Diversity versus variability in Megaloolithid dinosaur eggshells

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ISSN 1567–2158

2 tables, 5 figures

Abstract

Variability of dinosaur eggshell assigned to Megaloolithidae, from the Upper Cretaceous of Suterranya (Upper Campanian–Early Maastrichtian, Catalonia, South–Central Pyrenees), is described and compared with other Catalan, Argentinean, French, and Indian contemporaneous eggshells. Two–variable statistics using eggshell thickness and external diameter of eggshell units show discontinuous heterogeneity in the studied sample. Highly significant, stronger heterogeneity is also observed when comparing eggshell thickness from Suterranya to other neighbouring samples (Basturs, Coll de Nargó, Pioch Herbaut and Les Vignes) and India. Heterogeneity is interpreted as probably indicative of dinosaur polytypic diversity, instead of polymorphism of eggshell from one dinosaurian paleospecies. Variability distribution of eggshell thickness suggests a 15% coefficient of variation as the upper limit of a homogeneous intraspecific eggshell sample. The utility of eggshells as an indicator of nesting dinosaur diversity, particularly in the Catalan Pyrenees, is discussed.

Contents

1. Introduction

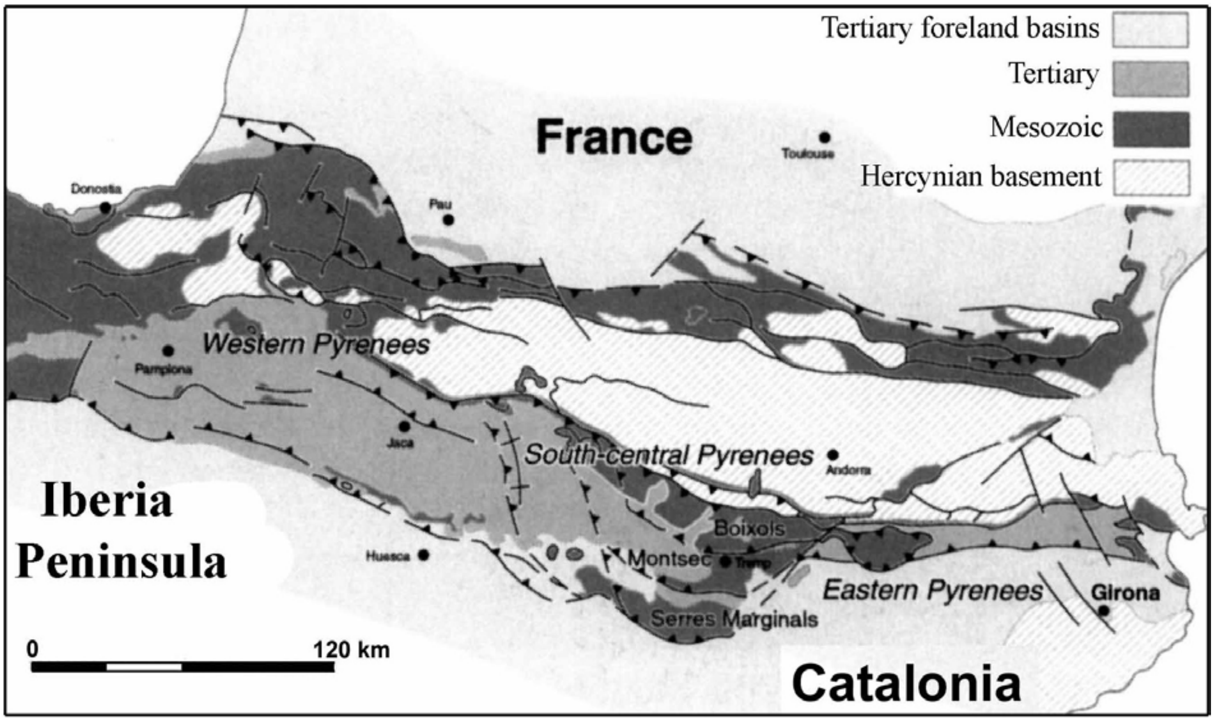

Figure 1. Geological map of the Pyrenean orogeny (modified from López–Martínez, 2000).

The Pyrenean realm contains well–exposed outcrops of the Cretaceous–Tertiary transition deposits (figure 1), where dinosaur eggshells are more abundant than dinosaur bones (Vianey–Liaud & López–Martínez, 1997; López–Martínez, 2000; Garcia & Vianey–Liaud 2001a, b; López–Martínez, 2003). These fossils, by means of parataxonomic studies, yield an important source of information on the diversity of dinosaurs during the Late Cretaceous. Oospecies from the Megaloolithidae oofamily, at least partly attributed to sauropods by Chiappe *et al*. (1998), have been used to infer the diversity of dinosaurs on both sites of the Pyrenees as well as of China, India and other European sites where they are particularly abundant (Zhao, 1979; Mikhailov, 1991; Vianey–Liaud *et al*., 1994; Mohabey, 1998, 2000).

The utility of eggshell features as indicators of biodiversity has been debated. Because of their high intraspecific variability in morphological features and surface patterns, Megaloolithidae ootaxa, unlike those of Elongatoolithidae (Zelenitsky *et al*., 2000), Spheroolithidae (Zhao, 1979; Zhao & Jiang, 1974; Zhao *et al.,* 1991; Mikhailov, 1994; Zelenitsky & Hills, 1997) and Ovaloolithidae (Mikhailov, 1994) are very difficult to recognise (Mikhailov *et al*., 1996). Peitz (1999) consider that *Megaloolithus* oodiversity at the oospecific level is artificial, because both metric and morphological eggshell characters show a large, continuous variability within egg clutches, as well as between eggshells from different localities and ages. Peitz (1999) also stated that all oospecies recognised in the South Pyrenean megaloolithid eggshell samples belong to a single oospecies, bearing a high variability and thus useless for biosystematics or biostratigraphic studies. However, Peitz (1999) did not run statistics analysis of the eggshells to test the homogeneity of his samples and the significance of his results. However, Panadés I Blas (2002) identified highly significant statistical differences in eggshell thickness between Catalan oospecies from Basturs, Coll de Nargó, and Suterranya.

