HISTORICAL AND NEW PERSPECTIVES ON THE PARATAXONOMY OF FOSSIL EGGS

par

Monique VIANEY-LIAUD* and Darla ZELENITSKY**

ABSTRACT

A critical review on the literature about the parataxonomy of amniote eggshells reassert the great interest of this systematics tool for the progress of dinosaur eggshell paleontology. However, shedding light on its limits, we propose to give up the use of the basic types – morphotypes key system.

RESUME

Une revue critique des travaux utilisant la parataxonomie des œufs d'amniotes réaffirme le grand intérêt de cet outil systématique pour progresser dans l'étude paléontologique des coquilles d'œufs de dinosaures. Cependant, en mettant l'accent sur les limites de l'outil, nous proposons d'abandonner le système de clé taxonomique des " basic-types " et morphoptypes.

* Institut des Sciences de l'Evolution, Université Montpellier II, Place Eugène Bataillon, 34095 Montpellier cedex 05, France.

** Departement of Geology & Geophysics, University of Calgary, 2500 University Drive NW, Calgary, Alberta T2N4, Canada.

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During several decades, the absence of an universal system of nomenclature for amniote eggs and eggshells has obstructed the progress of their use in paleontology, and limited their interest in phylogeny, paleobiogeography and stratigraphy. Since 1860, some biologists, like Landois (1865), Blasius (1867) or von Nathusius (1869, 1870, 1883) characterized the microstructure of eggs of modern amniotes, turtles and birds , and paleontologists (for ex. Gervais, 1877 ; Van Straelen & Denayer, 1923; Van Straelen, 1925;) described eggs and try to identify them on the basis of a few morphological characters, and a few available data. Among these authors, only a few apply a formal nomenclature, giving a binominal name. It was the case for Buckman (1860), naming *Oolithes bathonicae*. Then, Young (1954, 1965) give the same generic name to dinosaur eggs from Asia, and define different oospecies (*elongatus* and *rugustus*), on the bases of size and shape. Dughi & Sirugue (1957, 1958, 1962, 1966) defined an oofamily Ornithoolithidae for early tertiary birds, refered to an oogenus *Ornithoolithus*, and to various oospecies (i.e. *arcuatus*) . These authors try to find features in the shapes and microstructures of fossil eggs in order to establish phylogenetic relationships within reptiles or birds.

Since the last seventies, these two ways (naming eggs, explorating their structures) were explored independently. On the one way, Sochava (1969, 1971), then Erben (1970), Erben & Newesely (1972), Erben *et al.* (1979), established a first terminology for eggs microstructures. Sochava emphasized the structure of the pore system to define first three morphotypes, then two types of dinosaur eggshells: ornithoid, for avian like, and testudoide, for turtle like. Erben proposed six groupings among extant and fossil amniote eggshells. On the other way, Zhao (1975, 1979, 1994) expand the parataxonomy of the dinosaurs eggshells, creating oofamilies, oogenera for oospecies previously defined by Young and for new oospecies.

Using the work of Erben, Sochava and Zhao as a foundation, Mikhaïlov (1991, 1994, 1997 a & b; Mikhaïlov *et al.* 1994) and Hirsch (1989, 1994 a & b, 1996; Hirsch & Quinn 1990), converge the two ways and formalized a parataxonomic nomenclature and classification. At the same time, they established hierarchical groupings based on shell structures: the basic types and morphotypes. They use mainly micro and ultra structural characters for these groupings. The morphological features, like outer ornamentation, or shape of eggs, the size and thickness appears in the definition of the taxa. Mikhaïlov, by his wide and detailed works on eggs biomineralizations underline their potential use, first to evaluate relationships within the Archosauria, second to trace phylogenetic lineages peculiarly among birds (Mikhaïlov, 2000).

Mikhaïlov and Hirsh have provided three tools to the researchers community: an uniform terminology, a nomenclature and a key to combine the observed characters and classify their taxa. Later, they summarized their system with Emily Bray (Mikhaïlov *et al.*, 1996). On that bases, since 1990, the number of papers on eggshells, and pecularly on dinosaurs eggshells, increased strongly (see div. papers in Carpenter & Horner eds., 1994; id. Bravo & Reyes eds., 2000; Bray, 1998; Khoring, 1999; Khosla & Sahni, 1995; Packard & Hirsch, 1989; Penner, 1985; Sabath, 1991; Sanz-Garcia *et al.*, 1995; Vianey-Liaud, 1999; Vianey-Liaud *et al.*, 1997; Williams *et al.*, 1984, Zelenitsky & Hirsch, 1997 etc...). The authors fit their observations into the Mikhaïlov *et al.* system. Using that, by description of new taxa, defined by clear characters, their comparisons through

an uniform terminology, it became possible to suggest phylogenetic relationships and paleobiogeographical implications. With these fossil discrete entities, we can have an idea of the eggs diversity and, by the way, an approach of dinosaur diversity. Therefore, it has been possible to use the oospecies for biostratigraphical purposes (Vianey-Liaud & Lopez-Martinez, 1997; Vianey-Liaud, 1999; Garcia & Vianey-Liaud, 2001...).

