



# THE THEROPOD REPRODUCTIVE SYSTEM

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**ABSTRACT:** Soft tissue preservation in theropods is extremely rare, and preservation of reproductive soft tissue in vertebrate fossils is virtually unknown. It is possible, however, to draw conclusions about the theropod reproductive system by direct observation of fossil evidence, along with inferences based upon the reproductive systems of extant crocodiles and birds - theropods' closest living relatives. The gender of a theropod probably was determined by sex chromosomes, with females the heterogametic sex. Male theropods possessed internal testes and a retractable penis. Females possessed paired ovaries and oviducts, along with a crocodylian-like system of storing mature eggs awaiting fertilization. Egg clutches of one to two dozen, or more, were laid at one sitting with the female laying a pair of eggs and then pivoting around the center of the clutch a few degrees before she lay her next pair. At least some theropods incubated their eggs, again confirming that they were very probably endotherms.

**RÉSUMÉ:** La préservation des parties molles des théropodes est extrêmement rare, tandis que celle des parties molles du système reproducteur est pratiquement inconnue en ce qui concerne les vertébrés fossiles. Cependant, il est possible d'arriver à des conclusions quant au système reproducteur des théropodes par l'observation directe des fossiles, ainsi qu'en faisant quelques déductions fondées sur le système reproducteur des crocodiles et des oiseaux, seuls parents proches des théropodes encore existants. Le sexe des théropodes était probablement déterminé par des chromosomes sexuels, les femelles représentant le sexe hétérogame. Les mâles théropodes possédaient des testicules internes et un pénis retractile. Les femelles possédaient des ovaires appariés et des oviductes, ainsi qu'un système de stockage des oeufs prêts à être fécondés proche de celui des crocodiles. Des grappes d'une à deux douzaines d'oeufs, voire plus, étaient pondus en une fois, la femelle pondant une paire d'oeufs puis pivotant autour du centre de la grappe de quelques degrés avant de pondre la paire d'oeufs suivante. Quelques théropodes au moins incubaient leurs oeufs, confirmant ainsi à nouveau qu'ils étaient très probablement endothermes.

## INTRODUCTION

Non-avian theropods have been extinct for 65 million years. Their demise and the subsequent destruction of their bodies by biological, chemical, and meteorological agents have made direct study of their soft parts impossible, except for a few rare occurrences. Virtually nothing remains, for instance, of their reproductive organs. Yet, it is still possible to reconstruct much of the basic information about these soft tissues by studying the fossil remains we do have: evidence found in theropod skeletons and nests. When this information is coupled with our knowledge about the reproductive systems found in theropods' closest living relatives, crocodiles and birds, we arrive at a better understanding of how these animals' reproductive systems functioned. [This method of soft tissue inference using an extant

phylogenetic bracket has been explained in detail by WITMER (1995)].

## SEXUAL DETERMINATION & DIMORPHISM

In critically examining the biological processes of extant species related to theropods, we can determine which of these processes were most likely found in theropods. In considering the reproductive system, analysis begins with sexual determination in crocodiles and birds.

Most reptiles, amphibians, fishes, insects, and all mammals have sex chromosomes, X and Y, which produce enzymes that determine the gender of the individual upon fertilization of the egg. The Y chromosome carries the genes for maleness in mammals and most insects. However, the Y chromosome carries the genes for femaleness in birds,

reptiles, and some amphibians and fishes, and it is assumed to be the primitive condition in vertebrates. Females, in these cases, are the heterogametic sex, the gender with XY chromosomes (as opposed to the homogametic gender, which carries only XX).

Sexual determination does not stop there, however. Despite the presence or absence of these chromosomes, bird and crocodile embryos begin life with the essential primordia for developing into either sex. For example, while the sex of a bird is normally determined by the Y chromosome, in rare occasions in nature, and under experimental laboratory conditions, birds have been known to reverse their sex (WELTY & BAPTISTA, 1988). Equally exceptional is the effect of the temperature of incubation upon the sex of a crocodile. Utilizing a derived character shared with many species of turtles and some lizards, if crocodile eggs develop in temperatures of 28 - 30 °C, they produce females. If they develop in temperatures of 32 - 34 °C, they produce males. With intermediate temperatures, both sexes are produced (MAGNUSSON *et al.*, 1989).