A particularly intractable controversy has arisen about the eggshell sample composition of Suterranya (South Central Pyrenees, Catalonia, see Ardèvol *et al*., 2001 and figure 1). Moratalla (1993) distinguished two oospecies (*M. cf. mamillare* and '*M. trempii*'), while Vianey–Liaud & López–Martínez (1997) identified a single oospecies, *M. pseudomamillare*. A third different eggshell type, possessing thicker eggshells and slender eggshell units, has been identified during the course of this study (Panadés I Blas, 2002).

The aim of this study is to statistically evaluate the variability of a Megaloolithidae eggshell sample at Suterranya, and to reassess the utility of oospecies as diversity indicators for dinosaurs laying eggs in a particular environment. By the bracket of extant dinosaurs and crocodilians, we can infer oviparity in extinct dinosaurian clades; thus osteology would be a good diversity index for 'egg laying dinosaurs' because most or all probably laid eggs. The mystery is why lepidosaurians have evolved ovovivipary and vivipary so often, while archosaurs seem to be terrible at it.

2. Materials and methods

In total 1225 measurements were used. Catalonian egg data from Faidella (11 measurements for ET (eggshell thickness) and 9 for DU (diameter of unit) from figure A, Suterranya 1 (24 eggshell fragments; 18 of those from Panadés I Blas, (2001), and 86 for ET and 116 for DU) and Suterranya 15 (one eggshell fragment and 9 for ET and DU) are from Panadés I Blas (2001); Basturs and Coll de Nargó are from Peitz (2000 16 for ET and ET; 52 for ET and DU); Biscarri clutch (mixed egg and one egg sample, and 204 for ET) are from López-Martínez *et al*. (2000). French data, Les Vignes (74 measurements) and Pioch Herbaut (120 measurements) were obtained from Vianey-Liaud & Crochet (1994), and Rousset Erben 3 (42 measurements) and A (300 measurements) from Vianey-Liaud *et al.* (1994). Tackli (16 for ET, and 15 for DU), Pisdura 2 (6 for ET and 14 DU), and Jabalpur (22 for ET and DU) data from India were obtained from Vianey-Liaud *et al.* (1987); Auca Mahuevo (11 for ET and DU) data were obtained from thin section from an eggshell from a crushed egg (figure B).

Although, several metric characters in the Suterranya sample were considered, measurements from eggshell thickness and diameter of eggshell units would only be used in the following study, as they are the most commonly employed by oologists (Vianey-Liaud & Crochet, 1994; Carpenter, 1999; Peitz, 2000; López-Martínez *et al.,* 2000).

Eggshell thickness measurements were directly obtained from calibrated pictures of thin sections from the base of the mamillae to the top of the node; and diameter of eggshell unit from the widest horizontal line in a complete unit (figures 4 & 5). Using the PC version of Image, Image J 1.33, which captures real world dimensional measurements. This procedure avoids inaccurate measurements, such as would occur with eroded eggshells or the inclusion of sedimentary non-eggshell material, which lead to artificial eggshell thickness ranges.

In addition, to test how the inclusion of inaccurate measurements can affect the results, we have also analysed twice two samples from Rousset Erben (Vianey-Liaud *et al.,* 1994: 155): the first instance including eroded eggshells signalled by the authors (Rousset Erben C and 3), and the second instance excluding them (Rousset Erben C* and 3*).

3. Descriptive comparisons

A first univariable statistical analysis has been performed using a percentile comparison, to evaluate the variability of the eggshell thickness between different samples from different localities in a histogram (figure 2). The distribution of eggshell thickness has been compared between samples possessing the greater number of metric values, such as Suterranya, Coll de Nargó, and Pioch Herbaut. The results show in this case that there is not a uniform increase of eggshell variability with the in sample size. To analyse the level of significance of the eggshell thickness average differences, a Student T–test has been performed among all the samples (appendix table 1).

Coefficient of Variation (CV) calculation was applied for separated oospecies (between Suterranya 1 and Suterranya 15 samples, for example); for mixed samples (for example Suterranya 1+15); and between localities (appendix table 2). As a test of sample homogeneity (Biscarri, see López–Martínez *et al*., 2000), the CV of a highly variable eggshell sample from a clutch with a bimodally distributed eggshell thickness has also been calculated.

Secondly, diameter of eggshell units and eggshell thickness were subjected to bivariate analysis, comparing those samples where both variables were available (Suterranya 1, Suterranya 15, Coll de Nargó, Basturs, Tackli, Pisdura 2, Jabalpur and Auca Mahuevo). Samples from France and Biscarri could not be used, as data of their unit diameter were unavailable. The only values known from '*M. trempii*' were also included, to observe its relative position within the remaining Suterranya sample.

Finally, to define the limits of heterogeneity among the discontinuities of the eggshell thickness distribution, the CV was calculated for each locality and sample. The CV is a frequently used parameter for estimating the taxonomic homogeneity of (palaeo–)biological samples (Heaton, 1993; Kelley & Plavcan, 1998; Chandra & Pandya, 2001). In fact, it has previously been used to demarcate a threshold of morphological variation among species and populations (Sherley, 1996; Arnold & Phillips, 1999; Pessoa & Strauss, 1999; Melissa & Clark, 2000; Ellison *et al.,* 2004).

