

# DINOSAUR REPRODUCTION AND PARENTING

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■ **Abstract** Non-avian dinosaur reproductive and parenting behaviors were mostly similar to those of extant archosaurs. Non-avian dinosaurs were probably sexually dimorphic and some may have engaged in hierarchical rituals. Non-avian coelurosaurs (e.g. Troodontidae, Oviraptorosauria) had two active oviducts, each of which produced single eggs on a daily or greater time scale. The eggs of non-coelurosaurian dinosaurs (e.g. Ornithischia, Sauropoda) were incubated in soils, whereas the eggs of non-avian coelurosaurs (e.g. Troodon, Oviraptor) were incubated with a combination of soil and direct parental contact. Parental attention to the young was variable, ranging from protection from predators to possible parental feeding of nest-bound hatchlings. Semi-altricial hadrosaur hatchlings exited their respective nests near the time of their first linear doubling. Some reproductive behaviors, once thought exclusive to Aves, arose first in non-avian dinosaurs. The success of the Dinosauria may be related to reproductive strategies.

## INTRODUCTION

Most aspects of reproduction and parenting behavior are accessible by direct observation in extant taxa; however, they are virtually impossible to elucidate from the fossil record. Some general reproductive characteristics can, however, be hypothesized from taphonomic studies of skeletons, eggs, and a variety of trace fossils derived from the extinct Dinosauria. These data can then be evaluated on the basis of whether the characteristics are shared with closely related extant taxa. The methodology, referred to as the “extant phylogenetic bracket,” uses crown groups (Bryant & Russell 1992; Witmer 1994, 1998) to regulate orders of inference. Of extant groups, crocodylians and birds bracket extinct dinosaurs, allowing a first order inference (Witmer 1998): If both crocodylians and birds possess a particular characteristic or behavior, extinct dinosaurs could share it as well. A second order inference may be hypothesized when a character occurs in only one crown group. The most unreliable inferences are those of the third order, based on features that neither crown group possesses.

Further inferences can be derived on the basis of more recent common ancestry. If members of one crown group share particular characteristics with members of

an extinct group, it is a reasonable second order inference to hypothesize that the most recent common ancestor of the two groups, and all the ancestor's descendants, could share the characteristic.

Coombs (1989) published an extensive review of extant nesting and parenting behaviors associated with crocodylians and megapode birds (e.g. Brush turkeys), and discussed the likely presence of these behavioral characteristics in dinosaurs. Other less comprehensive works have reviewed various behavioral subjects as new data have become available (Ostrom 1985, Coombs 1990, Farlow et al 1995, Horner 1997a, Paul 1997).

Here I review the morphological and geological data concerning mate selection, nesting, egg laying, incubation, perinatal development, and parental investment. I conclude with a synthesis of the data and a short deliberation on the presence or absence of these characteristics in extant crown groups and hypothetical ancestors.

## COURTSHIP

Courtship rituals of extinct dinosaurs will likely never be known, but there is evidence that some taxa were sexually dimorphic and that some may have engaged in hierarchical mate competition.

### Sexual Dimorphism

Among the extinct dinosaur taxa for which we have significant collections, morphometric and other analyses suggest bimodal populations, representing sexual dimorphism (Nopcsa 1929; Brown & Schlaikjer 1940; Kurzanov 1972; Dodson 1975, 1976, 1990; Chapman et al 1981; Lehman 1990; Carpenter 1990; Colbert 1990). In some cases where whole skeletons have been analyzed (Raath 1990), the female is interpreted to be the larger and more robust of the dimorphic pair (Carpenter 1990, Larson 1994), as in extant avian raptors (e.g. Weidensaul 1996). However, with the exception of *Protoceratops*, represented by dozens of specimens (Kurzanov 1972, Dodson 1976), samples of most dinosaur taxa are much too small for statistical analyses (Sampson 1997, Sampson et al 1997, Sampson & Ryan 1997).

A morphometric analysis of *Triceratops* skulls reveals a bimodal population that was interpreted as two distinct species rather than sexual dimorphism, because one species was much more abundant than the other (Forster 1996).

### Display and Mate Competition

Hadrosaurs, marginocephalians (ceratopsians and pachycephalosaurs), ceratosaurs, and a few tetanurans possessed elaborate headgear including horns, bosses, crests, shields, and spikes (Vickaryous & Ryan 1997). In the past, it was hypothesized that these structures were used as defensive weapons (Colbert 1948), but

they are now thought to represent visual display organs (Davitashvili 1961; Hopson 1975; Farlow & Dodson 1974; Molnar 1977; Spassov 1979; Sampson 1995, 1997, 1999) similar to the horns and antlers present in living ungulates (Geist 1966). The hollow crests of lambeosaurine hadrosaurs are hypothesized to have been used as acoustic resonators in vocal displays (Wiman 1931, Hopson 1975, Weishampel 1981). Nearly all extant reptiles, including archosaurs, lack bony display organs; instead, they have dewlaps, skin flaps, median body frills, and various other display features that are rarely fossilized (e.g. Horner 1984a).

Various data suggest that dinosaurs such as the hadrosaurs and ceratopsians traveled in large aggregations (Ostrom 1972, Currie & Dodson 1984, Currie 1989, Rogers 1990, Varricchio & Horner 1993) and that they used their elaborate cranial ornaments for visual display, hierarchical combat, and mate selection (Sampson 1999). Contact during hierarchical combat, such as head-to-head butting or flank butting, has been proposed for the pachycephalosaurs (e.g. Galton 1970, Sues 1978, Carpenter 1997, Goodwin et al 1998) and intimated for chasmosaurine ceratopsians (Forster & Sereno 1997), and “head-wrestling” or shoving has been hypothesized for hadrosaurs (Hopson 1975) and ceratopsians (Sampson 1997). Intraspecific fighting has also been suggested to explain bite marks on the heads of carnivorous dinosaurs (Tanke & Currie 1995).

Various centrosaurine ceratopsian species had horns with similar morphologies as juveniles that were very different from those of their adult counterparts (Sampson et al 1997). This pattern suggests that specific horn morphologies were not used until adulthood and that they therefore evolved primarily as mating signals (Sampson 1999).

Regardless of the behavioral rituals that regulated mate selection, extinct dinosaurs eventually engaged in mating (Halstead & Halstead 1981, Larson 2000) that produced a gravid female.