But, as well for ammonites, trilobites, fishes or mammals, like it happened in many scopes of paleontology, during their first steps of development, the same problems appears. Some are linked with the working methods of researchers. Splitters exists too for dinosaur eggshells, and variability is sometimes not enough taken into account, nor the rules of correct systematics, like accurate figurations, precise descriptions and measurements, extensive comparisons, etc.... Others are due to the bad preservation of the eggshells, fragmentary or weathered or recrystallized (Dauphin, 1990; Garcia & Vianey-Liaud, 2001; Vianey-Liaud *et al.*, 2003). When better material is discovered, changes in characters and nomenclature can occur. Moreover, the discoveries of embryos inside eggs, the possibility to make a bridge between eggs parataxonomy and dinosaurs taxonomy become a reality (Sochava, 1972; Horner & Makela, 1979; Norell *et al.*, 1994; Mateus *et al.*, 1997; Chiappe *et al.*, 1998; Mackovicky & Grellet-Tinner, 2000) .

And even if the general classification frame of Mikhaïlov *et al.* remains, some discrepancies appear. Their key classification forces ootaxa in a rigidly defined and ranked groupings. The alteration of group definition can be a matter of subjectivity of authors. We can list a few examples of the non-accuracy of a rigid classification into morphotypes.

1 - The discretispherulitic morphotype and its tubocanaliculate pore system has been defined with the genus *Megaloolithus* from Aix Basin, in France, probably on the basis of both oospecies *M. mamillare* and *M. siruguei* as seen in plate 23, figure 1a and 5 (Mikhaïlov, 1991). On more complete fragments we have noted that, if some pore canals are straight and regular, in *M. siruguei* there is a net of oblique or horizontal canals linking the straight transverse ones (Garcia & Vianey-Liaud, 2001). And our Spanish colleagues have proposed to define another pore canal type, the reticulate pore system (Elez & Lopez-Martinez, 2000). With a better knowledge of the variability of microstructural features, and with discovery of new eggshells, it will appear that the morphotypes and pore systems initially established cannot be applied to all the cases. It will be better to use the morphotype characteristics simply as one of the microstructural features of a taxon.

2 - The prismatic morphotype has been defined on the type oospecies and oogenus: *Prismatoolithus levis*, that appeared to be the egg of *Troodon formosus*, after the discovery of embryos. This morphotype was distinguished from that of birds eggshells by the presence of tabular structure instead of prismatic, in the outer layer, like in the mamillary zone. Better preserved eggs and eggshells have been redescribed (Zelenitsky *et al.*, 2002) and squamatic structure appears in the outer layer, like in birds. That would lead to a re-evaluation of the prismatic type, a new definition of the oofamily Prismatoolithidae, and to new phylogenetic implications.

3 - Moreover, the Ratite morphotype is characterized by Mikhaïlov first by an homogeneous outer zone, and then by well defined wedges in the mamillae. It appears

that the later feature is absent in *Apteryx* and *Tinamou*, and present in some Neognathous. It would be confusing to use a ratite morphotype that do not include all the taxa of the Ratites, and comprise some Neognathes (Zelenitsky & Modesto, 2003).

New perspectives have been introduced by the discoveries in eggs with embryos. Morphotypes seems now of limited phylogenetic value. It seems necessary to abandon their use as a classification in the parataxonomy of eggshells. They can be used, partially, as characters in the definition of oospecies and other taxa. It does not mean that parataxonomy becomes unuseful. Since each egg type will be found with embryos, we would have to define and to use ootaxa. Thus, morphological, micro and ultrastructural features, on the bases of the previous terminology would be precisely established, in order to clearly define the characters of the taxa. Like in the other scopes of paleontology, the definition of taxa will evolve with the progress of discoveries and methods. Then, for each oospecies, the description and analysis of the different characters, like for any fossil, would be at the bases of phylogenetic considerations, either the character analysis is made by cladistics or not. In any case, the difficulties lies here, and elsewhere, on the determination of characters polarities.

To conclude, we will underline the heuristic value of the basal work of Mikhaïlov, Hirsh & Zhao. They opened an avenue, where most of us introduce since the eighties, using their language to communicate, to bring light on the diversity of eggshell, to have a first sight on their relationships, to use them in stratigraphy. Now, the increase of eyes looking over the eggs, even if the eggshells scientific community is reduced, the increase of field works and discoveries, pecularly of embryos, shed light on the limits of the basic types – morphotypes key system, going with the parataxonomy. A new step has to be crossed, with the abandon of the former, that open new perspectives for the parataxonomy of the eggshells.

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