The amount of variation within samples can be measured using the CV. The standard variation as a measure of the dispersion of samples (Jones *et al*., 1998), is generally used as a percent ratio to the mean value, which allows an absolute, dimensionless value of the total variation. This statistic has the advantage that it can be calculated for any sample and compared by independent authors, while comparing canonical multivariate statistics requires a common database. The results of these relatively simple statistics can therefore be highly informative, and serve as a springboard for more sophisticated multivariate and landmark analyses.

4. Statistical results

The Suterranya sample exhibits almost the same distribution range of eggshell thickness (0.8–1.5 mm, range 0.7 mm) that Pioch Herbaut from France (0.7–1.5 mm, range 0.8 mm) and Coll de Nargó from Catalonia (1.9–3.2 mm, 1.3 mm) (figure 2 & 3). Therefore, Catalonian eggshells possess the same high variability of eggshell metric values observed in Megaloolithus oospecies from South America and India (Mohabey, 1998; Peitz, 2000; Garcia & Vianey–Liaud 2001).

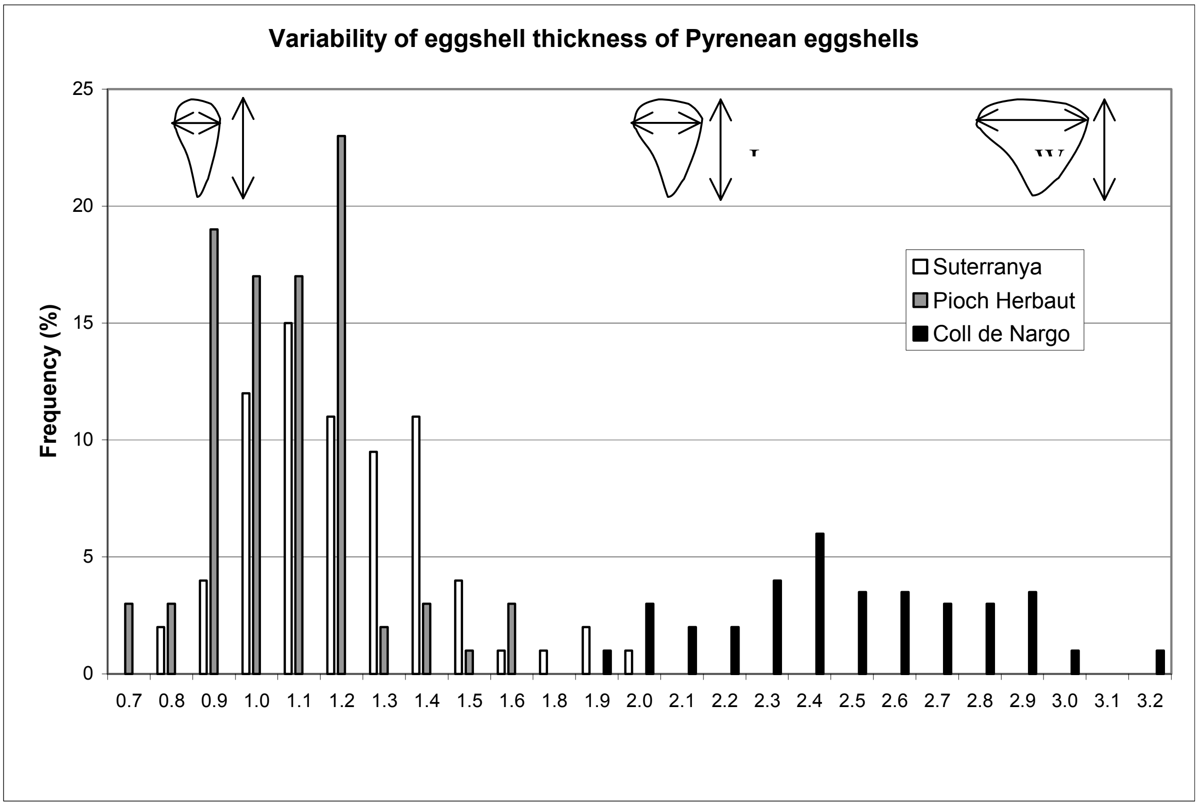

Figure 2. Variability of eggshell thickness between Suterranya, Coll de Nargó (Catalonia), and Pioch Herbaut (France). L = length; W = width.

In *Megaloolithus* oospecies, eggshell thickness is apparently the more variable feature, and its distribution has been suggested to be too uniform to be taxonomically significant (Peitz, 2000). However the Suterranya sample shows a discontinuous distribution in this variable. Instead of an incomplete sample from a continuous distribution, we interpret this discontinuity as a taxonomic gap. Discontinuous variation within a (palaeo–) biological sample can indicate a heterogeneous origin. In the case of fossil assemblages, taphonomic mixing must be first excluded, as presumably it is in this case because lack of reworking instances and high depositional rates (Ardèvol *et al*., 2000).

The discontinuous distribution in Suterranya *Megaloolithus* eggshell thickness is shown by the T–test (appendix table 1). Suterranya–15 and Suterranya–1 samples from the same locality differ from each other, showing statistically significant differences in eggshell thickness. Suterranya–15 groups instead with Faidella, Coll de Nargó and Basturs samples (appendix table 1 and figure 2). Suterranya–1 eggshells gather with Tackli, Pisdura 2, Jabalpur, and Auca Mahuevo (figure 2).

Eggshells from other Catalan localities and French sites also showed significant differences and discontinuous distribution in eggshell thickness (appendix table 1). Some of these differences are huge, such as between Biscarri and Les Vignes (probability p=7.4*10^–156). The statistical tests clearly demonstrate discontinuous distribution of the variables. These statistically significant differences suggest that *Megaloolithus* oospecies from Catalonia exhibit high heterogeneity and discontinuous variability.

