

DATING DINOSAUR OODIVERSITY: CHRONOSTRATIGRAPHIC CONTROL OF LATE CRETACEOUS OOSPECIES SUCCESSION

by

Nieves LOPEZ-MARTINEZ*

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*Departamento de Paleontología, Universidad Complutense, Facultad de Ciencias Geológicas, Ciudad Universitaria, 28040 Madrid, Espagne. lopezmar@geo.ucm.es

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ABSTRACT

An increasing fossil record of dinosaur eggs and eggshells allows putting ootaxa within a chronostratigraphic framework, in order to study their distribution pattern leading eventually to their use as biochronological markers. For these purposes, high-quality data exists in four major regions: North America, South America, Europe and Asia (Central Asia and India). Most of the highly diverse dinosaur egg record has been dated as Latest Cretaceous in age (Campanian-Maastrichtian), reaching the Cretaceous-Tertiary boundary closer than the dinosaur bone record. However, dating continental sections is problematic and need to be carefully verified, as it appears when comparing the European dinosaur eggshell record from two well-studied areas. Ootaxa distribution in both sides of the Pyrenees (Trempe and Aix basins) shows comparable oospecies successions, but different chronology. This disagreement probably indicates that one or both successions have a wrong chronostratigraphic calibration.

RESUME

Un registre fossile de plus en plus riche d'oeufs de dinosaures permet de situer la distribution des ootaxa dans un cadre chronostratigraphique précis, qui puisse éventuellement être la base de l'utilisation des coquilles d'oeufs comme des marqueurs biochronologiques. Dans ce but, des données de qualité existent en quatre continents: Amérique du Nord, Amérique du Sud, l'Europe et l'Asie (Asie Centrale et India). La plupart du registre d'oeufs de dinosaures, avec une haute diversité de types de coquilles, a été daté dans le Crétacé terminale (Campanien-Maastrichtien), arrivant plus près de la limite Crétacé-Tertiaire que le registre d'ossements de dinosaures. Cependant, les datations dans des séries continentales sont problématiques et ont besoin d'être soigneusement vérifiées, comme l'on voit en comparant le registre Européen de coquilles d'oeufs de dinosaures dans deux régions bien étudiées. La distribution des ootaxa des deux côtés des Pyrénées (bassins de Trempe et d'Aix) montre deux successions d'oospecies corrélables mais elles sont attribuées à des âges différentes. Ce désaccord probablement indique que l'une ou les deux successions ont une calibration chronostratigraphique erronée.

INTRODUCTION

The interest in fossil eggs is manifold. Besides their value as indicators of reproductive behaviour, fossil dinosaur eggs sometimes contain embryos, allowing to identify egg-laying dinosaur taxa (see Carpenter *et al.*, 1994; Carpenter, 1999; Chiappe *et al.*, 2001). The egg features and eggshell biomineralization have been proved to be reliable diagnostic characters bearing phylogenetic information (Mikhailov, 1992; Varrichio *et al.*, 1997; Grellet-Tinner, 2000; Zelenitsky *et al.*, 2002). Eggshell parataxonomy allows to differentiate ootaxa based on nests, egg and eggshell structural features, which document dinosaur distribution and oodiversity (Zhao, 1975; Vianey-Liaud *et al.*, 1994; Khosla & Sahni, 1995; Mikhailov *et al.*, 1996; Hirsch, 1996; Zelenitsky *et al.*, 1996; Garcia, 1998; Bravo & Reyes, 2000). Moreover, eggshell geochemistry provides a rich source of palaeoenvironmental and palaeoclimatic proxy data stored in the reservoir of original calcitic material and structural porosity (Erben *et al.*, 1979; Seymour, 1979; Williams *et al.*, 1984; Cojan *et al.*, 2003).

Eggshells are also relevant for biochronology. Late Cretaceous dinosaur eggshells are extremely abundant in an increasing number of regions (China, Europe, India, Mongolia, North and South America...). In many intervals devoid of other remains, they are the only fossils available to document the dinosaur record. The Late Cretaceous dinosaur succession, mostly based on fossil bones and teeth, can be enriched and completed by their egg record, which uncovers a hidden diversity in their last critical period. Dinosaur eggshells are useful markers for non-marine biochronological successions, where lack of reliable calibrations and elusive hiatuses cause poor age constraints (Vianey-Liaud *et al.*, 1994; Pickford *et al.*, 1995; Vianey-Liaud & Lopez-Martinez, 1997; Garcia & Vianey-Liaud, 2001; Difley & Ekdale, 2002; Khosla & Sahni, 2003; Zao *et al.*, 2002). Moreover, eggshells are less suspect than bones or teeth as possible reworked fossils in vertebrate assemblages, and clutches and eggs are reputed autochthonous fossils which guarantees their chronostratigraphical and palaeoenvironmental position. Finally, ootaxa successions can easily be established and correlated between regions, since fossil sites (eggshells) are frequently concentrated in areas along extensive egg levels usually repeated in successive beds, due to nesting fidelity behaviour and/or scarcity of favourable settings.

In this work we focus on the biostratigraphic value of Late Cretaceous eggshells as guide fossils for regional correlations and relative dating. The study of the rich fossil material of dinosaur eggshells can provide biostratigraphic scales for dating dinosaur successions, often being referred to diachronic lithostratigraphic units (Hell Creek Formation, Aren Sandstone, "Rognacian" limestone, "Garumnian" facies, etc.), or misleading chronostratigraphic terms in absence of true marine-continental correlations (Maastrichtian, Campanian...; see Lopez-Martinez *et al.*, 2001). These issues are particularly relevant for the record of the "non-avian" dinosaur extinction and its relation to the Cretaceous-Tertiary boundary (KTb). Thus, Late Cretaceous dinosaur eggs provide a rich source of information on the pattern of their fossil record at their most critical period. Particularly, the eggshell record is revisited in one of these areas, the Pyrenean-Provence basin, and their eggshell biostratigraphy is correlated in order to test its application for age determination.

DATING TOOLS

The Late Cretaceous period, more than 30 million years (Ma) long, is world-wide known for having the highest sea levels of the last 250 Ma, i.e. the whole dinosaur history. It is less known for concentrating the large majority of eggs and eggshell findings in the fossil record. Around 80% of the known world Mesozoic dinosaur eggshells and 95% of ootaxa come from this fascinating period, which includes the dinosaur mass extinction at its end. The dinosaur eggshell record in this period is considered representative enough for being used as evidence for different hypotheses of diachronic extinction patterns, supposedly pre-dating or post-dating the marine mass extinction in Europe and Asia (Galbrun, 1997; Zhao *et al.*, 2002).

The dating of these deposits uses numeric tools (geochronometry, radiometric

scale on eruptive rocks) and relative tools (subdivisions of geological time represented