Because a bird's sex is determined in a more primitive fashion than in crocodiles (via the effects of X and Y chromosomes as opposed to temperature during incubation), it is appropriate to assume that this primitive condition was present in birds' theropod ancestors. Also, like birds, the Y chromosomes must have carried the genes for femaleness.

In both crocodiles and birds, the male and female gonads lie in the posterior dorsal area of the abdominal cavity, near the kidneys. Extrapolating from this biological arrangement, it follows that the gonads of theropods must have been similarly positioned. These sex glands produce reproductive cells and secrete hormones which provoke sexual behavior such as courtship and mating. They are also responsible for secondary sexual characters (BELLAIRS, 1970; WELTY & BAPTISTA, 1988) seen as sexual dimorphism.

Both crocodiles and birds exhibit sexual dimorphism, as evidenced in gender-specific variations in birds' plumage, coloration, ornamentation, behavior, or size. We can use these types of clues as excellent tools to determine theropod gender. For example, depending upon the species, male or female birds may be larger than their counterparts, or the sexes may be relatively equal in size (GILL, 1995). In crocodiles, males are always the larger gender (MAGNUSSON *et al.*, 1989). Likewise, sexual dimorphism is evidenced in robust and gracile theropod dimorphs, where skeletons of the two sexes are clearly different (CARPENTER, 1990; RAATH, 1990; LARSON & FREY, 1992; LARSON, 1994, 1995). The question has been in determining which gender is which, a subject discussed in more detail below.

## MALE SEX ORGANS AND FERTILIZATION

Male crocodile and bird gonads, the testes, produce sperm only during the breeding season. During that time, testes size increases ten-fold in crocodiles (JOANEN & MCNEASE, 1980), and up to 200 to 300 times quiescent weight in birds (WELTY & BAPTISTA, 1988). [A duck's testes may equal one-tenth its body weight, with the left testis usually larger than the right (WELTY & BAPTISTA, 1988).] Millions of spermatozoa are generated, stored in a tube called the epididymis, and delivered during mating through a second tube called the vas deferens.

Egg fertilization (along with delivery of eggs in females) and removal of waste are performed through one opening, the cloaca. Male crocodiles (BELLAIRS, 1970) possess an intromittent organ, or penis, as do snakes, lizards, turtles, and some bird species, including ostriches, most water fowl, and galliceans, such as chickens and turkeys (GILL, 1995). It is constructed from the folding of a portion of the floor of the cloaca, which produces a seminal groove that conducts the sperm from the vas deferens (BELLAIRS, 1970). The penis is erected by the filling of expandable blood vessels within a spongy tissue. Once erected, the organ projects downward and forward from the cloaca, and thus may enter the cloaca of the female. During mating, the male usually climbs on the back of the female, and their tails twist toward each other until their cloacas contact. The seminal groove essentially becomes a canal because of the penile engorgement, and sperm empties from the vas deferens into the cloaca of the female, and finally into the oviduct to fertilize the eggs (BELLAIRS, 1970).

The possession of a penis is a primitive condition (WELTY & BAPTISTA, 1988), which the birds listed above derived from their theropod ancestors. Most birds, however, do not possess a penis; mating in these more derived avian forms usually involves only a brief cloacal contact (referred to as a "cloacal kiss") for the transferal of sperm.

In reviewing the biology and mating habits of theropods' closest relatives, we can sketch out the probable structure of the soft tissue of extinct theropods. Male theropods certainly possessed testes, and, in a manner similar to their living relatives, stored sperm in the epididymis and delivered it through the vas deferens. Theropods also must have possessed a cloaca. This seems probable because the generally more primitive crocodylians, and the more derived birds originating from theropods, possess them.

Male theropods also must have had a penis, or intromittent organ, that could be retracted back within the cloaca when not in use. This is the state in both crocodiles and primitive birds. However, even

stronger evidence for the existence of a theropod penis comes from direct correlations between theropod and crocodile skeletons.

After copulation, the crocodile penis is pulled back into the cloaca by special "penis retractor" muscles (BELLAIRS, 1970). These muscles are attached to the first chevron, or haemal arch, near the base of the tail (LARSON & FREY, 1992). To accomplish the attachment of this special muscle, male crocodiles have an extra chevron, located one vertebra forward of the first chevron of females (ROMER, 1956; LARSON, 1994, 1995).