Discontinuity is also shown by the bivariate statistical study. The plot between eggshell thickness and diameter of shell units is shown in figure 2, where the distribution clusters into two well–differentiated groups. The whole sample shows a similar range in the value of eggshell unit diameter, which varies roughly between 0.15 and 0.95 mm. The total sample was 1225 values; of those 268 were applied in the scatter and 889 for the

CV. The Suterranya 1 sample was composed of 202, and Suterranya 15 of 20 values. The value of eggshell thickness is much more scattered, ranging roughly between 0.7 and 3.7 mm and showing a clear bimodal distribution, with a sharp gap around 1.6–1.8 mm. This gap divides even small samples from a single locality, such as in the cases of Basturs and Faidella. The values of both variables are not correlated, and thus the highest and the lowest values in shell unit diameter correspond to similarly thin eggshells, while the thickest eggshells have intermediate values in eggshell unit diameter.

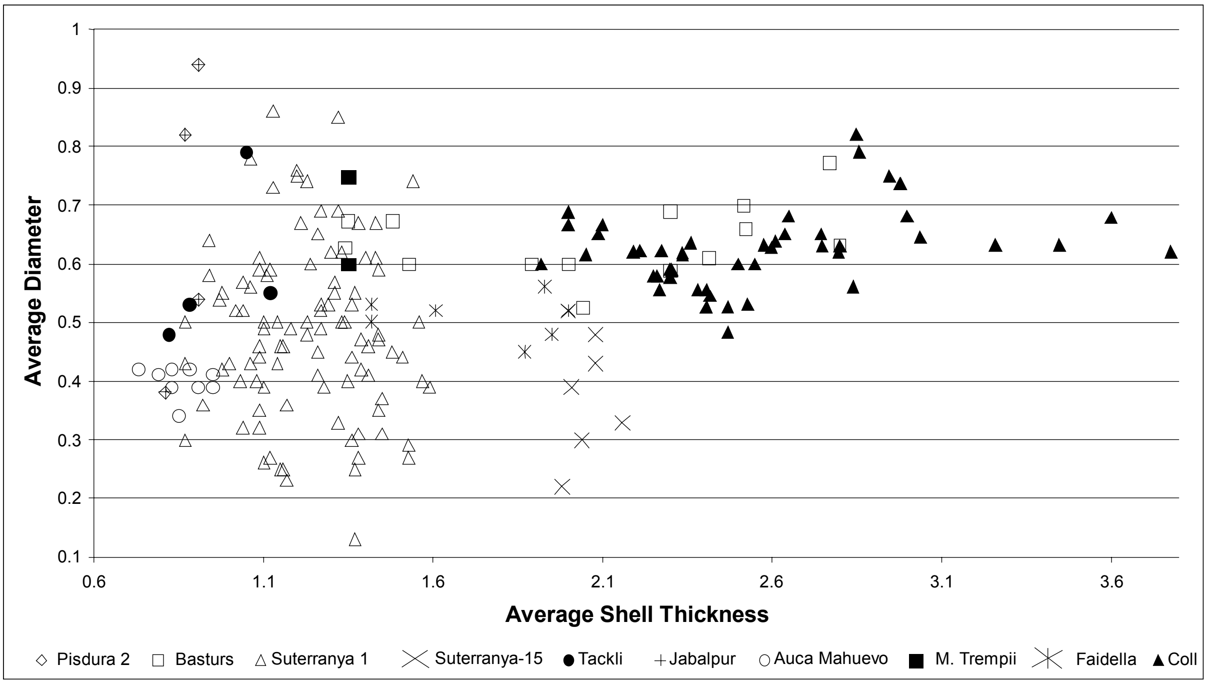

Figure 3. Relationship between eggshell thickness and diameter of unit of eggshells of samples from Peitz (1999) and Panadés I Blas (2001) (modified from Peitz, 1999). Most of eggshell thickness and Average diameter values from the Suterranya samples are paired, but, some are averages combining measurements.

In our study, localities that probably contain at least two oospecies (suspicious of taxic heterogeneity) exhibited the highest CV value (appendix table 2). Basturs possess the greatest value (CV=24.4%), followed by the whole Suterranya sample (1+15, CV=17.7%), Pioch Herbaut (CV=16.7%) and Coll de Nargó (CV=15.6%) (appendix table 2). Instead, localities and samples supposedly homogeneous have lower CV values, such as Biscarri One egg (CV=8.3%), Auca Mahuevo (CV=8.5%), Les Vignes CV=13.9%, Suterranya 1 (CV=14.1%) and Suterranya 15 (CV=14.5%). The amount of variation in eggshell thickness is not correlated with sample size. Comparing the CV for the 14 samples with highest homogeneity with sample sizes ranging from N=258 to N=4, the best correlation obtained with potential regression amounts R^2 = 0.106. Other regressions have even lower correlation coefficients.

In order to assess the oospecific diversity of each sample, we need to exclude heterogeneity due to differential preservation. The test made with two French samples with mixed, intact and eroded eggshells (Rousset Erben C and 3) shows that CV changes from 18.6% and 19.1% to CV=13.9% and 13.4% respectively when the values from the eroded shells are excluded (appendix table 2).

Therefore, a CV value of eggshell thickness of 15% marks a threshold between probably heterogeneous and homogeneous samples, either if heterogeneity is attributed to oodiversity or to differential preservation. This value is thus retained as a limit to the intra–specific variation in eggshell thickness. We propose the existence of a 15% upper limit for the CV value of eggshell thickness distribution for homogeneous, intra–specific eggshell samples.

