

Dinosaur Eggs and Babies

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Introduction

KENNETH CARPENTER,
KARL F. HIRSCH, AND
JOHN R. HORNER

We are currently enjoying a new Golden Age of Dinosaur Paleontology not seen since the interval between the two world wars. This revival stems from the hypothesis developed in the late 1960s and 1970s that perhaps dinosaurs were active endotherms. This suggestion came at a time when the Baby Boom generation was maturing and entering college. Many, including most of those contributing to this volume, were captivated by the idea that it was possible to determine something about dinosaur biology, physiology, and reproduction.

This volume, *Dinosaur Eggs and Babies*, was conceived while working on *Dinosaur Systematics: Approaches and Perspectives* (Carpenter & Currie, 1990). It was clear that a considerable amount of research had been done during the past two decades describing the microscopic structure of dinosaur eggs, structure of dinosaur egg clutches interpreted to be the remains of nests, and the skeletons of various very young hatchling dinosaurs. The editors of this volume felt that the time had come to organize and summarize this research before the sheer volume of material made this impossible. Hopefully, we could point the way for future research and possibly give it some cohesiveness.

Unlike other volumes in this series – *The Beginning of the Age of Dinosaurs* (Padian, 1986), *Dinosaur Tracks and Traces* (Gillette & Lockley, 1989) and *Dinosaur Systematics* (Carpenter & Currie, 1990) – this volume is not the result of a symposium. Instead, many of the contributors were solicited for specific overview chapters, while other chapters were voluntarily submitted for the volume.

The discovery of dinosaur eggs

Dinosaur eggs have often been considered novelties or museum curiosities not worthy of much scientific study. Consequently, they have been the subject of many misconceptions by the public and the film industry. Giant dinosaurs are assumed to have laid giant

eggs; thus Ringo Starr in *Caveman* (1981) is shown staggering under the load of a dinosaur egg bigger than he is. In point of fact, the largest dinosaur eggs are a little smaller than a basketball or a soccer ball. Most eggs are considerably smaller, and vary in shape from spheres, to ovals, to tapering elongated bodies.

Another myth is that dinosaur eggs were unknown before the 1920s when the American Museum of Natural History announced their discovery in Mongolia. Actually, dinosaur eggs have been known for thousands of years, however, the discoverers did not make a media event out of it. Instead, they chose to shape the shell fragments, possibly for jewelry. At least that is the conclusion reached by archeologists accompanying the Central Asiatic Expeditions of the American Museum of Natural History (Andrews, 1932, p. 255). The shaped eggshells were found at a late paleolithic or early neolithic site (Perle, personal communication) near Shabarakh Usu (now called Bayn Dzak), in Mongolia.

In historical times, a dinosaur eggshell was first reported in 1859 from the egg-rich area of southern France (Introduction-Table 1). This discovery, discussed by Buffetaut and Le Loeff (Chapter 2), came not long after the naming of the Dinosauria by Owen in 1841. This little-known discovery of eggshell occurred about 64 years before the well-publicized discoveries in Mongolia by the American Museum of Natural History in 1923. Less known is that in 1859 a clutch (nest?) of fossilized eggs was discovered in the “Great Oolite” of England (Buckman, 1859). The eggs were small, about the size and shape of “*Gobiopteryx minuta*” eggs (see Mikhailov, Sabath, & Kurzanov in Chapter 7). These were the first fossil eggs to be named (*Oolithes bathonicae*, Buckman, 1859). The identity of the eggs remains uncertain, although they have been ascribed to the crocodyles by Buckman (1859) and to the pterosaurs by Carruthers (1871). Pending a restudy of the specimens, we cannot rule out the possibility that they are the eggs of a small dinosaur.

Since 1859, dinosaur eggs and eggshells, as well as baby dinosaurs, have been found on almost every continent, as documented by Carpenter and Alf in Chapter 1.

Studies of dinosaur eggshells

Not long after the discovery of dinosaur eggshells, Paul Gervais (1877) sought to identify the large eggshell fragments from the Provence region of France (Buffetaut & Le Loeff in Chapter 2). Gervais made the first detailed microstructural study of these eggs by comparing them with those of modern turtles, crocodiles, geckos, and birds. From this study, he concluded that the eggs from Provence were structurally most like those of turtles. However, because of the large size of the eggshells, he could not rule out the possibility that they were dinosaurian. Many years later, Sochava (1971) also concluded that the eggshells from France resembled those of turtles and assigned them to his testudoid group.

The technique of comparative microstructural analysis was continued by van Straelen and Denaeyer (1923) who used both normal and polarized light to study both radial and tangential sections of the Provence eggshells. van Straelen later conducted the first study of eggs collected by the American Museum of Natural History expeditions to Mongolia (van Straelen 1925, 1928). Originally, he recognized only a single egg type from Bayn Dzak and suggested that it was possibly the egg of *Protoceratops andrewsi*. A few years later, he con-

cluded that a second egg type was present, based on shell thickness, surface ornamentation, and number of pore openings (van Straelen, 1928). This time he did not suggest who might be the egg-layer.