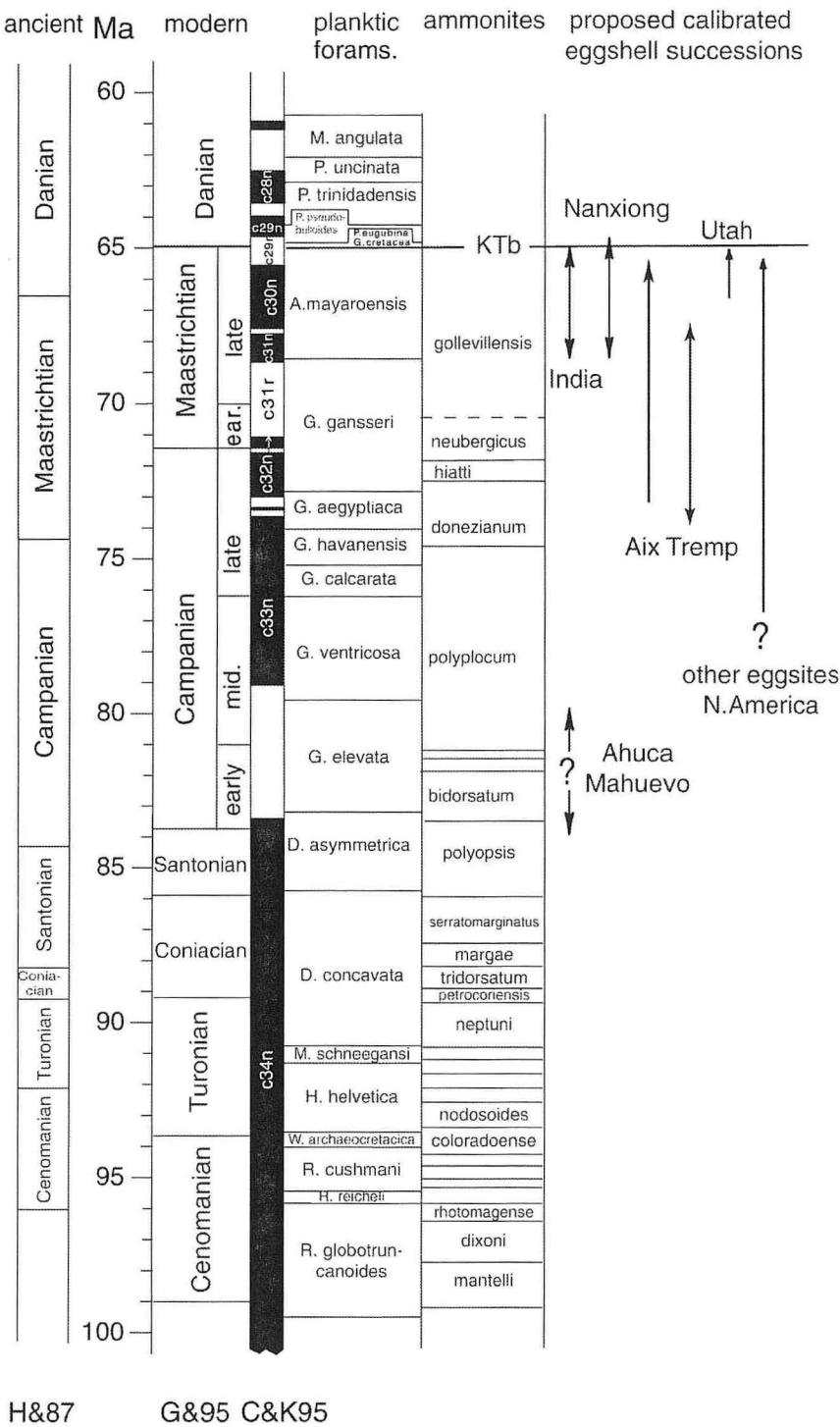


Figure 1.— Upper Cretaceous global chronostratigraphic scale, before and after its geochronometric modification (Gradstein *et al.*, 1995). Magnetostratigraphic, ammonite and planktic foraminifera biochronological scales are also shown., with the distribution of several eggshell successions.

by deposits, fossils and geophysical or geochemical signals in the rocks).

In the first case, a direct measurement of the age of the rock is obtained, surrounded by a confidence interval; therefore the only theoretical problem would be this interval being reduced as much as possible. However in practice, geochronometers show other problems, such as too large spread of data taken from the same sample. The modern $^{40}\text{Ar}/^{39}\text{Ar}$ techniques provide a more accurate method than older K/Ar ones, but in order to stabilize the results, whole rock analyses need to be replaced by single crystal analysis (Hofmann *et al.*, 2000). The calibration of Upper Cretaceous global chronostratigraphic scale has been strongly modified according to the different ages obtained for the Western Interior bentonites correlated to ammonite biostratigraphy (Gradstein *et al.*, 1995). As a consequence, the age of system and stage boundaries and their time span have changed (Fig. 1).

In case of relative dating, time estimation by rocks (lithostratigraphy) is by far the worst geochronologic reference. Groups, Formations and Members are often diachronic ("time transgressive") even in relatively short distances. The reason is the lateral migration of facies belts, formulated in the Walter's Law. This is also the case for marine transgressive deposits, considered in the past as isochronous references marking the base of the stages, and now merely indicating one step in a continuous process of coastal onlap. Therefore, the use of lithological units or facies for dinosaur dating (Hell Creek Formation, Aren Sandstone, Rognacian, etc.) must be avoided, being a misleading term indicating at the best just a palaeoenvironmental context.

However, sequence stratigraphy is a method leading to divide the rocks in isochronous units (depositional sequences) separated by short discontinuities or events (sequence boundaries). Such boundaries can be traced along entire basins and correspond to time-lines, which correlates the geological record across facies belts. An example of sequence stratigraphy for Upper Cretaceous, dinosaur-bearing Pyrenean deposits can be found in Lopez-Martinez *et al.* (2001) (Fig. 2). Such examples are extremely rare, because sequence stratigraphy only applies for non-marine deposits when they are in continuity with marine deposits.

Time estimation by fossils (biostratigraphy-biochronology) is the main chronostratigraphic method. At the first sight, any fossil type can be used as time-marker: planktic or benthic, aquatic or terrestrial, marine or continental, member of a surviving clade or extinct, known as a whole organism or treated as a piece of uncertain origin. In a second selection, the first types of each pair are frequently better guide fossils. In our case, the Upper Cretaceous has been subdivided by world-wide biochrons of ammonites and planktic foraminifera, although nannoplankton and dinoflagelates biozones are also widely used (free-living marine organisms). Other marine time-marker species, such as benthic foraminifera, rudists, echinoids and chondrichthyes are geographically more restricted. An example of biostratigraphic correlation based on rudist horizons, across two different tectonic units from the Upper Cretaceous of south-central Pyrenees is shown in Fig. 3.

In continental settings, favourite guide fossils for Upper Cretaceous deposits are palynomorphs, charophytes and mammals. The palynostratigraphy is not yet well developed for this period, palynotaxa are used as circumstantial time markers. Charophyte standard zones have been established by Rivelino *et al.* (1996) and are a

useful tool for approaching the age of non-marine European deposits. Mammals in this period are too rare for being a dating tool except in North America, where an example of Upper Cretaceous and Lower Paleocene non-marine biostratigraphy based on mammals can be found in Lillegraven & Eberle (1999). These authors found a vertebrate succession across the Cretaceous-Tertiary boundary in Wyoming, where mammal biostratigraphy shows a rather sharp boundary interval between Lancian and Puercan, two non-marine biochronological units corresponding a priori to latest Cretaceous and earliest Paleocene. The correlation of this basin with marine deposits is not possible; thus the position of the global KTb needs to be verified by indirect criteria (iridium anomaly, palynology, etc.).

The world-wide iridium anomaly, together with other signs of extraterrestrial impact at the KTb, is an example of a time-line signal for chemostratigraphic correlation. Other examples of dating by chemostratigraphic signals are:

1) the $^{86/87}\text{Sr}$ radioactive isotope curve, useful only for marine deposits. The ratio between both strontium isotopes in the seawater is uniform all over the world, and can be measured in marine carbonates. The secular change of this ratio has been calculated along the geological record, thus the resulting global curve allows assign an age to a particular Sr isotopic value of a rock or fossil.

2) the ^{13}C stable isotope anomalies, useful for both, marine and non-marine deposits. Organic productivity modulates the ratio of the carbon isotopes $^{13}\text{C}/^{12}\text{C}$ (^{13}C) in carbonates. Global events decreasing organic productivity result in strong decreases of the ratio, by releasing the light carbon in the water instead of being sequestered in the organisms. Their effect usually appears as short, rapid low peaks of the (^{13}C curve (Lopez-Martinez *et al.*, 1998, Fig. 4; Cojan *et al.*, 2000).

On the other hand, the physical signals in rocks also offer an opportunity for dating. Remnant magnetism in many types of deposits containing iron minerals allows recognizing normal and inverse polar magnetic periods (magnetostratigraphic chrons). This method is widely used for dating, by correlation of the local succession with the global magnetostratigraphic scale calibrated by geochronometry (Fig. 1).

