

HISTORICAL AND NEW PERSPECTIVES ON THE PARATAXONOMY OF FOSSIL EGGS

par

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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 morphotypes.

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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, referred 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, exploring 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 peculiarly 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, peculiarly 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.

LITERATURE

- BRAVO, A.M. & REYES, T., Eds. 2000. — "First International Symposium on Dinosaur Eggs and Babies", Isona, Spain, Extended Abstracts.
- BRAY, E., 1998. — Dinosaur eggshell *Boletuoolithus carlylensis*, oogenus nov. from the Lower Cretaceous Cedar Mountain Formation of Utah. In "Lcas, S.G., Kirkland, J.L. & Estep, J.W., eds, Lower and Middle Cretaceous terrestrial ecosystems. *New Mexico Museum of Natural History and Science*, Mexico, Bull. 14: 221-224.
- BUCKMAN, J., 1860. — Fossil reptilian eggs from the Great Oolithe of Cirencester. *Quarterly Journal of the Geological Society of London*, 16: 107-110.
- CHIAPPE L.M., CORIA R.A., DINGUS L., JACKSON F., CHINSAM Y.A. & FOX M., 1998. — Sauropod dinosaur embryos from the Late Cretaceous of Patagonia. *Nature*, 396: 258-261.
- DAUPHIN, Y., 1990. — Incidence de l'état diagénétique des coquilles d'oeufs de dinosaures sur la reconnaissance des morphotypes - exemple du Bassin d'Aix en Provence. *Comptes Rendus de l'Académie des Sciences*, Paris, 310, II: 849-854.
- DUGHI, R. & SIRUGUE, F., 1957. — Les œufs de dinosauriens du bassin d'Aix-en-Provence. *Comptes Rendus de l'Académie des Sciences*, Paris, 247 : 907-909.

- DUGHI, R., & SIRUGUE F., 1958. — Sur les oeufs de dinosaures du bassin fluvio-lacustre de Basse-Provence. *83ème Congrès des Sociétés Savantes, section des Sciences*: 183-205.
- DUGHI, R. & SIRUGUE, F., 1962. — Distribution verticale des œufs d'oiseaux fossiles de l'Eocène de Basse Provence. *Bulletin de la Société Géologique de France*, 7 : 69-78.
- DUGHI, R. & SIRUGUE, F., 1976. — L'extinction des dinosaures à la lumière des gisements d'œufs du Crétacé terminal du Sud de la France. *Paléobiologie Continentale*, Montpellier. 7 : 1-34.
- ELEZ, J. & LOPEZ-MARTINEZ, N., 2000. — Interrelationships between growth of mineral phase and pore system in dinosaur eggshells. In "First International Symposium on Dinosaur Eggs and Babies", Isona, Spain, Extended Abstracts.: 43-50
- ERBEN, H.K., 1970. — Ultrastrukturen und Mineralisation rezenter und fossiler Eischalen bei Voegeln und Reptilien. *Biomínéralisation*, 1: 1-66.
- ERBEN, H.K. & NEWSELY, H., 1972. — Kristalline Bausteine und Mineralbestand von kalkigen Eiershalen, *Biomínéralisation*, 6 : 32-48.
- ERBEN, H.K., J. HOEFS & WEDEPOHL, K.H., 1979. — Paleobiological and isotopic studies of eggshells from a declining dinosaur species. *Paleobiology*, 5: 380-414.
- GARCIA, G., 2000. — Diversité des coquilles "minces" d'œufs fossiles du Crétacé supérieur du Sud de la France. *Géobios*, 33 (1) : 113-126.
- GARCIA, G. & VIANEY-LIAUD, M., 2001. — Nouvelles données sur les coquilles d'œufs de dinosaures Megaloolithidae du Sud de la France : systématique et variabilité intraspécifique. *Comptes Rendus de l'Académie des Sciences, Paris, Sciences de la Terre et des Planètes*, 332 : 185-191.
- GARCIA, G., FEIST, M., CABOT, A., VALENTIN, X. & VIANEY-LIAUD, M. 2000. — Les œufs de dinosaures du Crétacé supérieur du bassin de Villeveyrac – Mèze (Hérault, France) : description d'une nouvelle espèce de *Prismatoolithus*, *Bulletin de la Société Géologique de France*, 171 (3) : 282-289.
- GERVAIS, P., 1877. — De la structure de coquilles calcaires d'œufs et des caractères que l'on peut en tirer. *Comptes Rendus de l'Académie des Sciences, Paris*. 84 : 159-165.
- GRELLET-TINNER, G., 2000. — Phylogenetic interpretation of eggs and eggshells of Paleognathae. In "First International Symposium on Dinosaur Eggs and Babies", Isona, Spain, Extended Abstracts: 61-76
- HIRSCH, K., 1989. — Interpretations of Cretaceous and pre-Cretaceous eggs and shells fragments : 89-97, In Gillette, D.D. & Lockey, M.G. (eds.) *Dinosaur Tracks and Traces*, Cambridge University Press, New York.
- HIRSCH, K., 1994. — The fossil record of vertebrate eggs : 269-294, In Donovan, S.K. (ed.) : *The Paleobiology of Trace Fossils*, John Wiley & Sons, London.
- HIRSCH, K., 1994. — Upper Jurassic eggshells from the Western Interior of North America. in "Dinosaur Eggs and Babies", Carpenter K., Hirsch K. & Horner J.R. editors, Cambridge University Press: 138-150.
- HIRSCH, K., 1996. — Parataxonomic classification of fossil Chelonian and Gecko eggs. *Journal of Vertebrate Paleontology*, 16(4) : 752-762.
- HIRSCH, K. & QUINN, B., 1990. — Eggs and eggshell fragments from the upper Cretaceous Two Medicine formation of Montana. *Journal of Vertebrate Paleontology* 10: 491-511.
- HORNER, J.R. & MAKELA, R., 1979. — Nests of juveniles provides evidence of family structure among dinosaurs. *Nature*, 282 : 296-298.
- KHOSLA, A. & SAHNI, A., 1995. — Parataxonomic classification of Late Cretaceous dinosaur eggshells from India, 40 : 87-102.
- KOHRING, R., 1999. — Strukturen, biostratonomie, systematische und phylogenetische Relevanz von Eischalen amnioter Wirbeltier. *Cour. Forschungsinst. Senckenb.* 210: 1-307.