As noted earlier, it has long been recognized that the skeletons of many species of theropod may be divided into gracile and robust morphotypes. It has often been proposed that these morphotypes represent sexual dimorphs (RAATH, 1990; CARPENTER, 1990; LARSON & FREY, 1992; LARSON, 1994, 1995). It turns out that the gracile morphotypes, or the smaller and more lightly built individuals, possessed one more proximal chevron than did the robust morphotypes for at least some theropods (LARSON, 1994, 1995). This means that not only did theropods possess a retractible penis which necessitated the extra chevron, but also the phenomenon of sexual dimorphism in extinct theropods was similar to the condition in many birds (including raptors), where females are larger than males (WELTY & BAPTISTA, 1988; GILL, 1995).

Crocodiles breed once a year in spring (JOANEN & MCNEASE, 1980). The breeding season varies among bird species, with some raising one or more broods per year (GILL, 1995). Therefore, while we cannot yet extrapolate the duration or timing of the theropod breeding season or breeding frequency, we can presume that during breeding, the male would mount the female from the rear, perhaps crawling up on her back. Their tails would twist until the cloacas aligned. The male's penis would enter the female, delivering sperm to the oviducts for fertilization of eggs.

## FEMALE SEX ORGANS AND PROPAGATION

Studying crocodile and bird processes of egg formation, fertilization, and laying, as well as eggshell morphology and nest structures, provides invaluable information to project onto theropods. Intriguing differences occur in these areas between crocodiles and birds, and we must add evidence from the fossil record to best outline the probable biology and behaviors of theropods.

### EGG FORMATION

The female's gonads, the ovaries, produce eggs as the primary haploid sex cells. Crocodile eggs are formed from a single germ cell derived from one of

the paired ovaries attached to a yolk and surrounded by a sac, or follicle. As the egg matures, it becomes larger and more heavily laden with yolk that will nurture the developing embryo. When it reaches a certain size, the follicle ruptures and the egg is ovulated into the body cavity. The egg then enters the corresponding paired oviduct and moves downward inside the oviduct toward the cloaca by aid of muscle fibers within the walls of the oviduct. As the egg moves toward the cloaca, it passes by special glands that produce albumin, fibrous protein membranes, and calcium carbonate eggshell (BELLAIRS, 1970). [Of the living nonavian reptiles, only crocodiles and turtles have a hard calcium carbonate eggshell (BELLARIS 1970). This would indicate that hard calcite shells are primitive for Reptilia, and that soft shells of lizards and snakes are a lepidosaur specialization.] The eggs may be released almost simultaneously from both ovaries (autochronic) or the ovaries may alternately release eggs (allochronic) throughout the breeding season (SMITH *et al.*, 1972). The large, mature eggs line up in each oviduct "like a chain of sausages" awaiting fertilization by the male (BELLAIRS, 1970).

Female bird reproductive organs are in some ways similar to those of female crocodiles, but there are also some important differences. Bird eggs begin their journey like crocodile eggs, freed from the ovary by the rupture of the enclosing follicle during ovulation. Unlike crocodiles, however, only the left ovary develops in birds. Atrophy of the right ovary and oviduct is thought to be an adaptation producing the necessary reduction of weight for flight (WELTY & BAPTISTA, 1988). It is also speculated that this loss of an ovary was related to the problem of producing enough calcium for two eggshells at the same time (TAYLOR, 1970).

After ovulation, the female germ cell and attached yolk enter the funnel-shaped opening of the oviduct, the infundibulum, where fertilization takes place. The fertilized egg continues to pass down the oviduct, propelled on its way to the cloaca by contractions of smooth muscle through distinct sections of the oviduct (GILL, 1995).

After entering the infundibulum, the ovum moves into a second section, the magnum. The magnum secretes layers of albumin around the egg and attached yolk. The albumin, or egg white, consists of protein and water taken from the bird's blood (WELTY & BAPTISTA, 1988).

The growing bird egg then passes into the third region, the isthmus, where it receives an inner keratin membrane surrounding the albumin and an outer keratin membrane upon which the shell will grow (WELTY & BAPTISTA, 1988). This outer layer is strengthened by albuminous cement and perforated

with tiny pores for the exchange of gases of respiration (GILL, 1995).