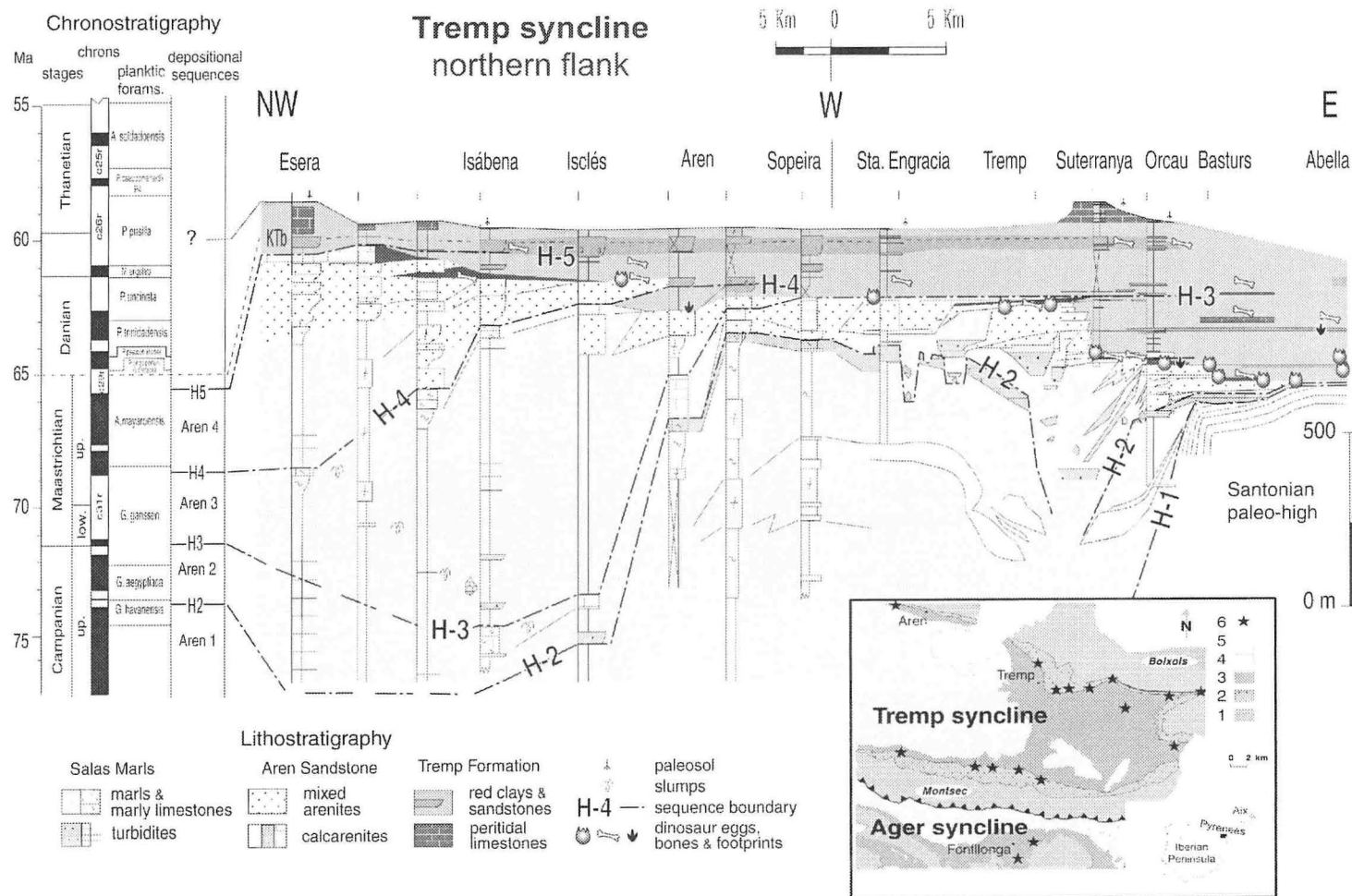


Figure 2.— Cross-section of Upper Cretaceous deposits in south-central Pyrenees, showing the depositional sequences and correlation of the sequence boundaries defined by Ardèvol *et al.* (2000). Their chronostratigraphic position is based on planktic foraminifera biostratigraphy by Orue-Etxebarria (UPV). Legend for the geological map: 1-Upper Cretaceous and older deposits; 2-Aren Sandstone; 3-Tremp Formation; 4-Lower Eocene; 5-Upper Eocene; 6-Dinosaur egg sites. From Lopez-Martinez (2003).

DATING DINOSAUR EGGSHELLS

Continental basins retain thick piles of sediments before they reach the starved marine basins, sometimes preserving intermediate, paralic areas with transitional marine and non-marine deposits. During the Upper Cretaceous, a global marine regression is recorded in most of the basins of the world, where hiatuses and non-marine deposits replaced the previous marine depositional systems in these basins. Dating hiatuses and non-marine deposits is a difficult task, specially when transitional and correlative marine deposits are not preserved, since non-marine fossils are less prone for biostratigraphical use because of local distribution and rarity. However, even if geochronometric radiochronology or marine-continental correlations are not available, magnetostratigraphy and local biostratigraphic scales of non-marine fossils (mainly palynomorphs, charophytes and vertebrates) can be useful for dating purposes, by correlation and calibration of regional successions.

The dating of dinosaur egg site successions in Europe, America and Asia has been approached by all these procedures. In most of these areas, eggshells have not yet been used as biostratigraphic markers but merely as indicators of dinosaur presence and diversity, often in relation to the KTb position; dinosaur eggshells are in the core of diachronic dinosaur extinction hypotheses (Stets *et al.*, 1996; Galbrun, 1997; Zhao *et al.*, 2002). We review below the dating of some of the main localities with abundant dinosaur eggs and eggshells of Late Cretaceous age.

Europe

Europe pioneered the studies in fossil dinosaurs and also in fossil eggshells, but the scientific tasks interested a relatively short number of persons.

The French Pyrenean-Provençal realm is where the first fossil dinosaur eggshells were collected and recognized as eggshells in 1859 by the priest J.J. Pouech. This region has yielded since a rich deal of egg sites from Late Cretaceous (Campanian-Maastrichtian) to Paleocene continental red beds from three main areas: North Pyrenees (Petites Pyrénées, Aude, Corbières), Languedoc (Villevieyrac, St. Chinian) and Provence (Aix basin) (Cousin *et al.*, 1994; Vianey-Liaud *et al.*, 1994; Garcia, 1998; Garcia & Vianey-Liaud, 2001). Egg sites are situated in continental red beds, in some cases from isolated tectonic units, therefore the chronostratigraphic context has not yet been accurately established. The egg sites from the central part of North Pyrenees can be correlated with marine deposits (Tambareau *et al.*, 1998), but their eggshells have not yet been studied. In contrast, a biostratigraphic scale has been based on egg distribution from the Aix basin, and calibrated by means of bio- chemo- and magnetostratigraphy as it will be detailed below.

In Spain, the Southern Pyrenean region has delivered diverse and abundant Late Cretaceous egg sites in transitional and continental sediments which contain similar species as the French counterpart (Vianey-Liaud & Lopez-Martinez, 1997; Lopez-Martinez, 2000; Escuer *et al.*, 2003; Vila *et al.*, 2003). The deposits from the central Tremp area allows a direct marine-continental correlation of the eggshell succession, which gives a rare opportunity for an accurate dating of the dinosaur ootaxa as it will be

detailed below. Other egg sites are reported from the Late Cretaceous Iberian Mountains in continental deposits with the usual inaccurate dating (Pol *et al.*, 1992; Moratalla, 1993).

The third European area providing dinosaur egg sites is Romania. Grigorescu *et al.* (1994) reported a clutch from red deposits of the Densu-Ciula Formation, Hateg basin (Transylvania), attributed to the Maastrichtian on the basis of a palynomorph taxon considered a time marker. Other locality from the same basin has been described by Codrea *et al.* (2002), with several levels containing eleven dinosaur clutches, eggshell fragments and vertebrate bones. It is located in a tectonized small outcrop of the Sanpetru Formation, a succession of near 2,500 m-thick attributed to the Maastrichtian but without reliable dating criteria.

North America

In North America, Difley and Ekdale (2002) use the eggshell stratigraphic distribution to characterise the Upper Cretaceous-Lower Tertiary North Horn Formation in central Utah (Western Interior basin). These 400 m-thick continental deposits contain dinosaur eggshells along its lower part (variegated unit 1 and lowermost part of the dark-coloured unit 2 which contain the KTb). Magnetostratigraphic calibration of this eggshell succession suggests a correlation with chrons c30n and c29r (Upper Maastrichtian). Eggshell diversity decreases along this succession, the last eggshell being recorded at 35 m below the KTb, which may correspond to a hiatus estimated elsewhere in 1 to 5 million years.

Other North American dinosaur egg sites appear mostly in single beds, not successive strata. Rich clutches and egg assemblages are known in Upper Cretaceous deposits from Colorado, Utah, Montana, Dakotas and Alberta (Western Interior basin); isolated eggshell findings are also reported from Mexico (Hirsch & Quinn, 1990; Carpenter *et al.*, 1994; Carpenter, 1999). Some of these eggs and eggshells were initially attributed to wrong dinosaur types because of misleading embryonic remains. Authors refers their stratigraphic position to different lithostratigraphic formations (Two Medicine, Judith River, Oldman, Lance, Belly River, Willow Creek, Saint Mary River, Hell Creek, etc.), approximately dated by plant and micromammal biostratigraphy within a regional chronological scale (Judithian, Lancian) loosely correlated from Campanian to Maastrichtian (Hicks *et al.*, 1999).

South America

South America contains important Late Cretaceous dinosaur egg assemblages in Argentina (Rio Negro and Neuquén, Patagonia), Brazil, Peru and Uruguay. The egg sites from Neuquén are notable for their extension and richness in embryonic remains, and allow connect Titanosaurid sauropod dinosaurs to eggshells belonging to the Megaloolithidae oofamily (but different from *Megaloolithus* oogenus) (Chiappe *et al.*, 1998, 2000). Rio Negro and Uruguay eggs bear the thickest eggshell record for known Amniota eggs (Powell, 1987; Facio, 1994). Brazil and Peru share eggshells from the Bauru Formation (Magalhaes Ribeiro, 2000). Upper Cretaceous Peruvian fossil localities from Vilquechico Formation were described as containing tubospherulitic

Megaloolithus pseudomamillare eggshells (Vianey-Liaud *et al.*, 1997), which seems to be probably a mistake due to mixed French fossil material. Dating of these assemblages are approached by continental biostratigraphic scales (Musacchio, 1989) and magnetostratigraphic correlations, which indicate an early Campanian age for the 40 m-thick Neuquén dinosaur nest levels (Chiappe *et al.*, 2000; Dingus *et al.*, 2000).

