LONG-TERM FIDELITY OF MEGALOOLITHID EGG-LAYERS TO A LARGE BREEDING-GROUND IN THE UPPER CRETACEOUS OF AIX-EN-PROVENCE (SOUTHERN FRANCE)

by

Géraldine GARCIA*, Yves DUTOUR, Isabelle COJAN*** , Xavier VALENTIN* & Gilles CHEYLAN****

SUMMARY

*Laboratoire de Géobiologie, Biochronologie et Paléontologie Humaine, UMR 6046, Université de Poitiers, 40 Avenue du Recteur Pineau, 86022 Poitiers cedex, France

**Muséum d'Histoire Naturelle, 6 rue Espariat, 13100 Aix-en-Provence, France

***Ecole des Mines de Paris, CGES-Sédimentologie, 35 rue St Honoré, 77305 Fontainebleau cedex, France

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ABSTRACT

We present here the preliminary results from a new nesting site "Sextius-Mirabeau", discovered close to the historical centre of Aix-en-Provence in Upper Cretaceous deposits. This extensive megaloolithid nesting ground, the first large scale excavation (3225 m^2) in France, yielded more than 530 eggs, some organized in clusters. Their study reveals the reproductive strategy of the megaloolithid egglayer group which indicates nesting fidelity and gregarious behaviour.

RESUME

Nous présentons ici les résultats préliminaires d'un nouveau site de ponte "Sextius-Mirabeau", découvert près du centre historique d'Aix-en-Provence dans des dépôts du Crétacé supérieur. Ce terrain de nidification étendu, la première fouille à grande échelle (3225 m^2) en France, a livré plus de 530 oeufs, certains disposés en groupes. Leur étude révèle la stratégie reproductive du groupe des mégaoolithidés qui indique une fidélité quant aux aires de nidification et un comportement grégaire.

INTRODUCTION

Dinosaur eggs have been mentioned in Provence (southern France) since the pioneer works of Philippe Matheron (1869), who attributed two "enigmatic spheres" either to a giant bird or to one of the large reptiles he had discovered in that region. Since, numerous discoveries of complete eggs and isolated clutches have been made in the foothills of the Sainte-Victoire mountain and everywhere in the outcrops of the Aix Basin (Derognat, 1935; Lapparent de, 1947; 1957; Dughi & Sirugue, 1957, 1958; Erben *et al.*, 1979; Ginsburg, 1980; Kerourio, 1981; Penner, 1983; Williams *et al.*, 1984; Vianey-Liaud *et al.*, 1994; Garcia, 1998, 2000). Recent studies provide new data in different areas of research (see for example Vianey-Liaud *et al.*, 1997; Garcia & Vianey-Liaud, 2001a; Vianey-Liaud *et al.*, 2003; Garcia & Barbin, in press). Most of the investigations, however have focused on eggs and eggshells and their macro- and microstructural features, rather than analysis of clutches in their nesting ground. For this reason, the nest structures (especially for French megaloolithid eggs) are still largely unknown and only some information on the reproductive biology of these extinct reptiles can be obtained (Dughi & Sirugue, 1976; Kerourio, 1981; Williams *et al.*, 1984; Garcia, 1998; Lorenz, 2000; Cousin, 2002).

During the construction works at Sextius-Mirabeau, in the city centre of Aix-en-Provence (Bouches du Rhône), we discovered an extensive dinosaur nesting ground in Late Campanian sediments, located several meters below archeological layers (roman history). For six months, our team conducted a salvage excavation, supported by the SEMEVA society. We present here a summary of the first large scale study of a megaloolithid nesting ground in Europe.

Structural context

Continental sedimentation in the Aix-en-Provence Basin began in the Santonian and lasted for more than 30 My (Durand & Guieu, 1980; Durand 1989). These upper Cretaceous to lower Tertiary deposits were unconformably overlain by Miocene marine facies. The present configuration of the Aix-en-Provence Basin corresponds to a subsurface pattern of a syncline, with blind thrust faults on the northern edge and generally small displacements. This structure is interpreted as the consequence of later compressional events (Durand, 1989). The NE/SW oriented Aix and Meyreuil faults correspond to a zone of strike-slip displacements which affect the basin as a whole (fig. 1a). During the Late Cretaceous, displacement was dominantly sinistral. Along the Meyreuil fault, the dextral oblique orientations are attributed to the Miocene displacement (Gaviglio, 1985).