The egg now receives water and salts through the shell membrane, "plumping" the egg (TAYLOR, 1970) before it enters the uterus or shell gland, where it acquires its hard shell (WELTY & BAPTISTA, 1988). The shell of a bird egg is composed of crystalline calcite (calcium carbonate), with interspersed proteins. These calcite crystals grow outward from raised portions of the outer keratin membrane called mammillary knobs, which are located between the respiratory pores (TAYLOR, 1970). This produces a cross-sectional morphology that gives bird eggshell its typical ornithoid structure, which is unique in the world of living egg-laying animals (ZELENITSKY & HIRSCH, 1997).

The calcium needed to produce bird eggshell is derived from the calcium ions in the blood (TAYLOR, 1970), which are ultimately derived from ingested food. The carbonate anion comes from carbon dioxide, normally eliminated from the body by respiration. However, the amount of calcium utilized in the production of an eggshell can be phenomenally large. Thus, laying birds store calcium in the marrow cavities of their skeletons as medullary bone (TAYLOR, 1970). This calcium may be rapidly stored and mobilized during the reproductive season. A domestic hen, for instance, can retrieve 2g, or 8-10% of its total skeletal calcium, within 15-18 hours (TAYLOR, 1970). Once the calcium carbonate shell is deposited, pigment (derived from the iron of old blood cells) adds color patterns to the surface of some bird eggs within a thin protective coating called the cuticle (GILL, 1995).

The egg moves rapidly through the fifth section of the oviduct, the vagina. From there it passes through the cloaca and is laid. The whole process, from ovulation to laying, takes only twenty-four hours in the domestic hen (WELTY & BAPTISTA, 1988), although it may take as much as seven days in boobies and hornbills (GILL, 1995). The ovary is stimulated by the laying of the egg and another follicle bursts. Ovulation is repeated and a new egg moves into the oviduct (WELTY & BAPTISTA, 1988). Only one egg is in a bird's oviduct at any one time, possibly helping to reduce ballast in a group whose majority of species depends upon flight. Some female birds are able to store sperm for up to ten weeks (TAYLOR, 1970), which was probably mandated by this serial ovulation process.

#### NESTING

Female crocodiles lay their fertilized eggs in nests excavated from sand or earth on the bank of a stream or near a body of water. They are excavated

by the female who "kicks" sand or earth with her rear (and sometimes front) limbs. The circular depression is roughly equal to her body length in diameter. Into this depression, she delivers from 16 to 80 eggs, all laid within the space of less than one hour (MAGNUSSON *et al.*, 1989). Alligators, the most temperate of living crocodylians, make mound nests using vegetation to cover their eggs. As the vegetation rots, it provides heat to maintain a higher incubating temperature (MAGNUSSON *et al.*, 1989). Because crocodiles are ectotherms, direct incubation of their eggs by transference of body heat is impossible, thus the temperature of incubation (which also determines the sex of the crocodile embryo) is left entirely up to the sun, the mean daily temperature, and/or the rotting vegetation. Incubation periods may vary from 65 days for the American alligator (*Alligator mississippiensis* DAUDIN) to up to 90 days for the Nile crocodile (*Crocodilus niloticus* LINNAEUS) (MAGNUSSON *et al.*, 1989).

Birds also lay their eggs in nests. These nests may be simply a randomly selected spot among the rocks on the open ground, like those of the night hawk (*Chordeiles minor* FORSTER) of western North America. Or the nest may be an elaborate affair constructed of branches, twigs, and downy feathers perched on the top of a tree, like those North American golden eagles (*Aquila chrysaetos* LINNAEUS) use year after year.

A more primitive ground nest is created through the movement of the bird's breast and feet. The bird presses its body downward, "snuggling" into the nesting material (plant or soil), while it kicks backward with its feet. The bird then rises and rotates its body about 36° and repeats the movements, eventually making two or three complete rotations. What results is a cup-like depression to receive the eggs (WELTY & BAPTISTA, 1988). Likewise, male and female pairs of maleo, *Magacephalon maleo* MULLER, of the Indonesian island of Sulawesi off the coast of Borneo, use their feet to dig holes in the black volcanic sands of the ocean beaches. The females deposit their eggs in separate or communal nests. The eggs are then covered with sand and left to the sun for incubation (WELTY & BAPTISTA, 1988).