Central Asia

Central Asia is rich in dinosaur eggs and eggshells, although accurate dating tools are lacking for most of the eggshells. In Mongolia, most of the findings probably belong to the Senonian (Santonian-Campanian), except an eggshell of possible Albian-Cenomanian age. Sections incorrectly attributed to early Cretaceous have been dated in late Cretaceous in base of their eggshell content (Mikhailov, 1994; Mikhailov *et al.*, 1994). The rich egg assemblages from Xixia (Henan, China), with 19 oospecies from more than 3,000 meter-thick sections, have not yet been accurately dated, moving from Early to Late Cretaceous (Zhao, 1994; Whyte *et al.*, 2000). The eggshells from South Korea, with 3 oospecies, share comparable ootaxa and may be from the same imprecise period (Huh & Zelenitsky, 2002). The best-calibrated eggshells correspond to the rich Nanxiong basin (Guangdong, China) detailed below. Less thick, similar deposits with egg assemblages from four shared oospecies are found in the Maoming basin (Guangdong, China), 500-km south-west of Nanxiong. Also the Laiyang region (Shandong, China) contains rich eggshells with 13 oospecies in the thick red beds of the Wangshih Series containing also hadrosaur and ceratopsian bones, similar to the Djadokhta Formation in the Nemegt basin of Mongolia, and thus probably also Late Cretaceous in age (Santonian-Campanian). Mismatched dinosaur eggs and associated juvenile bones have been frequent. Other scattered eggshell findings occur in many other less rich areas in Asia.

In the Nanxiong basin, Zhao *et al.* (1991, 2002) and Stets *et al.* (1996) have put dinosaur eggshells in a detailed stratigraphic framework. There, continental red beds from Upper Cretaceous to Lower Tertiary reach 3,000 to 7,000 meters in thickness. Zhao *et al.* (2002) summarize the presence of 12 oospecies during 1.5 Ma across a putative KTb, with an estimated 400 m/Ma average in sedimentation rate. The calibrations are based on radiometric dating, local bio- and chemostratigraphy and controversial magnetostratigraphic correlations discussed by Russell *et al.* (1993). The KTb was first situated between the Pingling and Shanghu Formations, marked by slight lithological differences and by the end of the dinosaur eggshell record, although eggshells above it have been reported by Buck *et al.*, (2004, they do not indicate if they correspond to avian eggshells). Both formations overlie the Yuanpu Formation, radiometrically dated at 67.2 Ma in its upper part (Zhao *et al.*, 1991). This boundary is situated in a reversal magnetic zone correlated to chron c29r.

However, Stets *et al.* (1996) situated the KTb right in the middle of the dinosaur eggshell succession, in a 21 m-thick interval at the upper part of the Pingling Formation around 78-161 m below its top. These authors record an important palynological change in this interval, from a diverse, fern-dominated flora to a less diverse, phanerogam-dominated flora. Although no palynozones have yet been calibrated with the KTb in the Old World, these authors propose the survival of Chinese dinosaurs into the Paleocene.

Zhao *et al.* (2002) study dinosaur eggshells across the pollen change interval, and adopt this criterion by noting six iridium anomalies within the eggshells affected also by pathologies that these authors relate to the KTb anomalies. Zhao *et al.* (2002) also refer to Sloan (1987) who attributed the upper part of the Pingling Formation to the Paleocene, because the presence of a specialized Polyglyphanodontinae lizard around 80 m below its top. According to Sloan (1987), this lizard also appears in the North Horn Formation of North America just below the KTb. However these dating arguments based on circumstantial evidence cannot be trusted unless a biochronological scale for palynomorphs or lizards can be established and calibrated.

Buck *et al.* (2004) discuss the controversial eggshell dating in the Nanxiong basin. They conclude that all dinosaur eggshells from the uppermost 101 metres of the Pingling Fm and the lower part of the Shanghu Fm are reworked fossils in Tertiary beds. In order to support their hypothesis, these authors reject the presence of complete dinosaur eggs in this interval, which contradict observations by Zhao *et al.* (2002). However, all authors agree that this interval contains frequent clusters of dinosaur eggshells, which together with the high sedimentation rate are arguments against the probability of reworking processes.

India

In Central and Western India, dinosaur eggs and eggshells typically occur in extensive, thin sedimentary beds (Lameta Formation, 1 - 40 m in thickness) overlaid or intercalated between thick basaltic layers (Deccan traps, more than 3,000 m in thickness) (Vianey-Liaud *et al.*, 1987; Tandon *et al.*, 1995; Khosla & Sahni, 1995, 2003). Around 15 oospecies have been retained, with three oofamilies, one oogenus (*Megaloolithus*) and probably at least one oospecies shared with other regions (France, Spain, Romania, Patagonia, Mongolia; Sahni *et al.*, 1994; Khosla & Sahni, 1995, 2003; Vianey-Liaud *et al.*, 2003). Besides to other contemporaneous fossils from shelfal, freshwater and terrestrial taxa, the Indian dinosaur eggshell ootypes shared with Europe and Asia bear additional arguments against the claimed isolated position of the Indian subcontinent during the Latest Cretaceous (Loyal *et al.*, 1996; Soler Gijon & Lopez-Martinez, 1998; Vianey-Liaud *et al.*, 2003).

The difficulty for establishing local eggshell successions in thin, distant stratigraphic sections has not allowed use of Indian dinosaur eggshells for biostratigraphic correlations. Dating the Indian dinosaur eggshells has been attempted by palynology, by direct radiometric measurements of associated Deccan basalts and by indirect correlation with marine sections bearing planktonic foraminifera. Palynological data are not always conclusive, since palynomarkers have rarely been calibrated against well-dated chronostratigraphic sections. For instance, *Aquilapollenites* is supposed to be a Cretaceous taxon in India because it is very frequent in North American Cretaceous, but it has also Tertiary representatives in North America, thus its presence in the Indian Tertiary cannot a priori be excluded.

Radiometric dating of Deccan traps has been controversial until recently, when single crystal $^{40}\text{Ar}/^{39}\text{Ar}$ dating are giving convergent results. According to Hofmann *et al.* (2000) and Courtillot *et al.* (2000), the massive Deccan volcanism started around 67 Ma in normal magnetochron c30n (Late Maastrichtian) and resumed in c29r and

c29n (Earliest Paleocene) after 1-2 Ma record of lacustrine deposits (inter-trappean beds). There, an iridium layer has been detected in Anjar (Western India) and attributed either to Late Cretaceous or to KTb (Bajpai & Prasad, 2000; Courtillot *et al.*, 2000). Planktic foraminifera below Deccan basalts in south-eastern India also belong to Upper Maastrichtian *A. mayaroensis* biozone (Khosla & Sahni, 2003). Therefore, more than 3,000 meters of Deccan basalts have supposedly been deposited in less than 3 million years at the very end of the Cretaceous.

The egg-bearing Lameta Formation underlies the Deccan basalts (infra-trappean beds). Eggs are preserved in limestones and calcretized sandstones attributed to semi-arid type soils. In some areas, a single egg layer is inferred, spreading along a palaeotopographic surface. Lameta beds contain rare palynomorphs, attributed to Upper Maastrichtian, and plant macrorests are absent excepting rhizolites. The Lameta Formation represents a condensed regolith deposit formed during a long period of pedogenetic alteration. According to some authors, it may be locally contemporaneous of the Deccan traps because it seems to change laterally to inter-trappean position in some areas, and its lower part contains clays that may derive from volcanic materials (Tandon *et al.*, 1995; Khosla & Sahni, 2003). However the cratonic weathered host rocks also contain volcanic materials. In contrast, inter-trappean beds roughly similar to Lameta beds differ by their abundant palynomorphs attributed to Maastrichtian, indicative of wet climate. They differ also by having very rarely dinosaur remains and eggshell fragments (Vianey-Liaud *et al.*, 1987; Prasad & Khajuria, 1995; Loyal *et al.*, 1996; Mohabey, 2000; Khosla & Sahni, 1995; 2003). This dinosaur distribution is suggestive of most of them being older than the Deccan basalts. Possibly the infra-trappean beds and the first basalts in different areas may have diachronic ages along these huge distances, as their high dinosaur oodiversity indicates.