## EGGS AND NESTS

There is extensive literature on extinct dinosaur eggs and eggshells, and their classification is beyond the scope of this review (see Thulborn 1991; Mikhailov 1991, 1997b; Carpenter & Alf 1994). Here I focus primarily on studies that are relevant to the actual reproductive behaviors of the extinct dinosaurs, touching only briefly on eggshell structure and classification.

### Egg Morphology: Internal Structure and Shape

It is a first order inference that all extinct dinosaurs laid eggs, and a third order inference to suggest live birth for any dinosaurian taxon (Marsh 1883, Sochava 1969, Charig 1979, Bakker 1980). Nevertheless, eggs have been attributed, on the basis of in ovo embryos, to only nine extinct dinosaurian taxa (Horner & Weishampel 1988, 1996; Currie & Horner 1988; Norell et al 1994; Li et al 1996;

Manning et al 1997; Mateus et al 1997; Chiappe et al 1998; Horner 1999). The eggshells of extinct dinosaurs have a characteristic microstructure that, for the most part, differentiate them from either crocodylian or bird eggshells (Hirsch & Packard 1987; Mikhailov 1991, 1992, 1997b; Zelenitsky & Hirsch 1997). Therefore, hypotheses about egg laying and nesting in extinct dinosaurs can be formulated even though the eggshell cannot always be matched to a specific parent taxon.

**Microstructure** Archosaurian eggshell must be thick enough to provide the calcium needed by the developing skeleton, and strong enough through incubation to withstand mechanical stress. It must also be thin enough to allow the conductance of respiratory gases and water vapor without inhibiting hatching (Hirsch & Zelenitsky 1997). Pores in the eggshell provide for the diffusion of gases (Ar et al 1974), and the inner surface of the shell is apparently resorbed for skeletal calcium (Jenkins 1975, Cox et al 1984, Board & Sparks 1991). The thickness of the shell can vary substantially in an individual egg (Norell et al 1994, Mikhailov 1997b), among eggs in a clutch (Zhao et al 1991), and among clutches of the same taxon (Horner 1999). Eggs containing embryos often have eggshell that is considerably thinner than eggs without embryos; this may be the result of calcium uptake by the embryo or a pathological condition (Horner 1999).

Eggshell has a variety of ultrastructural components and surface ornamentations, and these features, together with pore geometry and egg shape, form the basis of the parataxonomic classification (e.g. Young 1959; Zhao 1975, 1979; Kurzanov & Mikhailov 1989; Hirsch & Quinn 1990; Mikhailov 1991, 1992, 1997b; Hirsch 1994; Mikhailov et al 1996) (Table 1). Eggshell derived from the eggs of the hadrosaur *Maiasaura peeblesorum*, for example, is assigned the taxonomic binomial *Spheroolithus maiasauroides*. Eggs of the oofamily Spheroolithidae have a dinosauroid-spherulitic basic eggshell organization (Hirsch &

**TABLE 1** Correlation chart of dinosaur eggshell types (After Zelenitsky & Hirsch 1997).

<b>Eggshell Organization</b>	<b>Structural Morphotypes</b>	<b>Parataxonomic Families</b>	<b>Taxonomic Groups</b>	
Ornithoid	Ratite	Elongatoolithidae	oviraptorid	
	Angustiprismatic		<i>Troodon</i>	
Dinosauroid-Prismatic	Obliquiprismatic	Prismatoolithidae	?ornithopoda	
	Discretispherulitic		Megaloolithidae	sauropods
	Prolatospherulitic		Spheroolithidae	hadrosaurs
Dinosauroid-spherulitic	Filispherulitic	Faveoolithidae	?sauropods	
	Dendrospherulitic	Dendroolithidae	?segnosaurs	
	Angustispherulitic	Ovaloolithidae		
	?Dictospherulitic	Dictyoolithidae	?sauropods	

Quinn 1990), a prolatospherulitic structure, and a prolatocanaliculate pore system (Mikhailov et al 1996, Mikhailov 1997b).

**Pore Distribution** Pores in eggs allow the conductance of water vapor and respiratory gases. Eggs in subterranean nests have many more pores than those in open air. The number and geometric patterns of pores have been used to estimate environmental conditions during incubation of extinct taxa (Ar et al 1974), predict clutch size (Seymour 1979), and possibly predict the duration of incubation (Grigorescu et al 1994). Like eggshell microstructure, pore geometry is extremely variable among different extinct dinosaurian taxa (Mikhailov et al 1994). Seymour (1979) showed that pore space varies from 0.37% to nearly 25% of the total surface area in three dinosaur taxa, and Mikhailov and associates (1994) recently found other dinosaur eggs that have nearly 50% pore space. In most extant birds, pore space occupies less than 12% of the lowest values of any dinosaur eggs (Seymour 1979). Williams and associates (1984) linked the high porosity and thus high water vapor conductance of these dinosaur eggs to a nest environment with high humidity and low oxygen levels.

Pore density has been shown to vary over the surface of an egg (Hirsch & Quinn 1990) and may relate to its orientation during incubation (Mellon 1982). Pore density and distribution also vary in other archosaur eggs (e.g. Bertram 1992).

**Surface Patterns** Many dinosaur eggs have a variety of surface patterns (Moratalla & Powell 1994), ranging in degrees of ornamentation on single eggs (Powell 1995, Norell et al 1994) or between eggs of different taxa, from subtle striations on smooth eggshell (Horner 1987) to highly textured crenellations and deeply undercut caverns (Jensen 1970). The purpose of these structures is not well understood (Mikhailov 1997a), and the structures have no modern analogs. Mellon (1982) hypothesized that the patterns reflected the orientation of the eggs within subterranean incubation mounds and that they may have aided in gas exchange. Mellon discovered that the orientation of these structures matched the orientations of some eggs. Some eggs positioned with their long axis parallel to the horizon had randomly oriented surface structures, and eggs positioned vertically within the sediment had surface structures aligned vertically. Sabath (1991) speculated that the surface structures helped to keep the nest material from blocking the pores. According to Sabath, coarsely sculptured eggs could have been incubated in vegetation mounds and smooth-shelled eggs in sand, but there does not appear to be any direct evidence for these ideas.