- MAKOVICKY, P.J. & GRELLET-TINNER, G., 2000. — association between theropode eggshell and a specimen of *Deinonychus antirrhopus*. In "First International Symposium on Dinosaur Eggs and Babies", Isona, Spain, Extended Abstracts: 123-128.
- MIKHAÏLOV, K.E., 1991. — Classification of fossil eggshells of amniotic vertebrates. *Acta Paleontologica Polonica*, 36: 193-238.
- MIKHAÏLOV, K.E., 1994. — Theropod and Protoceratopsian Dinosaur Eggs from the Cretaceous of Mongolia and Kazakhstan. *Paleontological journal*, 28(2): 101-120.
- MIKHAÏLOV, K.E., 1997. — Avian eggshells: an atlas of scanning electron microphotographs: *Br. Ornithol. Club Occas. Pbl.*, 3: 1-88.
- MIKHAÏLOV, K.E., 1997. — Fossil and recent eggshell in amniotic vertebrates: fine structure, comparative morphology and classification. *Special Papers in Paleontology*, 56: 1-80.
- MIKHAÏLOV, K.E., SABATH K. & KURZANOV S., 1994. — Eggs and nests from the cretaceous of Mongolia, in Dinosaur Eggs and Babies, Carpenter K., Hirsch K. & Horner J.R. editors, *Cambridge University Press*: 138-150
- MIKHAÏLOV, K.E., BRAY, E. & HIRSCH, K., 1996. — Parataxonomy of fossil egg remains (Veterovata) : principles and applications. *Journal of Vertebrate Paleontology*, 16 (4) : 763-769.
- MIKHAÏLOV, K.E., 2000. — Eggshell structure, their identification and evolutionary implications: introductory statements. In "First International Symposium on Dinosaur Eggs and Babies", Isona, Spain, Extended Abstracts: 135-138.
- NORELL, M.A., CLARK, J.M., DASHEVEG, D., RHINCHEN, B., CHIAPPE, L .M., DAVIDSON, A.R., MCKENNA, M.C., ALTAZNGEREL, P. & NOVACEK, M.J., 1994. — A theropod dinosaur embryo and the affinities of the Flaming Cliffs dinosaur eggs. *Science*, 266 :779-782.
- PENNER, M.M., 1985. — The problem of dinosaur extinction. contribution of the study of terminal Cretaceous eggshells from southeast france. *Geobios*, 18: 665-669.
- SABATH, K., 1991. — Upper Cretaceous amniotic eggs from the Gobi desert. *Paleontologia Polonica*, 36 (2): 151-192.
- SANZ-GARCIA, J.L., MORATALLA, J.J., DIAZ MOLINA, M., LOPEZ-MARTINEZ, N., KÄLIN, O & VIANEY-LIAUD, M., 1995. — Dinosaur nest at the sea shore. *Nature*, 376:731-732.
- SOCHAVA, A., 1969. — Dinosaur eggs from the Upper Cretaceous of the Gobi desert. *Paleontological Journal*, 3: 517-527.
- SOCHAVA, A., 1971. — Two types of eggshells in Senonian dinosaurs. *Paleontological Journal*, 5: 353-361.
- SOCHAVA, A., 1972. — The skeleton of an embryo in a dinosaur egg. *Paleontological Journal*, 4: 527-531.
- VAN STRAELEN, V., 1925. — The microstructures of the dinosaur eggshells from the Cretaceous beds of Mongolia. *American Museum Novitates*, 173: 1-4.
- VAN STRAELEN, V. & DENAEYER, M.E., 1923. — Sur les oeufs fossiles du Crétacé supérieur de Rognac en Provence. *Bull. Cl. Sci. Académie Royale de Belgique*, 9 (5) : 14-26.
- VIANEY-LIAUD, M., 1994. — Les œufs de dinosaures du bassin d'Aix : 46-52 In Cheylan, G. (ed.) : Dinosaures en Provence, *Les cahiers de Sainte Victoire-I, Edisud, Aix-en-Provence*.
- VIANEY-LIAUD, M., 1999. — Coquilles d'œufs de dinosaures du Crétacé supérieur du Sud de la France : Parataxonomie, Diversité et Biostratigraphie ; Actes de la Conférence : Dinosaurs in the Mediterranean, Tunis, Novembre 1997. *Almadar, cité des Sciences, Tunis*, 11 : 171 - 184.
- VIANEY-LIAUD, M. & CROCHET, J.-Y., 1994. — Dinosaur eggshells from the late Cretaceous of Languedoc (Southern France). *Revue de Paléobiologie*, Genève, 7:237-249.
- VIANEY-LIAUD, M., MALLAN, P., BUSCAIL, O. & MONGELARD, C., 1994. — Review of French