This survey of some of the main dinosaur egg sites in the world shows a high concentration of ootaxa in the Latest Cretaceous (Campanian-Maastrichtian), in many cases closer to the Cretaceous-Tertiary boundary than the dinosaur bone record. However with some exceptions (Fig. 1), there is a general lack of accurate dating due to:

- few available radiometric ages,
- lack of associated reliable guide fossils,
- circumstantial use of palynomorphs and vertebrate associated taxa,
- few chemostratigraphic studies, and
- few reliable magnetostratigraphic sections.

This situation is similar to that other types of dinosaur fossil sites (bones, footprints), also frequently found in poor age-constrained settings. Rarely reference sections with dinosaur fossil successions are correlated and accurately dated. Eggshells are good candidates for such biostratigraphic function, as is discussed below, and they can serve as a criterion for dating other fossil sites (Garcia, 1998; see below).

EGGSHELLS AS BIOSTRATIGRAPHIC MARKERS

Ootaxa can serve to apply standard biostratigraphic procedures in continental deposits, where dating tools are frequently rare. These procedures are particularly suitable for egg site successions, since eggshells are frequently found in successive stratigraphic levels from the same sections (Lopez-Martinez, 2000). Several case studies have used this approach, which can follow three steps:

First of all, local or regional biostratigraphic successions are established by identifying different taxa in successive stratigraphic levels;

Then, local or regional biostratigraphic subdivisions (biozones) are defined by establishing boundaries across the biostratigraphic succession. If inter-regional correlations of biozones show general regularities it can lead to establish general biochronological units (biochrons, standard zones).

Finally, a chronostratigraphic correlation is proposed between the particular scale and a general chronostratigraphic framework (depositional sequences, regional or global stages), by calibration with geochronometry or with global reference scales (magnetostratigraphy, isotopic stratigraphy and standard marine biochronozones if direct correlations through paralic areas of transitional deposits are available).

This methodological approach makes possible to compare different regional calibrated eggshell successions and verify congruent patterns or detect possible mismatches due to hidden hiatuses, incorrect calibrations or other problems.

In Europe, an application of this method to eggshell successions has been made by Vianey-Liaud *et al.* (1994), Garcia (1998) and Garcia & Vianey-Liaud (2001), which establish an eggshell biozonation for the uppermost Cretaceous continental deposits of the Aix basin (France) where no correlative marine deposits are available. These authors adopt the parataxonomic approach pioneered by Zhao (1975) and distinguish 12 oospecies in 60 eggshell assemblages from nine stratigraphic successions in the Eastern and Western areas of the Aix basin. The local eggshell successions are then compared between the separated stratigraphic sections, and a biostratigraphic correlation is proposed, based on similar successions of shared ootaxa. This approach may be applied to other eggshell successions in any part of the world.

The eggshell distribution studied by these authors does not fit previous lithostratigraphic correlations between the Eastern and Western parts of the Aix basin. Based on the eggshell distribution, the authors show that the so-called "Rognac Limestone" is a diachronic lithostratigraphic unit, made by an older "Rousset Limestone" at the East and a younger "Rognac Limestone" *sensu stricto* at the West.

The resulting regional correlation panel is then calibrated by magnetostratigraphy, using partial magnetostratigraphic successions obtained by different authors and a correlation to global magnetocrons proposed by Westphal and Durand (1990). Finally, the authors divide the eggshell succession into three biostratigraphic units referred to previously defined continental stages and to marine chronostratigraphy. As a result, eggshell biostratigraphy allows dating the Upper Cretaceous continental deposits of the Aix basin and other basins (Languedoc, Corbières) and documents a decrease of

eggshell diversity around the Campanian-Maastrichtian boundary, a single oospecies reaching few meters below the KTb.

The Aix reference eggshell biostratigraphy presents in the base of the succession a diverse biozone (Assemblage 1), characterized by the ootaxa *Megaloolithus aureliensis* and *Cairanoolithus*, with *M. petralta* acme in its lower part and *M. siruguei* in its upper part, dated Late Campanian (magnetostratigraphic zones c33 and c32). It is overlaid by a less diverse biozone (Assemblage 2), characterized by the dominance of the oospecies *Megaloolithus siruguei*, with rare *M. petralta* in its lower part and *M. mamillare* in its upper part, dated around the Campanian/Maastrichtian boundary (magnetostratigraphic zones c32 and c31). Finally, it is overlaid by a poorly diverse biozone (Assemblage 3), characterized by *M. mamillare* in its lower part and *M. pseudomamillare* in its upper part. This uppermost biozone is correlated with chron c30 (late Maastrichtian) in the Eastern Aix basin, and with chron c31n in the Western Aix basin (Garcia and Vianey-Liaud, 2001), suggesting that the proposed calibration needs to be reassessed. These authors record the uppermost dinosaur eggshells more than 10 m below the assumed K/T boundary, inferred by magnetostratigraphy.

This procedure allows extend the biostratigraphic reference succession for dating other isolated sections if they share common ootaxa. Garcia (1998) study several isolated sections rich in eggshells from northern Pyrenean outcrops (Aude, Corbières, Languedoc), and assign them an age by correlation with the Aix-en-Provence reference succession. Villeveyrac and Corbières ootaxa successions perfectly fit and correlate with the three biozones defined in the Aix basin, strongly supporting the proposed scale. St.Chinian correlates with the lowermost biozone of the eggshell biostratigraphic scale (Assemblage 1).

The established biostratigraphic scale for the Provençal realm can be tested in other regions sharing similar ootaxa. If it holds, it can be referred to a more general biochronological succession. The large geographic extent of many ootaxa suggest that it may be the case. We will test the case of the south-central Pyrenean eggshell succession, where previous studies have shown the applicability of the Provençal eggshell biostratigraphy (Vianey-Liaud & Lopez-Martinez, 1997).

DATING THE SOUTH-CENTRAL PYRENEAN DINOSAUR EGGSHELL SUCCESSION

Vianey-Liaud & Lopez-Martinez (1997) study the eggshells of some isolated localities in south-central Pyrenees, and found that eggshell biostratigraphy previously established in Provence could also be applied there. The eggshell localities from south-central Pyrenees show a very diverse assemblage dominated by *Megaloolithus petralta* with *M. aureliensis*, and almost monospecific assemblages dominated either by *Megaloolithus siruguei*, *M. mamillare* or *M. pseudomamillare*. These eggshells could be respectively correlated to the Assemblages 1, 2 and 3 from Provence. The shared ootaxa recorded in both regions, linked to the Late Cretaceous paleogeographic continuity between them, allowed the application of the same biostratigraphic scale to

both successions (Vianey-Liaud *et al.*, 1994; Vianey-Liaud & Lopez-Martinez, 1997).

The magnetostratigraphic calibrations however did not fit in the schema, as it was noticed. The rocks containing Assemblage 1 eggshells in the Aix basin (lower Rognacian) were attributed to chron c32n and older by previous authors (Westphal & Durand, 1990), whereas the comparable assemblage Fontllonga-6 from south-central Pyrenees was correlated to chron c31r (Galbrun *et al.*, 1993). Since misfits in the magnetostratigraphic data from Aix basin due to remanentation were already noticed, the authors expected that this contradiction could be probably solved with more accurate data.

The rich eggshells in south-central Pyrenees have been increased since 1997 and put in a more complete chronostratigraphic framework (Lopez-Martinez, 2000, 2003; Lopez-Martinez *et al.*, 2001, 2002; Figs. 2-4). The sequence stratigraphic framework established by Ardèvol *et al.* (2000) allows correlate the continental and littoral eggshell-bearing deposits with the marine chronostratigraphy. The two main areas containing eggshells, the Tresp and Ager synclines (Figure 2) have been correlated to each other by means of rudist biostratigraphy (Vicens *et al.*, 2001, 2004, Fig. 3). The resulting correlations agree with the previous ones established by magnetostratigraphy by Galbrun *et al.* (1993). More works are in progress in order to confirm and complete these results, which offer a rare opportunity to obtain a continent-to-basin chronostratigraphic framework for a thick, very expanded record from the Campanian to the Danian.

The obtained correlations in the south-central Pyrenees shows that lithostratigraphic units are strongly diachronous ("time-transgressive") along a 70 km-long cross-section. It can be verified along the northern flank of the Tresp syncline (cross-section, Fig. 2). The basinward prograding clastic wedge built by the Aren Sandstone deposits is progressively younger north-westward. Each sandstone body pass landward to continental deposits (Tresp Formation) and basinward to deep marine marls forming large clinoforms (Salàs Marls) and basinal turbidites (Ardèvol *et al.*, 2000 and references therein). Only careful mapping and physical correlation allows to reconstruct this seismic-scale outcrop geometry, otherwise big mistakes can be made if vertical facies changes are taken as time-lines (*datum*). According to the sequence stratigraphic correlation and the planktic foraminifera dating (Figs. 2 and 3), the oldest eggshell sites in the eastern Aren Sst. outcrops (near Abella) are about 6 million years older than the youngest eggshells in the western Aren Sst. outcrops (near Aren).