Most birds, however, do not abandon their eggs, but sit on the nest, incubating the eggs with their own body heat. Incubation, maintaining a nearly constant temperature from 34 to 40 °C (GILL, 1995), does not just involve warming the egg when air temperature turns cool. It also necessitates keeping the egg cool in hot environments. This is accomplished with "brood patches" on the breast and belly of the bird, spots where feathers have been lost or removed and where circulation is enhanced through increased blood flow. Birds transfer heat between the brood patches and the egg through a network of

blood vessels in the skin of the brood patches (GILL, 1995). They may also stand over the eggs, shading them from the hot sun.

Birds lay and will incubate a clutch of one to a dozen or so eggs, depending upon the species. Incubation is usually, but not always, delayed until the clutch is complete. This is to facilitate synchronous hatching of all the eggs in the clutch (GILL, 1995).

During incubation, most birds (mound builders like the maleo are the exception) rotate their eggs on a regular daily basis. They do this by pulling and rolling each egg backward with their beaks. Turning eggs during incubation prevents the embryo from adhering to the inner surface of the shell (a critical factor when hatching time arrives). Aiding in this are twisted strands of albumin called chalazae, which are attached to the yolk and the inner shell and keep the developing embryo oriented right-side-up in the egg (GILL, 1995). These adaptations probably arose as a result of having eggs laid in an open nest, where they are subject to movements each time the brooding adult shifts positions or leaves or enters the nest.

#### INSIDE THE EGG

In both crocodylians and birds, the embryo must respire. It needs to obtain oxygen for metabolism and development, and it must get rid of the waste product, carbon dioxide. Passive respiration takes place in a structure called the chorioallantois, which is pressed tightly against the shell membrane. Gases are exchanged through the pores of the shell, most of which are at the blunt end of the egg. As the embryo matures, a system of blood vessels develops in the chorioallantois to allow for more efficient gas exchange (GILL, 1995). Exhaled carbon dioxide forms weak carbonic acid that slowly degrades the shell (MAGNUSSON *et al.*, 1989). Calcium ions from the dissolving shell are used by the embryo to construct its calcium phosphate skeleton (WELTY & BAPTISTA, 1988). As hatching approaches, the shell becomes progressively weaker and thinner (MAGNUSSON *et al.*, 1989; WELTY & BAPTISTA, 1988), an advantage to the embryo, who will soon seek escape.

Non-gaseous waste is stored in the egg. Crocodylians and birds, whose hard-shelled eggs develop in a gaseous environment, must expel nitrogenous wastes in a solid, insoluble form. They excrete uric acid in the form of insoluble crystals (unlike the water-soluble urea excreted by fish, amphibians, and mammals, who develop in an aqueous environment that sweeps poisons away). Uric acid and other solid waste is transferred to the allantois (the sewer system of the egg), which acts like a bladder, safely storing the poisonous waste away from the developing embryo (WELTY & BAPTISTA, 1988).

#### THEROPODS

Certainly a lot of what happens today in the female reproductive systems of crocodiles and birds must also apply to extinct theropods. As with our other biological extrapolations, we can safely conclude that theropod eggs were formed in a fashion similar to that shown in crocodiles and birds. However, to become more specific in applying the crocodile and bird models to the theropod female, we will add information directly from the fossil record. Evidence found in theropod nests not only sheds light on nesting habits of these extinct creatures, but also it provides an amazing glimpse into theropod anatomy.

Fossil egg nests are, of course, most useful in the study of extinct creatures when scientists know who laid the eggs. The only sure method of identifying the extinct species that produced a particular egg or nest of eggs is by the discovery of an identifiable embryo within the egg. As paleontologists discover more eggs, nests, and nesting sites, an increasing number of such specimens has been located. In this paper, I will refer to three groups of specific egg discoveries which point to an egg morphology that may reasonably be attributed to theropods. *Oviraptor* OSBORN (CLARK, 1995; NORELL *et al.*, 1995; DONG & CURRIE, 1996; WEBSTER, 1996); *Troodon* LEIDY (WEISHAMPEL & HORNER, 1994; VARRICCHIO *et al.*, 1997); and large, unidentified theropod embryos, whose eggs have been placed within the family Elongatoolithidae Zhao (ZHAO, 1994; CURRIE, 1996b), have been recognized to date, all with eggs also found in nearly complete clutches or nests.

The shape of these theropod eggs is elongate, typically two to four times as long as they are wide. The surface may be textured, with raised bumps or depressions, or it may be relatively smooth; all contain respiration pores, like bird eggs. In addition, all of the above eggs, as well as all of the clutches of various types of elongated (theropod) eggs I have personally examined from China, have three things in common: the cross-sectional morphology of the eggshell, a circular pattern formed by the laid eggs, and the eggs seemingly laid in pairs.