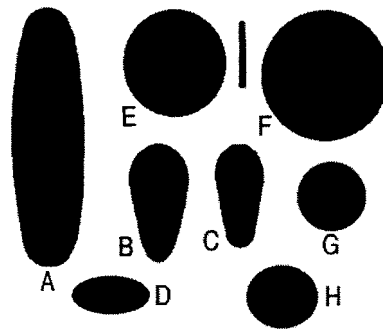
Moratalla & Powell (1994) suggested that the surface ridges also may have been useful for increasing overall shell thickness and strength without extending pore length. The pores occur in the valleys between the ornamentation (Jensen 1970, Hirsch & Quinn 1990).

**Egg Shape and Volume** Fossilized eggs attributed to extinct dinosaurs range from spheroids to modestly pointed, asymmetrical ellipsoids (Figure 1) (e.g. Currie 1996, Mikhailov 1997b), spanning the spectrum seen in other reptiles, including birds (Iverson & Ewert 1991, Smart 1991). The eggs identified on the basis of embryos as those of hadrosaurs (Horner & Currie 1994, Horner 1999) and sauropods (Chiappe et al 1998) are spheroidal or subspheroidal, whereas those of extinct theropods are ellipsoidal (Horner 1987, Norell et al 1994, Horner & Weishampel 1996). Segnosauroids may also have had spheroidal eggs (Manning et al 1997).

Egg shape in reptiles and birds is thought to be regulated by resistance within the oviducts (Iverson & Ewert 1991, Smart 1991). Extant non-avian reptiles ovulate and shell several eggs at a time, whereas birds ovulate and shell a single egg. "Assembly-line" non-avian production is thought to produce symmetrical eggs, whereas single-egg production yields asymmetrical eggs—blunt on one end and pointed on the other (Iverson & Ewert 1991). Nearly all non-avian dinosaur eggs are symmetrical except *Troodon* and *Oviraptor* eggs, which are elongated and asymmetrical (Horner & Weishampel 1996; Horner 1987; Varricchio et al 1997, 1999; Norell 1995), thus suggesting that these animals were producing a single egg at a time in their oviducts.

Although some variation in egg shape can be considered the result of oviduct resistance, it is also likely that shape contributed to the resistance to physical pressures in the nest (Zhao 1994). Using eggshell thickness and geometric shape, Zhao & Ma (1997) calculated the resistant pressures that particular eggs could have endured. Spheroidal eggs have the greatest overall compressive strength and predictably could have been laid irregularly in nests. Elongated eggs such as those of *Troodon* are most resistant to vertical pressure when their axes are perpendicular to the substrate.

**Figure 1** Various egg shapes (approximate) attributed to the non-avian Dinosauria. (A) Elongatoolithid (unknown taxon, cf. Theropoda), China. (B) Prismatoolithid (*Troodon*), N. America. (C) Elongatoolithid (*Oviraptor*), Mongolia. (D) Elongatoolithid (unknown taxa, cf. Theropoda), United States. (E) Megaloolithid (cf. Titanosaurid) S. America (Gondwana). (F) Spheroolithid (Lambeosaurinae), N. America. (G) Spheroolithid (Hadrosauridae, cf. *Maiasaura*), United States. (H) Ovaloolithid (unknown taxa, Ornithopoda), Mongolia. Scale is 10 cm.



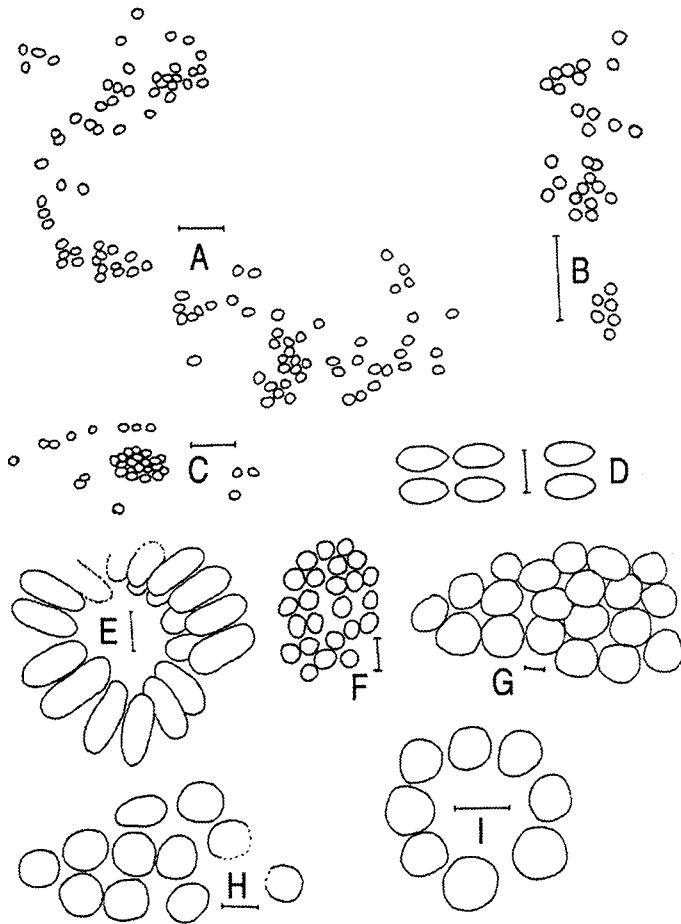
Egg volumes have been calculated for several taxa believed to be dinosaurian in origin (Dughi & Sirugue 1958a, Sabath 1991, Mikhailov et al 1994, Grigorescu et al 1994, Horner & Currie 1994, Chiappe et al 1998, Horner 1999), and they do not exceed the sizes known for some birds, particularly the extinct *Aepyornis* (e.g. Van Tyne & Berger 1976), which had eggs with an average volume of 9 liters. The largest identified non-avian dinosaur eggs (from lambeosaurine hadrosaurids) have volumes that slightly exceed 4 liters (Horner 1997a). Interestingly, closely related dinosaur taxa, such as some hadrosaurine and lambeosaurine hadrosaurids, produced eggs with a fourfold volume difference (Horner 1999). The average volume of the eggs attributed to sauropods is less than 1 liter (Chiappe et al 1998).

