

Upper Cretaceous titanosaur nesting sites and their implications for sauropod dinosaur reproductive biology

by

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With 14 text-figures

Summary

Megaloolithid dinosaur eggs are distributed nearly worldwide in Late Cretaceous terrestrial sediments, the most important regions of occurrence being southwestern Europe, central India, and the spectacular Auca Mahuevo site in Argentina. Based on finds from the Argentinian site, eggs classified within the oogenus *Megaloolithus* of the traditional fossil egg parataxonomy are believed to have been produced by titanosaurian sauropods.

Here we review the geologic context, taphonomy, nest structure, clutch morphology, shell thickness variation, and shell porosity of *Megaloolithus* occurrences from Europe, India, and Auca Mahuevo, Argentina. We focus on the implications of the data for the reproductive biology of sauropod dinosaurs. Although virtually all occurrences are from paleosols of varying maturity, there are striking differences between the European and Indian sites on one hand and Auca Mahuevo on the other. Clutch size is < 8 in the former and < 40 in the latter, shell porosity is very high in the former and low in the latter. Eggs at Auca Mahuevo are also smaller than those in Europe and India. Based on detailed data for inter-clutch and intra-clutch variation of shell thickness and porosity in clutches from the Spanish site of Coll de Nargó, all *Megaloolithus* eggs from Spain and probably from southern France pertain to a single oospecies, *M. mammilare*. Those from Auca Mahuevo belong to *M. patagonicus*.

Clutches from Europe and India were buried in the substrate and incubated by environmental heat, whereas those from Auca Mahuevo were deposited in an open nest structure and remained uncovered by sediment or plant material. Colonial nesting cannot be proven for the Indian and European occurrences, high density of clutches being the result of prolonged use of a site. Colonial nesting seems likely at Auca Mahuevo, but contradictions in the interpretation of this site remain.

Very small clutch size and clutch mass compared to estimated adult female mass suggests that the European and Indian titanosaurs produced multiple clutches per nesting season. In both the European and Indian as well as the Auca Mahuevo occurrences, small egg size and inferred large egg number suggests that titanosaurian sauropods were r-strategist. This reproductive strategy was obligatory due to the obligatory ovipary imposed by the calcareous eggshell combined with biomechanical limitations on maximum egg size.

Key words: *Megaloolithus* – Sauropoda – reproductive biology – r-strategy – Upper Cretaceous – Argentina – France – India – Spain

Zusammenfassung

Dinosaurier-Eier aus der Oofamilie Megaloolithidae kommen fast weltweit in oberkretazischen terrestrischen Sedimenten vor. Die wichtigsten Fundregionen sind Südwesteuropa, Zentralindien und die spektakuläre Fundstelle Auca Mahuevo in Argentinien. Aufgrund von Funden von Embryonen in Eiern von dieser Lokalität wird angenommen, dass Eier des Oogenus *Megaloolithus* von titanosauriden Sauropoden gelegt wurden.

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In dieser Arbeit geben wir einen Überblick über den geologischen Kontext, die Taphonomie, Neststruktur, Gelegeomorphologie, Dickenvariation der Schale und Schalenporosität von *Megaloolithus*-Eiern aus Europa, Indien und Auca Mahuevo, Argentinien. Wir konzentrieren uns auf die Implikationen dieser Daten für die Reproduktionsbiologie der sauropoden Dinosaurier. Obwohl fast alle Vorkommen aus Paläoböden unterschiedlicher Reife stammen, gibt es auffällige Unterschiede zwischen den europäischen und indischen Vorkommen einerseits und Auca Mahuevo andererseits. Die Gelegegröße ist < 8 Eier in ersteren, während sie < 40 Eier an letzterer Fundstelle beträgt. Außerdem ist die Porosität der Schalen bei den europäischen und indischen Vorkommen sehr hoch, aber gering in Auca Mahuevo. Die Eier von dort sind auch kleiner als jene aus Europa und Indien. Aufgrund unserer umfangreichen Daten über die Variation der Schalendicke und -porosität in den Gelegen aus der spanischen Fundstelle Coll de Nargó gehören alle *Megaloolithus*-Eier aus Nordspanien und vermutlich alle Funde dieser Gattung aus Südfrankreich zu einer einzigen Oospezies, *M. mammillare*. Die Eier aus Auca Mahuevo gehören zu *M. patagonicus*.

Die Gelege aus Europa und Indien wurden im Substrat vergraben und durch Umwelt-Wärme ausgebrütet, während die Gelege aus Auca Mahuevo in offenen Neststrukturen deponiert wurden und von Sediment oder Pflanzenmaterial unbedeckt blieben. Koloniales Nisten kann für die europäischen und indischen Vorkommen nicht belegt werden, sondern die hohe Dichte der Gelege in manchen Fundstellen ist das Resultat lang andauernder Belegung. Im Gegensatz dazu ist koloniales Nisten für Auca Mahuevo wahrscheinlich, aber es gibt noch Widersprüche in der Interpretation des Vorkommens.

Die sehr geringe Gelegegröße und -masse im Vergleich zur geschätzten Masse des Muttertieres in den europäischen und indischen Vorkommen macht es wahrscheinlich, dass diese Titanosaurier mehrere Gelege pro Saison produzierten. Sowohl die europäischen und indischen als auch das argentinische Vorkommen mit ihren geringen Eigrößen und daraus abgeleiteter hoher Eierzahl legen nahe, dass titanosauride Sauropoden r-Strategen waren. Diese Reproduktionsstrategie war wegen der Ovipary der Dinosaurier (aufgrund ihrer verkalkten Eierschalen) in Kombination mit der biomechanischen Obergrenze für die Größe von Eiern obligatorisch.