The use of polarized light microscopy (PLM) and normal light microscopy (LM) to study dinosaur eggshells continued with the studies of Lapparent (1947), Chow (1951, 1954), and Sochava (1969). A new technique, the scanning electron microscope (SEM), was introduced by Erben (1970) in his study of extant reptile and avian eggshells; also included were dinosaur eggshells from Provence, France. This technique, combined with PLM and LM, is becoming the standard for the analysis of fossilized eggshell (e.g., Hirsch & Quinn 1990).

Classification of dinosaur eggs

The early classification schemes for dinosaur eggshells apparently developed independently with little knowledge of other workers. Only recently, have attempts been made to utilize a single parataxonomical scheme as discussed in Chapters 7, 10, 11, and 12.

The earliest classification assigned names to the eggs on the basis of macrostructural characteristics. Size and shape were used by Buckman (1859) and Carruthers (1871). Their reasoning presupposed that such characters were as distinctive as the morphological features of bones used to separate dinosaur taxa. Shell thickness and surface ornamentation were also used by van Straelen (1928) for Mongolian eggs, but his conclusions were

Introduction Table 1. Chronological discovery of dinosaur eggs and babies

Date	Country	Material	Reference
1859	France	Eggshell	Buffetaut and Le Loewff; Chapter 2
1859	England	Nest?	Buckman, 1859
1883	U.S.A.	Baby	Marsh, 1883; Chapter 17
1908	Portugal	Egg	Lapparent and Zbyszewski, (1957)
1913	U.S.A.	Eggshell	Gilmore, field notes
1922	Mongolia	Egg	Andrews, 1932
1923	China	Eggs	Andrews, 1932
1923	Mongolia	Baby	Brown and Schlaikjer, 1940
1950	Tanzania	Eggs	Swinton, 1950
1951	Brazil	Eggs	Price, 1951
1954	Spain	Eggs	Lapparent and Aguirre, 1954
1961	Kazakstan	Eggshell	Bajanov, 1961
1964	Canada	Eggshell	Jepsen, 1964
1968	Peru	Eggshell	Sigé, 1968
1974	Argentina	Nest/baby	Bonaparte and Vince, 1974
1979	South Africa	Nest/baby	Kitching, 1979
1977	Uzbekistan	Eggs	Nesov and Kaznyshkin, 1986
1980	Uruguay	Eggs	Mones, 1980; Chapter 4
1982	India	Eggshell	Sahni and Gupta, 1982
1990	Romania	Nest	Chapter 6

contested by Brown and Schlaikjer (1940). Young (1954) used macrostructural characters to separate eggs from Laiyang, China, into two forms: a spherical egg (*Oolithes spheroides*) and an elongated egg (*O. elongatus*). Microscopic differences were not used in the original diagnosis, but appeared in a later paper (Chow, 1955). Length–diameter ratios were used by Young (1965) to separate *Oolithes rugustus* into two subforms, one of which was shorter and broader than the other. The shortcoming of this macrostructural classification became apparent, however, with Chao and Chiang's (1974) discovery that *O. spheroides* could be further divided into five types, based on the thickness of the shell layer, thickness of the mammillary layer, and number of mammillae per square millimeter. As a result, they recognized five different species of *Oolithes* (most of which have since been recognized as distinct egg genera; see Chapter 12 by Zhao).

Since pore canals had long been noted as differing among eggs (e.g., van Straelen, 1925), Sochava (1969) used these differences as the foundation for his classification scheme. Sochava separated eggshells into angusticanaliculate, prolatocanaliculate, and multicanaliculate. Erben (1970) introduced a new pore canal type, tubocanaliculate, and Nesov and Kaznyshkin (1986) introduced foveocanaliculate and lagenocanaliculate.

Sochava (1971) later placed his prolatocanaliculate and angusticanaliculate eggshells into a larger category he called the ornithoid group because of microstructural similarities with bird eggshells. The multicanaliculate eggshell (similar to the eggshells from Provence, France), were placed by Sochava into the testudoid group because of similarities with turtle eggshells. By doing so, Sochava formalized the distinction long noted that some dinosaur eggshells resembled those of birds, and others more closely resembled those of turtles. Dughi and Sirugue (1976) independently placed dinosaur eggs from southern France into a reptile and a bird group.

Other methods of classification that have been developed include designating the different egg types alphabetically (e.g., Jensen, 1966), numerically (e.g., Williams, Seymour, & K  rourio, 1984; Nesov & Kaznyshkin, 1986), and by shell-unit shape (Penner, 1985). The alphabetical and numerical systems of the various authors are usually not comparable; for example, one author's egg type A, is not necessarily the same as another author's type A (e.g., Jensen, 1966 versus Srivastava et al., 1986).