## Egg Clutches and Nests

**Clutch Geometry** Dinosaur eggs are generally found isolated, in disorganized assemblages, or in well-organized clutches (Figure 2). Disorganized assemblages of large round eggs of the Megaloolithidae oofamily (dinosauroid-spherulitic) found in France (K  rourio 1981, Breton et al 1986), Spain (Lapparent & Aquirre 1956), Argentina (Moratella & Powell 1994), Uruguay (Faccio 1994), and India (Sahni et al 1994, Sahni & Khosla 1994) appear to have been laid in circular to oval patterns in which the eggs are randomly spaced. These assemblages consist of three to eight eggs (e.g. Srivastava et al 1986), sometimes stacked or in single layers within pit-like structures (Erben et al 1979, K  rourio 1981, Mohabey 1984, 1998). Similar megaloolithid eggs are described as having been laid in large arcs (Beetschen 1985, Breton et al 1986, Powell 1995) of as many as 20 eggs (Figure 2A–B). K  rourio (1981) and Cousin and associates (1994) have reported numerous megaloolithid eggs from France that were found isolated as though laid one at a time, although they may have been “extras.” Ostrich nests often have a main clutch that is brooded, plus a number of extra eggs that are strewn about and abandoned (Bertram 1992) (Figure 2C).

A group of at least 34 prismatoolithid (dinosauroid-prismatic) eggs from Portugal, some containing embryonic elements, also appear to be a disorganized aggregation (Mateus et al 1997), but these have most likely been rearranged by post-nesting fluvial actions.

Some megaloolithid eggs from France were reported to occur in rows (Dughi & Sirugue 1958a, b, 1966, 1976) of two to five eggs per row. Other eggs found in rows include some unidentified (“ornithoid ratite”) eggs from Montana (Horner 1987, Hirsch & Quinn 1990) (Figure 2D), and a megaloolithid assemblage from Romania (Grigorescu et al 1990, 1994). Both were found in paired rows. Egg pairing is evident in a number of organized clutches (Sabath 1991, Mikhailov et al 1994, Carpenter et al 1994b) and has been supported by statistical analysis in *Troodon* (Varricchio et al 1997). Egg pairing is thought to result when both oviducts produce eggs at the same time (Sabath 1991, Mikhailov et al 1994, Varricchio et al 1997). The asymmetric shape of the *Troodon* and *Oviraptor* eggs



**Figure 2** Various egg distributions and egg clutches attributed to Dinosauria. (A) Megaloolithid assemblage, Rennes-le-Chateau, France (from Breton et al 1986). (B) Megaloolithid assemblage, Rio Negro, Argentina (from Powell 1995). (C) Ornithoid Ratite (Ostrich), Kenya, Africa (tracing of clutch in Bertram 1992). (D) Elongatoolithid, Two Medicine, United States (from Horner 1987). (E) Elongatoolithid (cf. *Oviraptor*), Laiyang, China (traced from Young 1954). (F) Prismatoolithid (*Troodon*), Two Medicine, United States (traced from Varricchio et al 1997). (G) Spheroolithid (Lambeosaurinae), Judith River, United States (traced from Horner & Clouse 1998). (H) Spheroolithid (Hadrosauridae, cf. *Maiasaura*), Two Medicine, United States. (I) Spheroolithid, Laiyang, China (tracing of clutch in Mikhailov et al 1994). Scale for A–C is 1 meter, others are 10 cm.

suggests that single eggs were being ovulated and shelled daily or at longer intervals (Varricchio et al 1997, 1999) in both oviducts. The neatly organized arrangement of the eggs within the clutches, however, has been used to argue in favor of a reptilian style en masse egg laying (Larson 2000).



The most common and well-known of the organized clutches are those from Mongolia belonging to *Oviraptor* (Norell et al 1994), some of which were previously believed to have been derived from *Protoceratops* (Andrews 1932; van Straelen 1925, 1928; Brown & Schlaikjer 1940; Thulborn 1991, 1992). These elongatoolithid (“ornithoid ratite”) eggs are found arranged in circular (Norell et al 1995) or spiral (Dong & Currie 1996) patterns in which the upper blunt ends of the eggs point inward toward the open center of the clutch (Sabath 1991, Mikhailov et al 1994) (Figure 2E). The number of eggs appears to vary from 20 to 36, and the nest often includes two to three layers of eggs (Brown & Schlaikjer 1940, Moratalla & Powell 1994, Norell et al 1995, Dong & Currie 1996). Similarly arranged clutches, also from Mongolia, have been assigned to *Protoceratops* (Mikhailov et al 1994), although embryonic specimens of this taxon (Dong & Currie 1993) have not been found associated with eggs.

The theropod dinosaur *Troodon* laid a clutch in which the upper, blunt ends of the eggs are directed inward toward a rather small open area (Horner 1984b, 1987; Varricchio et al 1997, 1999). *Troodon* eggs are much more steeply inclined than those of *Oviraptor*. *Troodon* clutches vary from 12 to 24 eggs, laid on a single level (Horner 1987) (Figure 2F). There is evidence of a spiral pattern in some clutches (Horner 1987).

Most of the spherical or subspherical eggs from Asia and North America are found in compact groups or circles (Young 1954, 1965; Mikhailov et al 1994; Horner & Currie 1994) (Figure 2G–I). Some of the Asian clutches that belong to the spheroolithid oofamily, also attributed to hadrosaurs (Mikhailov et al 1994), are found in circles with an open center (Young 1954) (Figure 2I). Spheroidal eggs of the dendroolithid oofamily, purported to contain possible segnosaur embryos (Currie 1996), are found in irregular clusters (Mikhailov et al 1994).

Eggs of the faveoolithid oofamily from Mongolia are found in tight clusters of up to 15 eggs in two to three layers, 1 to 1.5 meters in diameter (Mikhailov et al 1994).

**Egg/Sediment Relationships** A few egg aggregations, particularly some described from France and Spain, are suggested to have been either buried in shallow pits (Erben et al 1979, K  rourio 1981) or laid in open depressions (Cousin et al 1994). The bowl-shaped depressions that constitute some nests (Horner & Makela 1979, Varricchio et al 1999), and the neat and orderly arrangement of some of the clutches (Mikhailov et al 1994), suggest that the dinosaurs probably used their feet to construct nests and possibly manipulated their eggs after laying them (Moratalla & Powell 1994).