Schlüsselwörter: *Megaloolithus* – Sauropoda – Reproduktionsbiologie – r-Strategie – Oberkreide – Argentinien – Frankreich – Indien – Spanien

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1. Introduction

Titanosaurs were a highly successful and nearly cosmopolitan group of sauropod dinosaurs that survived until the end of the Cretaceous (WILSON 2002, UPCHURCH et al. 2004). Late Cretaceous eggs and eggshells classified as *Megaloolithus* in the traditional egg parataxonomy from the Upper Cretaceous of Europe, India, and South America are often associated with titanosaurs, based on osteological remains within the same horizon or formation (BUFFETAUT & LE LOEUFF 1994, SAHNI et al. 1994, MIKHAILOV 1997, CARPENTER 1999, MOHABEY 2001). Recent discovery of the first identifiable embryos in *Megaloolithus* eggs from Argentina (CHIAPPE et al. 1998, 2005, SALGADO et al. 2005) further supports this taxonomic assignment. Titanosaurs, therefore, are unique among sauropod dinosaurs in having a rich fossil record of eggs, extensive nesting horizons, and eggs with embryonic remains. In fact, the only other proven record of eggs containing embryos among sauropodomorphs are those of *Massospondylus* from the Upper Triassic of South Africa (REISZ et al. 2005).

Egg morphology, eggshell microstructure, geochemistry (eggshell and sediments), egg and clutch arrangement, and taphonomy also provide valuable information for understanding titanosaur reproductive biology. This important information may provide insights regarding the evolution of gigantic body size in this clade. In addition to containing previously unpublished information and observations, this paper attempts to synthesize what is known about titanosaur nesting sites worldwide and to consider possible implications of this data for titanosaur reproductive biology. Furthermore, we emphasize the importance of studying eggs within a taphonomic framework: once removed from the sediments, much scientific value is lost. A recent synthesis by CARPENTER (1999) and a review by HORNER (2000) on dinosaur eggs and nesting represent points of departure for discussing titanosaur reproductive biology.

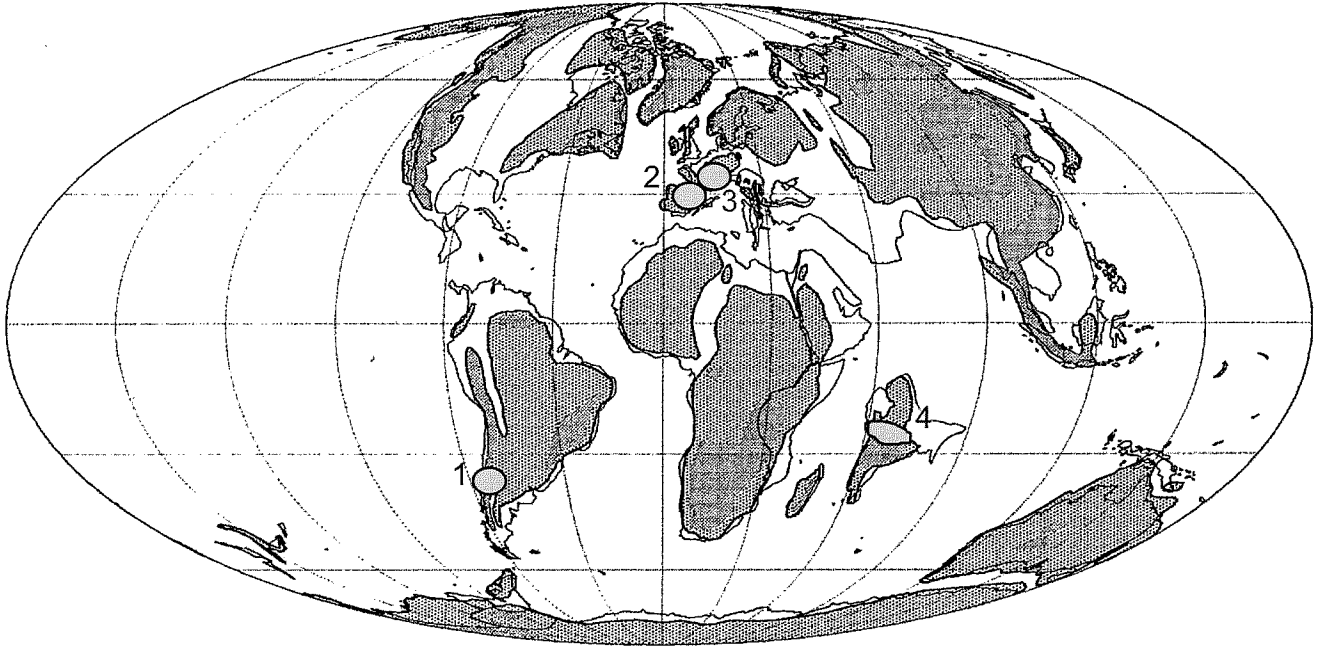
We review and analyze megaloolithid localities from Argentina, Europe, and India in detail, and discuss common patterns, including two different strategies of reproductive biology. The Catalan localities have been studied extensively by PMS and CP. Although the French localities have been examined cursorily by CP and PMS, we relied for much of the data on the work of DUGHI, SIRUGUE, KÉROURIO, COUSIN, BRETON, LE LOEUFF, and ERBEN, as reviewed in depth by COUSIN et al. (1994) and COUSIN (2002). The treatment of the Indian localities is solely based on the literature.