These correlations agree well with the biostratigraphic rudist scale established by Vicens *et al.* (2001, 2004), which allow to connect the Tresp cross-section chart to the Fontllonga section in the Ager syncline and its magneto- and chemostratigraphic calibration (Figs. 3 and 4). The Fontllonga section is only 25 km-southwards to the Tresp cross-section, but they belong to different tectonic units. The two synclines are separated by the Montsec fault (see map Fig. 2), interpreted as the verticalized frontal ramp of a southward-directed thrust with more than 15 km shortening. The condensed northern flank of the Ager syncline appears subdued by the Montsec thrust, and its thick southern flank shows a stratigraphic succession different from that of the Tresp syncline (Figs. 3 and 4). In the Ager syncline, the Aren Sandstone is lacking and its chronologically equivalent Les Serres Limestone is overlaid by thick peritidal

limestones assigned to the Tremp Formation.

The whole chronostratigraphic scheme shows a very clustered egg-site distribution, with most of the eggshell sites located in the Aren-2 sequence (Upper Campanian, between 73,3 and 71,3 Ma). Aren-2 eggshell assemblages are dominated by the Megaloolithidae oofamily, including the three almost monospecific assemblages containing *Megaloolithus siruguei* (Biscarri, Faidella), *M. mamillare* (Basturs, Abella) and *M. pseudomamillare* (Suterranya) which overlay each other. Very rich egg-sites (autochthonous clutches and eggs) are found in the Aren Sst. nearshore and beach deposits and in the lagoonal, tidal and coastal Tremp Fm. deposits as well (Sanz *et al.*, 1995; Lopez-Martinez *et al.*, 2000; Lopez-Martinez, 2000; Escuer *et al.*, 2003). No older eggshell assemblages have yet been discovered. Above the *M. pseudomamillare* assemblage, a transgressive episode is recorded, with fine-grained shelfal calcarenites overlying the Tremp Fm. lagoonal deposits (Fig.2).

The overlying deposits are less rich in dinosaur egg-sites; only eggshell fragments are found in Aren-3 and Aren-4 depositional sequences (d.s.), where the recurrent nesting localities that were so frequent in Aren-2 d.s. are completely lacking. This pattern in the south-central Pyrenean dinosaur record seems very consistent, since the three depositional sequences have comparable outcrop quality, contain very similar lithologies and facies and have been similarly explored.

The only relevant egg-site correlated with the Aren-3 d.s. is that from Fontllonga-6, one of the most diversified eggshell assemblages yet described, containing 7 oospecies dominated by *Megaloolithus petralta*. It belongs to the lower part of the chron c31r (Early Maastrichtian, around 70,5 Ma), and contains very abundant eggshell fragments in a fine-grained carbonatic deposit with oncolite-coated molluscs shells and vertebrate bones (fishes, turtles and crocodiles, with sauropod, theropod and ankylosaur dinosaurs; Vianey-Liaud & Lopez-Martinez, 1997; Lopez-Martinez, 2000).

The Aren-4 d.s. contains an important egg-site (Blasi-2 near Aren), with eggshell fragments associated with charophyte and small bones, sandwiched between two fossil sites containing partially articulated hadrosaur skeletons and scattered bones (Lopez-Martinez *et al.*, 2001). Hadrosaurs and theropods dominate the dinosaur assemblage, although a sauropod tooth has also been found. Other sauropod remains also appear in younger sites. Prismatic ornithoid eggshells (six different types) are predominant in the Blasi-2 eggshell assemblage, together with a new type of Megaloolithidae (Lopez-Martinez *et al.*, 1999). This eggshell type is rather thin (0,70-0,74 mm, Plate 1), although is the thickest eggshell type in this assemblage. The mamillae are scarce and well separated; the shell units are not differentiated in the external half, much more confluent than in *M. pseudomamillare*; the outer surface has rounded depressions surrounded by highs without individualized nodes. Pore channels must be very tiny and/or scarce, since they do not appear in the eggshell surfaces or fracture surfaces of the available fragments. The well-differentiated mamillae, distant to each other, is a typical feature of the Megaloolithidae oofamily. However, the peculiar characters of this ootaxon distinguish it from those already known.

The Blasi dinosaur sites correlate well with basinal deposits containing the planktic foraminifer *Abathomphalus mayaroensis*, dating the uppermost Cretaceous biozone. The first appearance of this species can be traced landward about 60 m below

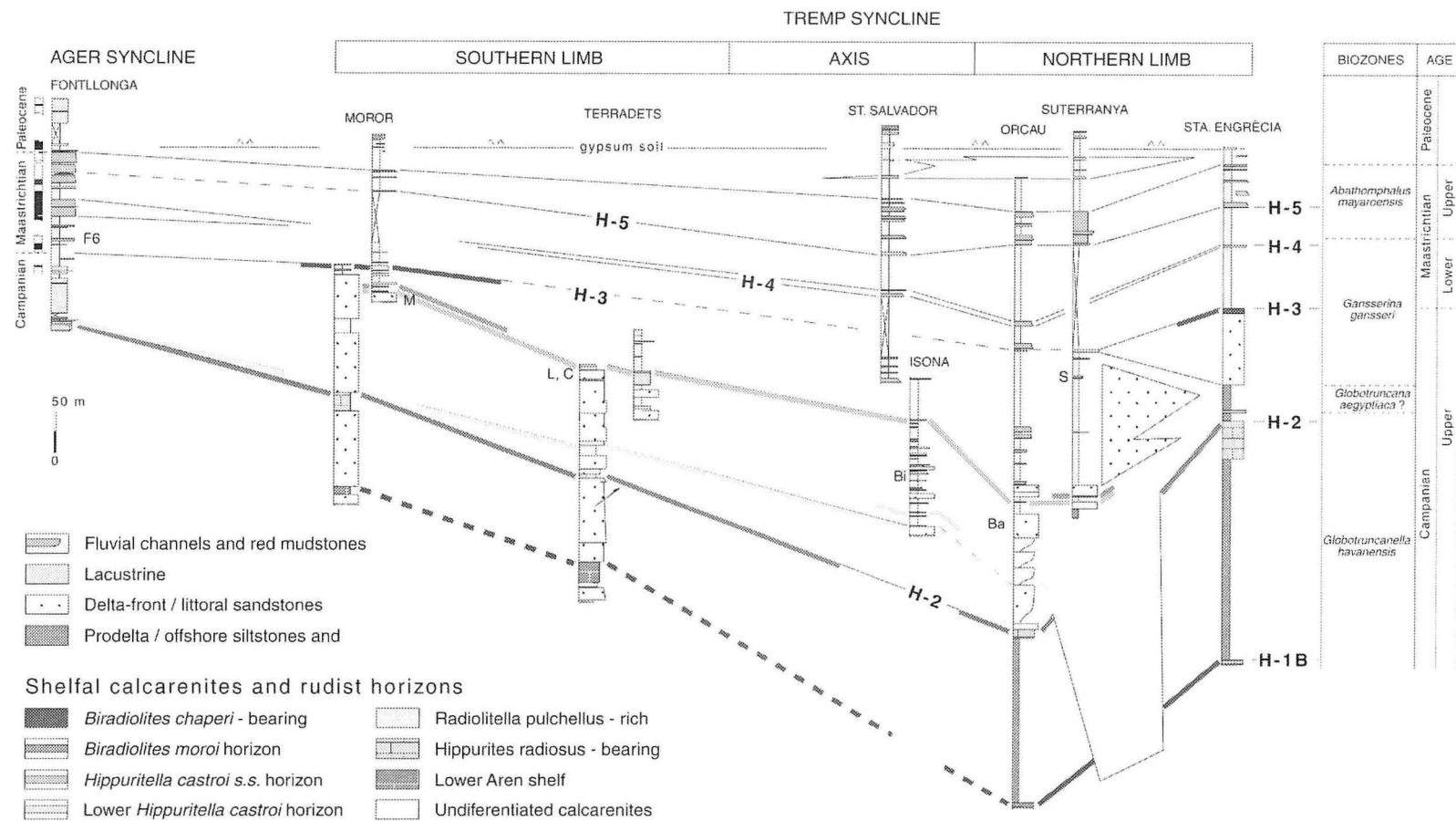


Figure 3.— Correlation of four rudist horizons in the Upper Cretaceous deposits from south-central Pyrenees, across two tectonic units, the Ager and Tresp synclines separated by the Montsec thrust (from Vicens *et al.*, 2001, 2004). The main egg sites are situated in the different sections: F6- Fontllonga-6; M- Moro; L-C- Llimiana-Cellers; Bi- Biscarri; Ba- Bastús; S- Suterranya.

the sites, and the Cretaceous-Tertiary boundary is about 200 m above them. Therefore, the thickness of the sediments correlated to the *A. mayaroensis* biozone suggests the Blasi-2 dinosaur egg site occupy a low position within this biozone, with an estimated age around 68 Ma (Lopez-Martinez *et al.*, 2001).