All the eggs attributed to Mesozoic dinosaurs appear to have been at least partially buried in sediment (e.g. Erben et al 1979; Seymour 1979; K  rourio 1981; Seymour & Ackerman 1980; Rahn & Ar 1980; Mohabey 1984; Williams et al 1984; Mikhailov et al 1994; Faccio 1994; Norell et al 1995; Varricchio et al 1997, 1999) rather than in the open air (Dughi & Sirugue 1958a, b, 1966; Cousin et al 1994). Grigorescu and associates (1994) described a clutch that was apparently “superficially” buried in fine sand and later blanketed by a coarser sediment.

The recent discoveries of adult non-avian dinosaurs in contact with the tops of eggs (Norell 1995, Dong & Currie 1996, Varricchio et al 1997) demonstrates that at least some taxa did not completely bury their eggs. The elongated, asymmetrical *Troodon* eggs from Montana stand on their pointed ends, half buried in sediment (Horner 1987, Varricchio et al 1997, 1999). Partial burial assured that the eggs would not be moved about, and could still be directly contacted by the parent (Figure 3). Typical reptilian eggs cannot be rotated because the eggs do not possess the albumen cords (present in bird eggs) that keep the embryos upright (Deeming 1991, Varricchio et al 1997).

**Nest Shape and Extent** The geometry of aggregate groups of eggs reveals the investment made by the parent in arranging its eggs. Eggs that appear scattered and random or in large arcs may have been made by quadrupedal animals that invested minimal energy, whereas well-organized clutches may have been laid by bipeds and manipulated with their “hands” (Moratalla & Powell 1994). Although it is parsimonious to presume that the outer edge of the egg clutch marks the inner periphery of the actual nest, there is evidence of a *Troodon* clutch with a 10-cm-high rim approximately 15 to 40 cm outside the clutch perimeter (Varricchio et al 1997, 1999). This rim marks the edge of a nest structure that was constructed independent of the egg-laying process, and it documents an added parental investment in delineating a particular area around the clutch. The rim likely reduced flooding and predation (Varricchio et al 1999).

Another rim-like structure hypothesized to have been constructed by a hadrosaur was apparently formed from a ring of “mud-balls” (Trexler 1997).

Mesozoic dinosaur eggs have been found in various kinds of sediments, but to date all known sites lack appreciable plant debris. The incorporating sediments include limestone (Srivastava et al 1986; Horner 1987; Sahni 1989; Cousin et al 1989, 1994) sandy carbonate (e.g. Sahni et al 1994), mudstone (e.g. Horner & Makela 1979, Grigorescu et al 1994, Horner & Currie 1994), and fine- to medium-grained sandstones (e.g. Faccio 1994, Mikhailov et al 1994, Vianey-Liaud et al



**Figure 3** *Troodon formosus* sitting on its clutch of partially buried, vertically oriented eggs.

1994). Some dinosaurs apparently nested near streams and rivers, and some may have nested near lakes, lagoons (Horner 1984b, 1987; Sahni et al 1994), and tidal flats (Srivastava et al 1986), or even possibly on beaches (Mikhailov et al 1994, Sanz et al 1995), although this interpretation has been contested for the Spanish egg sites (Sander et al 1998). Most of the rocks that yield eggs, regardless of their composition or depositional proximity to water bodies, are rose to red in color, suggesting that the sediment in which the eggs were deposited was well drained (Carpenter 1982).

Most nests are identifiable because they contain the remains of eggs, but a few contain skeletal remains (Horner & Makela 1979, Horner 1984b, Winkler & Murry 1989). One nest-like structure in Montana contained the remains of 15, 1-meter-long hadrosaurs referred to as *Maiasaura peeblesorum*, and another highly eroded structure nearby produced the remains of 7, 0.5-meter-long individuals (Horner & Makela 1979). Oval depressions near Proctor Lake, Texas have yielded as many as 11 hypsilophodontid individuals (Winkler & Murry 1989).

## Incubation

The eggs of all amniotes require an incubation period for embryonic development. Incubation temperature determines embryonic growth rates and the length of incubation (Deeming & Ferguson 1991b), and clutch size depends on nest respiration (Ackerman 1977). Temperature also determines sex in a number of non-avian reptiles (e.g. Bull 1980), including crocodylians, and affects thermoregulation, post-hatching rates of growth, and even pigmentation (Deeming & Ferguson 1991b).

Crocodylians use covered holes or vegetative mounds for passive incubation, and most birds have evolved specific brooding behaviors for active incubation (Campbell 1972, Jones et al 1995, Welty 1979).

**Passive Incubation** Although it has been hypothesized that some dinosaurs such as *Maiasaura peeblesorum* may have used vegetation for incubation (Horner & Gorman 1988), no fossil plant material has been found associated with egg clutches. As discussed above, it appears that most kinds of non-avian dinosaur eggs were buried in various types of soils. The notable abundance, size, and distribution of pores in dinosaur eggs have been used as evidence that many dinosaur eggs were incubated in vegetative mounds (Seymour 1979, Seymour & Ackerman 1980, Schmidt-Nielsen 1986, Williams et al 1984), much like those of megapode birds and some crocodylians. Although it is possible that the well-drained sediments in which most dinosaur eggs were laid (Carpenter 1982) may not have preserved evidence of vegetation, it is also possible that the large clutch sizes may have precluded the use of vegetative debris because nest gas tensions are higher in vegetative mounds (Seymour & Ackerman 1980).

**Active Incubation** The discovery of adult theropod skeletons straddling egg clutches was originally interpreted as evidence of nest plundering (Osborn 1924),

but this has recently been reinterpreted as evidence of parental brooding behavior (Norell et al 1995, Dong & Currie 1996, Varricchio et al 1997). Norell and associates (1995) define “brooding behavior” as the patterns of simply sitting on the eggs, but also explain that such behaviors are usually associated with processes of thermoregulatory incubation. Direct contact of the adult with its clutch of eggs (Figure 3) likely raised the egg temperature above ambient, as occurs in some reptiles (Campbell & Quinn 1975) and birds. An adult dinosaur in a squatting position, sitting with its abdomen in direct contact with a clutch of arranged eggs, displays features identical to bird-like brooding behaviors (Norell et al 1995), rather than crocodylian-like brooding behaviors (Geist & Jones 1996) in which only the throat and thorax may or may not rest on an incubation mound. Brooding behavior in *Oviraptor*, *Troodon*, and living birds suggests that it is a synapomorphy of the Coelurosauria (see Holtz 1996).