Stratigraphy

The continental stratigraphy of the Aix-en-Provence basin has been classically divided into five lithostratigraphic units. These were tied to marine stages over the last 20 years: Valdonian (Santonian), Fuvelian and Begudian (Campanian), Rognacian (Upper Campanian-Maastrichtian) and Vitrollian (Danian) (Babinot & Durand, 1980a; 1980b; Westphal & Durand, 1990; Cojan *et al.*, 2000; Garcia & Vianey-Liaud, 2001b). In situ dinosaur eggshells are laterally continuous in these formations, up to some 20 m below the Poudingue de la Galante Member (Garcia & Vianey-Liaud, 2001b).

Paleogeography

During the upper Cretaceous-lower Tertiary, the Aix-en-Provence Basin was located at 35° N latitude (Dercourt *et al.*, 2000; Camoin *et al.*, 1993).

This continental sequence is composed of shallow lacustrine carbonates interbedded with alluvial and fluvial deposits. The paleogeography corresponded to a fluvial network flowing into a permanent lake (Cojan, 1993). Numerous carbonate-rich paleosols developed over the silty alluvium of the floodplain or the palustrine facies that bordered the lakes (Cojan, 1999). Presence of carbonate-rich paleosols and the palynological record attests to a tropical to semi-tropical climate, with marked seasons (Medus, 1972). Proximal alluvial fans that were transverse to the main valley axis prograded occasionally into the floodplain due to favourable climatic or tectonic conditions. These were fed by the surrounding highlands (paleo-Ste victoire, -Ste Baume and -Nerthe). Lacustrine facies assemblages represent shallow lakes with evidence of subaerial exposure.