- dinosaur eggshells: morphology, structure, mineral, and organic composition: 151-183, in "Dinosaur Eggs and Babies", Carpenter K., Hirsch K. & Horner J.R. editors, *Cambridge University Press*, New York.
- VIANEY-LIAUD M., HIRSCH K., SAHNI A. & SIGÉ B., 1997. — Late Cretaceous Peruvian eggshells and their relationships with Laurasian and Eastern Gondwanian material. *Geobios*, 30 (1): 75-90
- VIANEY-LIAUD, M. & LOPEZ-MARTINEZ, N., 1997. — Late Cretaceous dinosaur eggshells from the Tremp basin (Southern Pyrenees, Lleida, Spain). *Journal of Paleontology*, 71: 1157-1171.
- VIANEY-LIAUD, M & GARCIA, G., 2000. — The interest of French Late Cretaceous dinosaur eggs and eggshells. In "First International Symposium on Dinosaur Eggs and Babies", Isona, Spain, Extended Abstracts: 165-176.
- VIANEY-LIAUD, M., KHOSLA, A. & GARCIA, G., 2003. — Comparisons of European and Indian dinosaurs eggshells ; paleobiogeographical implications. *Journal of vertebrate Paleontology*, 23(3) : 575-585.
- WILLIAMS, D.L.G., SEYMOUR, R.S. & KÉROURIO, P., 1984. — Structure of fossil dinosaur eggshell from the Aix basin, France. *Paleogeography, Paleoclimatology, Paleoecology*, 45: 23-37.
- YOUNG, C.C., 1954. — Fossil reptilian egg from Layiang, Shantung, China, *Scientia Sinica*, 3 :505-522.
- YOUNG, C.C., 1965. — Fossil eggs from Nanshiung, Kwantung and Kanchou, Kiangsi, *Vertebrata Palasiatica*, 9 :141-170.
- ZELENIISKY, D.K., MODESTO, S.P. & CURRIE, P.J., 2002. — Bird-like characteristics of troodontid theropod. *Cretaceous research*, 23: 297-305.
- ZELENIISKY, D.K., MODESTO, S.P., 2003. — New information on the eggshell of ratites (Aves) and its phylogenetic implications. *Canadian Journal of Zoology*, 81: 962-970.
- ZHAO, Z., 1975. — The microstructure of the dinosaur eggshells of Nanshiung, Kwantung. *Vertebrata Palasiatica*, 13: 105-117.
- ZHAO, Z., 1979. — The advancement of researches on the dinosaurian eggs in China. In: South China Mesozoic and Cenozoic "Red Formation". *Beijing: Science Publishing Co.*: 329-340.
- ZHAO, Z., 1994. — Dinosaur eggs in China : On the structure and evolution of eggshells : 184-203 in "Dinosaur Eggs and Babies", Carpenter K., Hirsch K. & Horner J.R. editors, *Cambridge University Press*, New York.