The most recent classifications (Sabath, 1991; Chapter 7 by Mikhailov, Sabath, & Kurzanov; Chapter 10 by Hirsch; Chapter 11 by Vianey-Liaud et al.; and Chapter 12 by Zhao) utilize the parataxonomic classification pioneered by Zhao (1975, 1979a). Zhao's classification scheme is now supplemented by the structural classification into basic groups, morphotypes, pore systems, and ornamentation (Mikhailov 1991, 1992). The

parataxonomic system, however, is not yet universally accepted. Sahni et al. (Chapter 13) prefer to use the identity of the egg-layer to identify the eggs from India, while Moratalla and Powell (Chapter 3) use the basic organizational groups of Hirsch and Quinn (1990).

Chemical analysis and organic material of dinosaur eggshell

The chemical analysis of dinosaur eggshell is a relatively new field of research, although the first study was conducted by van Straelen and Denaeyer (1923). They determined that the dinosaur eggshells from France were calcium carbonate (CaCO_3) and therefore little altered. Little additional analyses were conducted until sophisticated analytical equipment and techniques were developed in the 1960s. Voss-Foucart (1968) isolated two proteins by chromatography and verified their proteinlike macromolecular shape with SEM. She observed that the shell proteins were so similar to those of chicken eggs as to suggest a common ancestry.

The discovery of proteins in dinosaur eggshell is rather remarkable because they are not very stable chemically (Wyckoff, 1972). Usually, they degrade into amino acids which are more stable. But even these acids are soluble in water and so can be selectively removed from buried eggs by groundwater. Heat and pressure, such as found in the deep burial of sediments, can also affect amino acids. Nevertheless, Wyckoff (1972) was able to find various amino acids in a number of dinosaur eggshells. Kolesnikov and Sochava (1972) identified eighteen proteins from a dinosaur egg found in Mongolia, and noted a greater similarity between it and a chicken egg than between it and testudoid eggshell fragments from France. This suggests to us that amino acid studies of dinosaur eggshells might yet have some taxonomic value and perhaps might be an aid to evolutionary studies. Vianey-Liaud et al. discuss the results of their amino acid studies in Chapter 11.

Even more remarkable than the discovery of eggshell protein, is the report of organic material in eggshell. Van Straelen (1925) reported black organic material in the eggshell of *Protoceratops*. Chow (1954) identified what he interpreted to be the outer cuticle on some dinosaur eggs from Laiyang. This conclusion was challenged by Chao and Chiang (1974) who identified the material as calcite (see also Hirsch & Quinn, 1990). Vianey-Liaud et al. (in Chapter 11) suggest that the calcite skin, also seen on the dinosaur eggshells from France, is the result of the decomposition of the egg's soft tissue. Ammonia, a by-product of such decay, would raise the local pH and result in the deposition of CaCO_3 . The presence or absence of a cuticle on the dinosaur eggs is more than a minor point of debate because the presence or absence of the cuticle says a lot about the microenvironment of the nest. It was the apparent absence of such tissue on *Protoceratops* eggs that

led van Straelen (1925) to argue that these eggs were laid in an arid environment.

Chow (1954) also claimed that the albumin and yolk of one uncrushed egg had been replaced by calcite (see Dong & Milner 1988, p. 102 for a color photograph). A detailed analysis, however, is needed to substantiate this claim.

The cuticle, shell membrane (an organic structure that covers the inside of the eggshell), scleroprotein matrix, and organic material inside the pore canals were identified in a Mongolian egg (Kolesnikov & Sochava, 1972). The identification of the cuticle is suspect (see discussion above).

Oxygen and carbon isotopes of dinosaur eggshell from France are discussed by Vianey-Liaud et al. in Chapter 11. The first study of these isotopes was conducted by Folinsbee et al. (1970), who raised the possibility that isotopes might provide clues about the environment in which the egg-layers lived. Erben, Hoefs, and Wedepohl (1979) and Zhao, Yan, and Ye (1983) carried this further, suggesting that carbon isotopes might provide dietary clues. Dauphin (1990a), however, was not able to find a correlation between diet and eggshell composition.

Changes in the oxygen isotopes of eggshells were used by Zhao (1991) to indicate a possible climatic change toward the end of the Cretaceous. This climatic change, he argues, may be the cause for the extinction of the dinosaurs. Previously, Erben et al. (1979) had suggested thinning of dinosaur eggshell as a cause for the extinction. Paladino et al. (1989), on the other hand, suggest that the predominance of one sex among dinosaur hatchlings might have caused the dinosaur extinction.

A major problem with the use of isotopes from dinosaur eggshells is diagenesis, as pointed out by Dauphin and Jaeger (1990) and Dauphin (1992). For this and other reasons, Sabath (1991) urged caution about making environmental and dietary interpretations based solely on isotopic studies.