Therefore, in the south-central Pyrenees an interval about 2 Ma long at the end of the Campanian period (Aren-2 d.s. between 73,3 and 71,3 Ma) corresponds to an acme of nesting sites and abundant egg sites containing three successive *Megaloolithus* oospecies (*M. siruguei*, *M. mamillare*, *M. pseudomamillare*). This period ends with a transgressive episode, after what no more dinosaur clutches are found. The succeeding approximately 6,3 Ma long interval (Aren-3 and 4 d.s.) records rare egg sites with only eggshell fragments from diverse oospecies: 7 oospecies dominated by *M. petralta* around 70,5 Ma, and another site around 68 Ma with 7 different oospecies, among them a new ootaxon of a probable Megaloolithidae (Plate 1). This succession will be refined and completed in the future, when many of the rich egg sites will be studied, but the dating criteria available at the moment give us a different picture of that obtained from the Aix basin, as it will be compared below.

BIOSTRATIGRAPHIC CORRELATIONS BETWEEN THE PYRENEAN AND PROVENÇAL EGGSHELL SUCCESSIONS

The two compared Late Cretaceous eggshell successions proceed from two regions that were largely confluent in the past (Plaziat, 1984). From the early Campanian onwards, the southern and northern margins of the Pyrenean basin connect to each other by an eastern emerged area, belonging to the Catalanian-Thyrranian massif. The coastal and lagoonal sediments of this flat continent form the "red beds" of the modern Tresp and Aix basins. These regions share abundant fossil taxa and their former connection can still be recognized by isolated, fragmented tectonic units in Northern Pyrenees and Languedoc (see above).

The dinosaur eggshells in both regions share a high proportion of ootaxa. Figure 5 shows the compared distribution of the common ootaxa between Aix and south-central Pyrenees, together with some other types found only in one of the two areas. The chart shows the distribution of ootaxa from both regions beside each other, noticing the similarities and the main discrepancies between both eggshell successions.

The first eggshell-based biostratigraphic study on the south-central Pyrenees recorded the presence of *Megaloolithus petralta* and *M. cf. aureliensis* at Fontllonga-6 (Vianey-Liaud & Lopez-Martinez, 1997). This suggested a correlation between Fontllonga-6 and the French lowermost eggshell biozone from lower "Rognacian" deposits (Assemblage 1, according Garcia & Vianey-Liaud, 2001). The discrepancy with the magnetostratigraphic calibrations was already noted: early Maastrichtian chron c31r for Fontllonga-6, late Campanian chron c32n for the lower "Rognacian". However, this is not the only disagreement between both scales.

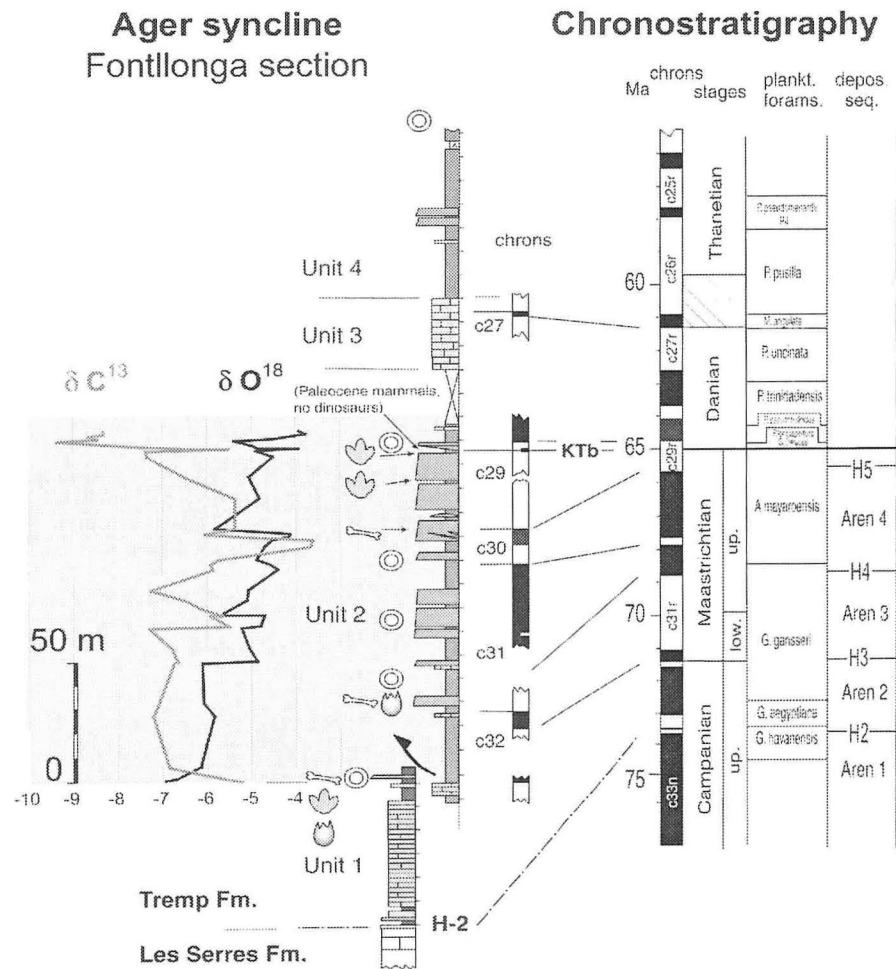


Figure 4.— Chemostratigraphic curves of ^{13}C and ^{18}O stable isotopes in the Fontllonga section, Ager syncline, south-central Pyrenees. The strong decrease of ^{13}C corresponds to the Cretaceous-Tertiary boundary anomaly, close to the top of c29r magnetochron (from Lopez-Martinez *et al.*, 1998).

Fontllonga-6 site is situated in Aren-3 depositional sequence at the base of chron c31r, according to magnetostratigraphic correlation (Early Maastrichtian in age, Figure 3). Thus, this assemblage dominated by *M. petralta* is probably younger than the Aren-2 egg sites containing *M. mamillare* (Bastús) and *M. pseudomamillare* (Suterranya), and certainly younger than the underlying *M. siruguei* assemblages (Biscarri, Faidella, etc.). The presence of *M. aureliensis* in Fontllonga-6 is not taken into account in this discussion, because only a fragment has been tentatively identified, which is not enough evidence.

Therefore in the South-central Pyrenees, four successive *Megaloolithus* oospecies appear in the order: *M. siruguei* - *M. mamillare* - *M. pseudomamillare* - *M. petralta*. This contradicts the biostratigraphic order observed in the Aix basin (*M. petralta* - *M. siruguei* - *M. mamillare* - *M. pseudomamillare*) because the conflicting position of *M. petralta*. This disagreement can just be the effect of a longer persistence of this eggshell type in the Southern Pyrenees.