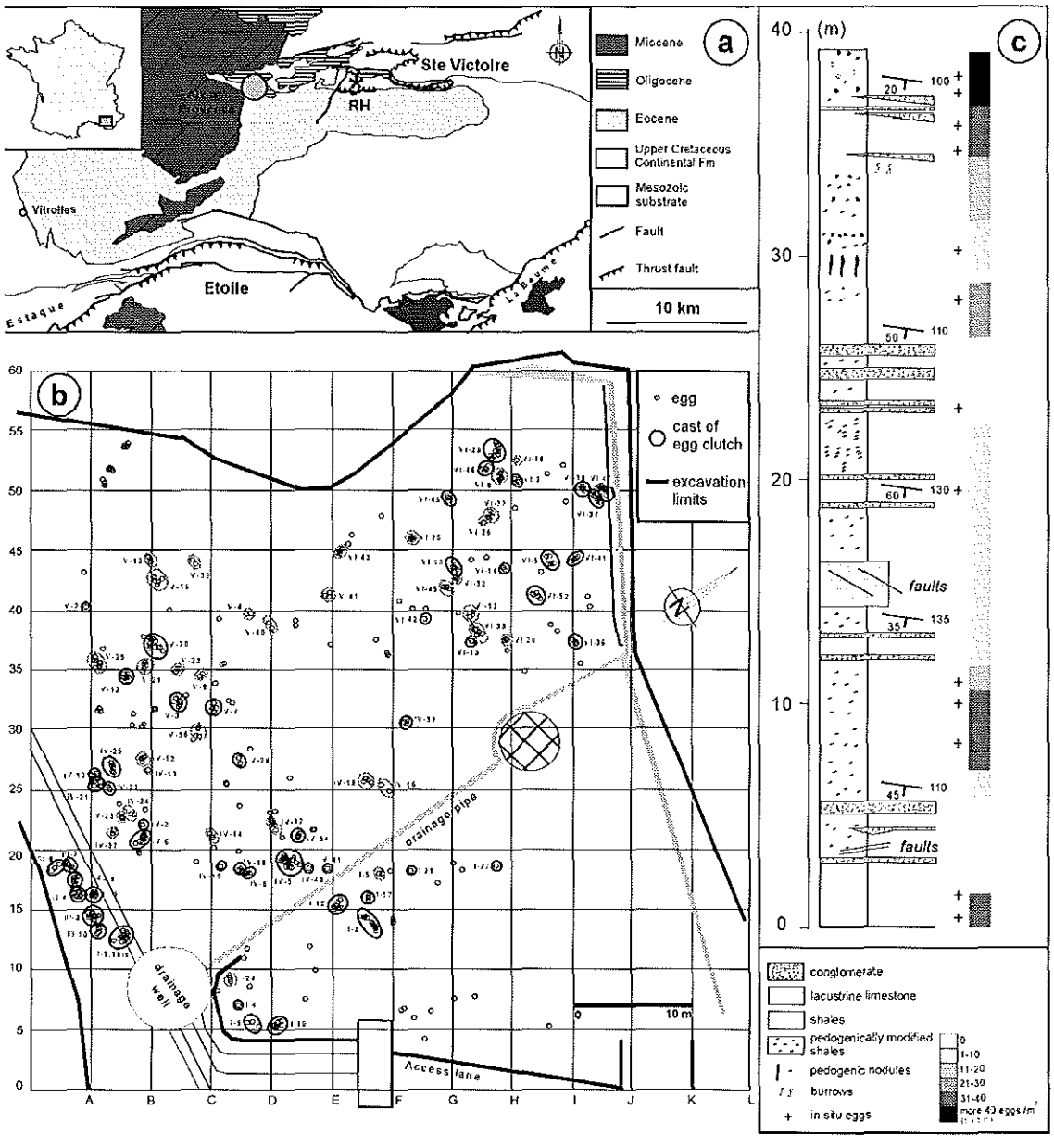

Figure 1.— a: Geological map of the Aix-en-Provence Basin (Southern France). b: Sextius-Mirabeau map showing egg clutches in plan view (realized with AutoCad software). c: Sedimentological section at Sextius-Mirabeau which reveals the presence of several stratigraphic layers. The distribution of megaloolithid eggs (using the association of French oospecies, Garcia & Vianey-Liaud, 2001b) give an Upper Campanian age.

MATERIAL AND METHODS

For the first time in France, we had the opportunity to excavate a large area, prior to construction of a parking structure. The excavation is close to the historical centre of Aix-en-Provence, in a new quarter: the Sextius-Mirabeau site (5 ha). From February to August 2000, we excavated, supported by the developer (the SEMEVA company), a 60 x 55 m surface (3225 m^2) to a 3 m depth (= 9600 m^3). Under the supervision of our team, two mechanical shovels were used to carefully skimmed the ground surface, removing 5 cm thick layers. Each time an egg was found, we investigated the immediate surroundings to detect the possible presence of other eggs. All the clutches were collected with plaster jackets. Some jackets, weighing over a ton, were extracted with the assistance of mechanical shovels. Excavation, parallel to the strata, was not possible due to the strong dip of the formation (20 to 60°), thus increasing the difficulty of interpreting the egg distribution in each layer.

A three-dimensional survey of notable sedimentary layers and all eggs was conducted during the course of the excavation, using a 5 x 5 m grid. In addition, one section measured along one of the edge of the central excavation pit, was described at a 5 cm interval (fig. 1b).

In the field, the macroscopic facies were described. Colour (with reference to the Munsell chart), granulometry and texture were noted. Sampling for different types of analysis (microscopic facies description, mineralogy, geochemical analysis) was made at the same time. Samples were primarily collected at regularly spaced intervals from overbank alluvium. Measure of dip and strike of beds was conducted through the measured section.

Except for one clutch, the eggs are missing their upper portions, which may be due to either hatching or erosion, or both. The number of eggs within some original clutches is questionable because several eggs may have been removed by erosion or tectonic processes. In the field, 530 eggs were mapped in situ. The preservation of the clutches is generally good but many eggs appear incomplete, flattened or crushed by compression of the sediments (for example see pl. 1, fig. f). Forty three well preserved clutches were extracted and prepared in the Aix-en-Provence Museum where the collection is now housed. Sediment around every clutch was screen-washed with hydrogen peroxide in order to collect possible thin eggshell types or small bone remains. Eggshells (more 200 fragments) often strongly recrystallized, were examined in thin sections using polarizing light microscopy (PLM) and scanning electron microscopy (SEM). Their thicknesses were measured using a micrometer. All the studied material are housed and catalogued in the collection of the Natural history Museum of Aix-en-Provence (Bouches du Rhône, France).