Physiology of dinosaur eggs

Physiological studies of dinosaur eggshell are not yet very common. The amniotic egg is thought to have freed tetrapods from having to reproduce in water by protecting the developing embryo from desiccation in a subaerial environment. Sochava (1969) took this one step farther by suggesting that the calcareous dinosaur egg developed in response to aridity during the Cretaceous. Such a hypothesis, Sochava argued, would explain the apparent rarity of Pre-Cretaceous dinosaur eggs; these eggs had a pliable shell that would rarely fossilize. Sochava's hypothesis is still advocated by Zhao in Chapter 12.

The use of negative evidence (the absence of eggshell) by Sochava and Zhao is not without danger, as indicated by Hirsch's description in Chapter 10 of eggs

and eggshell from the Upper Jurassic Morrison Formation. Carruthers (1871) and van Straelen (1928) have described what they thought were leathery-shelled eggs, but the taphonomic loss of a calcareous shell that left an organic residue cannot be discounted at this time. We do not rule out the possibility of leathery dinosaur eggshell, but demonstration of its existence is difficult (see Summary for one possible method).

The conductance of water vapor and respiratory gas exchange through the pore system of dinosaur eggshell has been examined by Seymour (1980). Grigorescu et al. attempt to estimate these values for eggs described in Chapter 6. The correlation between pores, surface ornamentation, egg shape, position of the eggs in the nest, and type of nest (vegetation mounds or soil) is discussed by Moratalla and Powell in Chapter 3, and by Mikhailov et al. in Chapter 7.

The presence of resorption pits in the mammillae was used for the first time by Schwarz et al. (1961) to show that an embryo had developed. Such pits form in the mammillae of modern eggs as a result of the embryo drawing calcium out of the egg for bone formation.

Dinosaur eggshell pathologies

Most dinosaur egg studies, such as those in this volume, were conducted upon healthy eggshell. Sometimes, however, various structural irregularities, like extra spherulitic structures, can be incorporated into the shell layer during shell formation. The most important pathologic condition is the multilayered eggshell, caused by unintentional retention of the egg (Zhao, Chapter 12). First reported by Dughi and Sirugue (1958), these multilayered shells provide important clues about the reproductive organs of the dinosaurs. In birds, the formation and shelling of an egg takes place in different regions of the oviduct in assembly-line fashion; thus only one egg is laid at a time (Taylor 1970).

Sometimes, however, the shelled egg in birds may be retained unintentionally rather than being layed because of stress, illness, or environmental conditions. This may cause a reverse peristalsis which sends the shelled egg back up the oviduct to where it meets the next egg (not yet shelled) being formed. These two eggs move together back down the oviduct and a shell is formed around both eggs, resulting in an egg within an egg, or "ovum in ovo" (Romanoff & Romanoff, 1949). The retention of an egg in the oviduct may cause illness or death of the female bird. The term "ovum in ovo" has been used incorrectly for multilayered eggshells (e.g., Erben et al., 1979). As yet, ovum in ovo has not been observed in the fossil record.

In noncrocodilian reptiles, the eggs are formed and shelled within a single region of the oviduct, and the entire clutch is laid simultaneously (Aitken & Solomon, 1979). Crocodiles, on the other hand, are somewhat like birds in that formation and shelling of the eggs occur in different parts of the oviduct, but the entire

clutch is laid at the same time (Palmer & Guillette, 1992). Unintentional retention of the eggs can occur for a variety of reasons, including a change in diet (Ewert, Firth, & Nelson, 1984). This retention can result in another egg membrane and layer of shell being deposited around the eggs. From this, we may conclude that dinosaurs did not have a avian-type reproductive system, but a reptilian-type. Ewert et al. (1984) also concluded from their study of turtles that multilayered eggs can occur if two or more clutches are laid per season. In addition, once retained eggs are laid, those at the bottom of a clutch (first laid) are more apt to be multilayered than those at the top. See Hirsch et al. (1989) for additional discussions.

Multiple layered eggshell is rare but widespread among different eggshell species. It does, however seem to be more common in *Megaloolithus* (Erben et al., 1979). This condition is fatal to the developing embryo because the pore canals of the layers are rarely aligned. This effectively blocks gas exchange.

Abnormally thin eggshell has also been reported by Erben et al. (1979), but contested by Penner (1985) who argues that different egg taxa are present. Some thinning is clearly diagenetic as discussed by Penner (1985) and Dauphin (1990b). Other pathological conditions have been reported by Zhao (1991). These include abnormal proportional thickness of the cone layer and columnar layer (i.e., part of the shell is too thick), misshapen calcite crystals in the columnar layer, and irregular spaces within the shell (but one of us, Hirsch, has evidence that this condition could sometimes be diagenetic). These pathologies are either rare or have not been recognized in other eggshells.

Effects of diagenesis

The study of eggshells must be undertaken carefully with the recognition that diagenetic overprinting can often occur as noted by Dauphin (1990a, 1990b, 1992) and Dauphin and Jaeger (1990), as well as Hirsch in Chapter 10 and Vianey-Liaud et al. in Chapter 11.