## NESTING COLONIES

Many bird species congregate in dense nesting colonies that occupy enormous geographic areas. Nesting colonies of the African Quelea, for example, cover several hundred hectares and contain more than 10 million nests (Welty 1979). Before their demise, passenger pigeons with a population of approximately 136 million individuals nested in central Wisconsin, in an area covering 2,200 km<sup>2</sup> (Schorger 1937). Crocodylians aggregate, but it is unclear whether there is any social interaction (see Coombs 1989).

## Geographic and Vertical Extent

A number of dinosaur egg localities cover huge geographic areas and incorporate the remains of hundreds or thousands of eggs (Williams et al 1984, Breton et al 1986, Horner 1982, Horner & Currie 1994, Sanz et al 1995, Chiappe et al 1998). As Sander and associates (1998) discussed, however, careful taphonomic and sedimentologic analyses of the Spanish sites have shown that the entire nesting horizon may not have been in use at one time. To the contrary, the evidence suggests that the dinosaurs nested in the area over a long period of time (10,000 years), but no evidence indicates that the dinosaurs were in specific nesting colonies. Cretaceous nesting horizons in Montana are hypothesized to have hosted concurrent nesting animals because the nests are approximately at equal vertical distances from ancient soil horizons, and there is no evidence of nest overlaps on individual horizons (Horner 1982, 1984b, 1987). A similar scenario is suggested by nest occurrences in Mongolia (Barsbold & Perle 1983).

“Site fidelity” is also hypothesized for most of the localities with extensive nests occurring on different levels (Horner 1982; Jain 1989; Cousin et al 1989, 1994; Sabath 1991; Sanz et al 1995; Sander et al 1998). Most of these sites appear to have been in use for many thousands of years.

## EMBRYOS AND NEONATES

Dinosaur embryos and neonates remain extremely rare (Carpenter & Alf 1994, Chiappe et al 1998, Horner 1999) and as a result we know little about the life histories of most Mesozoic dinosaurs (Weishampel & Horner 1994). Their scarcity was initially attributed to various factors (Jepsen 1964) including extremely long life cycles (Richmond 1965) and non-preservation of nesting areas (Sternberg 1955). Finding eggs with embryos, however, does not necessarily guarantee the ability to identify the eggs or the embryos (Sochava 1972, Kitching 1979, Horner 1997b). Juveniles of some non-avian dinosaurs experienced strongly allometric growth (Dodson 1975, 1976) and there can be considerable size and morphological difference between an embryo and adult (Horner & Currie 1994, Weishampel & Horner 1994, Paul 1994). Some individuals also had characteristics that changed after hatching or during early ontogeny (Horner & Varricchio 1997). Additionally, various juveniles can look very similar to one another, even across broad categories of taxa (Sampson et al 1997). As a result, no dinosaur embryos or neonates have been positively correlated to a specific dinosaur species, based on an adult individual.

### Taxonomic Identification

The only dinosaur species for which both in ovo embryonic and neonatal skeletons have been described and taxonomically assigned is *Hypacrosaurus stebingeri* from the Upper Cretaceous of Montana and Alberta (Horner & Currie 1994), and even in this instance, identification was primarily circumstantial rather than morphologic. None of the derived characteristics present in the adult holotype were present in the perinates. The perinates, recognizable as lambeosaurines (Currie & Horner 1988), were assigned to this species because it was the only lambeosaur species known from the stratigraphic horizon where the eggs and babies were found.

Other embryos found inside eggs, as opposed to specimens hypothesized to be embryonic or perinatal because of size (Bonaparte & Vince 1979, Dong & Currie 1993, Chure et al 1994, Britt & Naylor 1994), have been identified and assigned to the theropod genera *Oviraptor* (Norell et al 1994) and *Troodon* (Horner & Weishampel 1988, 1996; Varricchio et al 1997), two unknown taxa of theropods (Li et al 1996, Mateus et al 1997), a sauropod (Chiappe et al 1998), an unidentified lambeosaurine hadrosaur (Clouse & Horner 1993, Horner 1999) and cf. *Maiasaura* (Horner 1999). Other in ovo embryos have been discovered and are under study (see Currie 1996), but some are too immature to identify (Horner 1997b).

In addition to the in ovo specimens is a group of tiny skeletal hadrosaurine elements, representing individuals 45 cm in length, found in association with large pieces of spheroolithid eggshell in the Upper Cretaceous Two Medicine Formation of Montana (Horner & Makela 1979, Hirsch & Quinn 1990). These were

originally described as *Maiasaura* hatchlings because their teeth were worn, but the discovery of worn teeth in embryonic *Hypacrosaurus* (Horner & Currie 1994) falsified the hypothesis and indicated that the perinates might have been embryos instead of hatchlings. However, recent calculations of egg volume indicate that the young are very close in size to the range predicted for hatchlings (Horner 1999).

Small neonate dinosaurs are quite rare; they are found almost exclusively as disarticulated skeletal elements on nesting horizons (Horner 1987, 1994; Grigorescu et al 1994), in aggregate groups (Horner & Makela 1979, Barsbold & Perle 1983, Dong & Currie 1993), or as isolated elements or skeletons in other taphonomic situations (e.g. Coombs 1980, Fiorillo 1987, Jacobs et al 1994, Carpenter 1982, Carpenter & McIntosh 1994, Gallagher 1995). In China and Mongolia, most neonate specimens are found as isolated skulls or skeletons (Brown & Schlaikjer 1940), and nesting horizons are rare (Mikhailov et al 1994).

Aggregate groups of neonates are of particular interest because the skeletons, whether articulated or not, have been described as being within the confines of round or oval structures hypothesized to be nests (Horner & Makela 1979, Horner 1984b, Barsbold & Perle 1983). To date, only hadrosaur remains have been reported in such structures, although there is an unpublished cluster of 15 neonate *Protoceratops* in the National Museum of Mongolia (DB Weishampel, personal communication), and Coombs (1982) reported on a sibling group of seven *Psittacosaurus* specimens of identical size apparently found together, also in Mongolia.

