Dinosaur Egg Parataxonomy [1]

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Dinosaur egg [5] parataxonomy is a classification system that organizes dinosaur eggs by descriptive features such as shape, size, and shell thickness. Though egg [5] parataxonomy originated in the nineteenth century, Zi-Kui Zhao from Beijing, China, developed a modern parataxonomic system in the late twentieth century. Zhao's system, published in 1975, enabled scientists to organize egg [5] specimens according to observable features, and to communicate their findings. The eggshell protects the developing embryo, enables gas exchange between the embryo and the environment external to the egg [5], and the internal components of the egg [5] provide nutrients for the embryo. Those external and internal features that support a developing embryo leave their mark on eggshells. Dinosaur egg [5] parataxonomy classifies those characteristics and provides insight into dinosaur egg [5]-laying behaviors, reproductive physiology, and embryonic development.

James Buckman from Bath, England, was one of the first scientists to formally name and describe dinosaur eggs. He did so in his 1860 paper "On Some Fossil Reptile Eggs." Faced with the task of naming empty eggshells, Buckman applied a strategy similar to a system of biological classification, Carl Linnaeaus's eighteenth century system for organizing and naming species. The Linnaean system orders species into the hierarchical categories of Kingdom, Phylum, Class, Order, Family, Genus, and species. However, because preserved embryonic remains are rare, scientists have little evidence with which to assign the fossilized egg [5] to these categories. Instead, Buckman developed a classification strategy that scientists later developed into parataxonomy, a way to organize and study the eggs without any knowledge of an egg [5] layers' genus and species.

In his publication, Buckman named the eggs that he discovered *Oolithes bathonicae*, meaning stone eggs from Bath. He described the eggs' shapes and sizes. Buckman's method, which classified the eggs based on overall shape and size, could not apply to all recovered fossil egg [5], many of which were only egg [5] fragments. Additionally, researchers couldn't use Buckman's method to distinguish fossilized eggs from egg [5]-shaped rocks.

During the half-century following Buckman's publication, scientists suggested other properties of fossilized eggs for classification. Paul Gervais at the Museum of Natural History in Paris, France, argued in 1877 that researchers could use microscopic features of the shell units to classify the eggs. Additionally, in the 1920s, Victor Émile van Straelen in Brussels, Belgium, drew attention to the different ornamentation patterns that occur on fossil eggshell surfaces. However, fossilized eggs remained rare, and researchers adopted no cohesive or complete method of categorizing and studying the eggs.

In 1975, paleontologist Zi-Kui Zhao at the Institute of Vertebrate Paleontology and Paleoanthropology in Bejing, China, published an article in which he urged scientists to adopt universal parataxonomy as a system to classify dinosaur eggs. Zhao chose parataxonomy because it did not assume knowledge of the egg [5]-laying species prior to examining the structural components of the egg [5]. One historical episode in particular motivated Zhao and others to refrain from assuming knowledge about egg [5]-laying species, the story of *Oviraptor philoceratops* [6]. Scientists assumed that a group of eggs discovered in Mongolia in the 1920s belonged to the species *Protoceratops andrewsi* [7] based on *P. andrewsi*'s existence in the same strata as the eggs. Zhao's colleagues had previously questioned this identification, and soon after, scientists discovered that the eggs belonged to *Oviraptor philoceratops*, overturning a classification that had held for half of a century.

Zhao's parataxonomic system reinforced the practice of identifying egg [5] features, such as size, ornamentation of the shell, and microstructure of shell units. Zhao suggested that each parataxonomic rank depended not just on groupings of similar morphological characteristics of the eggshell, but must also reflect the evolutionary history of the characteristic. He said that a scientist working to categorize a fossilized egg [5] shell must consider how similarities in morphology [8] can signal functional and evolutionary divergence between related species. Zhao published his system in Chinese, and his work was not translated into English for over a decade. Therefore, his egg [5] parataxonomic system was not immediately available to the English-speaking world.

Parataxonomy gained wider acceptance in 1991 when Konstantin Mikhailov at the Paleontological Museum of Russian Academy of Science in Moscow, Russia, published research about Mongolian fossilized eggs. He used Zhao's system to discuss the eggs. Mikhailov illustrated the benefits of adopting Zhao's parataxonomy. Mikhailov's work was translated into English, and over the next few years, more paleontologists began to use about Zhao's system. Mikhailov wrote further about the lack of a universal schema for dinosaur egg [5] classification, including a 1996 paper titled "Parataxonomy of Fossil Egg Remains (*Veterovata*): Principles and Applications."