Certain features, such as a herringbone pattern or localized mineral deposits in the shell unit, have been described as part of the shell structure. It is now known that these and other features can distort or obliterate the true diagnostic features. Recrystallization of the eggshell calcium carbonate is a relatively common problem that can distort the exact size and shape of the prisms. Also, partial dissolution of the CaCO_3 can affect eggshell structures, especially the mammilla on the inner surface and the ornamentation on the outer surface. This dissolution can occur at any time and is controlled by local pH.

Nests and nesting behavior

The first possible dinosaur nest to be described was the clutch of eight or more eggs of *Oolithes bathonicae*. Buckman (1859) speculated that the eggs were

laid reptile fashion in sand (i.e., buried eggs). Since the 1859 discovery, dinosaur nests have been found worldwide (see Carpenter & Alf, Chapter 1). But whether the eggs were buried in the ground as Buckman (1859) implied or on the surface as Dughi and Sirugue (1958) concluded has been the subject of much debate as discussed by Cousin et al. in Chapter 5.

As a result of the discovery of the many dinosaur nests, several different nesting patterns have been recognized as detailed by Moratalla and Powell in Chapter 3. Their study expands the earlier review by Coombs (1989). Moratalla and Powell note that eggs may be arranged in spirals, concentric circles, irregular clusters, arcs, parallel rows, or double rows. A variant of the parallel row not mentioned by them is the alternating parallel row. Such an arrangement is proposed by Zhao (1979b) for *Youngoolithus xiaguanensis*.

Colonial nesting grounds have been described by Young (1965) for sites in Laiyang, China, where the nests were about 2 m apart. In Nanxiong Basin, the nests are about 7 or 8 m apart, and cluster into "sets" of five or six nests. Young suggested that a single gravid female was responsible for each "set." Horner (1982) described a regular spacing of *Maiasaura* and *Orodromeus* nests at the Willow Creek Anticline. The harsh conditions within a dinosaur nest are examined by Paul in Chapter 18.

Eggs and stratigraphy

The geographic distribution of eggshells in China was noted by Young (1965) who used them for correlation between various depositional basins. Chao and Chiang (1974) plotted the stratigraphic distribution of *Oolithes* near Laiyang and used the results to show the evolution of the various species within the basin. Zhao (1979a) discussed the use of egg species in biostratigraphy and regional correlations. The use of eggs for regional correlation has been accepted by Sabath (1991) and Mikhailov et al. in Chapter 7.

Discovery of baby dinosaur bones

The best-known baby dinosaurs are those of *Maiasaura* popularized by Horner (1984) and Horner and Gorman (1985, 1988). The underdevelopment of the joints suggested that the babies did not venture out of the nest, but that the adult(s) brought food to them. Parental care in dinosaurs had been predicted a year earlier by Case (1978). The subject has been examined by Coombs (1989). Lambert (1991) argues that altricial behavior only occurs in endotherms, therefore dinosaurs could not have been ectotherms. Paul expands on this argument in Chapter 18.

Other baby dinosaurs from Montana besides *Maiasaura* include an embryonic *Orodromeus* described briefly by Horner and Weishampel (1988). A new species of *Hypacrosaurus* is described from specimens of

numerous babies and an adult by Horner and Currie in Chapter 21.

The baby *Maiasaura* were not the first baby dinosaurs to be described. In 1883, Marsh briefly described a "foetal" sauropod associated with the holotype of *Morosaurus* (= *Camarasaurus*) *grandis*. The specimen is illustrated for the first time by Carpenter and McIntosh in Chapter 17. It and the other sauropod babies described in Chapter 17 are too large to be embryos. A possible embryonic *Camarasaurus* is described by Britt and Naylor in Chapter 16. At present, this may be the only embryonic sauropod known despite the thousands of "sauropod" eggs known from France, Spain, Argentina, and India (contrary to Mohabey, 1987; see Chapter 17).

The distribution of dinosaur babies, along with some reconstructed skeletons, is presented in Chapter 1 by Carpenter and Alf. They report that embryonic dinosaurs are very rare, occurring mostly in Mongolia and the Two Medicine Formation of Montana. The first Mongolian embryonic dinosaur to be found may be in a "*Protoceratops*" egg collected by the American Museum of Natural History expedition at Bayn Dzak. The specimen had been on exhibit for many years, until one of us (Horner) studied the specimen but was unable to verify whether the white material was bone. Considering the poor fossilization of many Djadohka bones, we cannot dismiss the possibility that it is embryonic bone.