Structural context and depositional environment

The excavated area is characterized by sedimentary horizons that present a fairly persistent strike, approximately N 120 10°, whereas the dip, varies from 20° to 60° to the South. The sedimentary layers dip from 45° at the base, up to 60° in the middle of the section then back to 20° in the upper part. Most of the faults present in the excavation show offsets that do not exceed a meter. Despite these tectonic structures, distinctive sedimentary horizons are correlative over most of the excavated area. The structural results indicate that the series now located in the center of Aix-en-Provence have been strongly affected by the late strike slip displacements along the Aix and Meyreuil faults.

The continental deposits are dominated by red shaly alluvium that are interbedded by some conglomeratic layers and lacustrine carbonates (fig. 1c):

- *Conglomeratic units.* These are composed of heterometric, angular carbonate clasts. Average size is 5 cm, largest clasts may attain 14 cm in diameter. The clasts derived from marine limestone are attributed to Jurassic or lower Cretaceous. The conglomerates are clast supported, with a reddish matrix. One stratigraphic level is characterized by clasts floating in a white carbonate matrix. Most of the conglomeratic units correspond to isolated, non erosive sheet deposits; channelized units are rare. No sole marks were observed due to the tectonic deformation and poor lithification of these units.

- *Shaly facies.* These represent to the dominant facies observed in the excavation. The rocks are reddish in color and they exhibit evidence of pedogenesis: mottling varying from purple (2.5YR 3/6 to 4/6) to yellow and orange colours (2.5YR 4/8 to 5/8) presence of carbonate nodules scattered or coalescenting into vertical rhizomorphs. These shaly facies contain small scattered carbonate clasts, occasionally a few centimetres in diameter but rarely exceeding 1 cm. The in-situ egg clutches were collected in these facies.

Limestone deposits. Two horizons of micritic limestone sediments are present in the excavation. These are chalky and contain some clasts that are floating in the calcium carbonate matrix.

Facies interpretation

These facies are attributed to a floodplain bordered by alluvial fans and a lake. These prograded from time to time towards the studied area. The lack of sandy deposits, that are present in other parts of the basin, indicates that this site distal to the main channel belt that flowed through the basin. Occurrence of numerous paleosols and absence of erosive features indicate a period of aggradation that favoured preservation of the egg clutches.

The Sextius site strongly resembles the Roques Hautes area, both in terms of egg clutches density and paleoenvironment. The Roques Hautes area (site Grand Creux) has been known for many years for the highest density of in situ dinosaur egg clutches in

the Aix-en-Provence (Garcia & Vianey-Liaud, 2001b). This site also represents a distal alluvial plain, bordered to the north by alluvial fans and invaded from time to time by lakes (Cojan *et al.*, 2003).

Egg systematic and distribution at Sextius-Mirabeau

Three oofamilies have been identified at Sextius-Mirabeau, among them, 2 represent eggs that were probably laid by dinosaurs. The most abundant (more than 90%) are discretispherulitic morphotype and correspond to the Megaloolithidae, an oofamily associated with sauropod dinosaurs on the basis of embryonic remains (Chiappe *et al.*, 1998; 2000). The two other egg types include prismatic (oofamily Prismatoolithidae) and geckonoid eggshell morphotypes (pl. 1).

The Prismatoolithidae, often preserved as fragments, are scarce in the Aix basin deposits (Garcia *et al.*, 2000a & b). Therefore, the discovery of four crushed eggs with numerous fragments (grouped without any associated nest) in this locality is exceptional. This oofamily is now related to theropod dinosaurs and birds by its associated embryos and possibly brooding adults (Varrichio *et al.*, 1997). The geckonoid type, which may have been laid by small reptiles, was known only from French Late Cretaceous localities, from fragments obtained by screen-washing (Garcia, 2000). For the first time, one very small egg (pl. 1, fig. g) was found at Sextius-Mirabeau, close to a clutch of megaloolithid eggs.

Three megaloolithid taxa have already been distinguished according to their microstructural features (Tab.): *Megaloolithus petralta* (N = 188 eggs), *M. aureliensis* (N = 36 eggs) and *Cairanoolithus dughii* (N = 6 eggs). But 300 eggs are still to be identified at the species level. The eggs, originally subspherical, have a diameter ranging between 14-20 cm but they are generally crushed due to tectonic processes and postburial compaction. The compactituberculate outer ornamentation for the three oospecies varies widely with the degree of weathering (pl. 1, fig. a). The eggshell microstructure, composed of well defined fan shaped units, is often altered by recrystallizations e. g. herring bone pattern.