We test this CV index value against a highly discontinuous sample from a single oospecies, studying the bimodal distribution of eggshell thickness from a clutch of seven eggs from Biscarri (Upper Campanian, Catalonia, López–Martínez *et al*., 2000). This large sample of well–preserved eggshells (N=312) has a highly variable eggshell thickness ranging from 2.1 mm to 3.5 mm, and a clear bimodal distribution either from a single egg (N=54) or from mixed eggshells from the clutch (N=258). In spite of the discontinuous, bimodal distribution, Biscarri sample shows homogeneous CV values (less than 15%) in eggshell thickness both from a single egg (CV=8.3 %), from mixed eggshells (CV=10.3%) and for both (CV=9.83%). These values are even lower than those belonging to other homogeneous, monospecific localities with smaller samples, as expected for the variability of a single clutch.

5. Discussion and conclusions

The two unpublished samples from '*M. trempii*' kindly provided by J.J. Moratalla (Museo Geominero, Madrid) exhibits round–shaped units and an eggshell thickness of 0.6 and 0.75 mm (Moratalla 1993). These eggshells fit perfectly well within the range of *M. pseudomamillare* (figure 2); therefore the distinction between the informal oospecies '*M. trempii*' and *M. pseudomamillare* is still insufficient to formalise its taxonomic status.

Conversely the Suterranya sample contains a different eggshell type, although it is represented by a single specimen labelled Suterranya 15. The fan–like shell units of *Megaloolithus sp*. from Suterranya 15 are higher, slender and more cylindrical than *M. pseudomamillare* and they overlap more against each other (figure 4). This morphology is more similar to other eggshells like Faidella or Biscarri that share slender units although a stronger eggshell thickness (appendix table 2 and figure 5; see López–Martínez, 2000: 108, Fig. 19). Apart from exhibiting morphological differences, *Megaloolithus sp.* also shows statistical significant differences in eggshell thickness to *M. pseudomamillare* (appendix table 1). However, a new oospecies name cannot be validated until more eggshell material from Suterranya can be studied.

In summary, Suterranya exhibits a diversity of two oospecies, *M. pseudomamillare*, by far the most abundant one, and *Megaloolithus sp.,* which cannot be well characterised until additional research would yield new material from this egg type. Therefore, at the end of the *Megaloolithus* record, its oodiversity is likely to be represented by at least two oospecies instead of only being represented by *M. pseudomamillare* as outlined by Vianey–Liaud and López–Martínez (1997).

Localities with mixed *Megaloolithus* eggshell samples, where possibly more than one oospecies is present, shared a CV higher than 15% in eggshell thickness. In contrast, when a single oospecies is probably present (*e.g.* when eggshells from the same clutch are compared), their eggshell thickness distribution always has a CV lower than 15% (appendix table 2). Therefore, a CV=15% is chosen as an upper boundary for assessing the homogeneity of eggshells from a sample. The Suterranya *Megaloolithus* eggshell sample is thus heterogeneous, as shown by the univariate and bivariate statistics of the shell units. This 15% limit may also confirm that Les Vignes possessed a single *Megaloolithus* oospecies, and Pioch Herbaut may contain two oospecies as suggested by Vianey–Liaud & Crochet (1994). Also, the homogeneity and morphological characteristics shared by Auca Mahuevo, Jabalpur and Rousset–Erben eggshells (appendix table 2, figure 2, figure 5; Vianey–Liaud *et al.* 1987: 415, Fig. 5A, B; Vianey–Liaud *et al.,* 1994: 159, Fig. 11.6D, E), may suggest a taxonomic relation among eggshells from these localities.

The heterogeneity of eggshell samples suggests diversity of egg–laying dinosaurs. It is not compatible with different dinosaurs laying similar eggs. In such case, it would be difficult to explain why there are localities with homogeneous eggshells. The observations also indicate statistically significant differences in *Megaloolithus* eggshell thickness between localities. Therefore, the hypothesis that all of the eggshells are variations of a single ootaxon (Peitz, 2000) is highly probable. If such uniformity would exist, it would imply a random distribution of variation among localities, a continuous distribution of eggshell thickness within each sample, and lack of statistically significant differences among samples. These predictions are not shown by the statistical results of this paper. Instead, the observed clustered distributions of variability among localities suggest that different oospecies coexist, represented by samples with CV less than 15% in eggshell thickness. Each oospecies probably was laid by a particular dinosaur species alike other dinosaur ootaxa mentioned above and extant reptiles (Schleich & Kastle, 1988). The observed discontinuous distribution in eggshell thickness of the Catalan samples strongly suggests that different oospecies were laid by different species of dinosaur, as stated by Vianey–Liaud & López–Martínez (1997), Mohabey (1998, 1999), and Garcia & Vianey–Liaud (2001a, b). Nonetheless, because no embryonic or postnatal sauropod skeletal remains have been found within or closely associated with the Catalan samples, the ownership of the different oospecies cannot be directly attributed to a particular species of sauropod dinosaur. This is however not necessary in order to estimate the diversity of dinosaurs based on ootaxa. Thus, it is concluded that the Megaloolithidae oospecies are valid indicators of the biodiversity of nesting dinosaurs in the Catalan Pyrenees during the Late Cretaceous period.