A possible embryonic *Psittacosaurus* has been described by Coombs (1980, 1982). The association of pelvic and hind-limb material with ?anterior dorsals, ?posterior cervicals, and scapula (distal ends overlapped) would be expected in an embryo. This conclusion is based on an unhatched *Orodromeus makelai* embryo that shows the skull tucked down between the bent knees (see Horner & Weishampel, 1988, Fig. 1A). Overlap of the distal ends of the scapulae in the *Psittacosaurus* is probably due to collapse of the rib cage (see Chapter 1, Fig. 1.13, for skeletal reconstruction). That this specimen is an embryo would also explain the disparity in size between baby and adult as noted by Coombs (1982). The apparent absence of eggshell in the specimens could be due to loss by erosion (many of the bones were apparently lying loose when found), by sacrifice during collection or preparation in order to get the bones, by failure of the eggshell to fossilize well (see below), or by loss of the shell through dissolution by groundwater as indicated by "ghosts" of eggs or egg "steinkerns" (e.g., Djadohka Formation, see Chapter 7).

Numerous other baby dinosaurs have been collected in Mongolia by Soviet, Polish, and Mongolian expeditions. An embryonic foot of an unknown dinosaur was found adhering to a small piece of dendroolithid eggshell (Sochava, 1972; Sabath, 1991). A baby *Protoceratops* skeleton has been collected and mounted for display next to an adult (see Rozhdestvensky, 1973, p.

36; see Chapter 1, Fig. 1.13B). Unfortunately, the specimen has never been described. A partial baby *Protoceratops* from Bayn Dzak, a baby *Bagaceratops* from Khermeen Tsav, and a baby *Breviceratops* (= ?*Protoceratops*) from Khulsan have been described by Maryanska and Osmólska (1975). Barsbold and Perle (1983) described a group of baby hadrosaurs and a baby *Protoceratops* from Toogreek. The hadrosaurs were found evenly spaced with a thin white powder around each of them (Currie, personal communication), suggesting that the babies were actually embryos and that the eggshells did not fossilize well. Phillipe Taquet (personal communication) suggests that the embryos are those of *Saurolophus*, a hadrosaur known from the younger Nemegt Formation; further study is needed to verify this identification. One of the few baby theropods known are the ingeniyids associated with an adult skeleton as described by Barsbold and Perle (1983). Other baby dinosaurs discussed in this volume include *Dryosaurus* by Carpenter in Chapter 19, an embryonic *Camptosaurus* by Chure, Turner, and Peterson in Chapter 20, and a nodosaurid ankylosaur by Jacobs et al. in Chapter 22. A nest full of baby dinosaurs would be a tempting source of food for many carnivores. Kirkland explores this possibility with terrestrial crocodiles in Chapter 9.

Growth of baby dinosaurs

The ontogenetic changes that accompany growth were examined briefly by Brown and Schlaikjer (1940), Rozhdestvensky (1965), Maryanska and Osmólska (1975), and Dodson (1976). These studies are based upon Mongolian specimens, especially of protoceratopsians. The ontogenetic growth of a new species of *Hypacrosaurus* is discussed by Horner and Currie in Chapter 21.

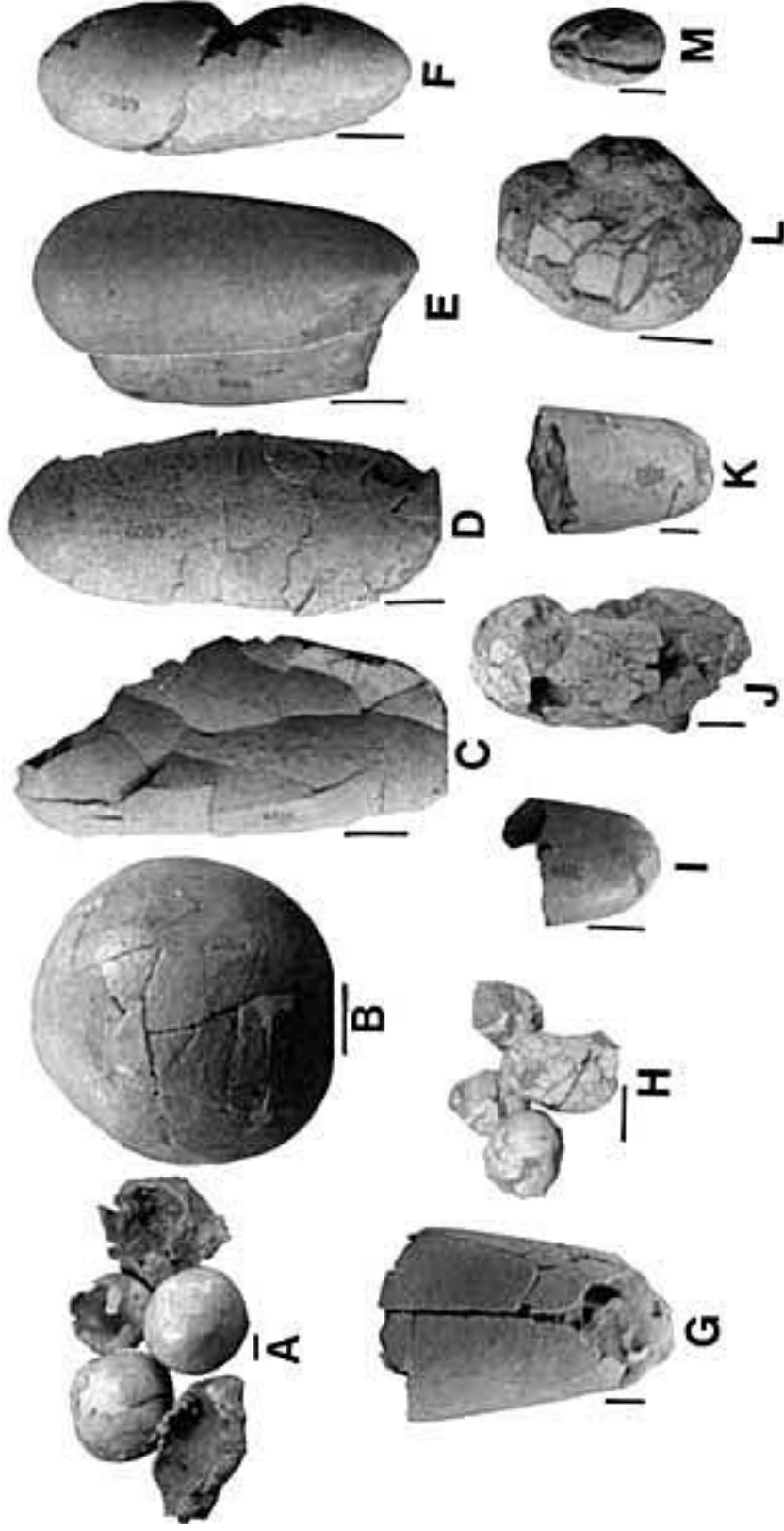
Rate of growth is a new area of research, although it has been the subject of previous speculation (e.g., Case, 1978; Dunham et al., 1989). Ongoing histological research by one of us (Horner) on an entire growth series of the new *Hypacrosaurus* species should permit the first comprehensive growth curve for a dinosaur. Preliminary curves for another hadrosaur, *Maiasaura*, has been presented by Morell (1987) and used by Lockley in Chapter 23 for his population studies of footprints.