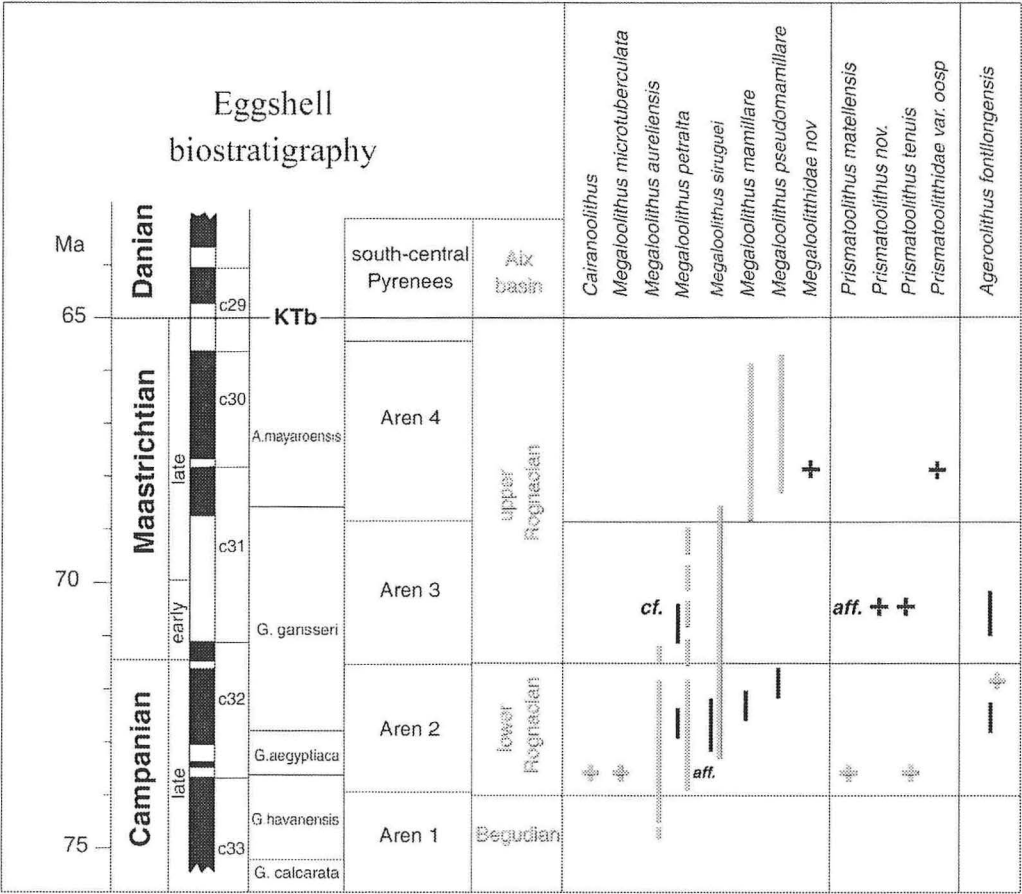


Figure 5. — Compared biostratigraphic distribution of eggshell ootaxa between south-central Pyrenees and Aix basin. The signs for the Pyrenean distribution are black-coloured, those for the Aix are grey coloured. Calibrations of eggshell successions in both basins result in a distorted ootaxa distribution. Data from Vianey-Liaud & Lopez-Martinez (1997), Lopez-Martinez (2000) and Garcia & Vianey-Liaud (2001).

Therefore, the successive appearance of the three oospecies *M. siruguei* - *M. mamillare* - *M. pseudomamillare* is common to both regions and confirmed in all observed cases. However, the calibration in each region is rather different, and differs also within the Aix basin. In the south-central Pyrenees, the three oospecies are recorded in the Aren-2 d.s., dated Upper Campanian (top of *G. havanensis* - middle part of *G. gansseri* biozones). In the Western Aix basin they are correlated with magnetochron c31n (latest Campanian-early Maastrichtian), while in the Eastern Aix basin these three oospecies are situated in magnetochrons c32n to c30n (latest Campanian-latest Maastrichtian), very close to the Cretaceous-Tertiary boundary. The misfit of the calibrations of the eggshell biostratigraphy is shown graphically in Figure 5. One or both successions are probably wrongly calibrated. As it has already been commented, the magnetostratigraphic correlations in the Aix basin are not yet reliable enough, and can be responsible for the lack of agreement between both eggshell-based biostratigraphic successions.

As in many other biostratigraphic conflicts, good guide fossils can show correlation problems. The biochronologically irrelevant fossils do not show conflicts because they have mostly random distribution. The quality of the eggshell biostratigraphy needs yet to be proved, since it is at its beginnings. However, its test in the Pyrenean-Provençal regions suggests that it can be a reliable dating tool, which will be verified when confident calibrations would be available.

CONCLUSION

The record of the Late Cretaceous dinosaur eggshells is sufficiently large, frequent and extended in time and space to be a very important fossil record for dinosaur dating. Four continents contain a potentially rich source of biostratigraphic information, since different ootaxa assemblages appear in successive strata, and similar ootaxa are shared across wide regions. However, there are few cases with reliable calibrated eggshell successions. As a test case, the comparison between two eggshell-based biostratigraphic successions in two European basins, South-central Pyrenees (Spain) and Aix-en-Provence (France), reveals common patterns in the distribution of the same ootaxa, allowing establishing biostratigraphic correlations.

The eggshell succession in both regions shows the appearance of three successive oospecies, *Megaloolithus siruguei* - *M. mamillare* - *M. pseudomamillare* in the same order. However, the chronological calibrations of both successions do not fit to each other. In the south-Pyrenean basin this oospecies succession appears in the lowermost depositional sequence Aren-2, dated in Late Campanian. Two more overlaying depositional sequences contain different oospecies including new ootaxa (Plate 1). The dinosaur eggshell record stops there around 3 Ma before the KTb. In contrast, in the Aix basin the three oospecies succession is dated from latest Campanian to Latest Maastrichtian, very close to the Cretaceous-Tertiary boundary. This significant disagreement in the chronostratigraphic calibrations appears not only between both regions, but also within the Aix basin, when comparing magnetostratigraphy from the

Eastern and Western parts. Thus the validity of eggshell biostratigraphy for dating continental sediments is supported by the consistent oospecies succession. The disagreement in chronostratigraphy may be probably caused by unreliable calibrations.

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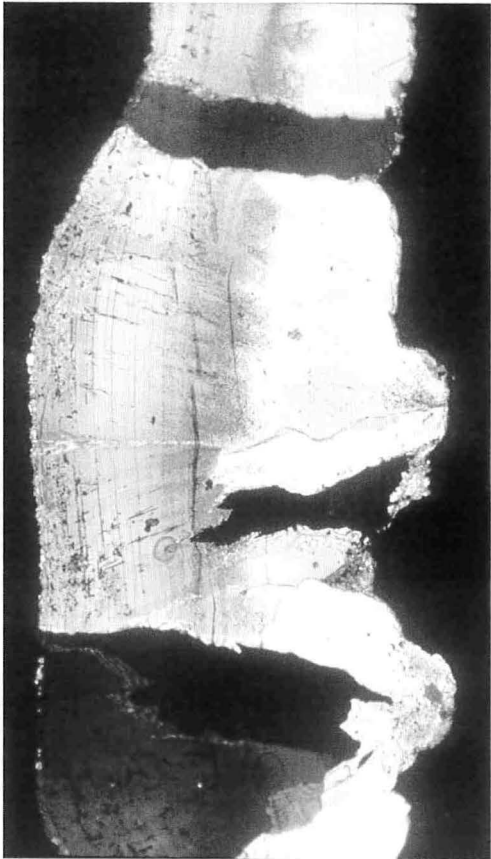
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PLATE 1

New ootaxon, aff. Megaloolithidae nov., from Blasi-2 (Huesca, Upper Maastrichtian); a) thin slide view through transmitted light; b) id. through polarized light, crossed nichols; c) SEM radial view; d) SEM external view.

The scarce, well-differentiated mamillae characterize the Megaloolithidae oofamily attributed to sauropod dinosaurs. Sauropod bones and teeth have been recorded also from Upper Maastrichtian deposits in Blasi and younger sites. Blasi-2 is the youngest dinosaur egg site of the south-central Pyrenean record, at least 2,5 Ma younger than its closest site (see Lopez-Martinez *et al.*, 1999; 2001).



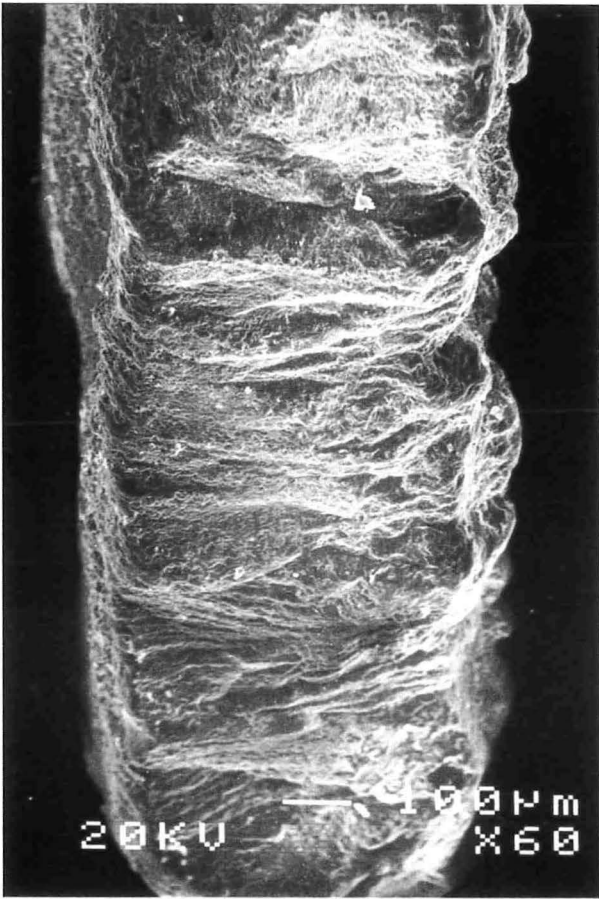
b



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a



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