The study of *Megaloolithus* eggshells to evaluate the diversity/variability has encountered the same problems by taxonomists working with bone or tooth structures. The method applied here and the results on eggshells are similar to those in ordinary biosystematics:

- Inter–specific is less than intra–specific variation
- Mixed associations composed of two or more taxa exhibit discontinuity (heterogeneity) in the distribution, that can show significant statistical differences within two taxa coexisting together

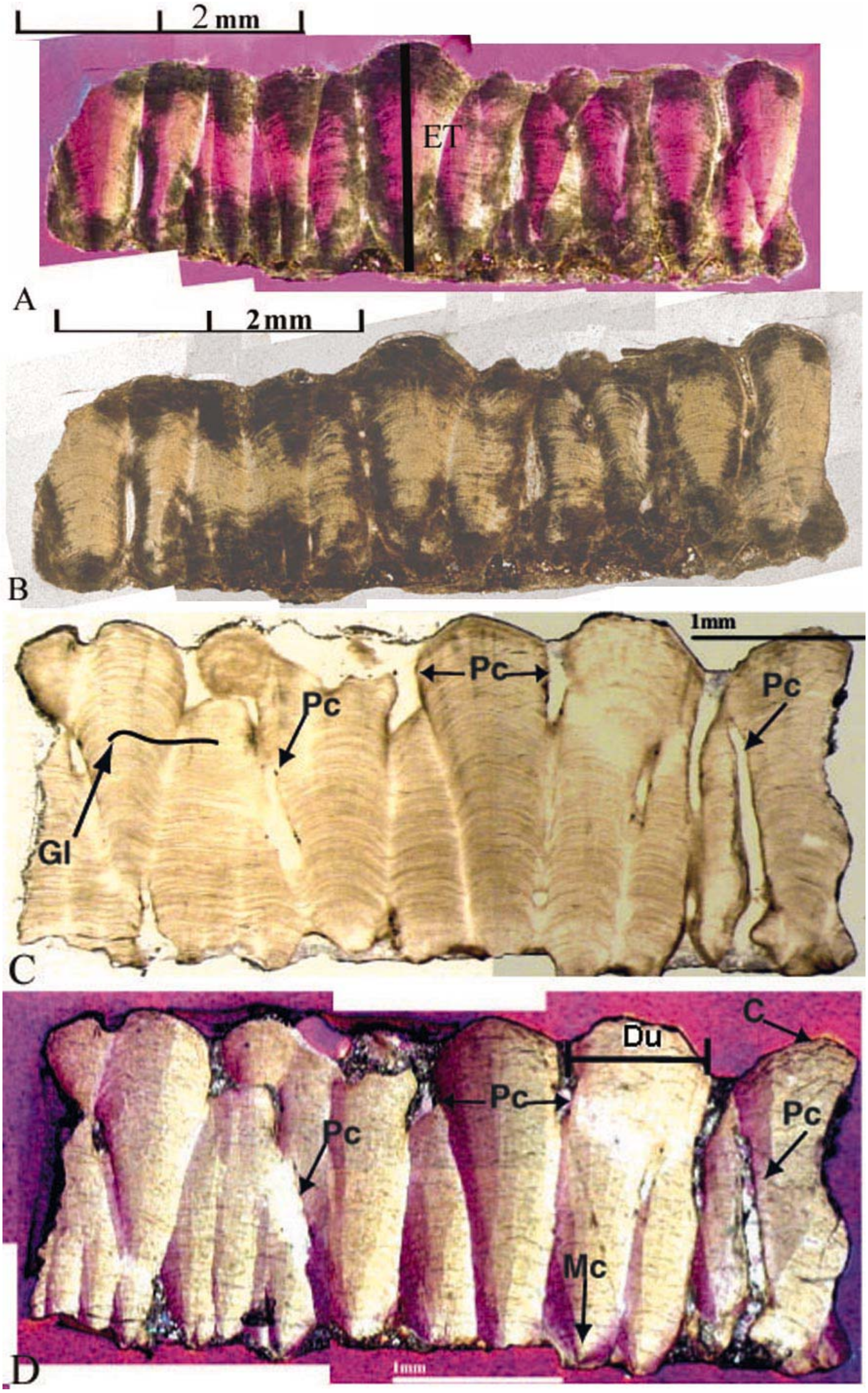

Figure 4A, B. Cross–section view of S1, Megaloolithius pseudomamillare; *figure 4C, D. S15* Megaloolithius nov.*; A and C under light and B and D under petrographic microscopes respectively. The eggshell materials will be deposited at the l'Institut d'Estudis Ilerdencs (Catalonia); S1=Suterranya 1, S15=Suterranya=15, C =cuticle, Du=Diameter of units, ET=Eggshell Thickness, GL=growth layers, MC=mamillare core, and PC=pore canals.*