The implications of ontogeny for understanding the evolution of the Dinosauria is discussed in Chapter 14 by Weishampel and Horner. Paul, in Chapter 15, concludes that dinosaurs were r-strategists, with rapid rates of growth.

Taphonomy of eggshell and baby bones

The taphonomy of eggshells is still in its infancy, and little of this is devoted exclusively to dinosaur eggshells. One of us (Carpenter, 1982) presented a brief discussion on the effect local pH has on the preservation

Introduction Figure 1. Some of the eggs recovered by the American Museum of Natural History expeditions to Shabarakh Usu (= Bayn Dzak), Mongolia, and Iren Dabasu (= Ernhot), China. A. Five or seven(?) eggs collected from Ernhot; three of the eggs have been partially or completely restored (AMNH field number 707). B. Enlargement of the restored egg in the front center of A (≈ 8.3 cm in diameter, ≈ 26.8 cm in circumference). A, B: *Paraspheroolithus irenensis* (Zhao, 1979a). C. *Elongatoolithus* sp. egg (AMNH 6510); cited in van Straelen, 1925). D. *Elongatoolithus* sp. egg (16.6 cm long, AMNH 6511, cited in van Straelen, 1925). E. Two smooth eggs (most complete is 11.4 cm long, AMNH 6513), F. Smooth egg from clutch of five (11.3 cm long, AMNH 6511, cited in van Straelen, 1925). G. Hatched(?) smooth egg (AMNH 6505). H. Clutch of four '*Gobiopteryx minuta*' eggs (egg in foreground 4.1 cm tall, egg to left 4.3 cm long, egg in rear center 4.2 cm tall, partial egg to right >2.8 cm tall, AMNH 6642). I. Hatched(?) egg (AMNH 6512). J. *?Laevisoolithus sochavi* or large avian egg (AMNH 6507). K. *?Laevisoolithus sochavi* or large avian egg (AMNH 6657). L. Crushed *?Laevisoolithus sochavi* or large avian egg (14.4 cm long, 11.6 cm in circumference, AMNH 6652). M. Steinkern of a small egg (AMNH 6654) (see Sabath, 1991). Scale for A–F, H = 2 cm; G, I–K = 1 cm.



potential of dinosaur eggshell and baby bones. Tokaryk and Storer (1991) concluded from experimental evidence that eggshell can be transported a considerable distance with minimal abrasion.

In extant eggs, dissolution may actually occur in the nest due to microbial decay of nest vegetation and the production of acidic metabolites. Such dissolution may enhance gas exchange due to increased shell porosity, while at the same time making it easier for the hatchling to escape by weakening the shell. This type of dissolution produces very distinctive concentrically stepped erosion craters (Ferguson, 1981). As yet, such features have not been reported for dinosaur eggshells, although they may be predicted for those species having long incubation times.