## Skeletal Development

The degree of epiphyseal development and ossification in embryonic and neonatal dinosaurs has been used to hypothesize stages of overall development and to speculate on altricial and precocial post-hatching behaviors (Horner & Weishampel 1988, 1996). It was observed that the epiphyseal ends of the embryonic femora of the coelurosaur *Troodon*, originally misidentified as the hypsilophodontid *Orodromeus* (Horner & Weishampel 1996), consisted of a thick pad of calcified cartilage penetrated by an opening that appeared to contain a cartilage cone. In contrast, the epiphyseal ends of an embryonic femur hypothesized to belong to the hadrosaurid *Maiasaura* was described as having a thin calcified cartilage pad overlying a very spongy endochondral metaphysis. The ends of the *Maiasaura* femur were described as spongy and incomplete, and incapable of withstanding the rigor of locomotor activity. *Maiasaura* was hypothesized to have been altricial, or nest-bound, and in need of parental assistance for acquiring food (Horner & Weishampel 1988). *Troodon* was regarded as capable of locomotor activities and precocial. Later discoveries of other non-avian dinosaur skeletons that had limb bones with incomplete condyles were interpreted as representing altricial young (Jacobs et al 1994, Chure et al 1994), and those with well-formed limbs were regarded as precocial (Coombs 1980, Winkler & Murry 1989). A compi-

lation of data and cladistic analysis (Weishampel & Horner 1994) of the evolution of dinosaur life histories with regard to mode of development suggested that several hadrosaurid taxa were altricial.

Geist & Jones (1996) challenged the interpretation of the epiphyses by correctly pointing out that the reason that the neonate *Maiasaura* femora appeared incomplete was that they were missing their articular fibro-cartilage caps (Reid 1997). Geist & Jones suggested that the *Maiasaura* neonates (perinates) and various other embryonic and neonatal individuals all possessed well-ossified skeletons, and showed no characteristics suggestive of altricial behaviors. The Geist and Jones study, however, was based on morphological observation rather than histology. Horner (1996; see also Horner et al 2000a) re-examined the bones using histological techniques, and showed that there were major differences in metaphyseal development separating *Maiasaura* from *Orodromeus* and *Troodon*. *Maiasaura* possessed massive calcified cartilage pads. However, a thin calcified pad overlying endochondral bone was evident in both *Troodon* and *Orodromeus*. Horner (1996) and his colleagues (Horner et al 2000a, b) showed that the epiphyseal ends of the limbs of hadrosaurs possessed calcified cartilage structures that would have severely limited active locomotion during the time between hatching and when the hatchling doubled in size. Within the avian altricial-precocial spectrum (Stark & Ricklefs 1998b), the maiasaurids appear to have been semi-altricial, requiring adult care until they at least doubled in linear dimensions from hatching (Horner et al 2000a, b).

## Parental Care

Case (1978) determined that if dinosaurs grew at rates equivalent to extant ectotherms, the largest of them would not have reached maturity for several decades. From these calculations, he hypothesized that selection may have favored high juvenile survivorship by extended parental care. More recent calculations of growth rates (e.g. Varricchio 1993, Reid 1997, Curry 1998, Horner et al 2000b), however, suggest that most dinosaurs grew much more quickly than extant non-avian reptiles, and therefore an argument for parental care cannot be based on growth rates alone.

In the context of this review, parental care is defined as any protective or nurturing parental investment in its eggs or hatched offspring (Horner 1997a). The most direct evidence of parent/offspring relationships are the occurrences of adult *Oviraptor* and *Troodon* sitting on their nests (Norell et al 1995, Dong & Currie 1996, Varricchio et al 1997). In no other instance has an adult skeleton been found in direct association with its eggs or young, contrary to previous reports (Coombs 1982, Geist & Jones 1996).

Two localities have provided data from which parental feeding of young has been hypothesized. One is based on the presence of nestlings (Horner & Makela 1979, Horner 1984b) incapable of strenuous locomotion (Horner & Weishampel 1988; de Ricqlès et al 1998; Horner et al 2000a, b); the other is based on taphon-

omic speculations concerning neonate theropod tooth marks on adult carcasses (Bakker 1997).

Coombs (1980, 1982) argued that parental care would have been unlikely in situations when there was a great size discrepancy between the perinates and adults. Coombs argued that it would have been difficult for an adult to actually attend the needs of tiny offspring, and would likely crush them underfoot. Horner (1984b) countered that had the young been attended in a nest, the nest perimeter could have provided a protective limit for the eggs and young, as observed in birds (Welty 1979).

Crocodylian hatchlings are transported by a parent to a nursery pool, where they remain together under protective surveillance by the parents (see Coombs 1989). Crocodylians are amphibious animals, and the young are obviously better protected by the parents while they are in the water than if they were in their original nest on land. Dinosaurs, however, were terrestrial animals, and it would make little sense to move the young from one terrestrial location to another. The most parsimonious explanation for finding post-hatchling juveniles in nest-like structures (Horner & Makela 1979, Horner 1982) is that the juveniles (*Maiasaura*) remained in their nests for some period of time following hatching (Horner et al 2000a). Histological studies of the tiny perinate hadrosaurs suggest that their limbs were not well ossified; instead, their leg bones contained vast regions of calcified cartilage (de Ricqlès et al 1998; Horner et al 2000a, b). The nestling dinosaurs fall within the spectrum of altricial as recently defined by Starck and Ricklefs (1998b); possibly they were brought food by a parent (Horner & Makela 1979, Paul 1994). Altricial dinosaur perinates and parental feeding may have been rare (Horner 1999).

## CONCLUSIONS

It was not within the scope of this review to cover the reproductive and parenting behaviors of crocodylians and birds, but I direct the reader to the various references reviewed by Welty (1979), Shine (1988), and Coombs (1989), for reproductive comparisons with crown groups.

Some non-avian dinosaur groups, particularly those with accessory cranial features such as horns, bosses and crests, probably exhibited sexual dimorphism (e.g. *Protoceratops*: Dodson 1976) that may have been elaborated by differences in body robustness, as in numerous extant archosaurs. Extinct dinosaur taxa, like most other extant amniotes, probably engaged in some form of display in competition for mates (Sampson 1999), and at least some non-avian dinosaurs apparently possessed elaborate bony display structures unlike most extant archosaurs. The hadrosaurs and ceratopsians, the two most common groups with cranial ornamentations, are commonly found in extensive bonebeds, interpreted as evidence for large, monospecific aggregations or herds (e.g. Rogers 1990, Varricchio & Horner 1993).