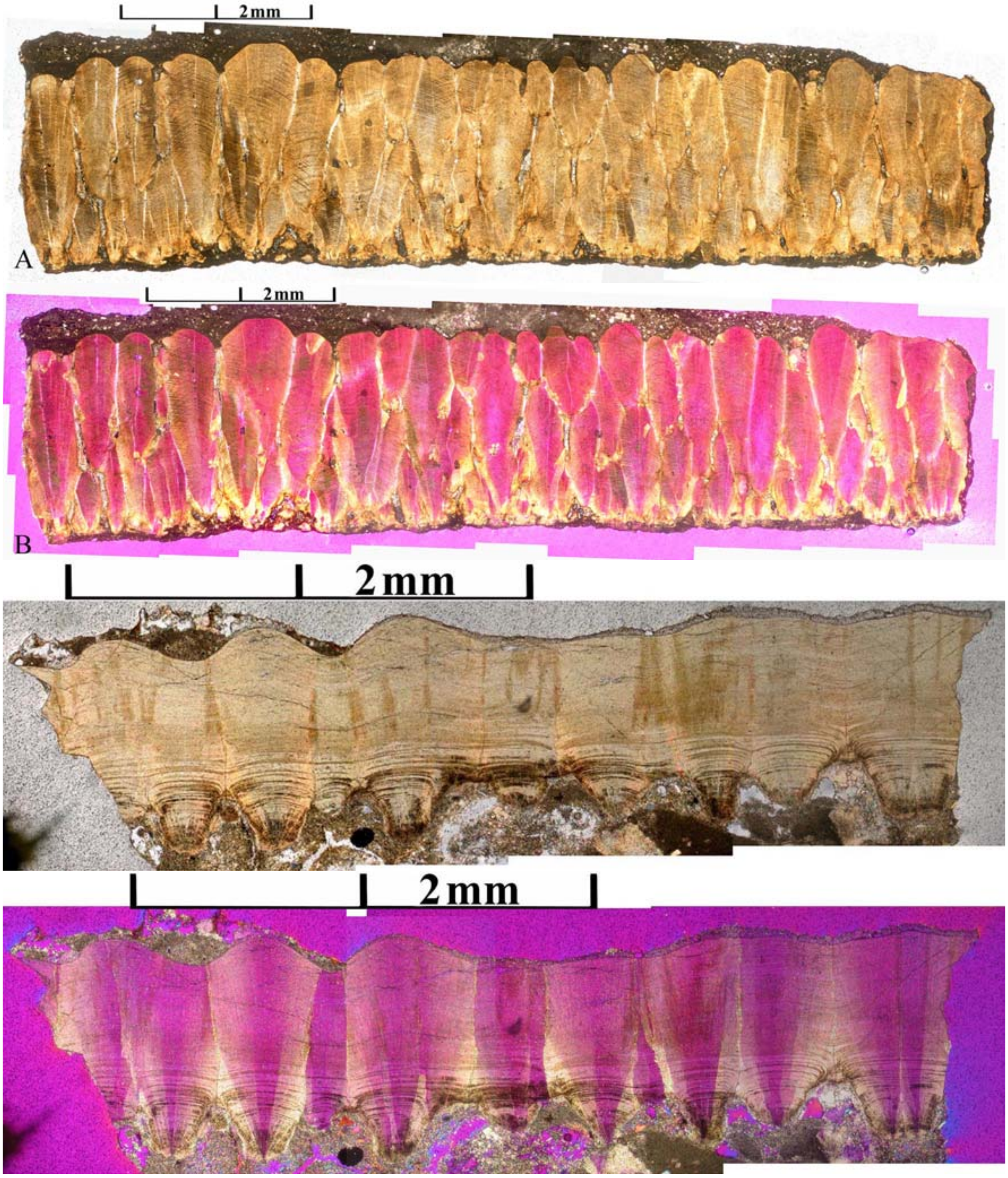

Figure 5A, B. Cross–section view of F1, Megaloolithius nov. *from Faidella (Catalonia); figure 5C, D. AM1* Megaloolithius patagonicus *from Argentina oospecies; A and C under light and B and D under petrographic microscopes respectively. The eggshell materials will be deposited at the l'Institut d'Estudis Ilerdencs (Catalonia); F1=Faidella 1, AM=Auca Mahuevo 1, ET= eggshell Thickness, GL= growth layers, MC= mamillare core, and PC=pore canals.*

- A (oo–) taxon shows homogeneity when its populations from different associations are compared, particularly if geographically separate, such as is the case of *M. pseudomamillare* from both sides of the Pyrenees.

In addition, the inclusion of eggshell thickness values from eroded eggshells dramatically alters *Megaloolithus* eggshell analyses. Eggshells from Rousset–Erben samples must be interpreted as belonging to a single oospecies since they come from a single clutch, and thus they had to show homogeneity. However, homogeneity test (CV less than 15%) is only achieved when values from eroded eggshells are excluded from the analyses (which would be expected). Therefore, accurate oodiversity results need eggshell measurements to be taken only from complete crystal units, as directly from the thin sections. Measurements obtained in the field are less accurate and may contain inexact values. Thin sections allow observation of the completeness of eggshell units, and a software program can provide exact measurements on the pictures. Thus, including values of eggshell thickness from incomplete units could lead to unrealistic ranges, and hence to misleading statistical analyses.

6. Acknowledgements

Support is gratefully acknowledged from the project BTE2002–01430 (Ministerio Ciencia y Tecnología, Spanish State), particularly from Dr. Nieves López–Martínez (UCM) for her constant help during the two years of developing the study. Also thanks to Dr. Mike Benton for giving me the opportunity to undertake a Masters in palaeontology and dinosaurs at Bristol University; Lluis Ardèvol for all the geological and moral help; and Dr. J. Moratalla for sending information from his PhD thesis and instructive talks. Many thanks also to my partner Stephanie, who has supported in the many bad moments and encouraged me to carry on with this project and in this field.