Megaloolithid species	Average thickness mm	Taphonomy of eggshells	n clutches	Egg number (average)	Range (eggs per clutch)	Total number of identified eggs
M. aureliensis	1.085 0.043	variable preservation	10	3.6	1-10	36
M. petralta	1.452 0.103	often recrystallized	32	5.9	1-13	188
C. dughii	1.896 0.151	good preservation	1	-	-	6

Table 1.— Characteristics of the studied megaloolithid eggs from the Sextius-Mirabeau site (Southern France, Upper Cretaceous).

Spatial analysis showed the eggs were not randomly grouped but organized in clutches and often associated with pedogenic carbonate nodules or burrow casts, suggesting that they are in situ. Eggs have occur exclusively in mudstone layers representing probable overbank deposits far away from the main channel. The distribution of each oospecies differs along the section: *M. petralta*, the commonest ootaxa is widely represented from the base to the top of the section. *M. aureliensis* as well as *C. dughii* are represented only by some clutches that are mainly in the basal layers. In the mapped area, the egg density varies from 0 to 40 egg/25 m^2, with high differences between the oospecies. The distinctive clutches of *M. petralta* (mean = 5.9 eggs) and *M. aureliensis* (mean = 3.6 eggs) (Tabl. 1) average fewer eggs than the 8-12 commonly reported megaloolithid clutches (Moratalla & Powell, 1994; Cousin, 2002). Two large clutches contain up to 15-20 eggs, and we interpret them as an accumulation over time in the same nest. In addition, we regard 75 "isolated" eggs as being either eggs removed from original clutches before burying or as eggs perhaps laid by young females in their first years of breeding. Apparently (especially from field observations), only one clutch is unhatched, but no embryo was found in it. Nevertheless, because the clutches were prepared upside down, this conclusion needs confirmation.

No bones, either juvenile or adult, were discovered. The same is true for other organic elements, except for some microscopic gastropod shells and coral fragments from the unconformably overlying Miocene deposits. The lack of any vertebrate remains in the Cretaceous deposits may be attributable to the chemical dissolution of the phosphate material.

CONCLUSION

Sextius-Mirabeau appears as an original site underlying the Miocene deposits and located several meters below archeological layers (roman history) in the town of Aix-en-Provence. The distribution of megaloolithid eggs, which differs along the section, shows strong evidence of communal nesting and gregarious behavior of ? titanosaur groups and it indicates a stable paleoenvironment with favourable breeding conditions during a long period. The egg clutches are distributed in the shaly facies representing paleosols associated to overbank alluvium. No discernable sedimentary nesting trace (e.g. ground depression) has been observed, which is consistent with Lorenz (2000) and Cousin (2002) observations, but pedogenesis may have destroyed the sedimentary features. This is not contrary to the Chiappe *et al.* observations (this volume) of eggs laid in a ground depression, as these structures could also be covered with vegetal matter. The megaloolithid eggs were found in situ and may have been protected by a mound of vegetal layers. Thus, we interpret the large number of undisturbed clutches found as an accumulation of eggs in the same nests over time.

Neither bone nor embryonic remains were discovered, suggesting either unfavourable conditions of fossilization due to a chemical dissolution process or the quick dispersion of juveniles from the colony. The lack of juvenile and adult bones in the nest structures, also observed in the sauropod nesting grounds from Argentina

(Chiappe *et al.*, 1998; 2000) and India (Sahni *et al.*, 1994), suggests parental care less derived than that inferred for the hadrosaur *Maiasaura* (Horner & Makela, 1979).

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PLATE 1

a: weathered outer surface with pore openings of a megaloolithid fragment, scale = 5 mm [III-4].

b: *Megaloolithus petralta*, thin section, scale = 1 mm [IV-21].

c: Clutch of *M. petralta*, scale = 5 cm [III-4].

d: *M. aureliensis*, thin section of a recrystallized eggshell, scale = 1 mm [I-21].

e: *Cairanoolithus dughii*, thin section, scale = 1 mm [III-8].

f: megaloolithid crushed eggs affected by a strong pressure, scale = 5 cm [IV-10].

g: geckonoid egg [V-2] scale = 5 mm.

h: prismatoolithid egg, scale = 2 cm [I-19].

i: cf. *Prismatoolithus* sp., thin section, scale = 1 mm [V-19a].

PLATE 1