1.1 Terminology

Various descriptive terms are applied to dinosaur eggs and nesting horizons. To avoid confusion, we briefly discuss terminology used in this paper. Eggshell refers to both the mineralized outer covering of the egg and to dispersed fragments in the rock. The upper portion of the egg, that in some modern species becomes separated during hatching, is referred to as the cap (MUELLER-TÖWE et al. 2002). This feature was first referred to as the "operculum" by COUSIN et al. (1989) and later changed to "hatching window" by these authors (COUSIN et al. 1994). Clutch refers to a close association of multiple, in situ eggs that occur within sediments and show no evidence of transport; the term nest is restricted to a preserved trace fossil that shows truncation of primary sedimentary structure resulting from excavation by the adult dinosaur. Cover refers to soil and/or significant vegetation surrounding and covering a clutch in which eggs are incubated (i.e. substrate burial or vegetation mound).

1.2 *Megaloolithus* eggs: affinities, distribution, parataxonomy

The parataxonomic oofamily Megaloolithidae includes several egg genera: *Megaloolithus*, *Cairanoolithus*, *Dughioolithus*, and *Sphaerovum* (MIKHAILOV 1997, CARPENTER 1999, VIANEY-LIAUD et al. 2003). Only *Megaloolithus* from Argentina, however, is referable to a biological species of titanosaurid sauropod based on identifiable embryonic remains within an egg (CHIAPPE et al. 1998, 2000, 2001, 2005, SALGADO et al. 2005). Therefore, we limit the following discussion to this oogenus and assume that titanosaurs of different biological species also produced similar *Megaloolithus* eggs from elsewhere in South America, Europe, Africa and India. By virtue of their exclusive occurrence in Upper Cretaceous rocks, we consider it likely that other oogenera of the oofamily Megaloolithidae were also produced by titanosaurian sauropods because titanosaurs are the only sauropods known from this time period with certainty (CURRY ROGERS 2005).



Text-fig. 1. Localities of *Megaloolithus* nesting sites plotted on a world map of the Late Cretaceous (Maastrichtian). 1 = Auca Mahuevo, Neuquén Prov., Argentina; 2 = Tremp Basin and Coll de Nargó, Catalunya Prov., Spain; 3 = localities in the Aix Basin and the northern Prepyrenees, France; 4 = localities in central India. Age of localities is Campanian (Auca Mahuevo) or Maastrichtian (Europe, India). Map base from SMITH et al. 1994.

The most thoroughly documented localities of *Megaloolithus* occur in Argentina, northern Spain, southern France and India (Text-fig. 1), as reviewed in detail below. Other occurrences are known from Romania (GRIGORESCU et al. 1990, 1994, CODREA et al. 2002), Korea (PAIK et al. 2004) and Africa (DANTAS et al. 1992; SWINTON, 1950, GOTTFRIED et al. 2004). Eggshell fragments were recently described from Tanzania (GOTTFRIED et al. 2004) from the same locality where a single egg was discovered previously (SWINTON 1950). The egg, however, shows significant diagenetic alteration and surface weathering that obscures the eggshell structural characteristics and therefore cannot be definitively referred to *Megaloolithus*.

GRIGORESCU et al. (1990, 1994) referred megaloolithid eggs from a site near the Romanian village of Tustea to the hadrosaurid *Telmatosaurus* on the basis of embryonic or hatchling bones found in the mudstone that contained the eggs (GRIGORESCU et al. 1990, 1994). However, the fossil material from this site was not in situ, but collected from a rock fall and the presence of a small theropod tibia "in the vicinity" further complicates the site taphonomy (GRIGORESCU et al. 1990). Furthermore, the eggshell structure differs from the *Spheroolithus* microstructure of hadrosaur eggs containing embryos from Montana (HIRSCH & QUINN 1990). For this reason, CARPENTER (1999) doubted the identification of the Romanian embryos and the assignment remains questionable. However, in 2002, new eggs with *Megaloolithus* microstructure were found at the same stratigraphic level as the earlier specimens described by GRIGORESCU et al. (1990, 1994). These clutches were again associated with a few hadrosaur hatchling limb bones and vertebrae (GRIGORESCU 2003). Future publication of a detailed taphonomic study of this locality and eggs containing identifiable embryos may clarify the phylogenetic affinities of these eggs. Until further evidence is presented, we assume that *Megaloolithus* eggs were laid by animals belonging to only one taxonomic group of dinosaurs (contra VIANEY-LIAUD et al. 2003), in this case titanosaurid sauropods. Note, however, that assignment of an egg to a taxon on any evidence other than embryonic remains within an egg (or an egg within a female, e.g. SATO et al. 2005) is uncertain, and such assumptions have proven fallacious (NORRELL et al. 1994, HORNER & WEISHAMPEL 1996).

Named *Megaloolithus* oospecies include a perplexing array of overlapping ranges of egg size and shell thickness. Over 20 oospecies are currently assigned to *Megaloolithus*; often only minor differences in microstructure characterize these different oospecies. As noted by CARPENTER (1999), the diversity of eggshell

“species” far exceeds the diversity of dinosaurs in some localities. Until recently, investigation of the variation that exists in a single egg and eggs within the same and different clutches was lacking. However, significant reduction in the number of megaloolithid oospecies appears justified by recent studies (PEITZ 1999, 2000a, VIANEY-LIAUD et al. 2003, see also below).