In this paper, Mikhailov and his colleagues argued that the methods and criteria used to identify and classify fossilized eggs is fragmented and likely resulted from the rare nature of the fossils, as well as from the geographical isolation of separate egg [5] discoveries. They suggested that an increase in fossil egg [5] discoveries required scientists to adopt a universal nomenclature.

Noting that Zhao and others in China had successfully used Zhao's method for decades, the group suggested using Zhao's parataxonomy more widely. Mikhailov and his team stressed that as the number of discovered eggs increased, then the species diversity of the egg [5] types increased as well. Without a way to categorize that diversity, the nuanced differences between the specimens could be lost.

Mikhailov's papers formalized dinosaur egg [5] parataxonomy, establishing it as the system for scientists to study and communicate their results on fossilized eggs. Mikhailov and his colleagues suggested a few additions to Zhao's system so that it included more microscopic characteristics in the eggshell. They also proposed that the system follow the method of the International Code of Zoological Nomenclature, which are internationally standard guidelines for naming organisms. Mikhailov's modified system, which also integrated suggestions from Zhao, required that the name of any new species associated with focalized dinosaur eggs contain the term oolithus, meaning stone egg [5]. Mikhailov and his team also suggested fitting dinosaur egg [5] parataxonomy within a larger category called Veterovata, meaning old eggs. That category enabled scientists to situate dinosaur eggs within larger categories of other fossilized eggs, for example those of ancient birds [9] and crocodiles.

The parataxonomic system divides eggs into the categories of family, genus, and species. Scientists assign fossil eggs to species based the egg [5] size, including length, width, and volume, the range of eggshell thickness, the eggshell's surface pore patterns, and the ornamentation details of the shell. The genus classifies the fossilized egg [5] within a slightly wider range of egg [5] size, type of pore canals, and surface ornamentation grouping. Above the genus level, there are three main categories based on shapes that commonly occur, small round bodies (Spherulitic), prism shaped (Prismatic), and resembling a bird (Ornithoid). These categories classify the eggshell's structure, with particular attention to shell units.

A part of the parataxonomic system requires scientists to collect evidence from extant avian and crocodilian eggs for comparison with dinosaur eggshell. Crocodiles and birds [9] are the closest living relatives to dinosaurs. The comparison enables scientists to hypothesize about dinosaurian structures that they cannot see in fossils, such as reproductive organs, based on evolutionary relationships. For example, birds [9] and crocodiles have a part of the reproductive tract that adds a specific layer to the egg [5] as it moves down the oviduct [10], called assembly-line oviducts. Thus, scientists infer that dinosaurs also had assembly line oviducts. Scientists compared the eggshell of dinosaurs to those of crocodiles and birds [9] and found that they all share common microscopic features including a hard calcite construction. Therefore, scientists theorize that dinosaur reproductive organs were likely similar to birds [9] and crocodiles.

Scientists infer aspects of the dinosaur reproductive tracts by comparing the shape of dinosaur eggs with those of other archosaurs. For example, some birds [9] lay asymmetric eggs, compared to round crocodilian eggs. Certain dinosaur eggs, including those containing embryos of the birdlike dinosaur, *Troodon formosus* [11], are also asymmetric, which suggests that dinosaurs such as *Troodon* had birdlike reproductive tracts.

Features of the eggshell, identified using parataxonomy, also provide clues about dinosaur reproductive behavior, such as how dinosaurs could have constructed their nests and whether or not parents incubated those nests. The density of pores across the eggshell indicates the amount of gas exchanged between the embryo and the outside environment. Many dinosaur eggshells have a high density of pores, which could have facilitated gas exchange in environments where oxygen was not readily available. Living reptiles lay eggs with high pore density and incubate their eggs using either sediment or dense vegetation. Scientists hypothesize that some dinosaurs may have used similar methods to build nests.

Eggs can also indicate the developmental stages [12] dinosaurs have reached upon hatching. Living animals emerge from their eggs in a variety of developmental states. For example, crocodiles can move around and eat on their own, and scientists call them precocial young, whereas some birds [9] hatch unable to leave the nest to feed themselves without the help of their parents, called altricial young. Precocial young require fully developed teeth and bones upon hatching, enabling them to support their own weight and to consume food. Altricial young are less developed, and must remain in the nest after hatching. While scientists examine the correlation between egg [5] size, growth, and the developmental stage of hatching, they debate whether dinosaurs produced either precocial or altricial young.

In to the first decades of the twenty-first century, the majority of paleontologists who studied fossil eggs used the formalized parataxonomic scheme. However, not all scientists used this method, and some argue that it has faults. By establishing methods for classifying, explaining and communicating results/discoveries about dinosaur eggs, paleontologists such as Zhao and Mikhailov enabled scientists to study eggs in detail, and to discuss features such as pore systems and eggshell ornamentation.

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