The cross-sectional morphology of the eggshell, examined by cutting slices of the shell material, has been studied intensely by Karl Hirsch and others (ZHAO, 1994; MIKHAILOV, SABATH & KURZANOV, 1994; ZELENITSKY & HIRSCH, 1997). They have concluded that the cross-sectional morphology of the elongated eggs is virtually identical to that of extant birds (ZELENITSKY & HIRSCH, 1997). The material is composed of the same tightly packed radial calcite crystals, growing from mammillary knobs with interspersed respiration pores. This reminds us how close living birds are to their theropod ancestors,

and supports the proposed biological similarity between the reproductive anatomies of birds and theropods.

The eggs of *Oviraptor* (MIKHAILOV, SABATH & KURZANOV, 1994; WEBSTER, 1996), *Elongatoolithidae* eggs (CURRIE, 1996b), and most of the other above-mentioned Chinese elongated eggs are laid in a circular pattern. The long axis of each egg points toward the center of the circular nest. The eggs usually form one, two, or three tiers and there are generally one to two dozen eggs in a complete clutch (although I have seen one phenomenal nest on exhibit at the Natural History Museum in Beijing with nearly one hundred small, elongated eggs in a beautiful circle). The *Troodon* nests from Montana, although departing from the long axis arrangement of most elongated egg clutches, were still laid in a circular-spiral arrangement, with the long axis of each egg pointed upwards and inwards toward the center of the spiral (VARRICCHIO *et al.*, 1997).

In addition, the pairing of these eggs as they were laid (MIKHAILOV, SABATH & KURZANOV, 1994; WEBSTER, 1996; CURRIE, 1996b; VARRICCHIO *et al.*, 1997) provides a most compelling component to the study of theropod egg nests. This is unlike any modern arrangement of eggs within nests created by extant vertebrates.

When compared to the nests of birds, the arrangements of theropod eggs demonstrates distinct differences in nesting habits. The arrangement is also distinctly different from crocodile nests, in which the eggs are randomly dumped and covered, with no intentional arrangement. HORNER (1987) was so impressed with theropod nest arrangement, he actually speculated that the eggs were manipulated after laying. Other researchers (COOMBS, 1989) disagree with this analysis. I believe that the arrangement of eggs within theropod nests gives us a glimpse at how female theropod ovaries and oviducts operated.

The pairing of theropod eggs seems to indicate that both oviducts delivered an egg at the same time. This would mean that a pair of eggs would enter the cloaca simultaneously, one from the right and one from the left oviduct. After passing through the oviducts side by side, the two eggs would be delivered through the opening of the cloaca. In order to remain in this position, they must have been pushed partially into the loose sand or silt at the bottom of the nest by the muscular contractions of the oviduct and cloaca. In order to remain paired, the eggs must have been forced out by the following pair of eggs. The circular arrangement could indicate that the mother pivoted (COOMBS, 1989) as she delivered each pair of eggs. Up to three tiers of eggs would be laid in the nest, and each tier of eggs represents a

complete circling of the nest as she paused to lay each pair of eggs.

The pairing of eggs points to the presence of two functioning ovaries that simultaneously deliver a single egg to each oviduct, via autochronic ovulation (SMITH *et al.*, 1972, 1973; VARRICCHIO *et al.*, 1997). This indicates that the single functioning (left) ovary of birds is a derived condition not shared by their theropod ancestors, who obviously retained both functioning ovaries.

The paired eggs and the circular arrangement of the pairs of eggs also point to the more primitive condition of theropod ovaries and oviducts. As was noted, birds retain only one egg in their single oviduct at a time, with ovulation not occurring again until that egg is laid. Bird eggs are laid from one a day to one every several days, until the clutch is complete, with each successive egg passing down the oviduct for its layers of albumin, membranes, and shell. The circular and sometimes tiered arrangements of theropod eggs, however, indicate that they were laid in one sitting, within a period of minutes, rather than days. It would make no sense that a female would, or could, locate her exact position to continue her pivot after 24 hours or more had elapsed. This also suggests that we may more closely pinpoint the biological model to apply to the female theropod reproductive system. For the theropod to be able to lay her eggs in one sitting, the large, mature eggs would line up in the oviducts "like a chain of sausages" awaiting fertilization, as in crocodiles. Although theropod egg construction was virtually identical to that of birds, their eggs did not pass through their systems as in the birds' more derived fashion of one at a time.