1.3 Previous work on megaloolithid dinosaur eggs

The first dinosaur eggshell to be discovered in the mid-19th century in southern France belongs to *Megaloolithus* (see historical review by BUFFETAUT & LE LOEUFF 1994) but the oogenus was only named in 1994 (VIANEY-LIAUD et al. 1994). Beginning in the 1950s, French and German workers speculated on dinosaur nesting biology, based primarily on the localities in France (DUGHI & SIRUGUE 1958a, b, 1966, ERBEN et al. 1979, KÉROURIO 1981a, b). However, a better understanding of dinosaurs and their reproductive biology has superseded much of this work. Modern analytical equipment and field techniques, including facies analysis, archaeological excavation procedures, and site taphonomy have contributed significantly to changing perceptions. Seymour’s work on *Megaloolithus* eggshell porosity represented a great advance for its sound predictions, based on egg physiology and nesting mode in modern taxa (SEYMOUR 1979). DEEMING (2006) also included much *Megaloolithus* material in his study on eggshell porosity and gas conductance, concluding that dinosaur eggs in general have porosity values indicative of incubation buried in a substrate. MOHABEY (1990, 1996) provides a brief but accurate interpretation of titanosaur nesting in India, based on field data from this country. Although criticized for over interpretation of the spatial distribution of the eggs (CARPENTER 1999), COUSIN et al. (1994, see also COUSIN 2002) give an important and detailed account of appropriate excavation techniques. A northern Spanish site analyzed by SANZ et al. (1995) purportedly provides evidence for colonial nesting in a beach habitat. This hypothesis, however, is no longer considered tenable and an emerged, abandoned beach sand is hypothesized instead (SANDER et al. 1998, LÓPEZ-MARTINÉZ 2000, see below). CALVO et al. (1997) described the first *Megaloolithus* eggs from the Neuquén Group in Neuquén Province, Argentina. The discovery of titanosaur embryos enclosed within *Megaloolithus* eggs from another locality in Neuquén Province (CHIAPPE et al. 1998) represented the most crucial discovery in the current context, providing this egg genus with its full biological meaning.

2. The four nesting sites: introduction and geologic setting

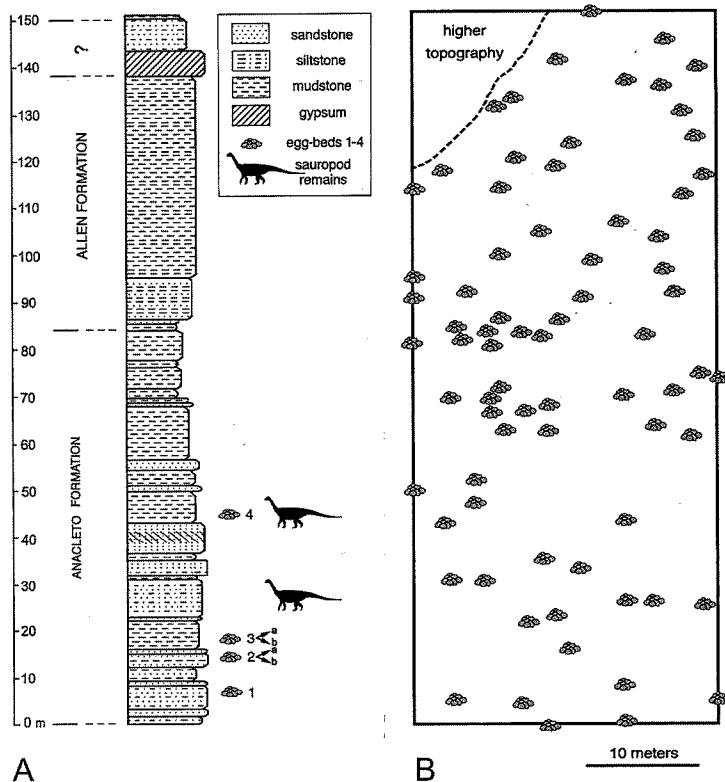
2.1 Auca Mahuevo, Argentina

In 1997, the extensive Auca Mahuevo nesting locality was discovered in Upper Cretaceous rocks of northwestern Patagonia, Argentina (Text-fig. 2). Located approximately 120 km north of Neuquén City, Neuquén Province, Argentina, Auca Mahuevo and adjacent sites have produced thousands of in situ titanosaur egg clutches (Text-fig. 2), many preserving embryonic bone and integument (CHIAPPE et al. 1998, 2000, 2001, 2005, DINGUS et al. 2000, CHIAPPE & DINGUS 2001, SALGODO et al. 2005). Auca Mahuevo is the only locality where titanosaur embryos are preserved within *Megaloolithus* eggs and where abnormal eggs have been found in situ.

2.1.1 Embryos from Auca Mahuevo

The embryos were originally identified as neosauropods within Eusauropoda, a taxon more closely related to *Saltasaurus loricatus* than to *Vulcanodon karibaensis* (WILSON & SERENO 1998). However, recent discovery of articulated embryonic skulls allows assignment to titanosaurid sauropods. The embryonic remains represent some of the most complete cranial material for any titanosaur taxon (CHIAPPE et al. 2001, SALGADO et al. 2005).

Eggs containing the embryonic remains often occur as weathered “float” on the erosional surface of egg bed 3. These well-cemented, partial eggs contain diagenetic calcite and the zeolite mineral analcime (JACKSON et al. 2004) and occasionally preserve soft tissue in the form of embryonic integument and eggshell membrane (CHIAPPE et al. 1998, GRELLET-TINNER 2005, SCHWEITZER et al. 2005), suggesting that very rapid burial coincided with unusual conditions during early diagenesis. Other eggs from the quarry in egg bed 3 contain



Text-fig. 2. Stratigraphic section (A) and contemporaneous clutches (B) from a site at Auca Mahuevo, Argentina. There are four distinct egg-bearing horizons, two of which are subdivided into two layers. (B) Egg clutches in the horizons are rather densely and regularly spaced as seen at site 1 in egg-bed 3. From CHIAPPE et al. 2005.

