmental-habitat differences? On alligators there are said to be some data and we have a report on one population of *Crocodylus niloticus* in this volume, but the enormous ranges occupied by this species, and *Crocodylus porosus*, have been utilized for only limited studies thus far. Are these animals generalists which have a basic pattern that matches all habitat variants or specialists which show some degree of local adaptation? Do the island populations of *Crocodylus porosus* show any genetic restriction possibly due to past founder effects? Or is the present distribution the restriction of a once much more extensive range in which gene exchange was once common?

Then there are various behavioral aspects which deserve more attention. The few observations on food acquisition by crocodilians are mostly serendipitous. Do crocodilians trap or specifically hunt individual prey? Do the few reports on cooperation represent accidental events or part of a more general phenomenon? What about the issue of interspecific interactions; were the ranges, for instance of *Caiman, Melanosuchus* and *Paleosuchus*, ever in contact?

Many of the things we have learned apply to only one or a few species. There is a vast gap in our understanding of the comparative biology of crocodilians, of the patterns disclosed by their species and genera. There are summaries of the elements of the skull, but we still lack a comparative anatomy of the soft tissues. There is almost no comparative functional morphology, only quite inadequate individual reports on feeding and on locomotion, crocodilian

ventilation having been reported for only two species and then for a restricted range of sizes. The crocodilian heart has similarly been studied in only a very few species and for a limited size range. Development has been described for *Alligator*, but there are many other species and, in some, nursing activities extend over 65 degrees of latitude and 70 degrees of longitude; is the developmental pattern vagile or does it proceed independently of environmental influence? Are there intraspecific and possibly adaptive differences among crocodilians or is the partition of the world among Recent crocodilian species only the remnant of a series of historical accidents?

Comparative functional morphology is important because it may allow some conclusions not just about the placement of fossils, but about their behavior, physiology and perhaps ecology. The number of times that certain structural patterns have appeared in the skull needs to be matched with better treatment of the postcranial system. An obvious set of questions concerns the crocodilian gallop, morphological attributes of which have never been characterized. Reconstruction of the locomotor patterns of extinct forms, mainly appears to assume that locomotor pattern is a function of the length of limb segments, and of the ratio of pectoral to pelvic proportions. However, we seem to have no analysis of how this differs in Recent forms, how it changes in ontogeny and how it related to joint motility and muscle placement.

This may let us introduce the issue of the enormous range of crocodilian growth, which seemingly incorporates only minor morphologic differences although the size shifts over orders of magnitude. One gets the impression that the insectivorous jumping pattern seen in juveniles grades gradually into the sit-and-wait behavior of adults, but one lacks information about probable adaptive compromises or the question whether the motor patterns scale evenly with size.

We do know that the proportions of brain and sensory tracts grow allometrically. However, there is little information about possible comparative differences in brain components and about the way that these correlate with sensory attributes. Do these correlate with neurobehavioral changes in ontogeny, or do they reflect only allometric changes?

One notes the curious pattern of parental care, seemingly unique among reptiles. Adult crocodilians dig up and protect their young which first cluster in their vicinity and later show a behavioral switch, scattering away from subadults and adults. Does this set of behaviors allow any suggestions about the environments ancestral to crocodilians and why does it differ so markedly from the reproductive patterns seen in turtles? Does this limited parental care presage an early evolutionary stage for the parental care shown by birds (and mammals?)? How does it relate to the suggestion that amniote parental care represents the reinvention of a kind of metamorphosis?

The current success of conservation and the extensive availability of crocodilian materials provide an excellent opportunity for further studies. These should not only enhance our understanding of crocodilian biology but also provide data facilitating conclusions and furnishing perspectives for the understanding of the biology of other animals, large and small.

ACKNOWLEDGMENTS

It is a pleasure to acknowledge with gratitude the opportunity to talk about these animals and to see them in the field in the company of Francisco S. Pereira, CMF, Wilfred T. Neill, E. Ross Allen, Heinrich Mendelssohn, Tony Pooley, C. O. Dieffenbach, Harry Messel, Graeme Webb, Jeff Lang and Rom Whitaker. Preparation supported by NSF grant G-BSR-850940.