Indeed, delivering an entire clutch of eggs in one sitting is a character of crocodiles, who lay 16 to 80 eggs in less than one hour (MAGNUSSON *et al.*, 1989). The clutch size of theropod eggs varies from three (probably truncated by weathering) to 24 in the case of *Troodon* eggs (HORNER, 1987), to at least 20 and perhaps more than 30 eggs in *Oviraptor* nests (MIKHAILOV, SABATH & KURZANOV, 1994), and 26 eggs in a clutch of the huge *Elongatoolithidae* eggs from China (CURRIE, 1996b). In addition, the incredible 100-egg nest in Beijing contained a three-tiered circular arrangement. Most of the as-yet unidentified elongated "theropod" eggs are moderately or highly textured and occur in circular clutches that contained one to two dozen eggs. But surely this number was variable from species to species, as with modern birds and crocodiles.

Probably the best recorded theropod nest was reported by VARRICCHIO *et al.* (1997). This complete *Troodon* nest contains a clutch of 24 hatched eggs laid within a shallow bowl-shaped depression with a distinctive rim. The rim measures 10 cm high and 20

cm wide. It encircles a depression 100 cm in diameter. The egg clutch is about 50 cm across and slightly off center from the rim (VARRICCHIO *et al.*, 1997). *Troodon* is a relatively small theropod, measuring at most a meter tall at the hips.

It seems likely that this nest was made with kicking motions of the rear feet, similar to crocodylian behavior (COOMBS, 1989), while bracing with the breast and forelimbs. The nest would attain a circular rim if the female were to rise and turn 30° or so, and repeat the movements until she had turned in a circle several times, in a manner similar to modern ground nesting birds who produce a cup-like depression for their nests (WELTY & BAPTISTA, 1988). As the eggs were laid, they were forced into the loose sediment at the bottom of the nest. There is no evidence of vegetation in this or any other described theropod nest (VARRICCHIO *et al.*, 1997). I have seen no plant material in any of the many clutches I have studied. This nest was apparently open (VARRICCHIO *et al.*, 1997) with the tops of the eggs exposed and each of the eggs held in position by the surrounding sediment. These observations are in direct contrast to conclusions assuming theropod eggs were buried after laying (COOMBS, 1989) and incubated by the sun or rotting vegetation (MIKHAILOV, SABATH & KURZANOV, 1994).

Recent discoveries in China (CURRIE, 1996a; DONG & CURRIE, 1996) and Mongolia (NORELL *et al.*, 1995; WEBSTER, 1996) have brought to light some remarkable specimens that provide additional insight into the reproductive system of theropods. These specimens each clearly show an adult theropod, *Oviraptor*, sitting on a clutch of *Oviraptor* eggs. The bones, and hence the body, of each adult is in direct contact with the eggs. A *Troodon* nest from Montana also preserved a partial, articulated adult in direct contact with a clutch of *Troodon* eggs laid in an open nest (VARRICCHIO *et al.*, 1997). These findings offer strong evidence for theropod incubation of eggs, evidence that does not support other behavioral or physiological conclusions.

Several examples can illustrate why other behaviors are not indicated. 1) The nests of ectotherms commonly are covered and abandoned in a terrestrial environment. 2) Although it is common practice for incubating birds to shield eggs from the direct rays of the sun during the heat of the day, an ectotherm would be in as great a peril as its eggs in a parallel situation. 3) Brooding females might remain on their nests during a sand storm, where non-brooding ectotherms as a rule do not remain with their eggs once they are laid. 4) The act of a parent's wrapping its body about its eggs to protect them from a predator would mandate the death of the mother as well as the embryos, hardly favorable under natural selection. Contrast this behavior with that of crocodiles,

who, unlike nearly all ectotherms, often remain near their nests to protect their eggs from predation (MAGNUSSON *et al.*, 1989) but are never in direct contact with their buried eggs, or with that of birds, who rely upon camouflage or who lead predators away from a nest by feigning injury. [DONG & CURRIE (1996) speculated that in one specimen of *Oviraptor* the mother may have been caught in the act of laying her eggs when she was buried by a sand storm, but they still favored the brooding scenario.]