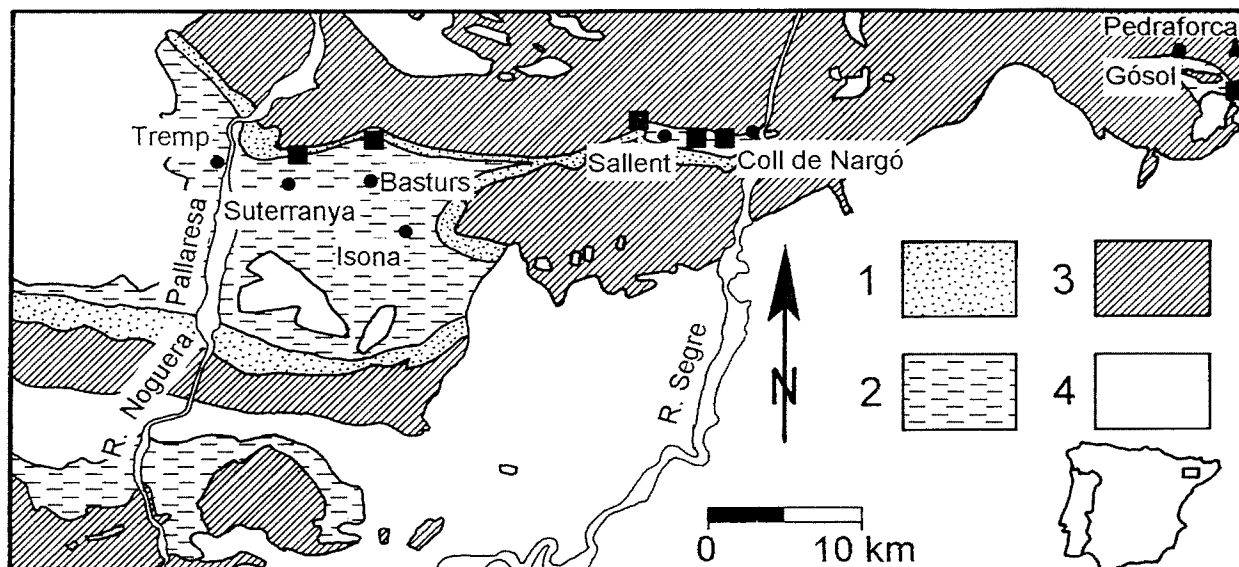
nearly complete, articulated embryonic cranial material (CHIAPPE et al. 2001, SALGADO et al. 2005) or bones that are disarticulated and compressed against the bottom of the egg (CHIAPPE et al. 1998). At Auca Mahuevo all embryos thus far discovered occur in egg bed 3 (CHIAPPE et al. 2000). However, two new localities 15 and 22 km south of Auca Mahuevo, Barreales Norte and Barreales Escondido, have also produced embryonic remains.

2.1.2 Abnormal eggs from Auca Mahuevo

Abnormal, multilayered eggshells occasionally occur in megaloolithid specimens. However, egg bed 2 and 3 at Auca Mahuevo produced the first in situ dinosaur clutches containing abnormal, multilayered eggs. Furthermore, these clutches represent the first abnormal eggs referable to an identified taxon, titanosaurid sauropods (JACKSON et al. 2004). Two study sites in egg beds 2 and 3, covering 3.000 m² and 35.000 m², respectively, contain 14 and 329 in situ egg clutches. These two study sites produced one clutch from egg bed 2 and five clutches from egg bed 3 that contain both normal and abnormal eggs within the same clutch. Excavation of a clutch from egg bed 3 revealed 30 eggs: 27 normal eggs and 3 abnormal, multilayered eggs. The three eggs occur adjacent to each other, at the highest level within the clutch, and represent the last eggs laid by the female sauropod. Abnormal shell morphology varies among the clutches and even within a single egg; the abnormal morphology encompasses that found in both modern reptiles and birds, thus providing little evidence of reproductive anatomy (JACKSON et al. 2004).

2.1.3 Geologic setting and age of Auca Mahuevo

The Upper Cretaceous rocks of Auca Mahuevo provide exceptional exposures of one of the most fossiliferous units in Patagonia. The nesting sites occur in the Anacleto Formation that overlies the Bajo de la Carpa Formation of the Neuquén Group. A disconformity (ARDOLINO & FRANCHI 1996) separates the Anacleto Formation from the overlying Allen Formation of the Malargüe Group (Text-fig. 2). The Anacleto Formation is 85 meters thick in the study area and characterized by reddish and reddish-brown mudstones, siltstones, and



Text-fig. 3. Catalan sites (black squares) with *Megaloolithus* discussed in this review plotted on a geologic map. The Tremp Basin is the synclinal structure in the left third of the map. 1 = Aren Sandstone Formation (middle Campanian to upper Maastrichtian), 2 = Tremp Formation (upper Campanian to lower Paleocene), 3 = older Cretaceous marine rocks, 4 = Eocene and younger cover.

interbedded gray-green, thin sandstone bodies (Text-fig. 2, DINGUS et al. 2000, CHIAPPE et al. 2000). These rocks represent fine-grained overbank, channel, and crevasse splay deposits characteristic of a distal floodplain environment. The purported age of the Anacleto Formation is early to middle Campanian (LEGARRETTA & GULISANO, 1989), an age recently confirmed by a reverse magnetozone within the section, tentatively correlated with Chron 33R which is dated as between 83.5 and 79.5 million years ago (DINGUS et al. 2000).

2.2 Catalan sites, Spain

Catalunya Province in northeastern Spain harbors extensive nesting sites with *Megaloolithus* eggs, many of which were studied in considerable detail by two of us (SANDER et al. 1998, PEITZ 1999, 2000a, b). A review of these and several other sites can also be found in LÓPEZ-MARTINÉZ (2000). Here, we will only discuss those sites studied by SANDER & PEITZ personally.