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Appendix

	Basturs	Suterranya 1	Suterranya 15	Faidella	One egg	Mixed egg	Tackli	Pisdura 2	Jabalpur	Les Vignes	Pioch Herbaut	Rousset Erben 3	Rousset Erben 3*	Rousset Erben C	Rousset Erben C*	Auca Mahuevo
Coll	5.0E-03	2.1E-30	1.5E-05	3.8E-11	2.1E-05	2.8E-04	6.8E-30	8.0E-30	2.8E-21	1.1E-32	1.9E-31	2.8E-33	3.2E-31	4.8E-34	2.8E-31	2.2E-34
Basturs	X	2.4E-05	5.1E-02	8.4E-01	6.7E-05	1.7E-04	5.0E-07	5.2E-07	5.2E-05	3.9E-06	8.0E-06	1.2E-05	2.8E-05	6.7E-06	2.1E-05	4.3E-07
Suterranya 1	X	X	1.5E-03	8.2E-20	7.6E-61	1.2E-145	3.0E-06	2.9E-06	3.6E-02	2.4E-09	1.4E-04	1.6E-10	5.3E-01	2.7E-03	7.9E-01	1.6E-10
Suterranya 15	X	X	X	1.5E-02	7.0E-06	2.4E-05	3.7E-05	6.4E-05	2.9E-03	3.3E-04	5.9E-04	5.4E-05	1.6E-03	4.5E-04	1.3E-03	5.4E-05
Faidella	X	X	X	X	3.7E-25	4.0E-18	2.0E-15	2.7E-10	3.0E-18	5.0E-20	1.3E-18	1.1E-24	6.0E-22	2.6E-27	2.5E-22	9.6E-17
One egg	X	X	X	X	X	7.6E-02	2.4E-26	5.1E-23	9.7E-49	5.1E-62	3.6E-60	1.6E-53	3.3E-51	2.6E-67	4.1E-61	1.7E-38
Mixed egg	X	X	X	X	X	X	3.8E-19	1.8E-11	5.5E-42	7.4E-156	1.6E-202	8.2E-47	2.6E-44	6.1E-85	4.6E-82	1.9E-23
Tackli	X	X	X	X	X	X	X	3.7E-01	1.8E-07	6.0E-03	2.5E-04	1.3E-23	1.0E-06	4.3E-04	3.8E-06	2.2E-01
Pisdura 2	X	X	X	X	X	X	X	X	1.4E-07	3.5E-04	7.3E-05	2.8E-07	2.6E-08	4.7E-06	5.4E-07	6.2E-01
Jabalpur	X	X	X	X	X	X	X	X	X	1.1E-09	1.4E-06	9.7E-03	2.7E-01	1.7E-05	3.1E-02	8.3E-10
Les Vignes	X	X	X	X	X	X	X	X	X	X	6.3E-03	4.0E-03	2.7E-06	6.0E-02	6.0E-07	2.2E-06
Pioch Herbaut	X	X	X	X	X	X	X	X	X	X	X	1.9E-01	1.2E-03	8.9E-01	2.2E-03	5.9E-08
Rousset Erben 3	X	X	X	X	X	X	X	X	X	X	X	X	1.4E-01	2.2E-01	3.5E-01	2.9E-09
Rousset Erben 3*	X	X	X	X	X	X	X	X	X	X	X	X	X	3.4E-03	4.3E-01	2.0E-11
Rousset Erben C	X	X	X	X	X	X	X	X	X	X	X	X	X	X	1.0E-02	1.9E-08
Rousset Erben C*	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	6.0E-11
Auca Mahuevo	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X

Table 1. Results of the Student t-test comparing the average eggshell thickness between Catalan, French, Argentinean, and Indian samples. means without eroded eggshells.*

	Basturs	**Suter-ranya 1**	**Suter-ranya 15**	**Faidella**	**One egg**	**Mixed egg**	**Tackli**	**Pisdura 2**	**Jabalpur**	**Les Vignes**	**Pioch Herbaut**	**Rousset Erben 3**	**Rousset Erben 3***	**Rousset Erben C**	**Rousset Erben C***	**Auca Mahuevo**
Coll (15.9)	19.6	40.9	19.3	16.8	13.3	11.6	35.2	24.4	30.7	47.2	45.6	39.4	35.4	44.6	39	31.4
Basturs	24.4	28.9	23.6	19	16.4	12.3	46.9	37.6	31.9	36.6	30.6	36.1	33.1	36.3	32.4	45.4
Suterranya 1	X	14.3	17.4	21.9	44.7	31.6	16.9	15.3	13.5	15.9	15.6	18.9	18.1	19.2	17.5	20.0
Suterranya 15	X	X	14.5	12.2	15.8	12	36.9	33.7	17.9	22..3	19.7	23.8	20	24.3	19.3	38.9
Faidella	X	X	X	3.2	13.1	11.3	42.7	33.8	24.4	13.9	15.7	29.7	26.2	30	25.4	42.7
One egg	X	X	X	X	8.3	10	33.4	20.5	30.1	49.9	49.7	40.5	36	29.3	40.7	28.8
Mixed egg	X	X	X	X	X	10.3	18.3	13.4	17.8	31.6	35.9	24	21.3	20.4	24.9	16.5
Tackli	X	X	X	X	X	X	17.3	15.6	19.2	15.2	16.8	21	19.7	19.8	17.6	14..9
Pisdura 2	X	X	X	X	X	X	X	5.4	15.2	14.3	16.1	19.7	16.8	18	15.1	7.5
Jabalpur	X	X	X	X	X	X	X	X	8.2	15.1	15.4	16.1	11.9	17.1	12.1	19.5
Les Vignes	X	X	X	X	X	X	X	X	X	13.9	15.3	19.9	15.8	17	15.1	14.9
Pioch Herbaut	X	X	X	X	X	X	X	X	X	X	15.7	16.6	15.8	17	15.3	16.7
Rousset Erben 3	X	X	X	X	X	X	X	X	X	X	X	18.6	16.7	19.1	15.8	21.1
Rousset Erben 3*	X	X	X	X	X	X	X	X	X	X	X	X	13.9	18.2	13.4	19.5
Rousset Erben C	X	X	X	X	X	X	X	X	X	X	X	X	X	19.4	17.2	20.5
Rousset Erben C*	X	X	X	X	X	X	X	X	X	X	X	X	X	X	13.2	17..2
Auca Mahuevo	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	8.5

*Table 2. Coefficient of variability from and between the eggshell thickness of megaloolithid dinosaur eggshells from Catalonia, France, Argentina, and India. Data source: see material and methods. Coll de Nargo's Coefficient of variability within brackets. * means excluding* eroded eggshell.

Submitted: 27 September 2004.
Published: 1 April 2005.