With an unhatched egg, dissolution can begin shortly after the death of the egg or embryo. Decay of the organic material in the presence of oxygen produces carbon dioxide (CO₂) in large amounts making the calcium carbonate (CaCO₃) of the shell more soluble. If, however, access to air is restricted (e.g., burial of the nest by fluvial sediments), the process of decay is more complicated, and the effects on the eggshell is not always predictable (Krauskopf, 1979). Any CO₂ or hydrogen sulfide (H₂S) produced would lower the pH of the water in the vicinity of the egg, causing an increase in solubility. On the other hand, ammonia is often a by-product of organic decay, and this would raise the local pH, resulting in the deposition of CaCO₃. In some instances, this ammonia may be the cause for the thin carbonate skin reported on eggshells (e.g., Vianey-Liaud et al, Chapter 11), mistakenly identified as the cuticle by Chow (1954).

Even if the egg hatches, shell fragments may still undergo dissolution before burial if the pH of the local environment is low (Carpenter, 1982; Hayward, Hirsch, & Robertson, 1991). After burial, dissolution can occur by hydrolysis involving groundwater (Krauskopf, 1979), or by carbonic acid (H₂CO₃) produced by CO₂ dissolved in rainwater. Carbonic acid is probably most responsible for dissolution of the fossilized eggshell that occurs after

weathering and erosion have returned the eggshell to near the ground surface.

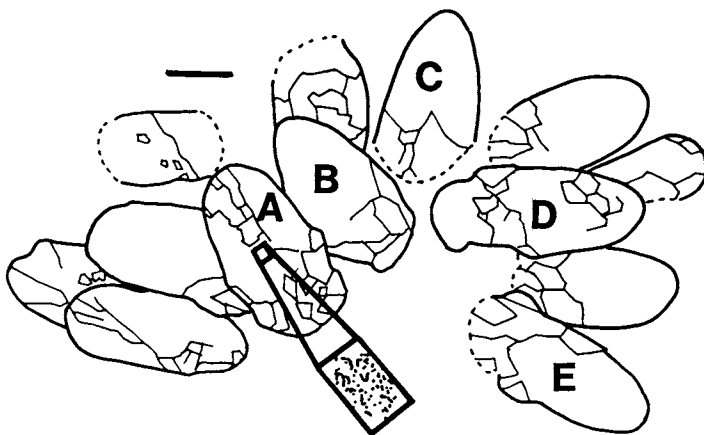
The rate of dissolution is undoubtedly affected by how acidic conditions are, as well as by the thickness of the eggshell. In a similar vein, thin shells are more affected by diagenesis than thicker shells because of their greater surface to volume ratio.

The taphonomy of nesting grounds has only recently been examined. One of the first studies was made by Barsbold and Perle (1983) for sites at Toogreek, Mongolia. A more detailed study was presented by Winkler and Murry (1989) for a hypsilophodontid nesting ground in Texas. Hayward, Amlaner, and Young (1989) conducted a taphonomic study of an extant avian nesting colony buried by a volcanic ash fall, and their results should shed light on dinosaur nesting sites. In Chapter 8, Horner compares the taphonomy of an extant pelican nesting colony with those of two dinosaur nesting sites in Montana.

Egg collection by the Central Asiatic Expeditions

We feel it appropriate to close the Introduction by briefly discussing the historically important collection made by the Central Asiatic Expeditions of the American Museum of Natural History. Despite the importance of these eggs, they have been treated as curiosities, and only brief descriptions have appeared (e.g., van Straelen, 1925, 1928; Brown & Schlaikjer, 1940; Erben et al., 1979). We illustrate for the first time a representative sample of the eggs in Introduction-Figure 1. This sample includes eggs now referred to as *Paraspheroolithus irenensis* and to *Elongatoolithus* by Mikhailov et al. (Chapter 7) and Zhao (Chapter 12). Also shown are smooth protoceratopsian eggs, "*Gobiapteryx minuta*" eggs, possibly some *Laevisoolithus sochavi* eggs, and a single small steinkern of an egg Sabath (1991) has referred to Problematica.

The abundance of egg types from Bayn Dzak has resulted in confusion about which eggs are those of *Protoceratops*. Van Straelen unfortunately did not illustrate



Introduction Figure 2. Nest of eggs (AMNH 6508 described by van Straelen (1925) as *?Protoceratops andrewsi*. Enlargement shows ramotubercular ornamentation in the equatorial portion. Most of the eggs are slightly crushed, thus exaggerating their width. Measurements for eggs: A. 14.9 cm long (partially telescoped), 7.7 cm wide; B. 14.7 cm long (partially telescoped), 6.7 cm wide; C. >14.3 cm long, 7.4 cm wide; D. 16.2 cm long, 6.7 cm wide (least crushed egg); E. 16 cm long, 7 cm wide. Dashed lines indicate portion still buried. Scale = 5 cm.