The Catalan nesting sites are in the southern Pyrenees of western Catalunya, primarily in the Tremp Basin to the west (Text-fig. 3) and in the drainage of the Riu Sallent, 20 km to the east. In this drainage, several extensive badland areas occur west of the village of Coll de Nargó, representing the principal sites, collectively referred to here as Coll de Nargó (Text-fig. 3). The nesting sites in the Tremp Basin and at Coll de Nargó occur in two formations, the Tremp Formation and the underlying Aren Sandstone Formation. The Tremp Formation is dated as late Maastrichtian based on ostracods (LIEBAU 1971, 1973) and charophytes (LÓPEZ-MARTINÉZ et al. 1998). However, more recent sequence stratigraphic and biostratigraphic dating indicates an uppermost Campanian age, at least for the beds in the Tremp Basin (ARDÈVOL et al. 2000, LÓPEZ-MARTINÉZ et al. 2000). At Coll de Nargó, palynomorphs (ASHRAF & ERBEN, 1986) date the egg-bearing horizons in the Tremp Formation as latest Maastrichtian. ASHRAF & ERBEN (1986) considered some egg horizons as earliest Paleocene in age because they occur above a distinctive change in the palynoflora, indicative of climatic cooling. This palynofloristic change is correlated with the Cretaceous-Tertiary boundary by these workers. However, independent confirmation for an earliest Paleocene age for the Coll de Nargó section (such as unequivocal biostratigraphic markers or radiometric dates) is lacking.

The rocks of the uppermost Aren Sandstone and Tremp Formations vary greatly in lithology. Interpreted as alluvial to marginal marine deposits shed by a rising anticline to the north, they represent the initial orogenic

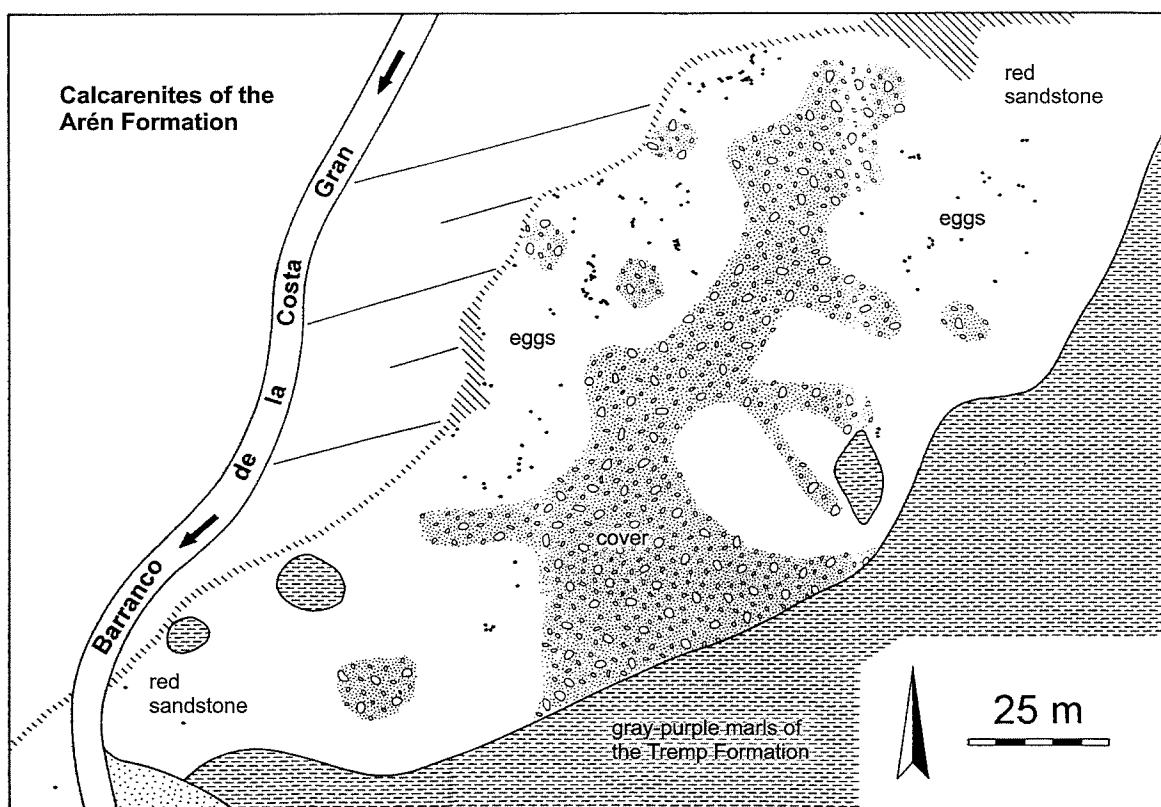
phase of the present-day Pyrenees (LIEBAU 1973, NAGTEGAAL et al. 1986, KRAUSS 1990, LÓPEZ-MARTINÉZ et al. 2000). The following significant localities are discussed from west to east (Text-fig. 3), with an emphasis on lithologic differences.

2.2.1 Suterranya

In the central portion of the Tremp Basin, the Suterranya locality preserves egg clutches but no dispersed eggshell. The medium-grained yellow sandstones that contain the eggs represent the two highest horizons of the uppermost Aren Sandstone Formation. The sandstones are fluvio-deltaic deposits with a slight pedogenic overprint (PEITZ 2000a).