The *Oviraptor* and *Troodon* discoveries also lead to the further conclusion that theropods possessed brood patches for the transference of heat. Incubation of eggs, of course, would strongly suggest that theropods, like their avian descendants, were endotherms. [The incubation of eggs in extant ectotherms is limited to only a few species of pythons, including *Python molurus* LINNAEUS. These snakes are able to become temporary endotherms by rapid periodic muscular contractions of the coils surrounding their eggs yielding thermogenesis similar to that brought about by shivering in mammals and birds (HUTCHINSON, DOWLING & VINEGAR, 1966; VINEGAR, HUTCHINSON & DOWLING, 1970; VAN MIEROP & BARNARD, 1976.)]

It is clear that the eggs in theropod nests were not periodically turned, as are those of modern birds. These eggs were "planted" in the substrate (VARRICCHIO *et al.*, 1997). It was apparently unnecessary for these non-avian theropods to rotate their eggs because the embryos would remain upright, undisturbed by the comings and goings of the adult. Thus, theropod eggs lacked chalazae (VARRICCHIO *et al.*, 1997), the twisted strands of albumin that orient developing bird embryos.

#### HATCHING

Bird chalazae, the rotation of bird eggs during development, and the importance of the bird embryo not fusing to the eggshell all begin to make sense at the time of hatching. After puncturing the inner membrane and outer shell with its egg tooth, the bird begins respiration and its ordeal of hatching. The chick thrusts with a special hatching muscle of its neck, at the same time thrusting with its left leg. This turns the chick slightly as its egg tooth rotates for each successive strike, weakening the shell along a circle, eventually allowing the chick to break open the top of the egg and crawl out (WELTY & BAPTISTA, 1988). These motions would have been impossible if the egg had not been turned during incubation and the chick had stuck to the inner surface of the egg. Avian parents do not assist their chicks in hatching (GILL, 1995).

As alligator eggs near the end of their incubation period, the young emit grunts from within the egg.

Females who have guarded their nests hear these sounds and tear open the nest. The mother individually lifts each unhatched egg from the nest, and, within her jaws, rolls the eggs against the roof of her mouth with her tongue, opening the shell and freeing the young (MAGNUSSON *et al.*, 1989).

Based upon incubation periods from living crocodiles and birds, theropod incubation was probably from 60 to 90 days. Because theropods partially buried their eggs (VARRICCHIO *et al.*, 1997) and did not rotate their eggs the way birds do, hatchlings may have needed help from attending adults in order to escape from their eggs. Hatched theropod eggs from China and Montana (VARRICCHIO *et al.*, 1997) with the bottom half undisturbed indicate that for *Troodon* and some other theropods, any adult assistance must have taken a different form than in crocodiles. Perhaps adults nudged and cracked the top part of the egg with their muzzles, freeing their young.

## CONCLUSION

The sex of a theropod embryo was almost certainly determined by sex chromosomes. As in birds, reptiles, amphibians, and fishes, females were the heterogametic sex. Male theropod testes, like those of birds and crocodiles, were positioned within the posterior dorsal portion of the abdominal cavity. At least some theropods possessed an intromittent organ, or penis, that penetrated the female cloaca during copulation and was retracted back into the cloaca of the male when not in use.

Female theropods possessed paired ovaries and oviducts like their more primitive relatives, the crocodiles. Also, like crocodiles, female theropods probably carried an entire clutch of mature eggs inside the oviduct, awaiting fertilization. Unlike in any living animal, eggs were delivered in pairs, simultaneously, from the right and left oviducts. Theropod egg clutches were laid at one "sitting," with the female standing in the center and circling the nest as she laid the egg pairs. Theropods may not have had a reproductive system as specialized as a modern bird's, but there was much about theropod reproduction that was very bird-like, including the cross-sectional morphology of the eggshells themselves.

Each unfertilized egg contained a sex chromosome for sex determination, either an X chromosome for maleness or a Y for femaleness. Sperm carried only an X chromosome. This is the same primitive condition we see in birds, descendants of theropods. As the embryo grew, it expelled insoluble uric acid. Adult theropods, then, were as water conservative as living birds because, unlike mammals, they did not need to expel huge quantities of water to purge their systems of urea. Finally, the discoveries

of the open nest of *Troodon* and nesting *Oviraptors* point to contact incubation, brood patches, endothermy of theropods, and a more bird-like behavior than most paleontologists ever imagined.

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