Hadrosaurian dinosaurs may have been exceptionally gregarious because their neonate remains are commonly found on nesting horizons with egg clutches. These patterns suggest colonial nesting in addition to the possible aggregate groups of adults represented by bonebeds. Numerous other taxa were also apparently gregarious in the sense that they nested in colonies.

Some extinct dinosaurs, particularly *Troodon*, and perhaps all the Coelurosauria (Holtz 1996), invested energy in the construction of their nests, forming an outer sediment rim. The eggs, apparently laid two at a time, were placed partially in soil, in circular or spiral patterns. The laying of 12 to 30 eggs with two active oviducts probably took 6 to 15 days, and there could have been some manipulating of the eggs after laying that organized the eggs into the neat circles. Sauropods and ornithischians may have constructed concavities in built-up mounds (Horner & Makela 1979), dug pits into the surface of the ground (K  rourio 1981), or laid the eggs in shallow depressions. Pore size and distribution suggests that all Mesozoic dinosaur eggs were most likely at least partially buried, and that the non-avian coelurosaurs probably provided some body heat during incubation.

It has been suggested that non-avian dinosaurs may have been subject to temperature-dependent sex determination (Paladino et al 1989) because they were closely related to crocodilians. However, non-avian dinosaurs are even more closely related to birds than to crocodilians, so there is no particular reason why crocodiles should be the default model for dinosaurian life history strategies, as shown above. Both genetically fixed and temperature-dependent sex determinants are second order inferences, and neither hypothesis is stronger than the other. It may have been that the passively incubated eggs were temperature dependent, whereas the actively incubated eggs were genetically fixed.

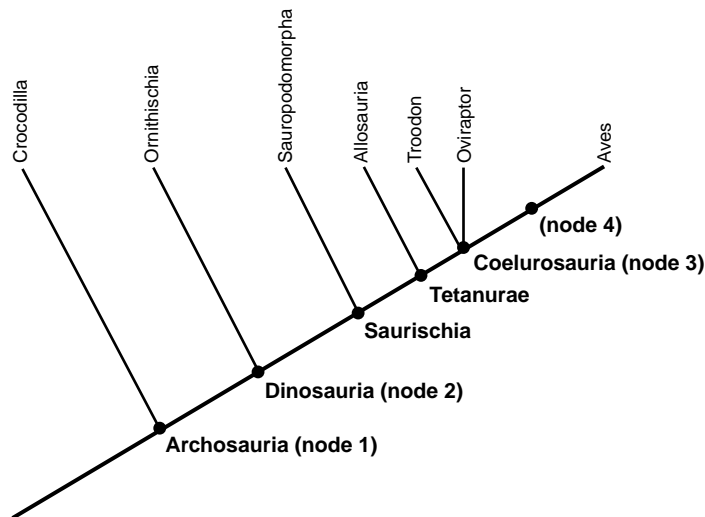
Parental care and protection among non-avian dinosaurs was probably as varied as among living archosaurs (Shine 1988, Welty 1979). Nesting horizons with eggs and neonate bones suggest that the young of many taxa remained in the nesting areas, probably in cr  che-like groups, for some period following hatching. Parental feeding of the young may have been uncommon, but parental care and protection are both present in crocodilians and birds, and presumably in non-avian dinosaurs. Parental feeding is absent in extant non-avian reptiles, and considered derived for birds (Pond 1983).

Initial growth rates of most non-avian dinosaurs appear to have been greater than those of crocodilians, and in many cases they probably approached the rates of most extant birds (e.g. Varricchio 1997; Horner et al 2000a, b).

Sexual dimorphism, sexual display, nest construction, aggregate nesting, egg guarding, and parental care (protection) of the young are all first order inferences for extinct dinosaurs because these behaviors are observed in most extant archosaurs (see Coombs 1989). Parental feeding of altricial (semi-altricial) young is a second order inference, exhibited by various birds but not by crocodilians. If *Maiasaura* fed its young, it is possible that this behavior evolved twice—once among some hadrosaurs or a broader group within ornithischians, and again among various birds (and perhaps a wider group within saurischians).

Mapping the known reproductive behaviors of non-avian dinosaurs on a cladogram (Figure 4) (previously devised from morphological data, Currie & Padian 1997) suggests that many of the reproductive traits of birds may have been derived from both their archosaurian and dinosaurian ancestors. From a phylogenetic point of view, it cannot be stated that non-avian dinosaurs possessed reproductive behaviors that were intermediate between crocodylians and birds (Varricchio et al 1997), but rather that they were derived from the common ancestor of the two groups. Traits and behaviors shared by both crown groups were most likely derived from the common ancestor and may have been present in any of its descendants.

From a speculative perspective, it can be hypothesized that sexual dimorphism and parenting characteristics imply that Mesozoic dinosaurs inhabited unstable environments (e.g. Wilson 1980), the result of relatively rapid changes in sea level and concomitant rapid speciation events (e.g. Horner et al 1992). Non-avian dinosaurs produced relatively large numbers of offspring that provided them with the capacity to rebuild populations quickly following environmental disturbances



**Figure 4** Cladogram of the Archosauria with selected reproductive characteristics at selected nodes (modified after Varricchio et al 1997). Characteristics of Node 1: assembly-line oviducts, hard-shelled eggs, embryonic use of eggshell calcium, nest construction, aggregate nesting, clutch attendance, parental care (protection), juvenile crèches. Node 2: monoautochronic ovulation (two eggs deposited at a time), reduced clutch sizes, increased perinate growth rates. Node 3: loss of egg retention, potential for asymmetric eggs, relatively larger egg/adult size ratio, eggs only partially buried, brooding of eggs, open nest. Node 4: loss of right ovary and oviduct function, eggs free of sediment, larger egg/adult size ratio, egg rotation, chalazae.

(Janis & Carrano 1992). Such a reproductive scenario may have been a factor in the ultimate success of the Dinosauria (Paul 1994).

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