2.2.2 Basturs

East of Suterranya, the impressive Basturs locality (Text-fig. 4) preserves clutches, eggs, and eggshell within a bright red, medium-grained sandstone (SANZ & MORATALLA 1997, SANDER et al. 1998). Although much less abundant, fossil egg material also occurs stratigraphically lower in gray sandstone strata. These units represent similar depositional environments, but exhibit less pedogenic overprint than the overlying red unit. The rocks at Basturs were initially deposited by alluvial fans prograding into the Tremp Basin, but the sediment was reworked in a nearshore or beach setting. The red sandstone exhibits a dominance of quartz grains, supported by a matrix of microsparite that resulted from dissolution of carbonate grains. Hematite grain coatings document a subsequent pedogenic history consistent with a mature paleosol (SANDER et al. 1998, LÓPEZ-MARTINÉZ 2000). While SANDER et al. (1998) showed that nesting activity occurred during soil formation, LÓPEZ-MARTINÉZ (2000) emphasized that there was a second pedogenic phase after nesting activity had ceased. Although the sandstone was deposited as coastal sand, egg laying occurred only after the onset of soil formation on the former beach sands, thus claims that dinosaurs nested on the seashore appear unfounded (SANDER et al. 1998).



Text-fig. 4. Map of nesting horizon Basturs West, Tremp Basin, Catalunya, Spain. The nesting horizon is developed on the upper surface of a tongue of the Aren Sandstone Formation. Each individual egg mapped in outcrop is represented by a small dot.

2.2.3 Sallent

A number of smaller sites occur near the abandoned village of Sallent at the head of the Riu Sallent valley. Strong local tectonic deformation affects the eggs and the surrounding reddish indurated mudstone. For example, one nesting site is present in the tight core of a fold! This tectonic deformation and limited outcrop exposure contributes to the difficulty of facies analysis.

2.2.4 Coll de Nargó area

West of the town of Coll de Nargó, extensive badland exposures contain sites equally instructive as the Basturs localities. The sites occur along the incised valley of the Riu Sallent and tributary streams draining into the river from the north (ASHRAF & ERBEN 1986, SANDER et al. 1998, PEITZ 2000b). Underlain by the uppermost Aren Sandstone Formation, the 170 meter-thick section of calcareous mudstones of the Tremp Formation contains several distinctive egg horizons (Text-fig. 5).

The lower member of the Tremp Formation in the study area exhibits thin intercalated coals, calcareous mudstones, and limestone beds. The lithology and the charophyte oogonia that occur on the bedding surfaces provide evidence of standing water or a high water table. The lower member of the Tremp Formation attains a thickness of up to 20 meters. No eggshell or eggs occur in this unit (Text-fig. 5).

In the 150 m-thick middle member of the Tremp Formation, these facies disappear, leaving only mudstones with mottling, caliche nodules, and other evidence of pedogenesis (Text-fig. 5). The overall color of the mudstones changes from gray to a reddish hue upsection, with the gray-dark red mottling changing to a light red-yellow mottling. The section also shows occasional small to medium-sized (< 4 m thick) channel fills incising into the mudstones. In most cases these fills consist of mudstones as well and only rarely of sandstones or fine conglomerates. The mudstones of the middle member of the Tremp Formation (Text-fig. 5) probably represent rapid aggradation on a low-lying alluvial plain, dissected by occasional fluvial channels. Alternatively, the sediments could have been deposited on tidal flats colonized by mangrove vegetation (DÍAZ-MOLINA 1987). This hypothesis, however, is not supported by the palynoflora which lacks any indication of mangrove taxa (ASHRAF & ERBEN 1986, ASHRAF pers. comm. 2004), which had evolved by the Campanian.

Rapid deposition of the middle member of the Tremp Formation under increasingly drier conditions prevented mature soil development, resulting in immature, complex paleosol horizons. The immaturity of these paleosol contrast strongly to the mature profiles present in the red sandstone at Basturs. Several mudstone horizons at the Coll de Nargó site contain vertical burrows (Text-fig. 5) that can be assigned to the ichnogenus *Ophiomorpha*. However, there is no indication that these trace fossils represent calianassid shrimp burrows, as generally assumed for *Ophiomorpha*, nor that the traces were necessarily formed in a shallow water environment.

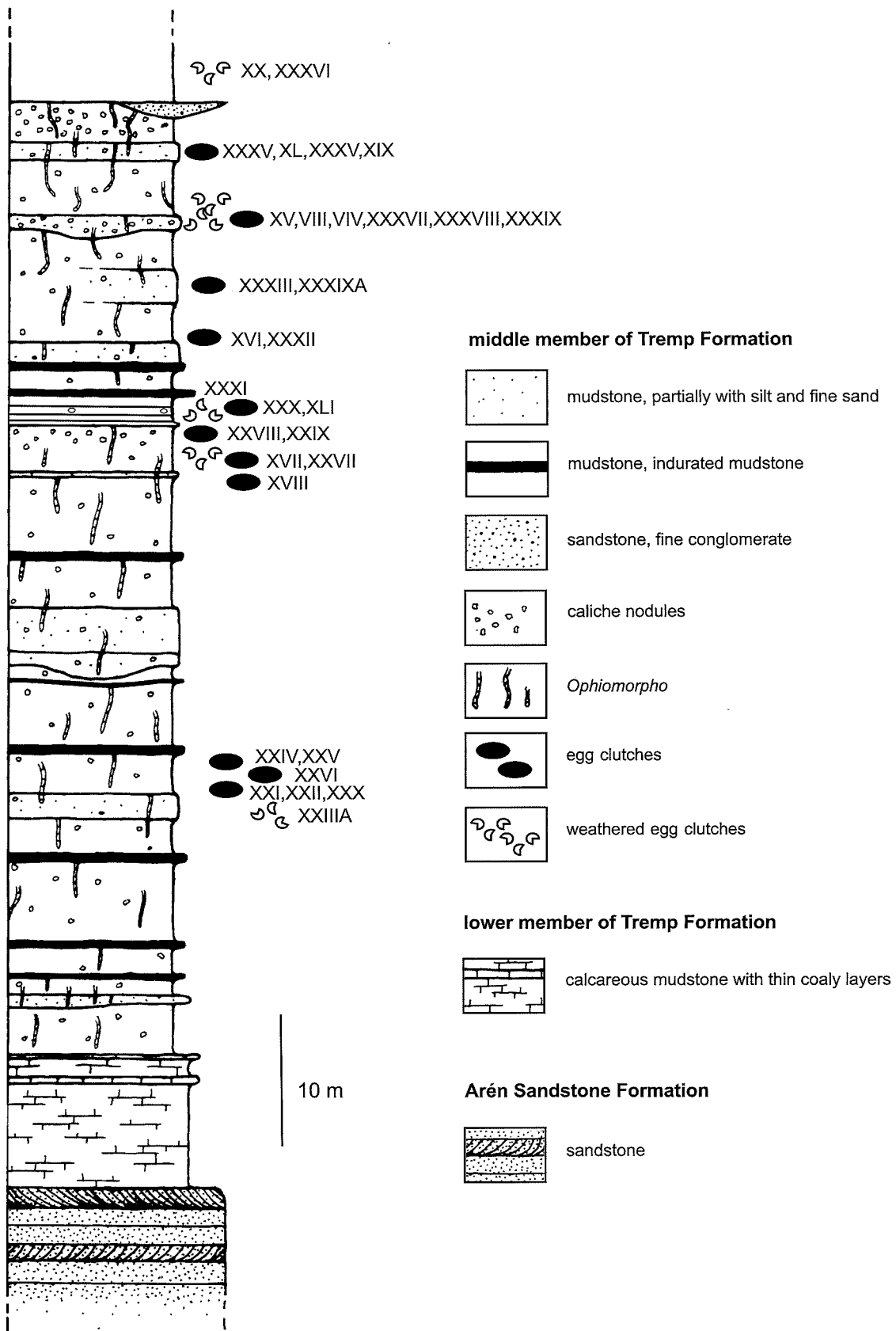
Individual indurated mudstone beds and egg horizons are traceable over a considerable distance in outcrop. Clutches occur throughout an interval of 56 m in the lower part of the section of the middle member of the Tremp Formation (Text-fig. 5), with no apparent association with a particular lithology (e.g. well indurated beds or beds with *Ophiomorpha*). More sporadically, clutches occur throughout the overlying roughly 90 m of the middle member of the Tremp Formation (PEITZ 2000b).

The upper member of the Tremp Formation, characterized by a dark red color, is devoid of any indication of dinosaur nesting activity and is believed to be earliest Paleocene (Danian) in age (ASHRAF & ERBEN 1986).

2.3 Sites in southern France

In southern France, where the study of dinosaur eggs began in 1859 (BUFFETAUT & LE LOEUFF 1994), egg-bearing sediments are present in two major regions, the Basin of Aix-en-Provence to the east (Departement Bouches-du-Rhone) and the foothills of the eastern Pyrenees (Departement Aude) (Text-fig. 1).

Megaloolithus eggs in southern France are generally preserved in red beds consisting of mudstones, siltstones, and fine to coarse-grained sandstones (COUSIN et al. 1994, COUSIN 2002). These rocks are assigned to the Rognacien and the underlying Begudien local stages. Based on index fossils such as charophytes, these units are generally dated as Late to latest Cretaceous (Campanian to Maastrichtian – COUSIN et al. 1994, COUSIN 2002, VIANEY-LIAUD et al. 2003). As noted by COUSIN et al. (1994), the sediments are laterally equivalent to the northern



Text-fig. 5. Measured section of egg-bearing beds of the middle member of the Tremp Formation in the valley of the Riu Sallent about 6 km west of the town of Coll de Nargó. Clutches were assigned Roman numbers in the field. Not all clutches discussed in the text were found in this section.

Spanish egg localities discussed in the previous section and formed a continuous facies belt with these, interrupted today by the Pyrenees.

2.4 Lameta Formation, India

The Lameta Formation contains nesting sites at several outcrops, distributed over a wide geographic region that covers several states of central, northern, and northwestern peninsular India (for reviews, see SAHNI et al. 1994, MOHABEY 2001, 2005). These sites have been extensively studied in terms of the sediment and associated fauna, but observations on the egg occurrence have not been published in sufficient detail. Nevertheless, it is clear that the Indian sites are comparable to other sites discussed in this paper, as previously noted by CARPENTER (1999).

The Lameta Formation is a relatively thin (± 20 m) sequence of nonmarine sediments deposited directly on Precambrian basement or “Gondwana” rocks (BAJPAI et al. 1990, TANDON et al. 1990, MOHABEY et al. 1993, MOHABEY 2001). These deposits underlie the extensive Deccan Traps flood basalts and intercalate in some places with individual basalt flows. These occurrences are referred to as the Intertrappean Beds of the Lameta Formation. Lithologies in the Lameta Formation are varied, indicating depositional environments that range from alluvial fans to lacustrine, with fluvial environments dominated by extensive overbank deposits (TANDON et al. 1990, 1995, SAHNI 1997, SAHNI et al. 1994).

The Lameta Formation is dated as latest Cretaceous (Maastrichtian), an age that is well constrained radiometrically and magnetostratigraphically due to extensive dating efforts in conjunction with the presumed role of the Deccan Traps in the Cretaceous-Tertiary extinction event (COURTILLOT et al. 1986, DUNCAN & PYLE 1988, VANDAMME et al. 1991, SAHNI 2000). The biostratigraphic evidence also indicates a Maastrichtian age (SAHNI & TRIPATHI 1990, SRINIVASAN et al. 1994, SAHNI et al. 1994).

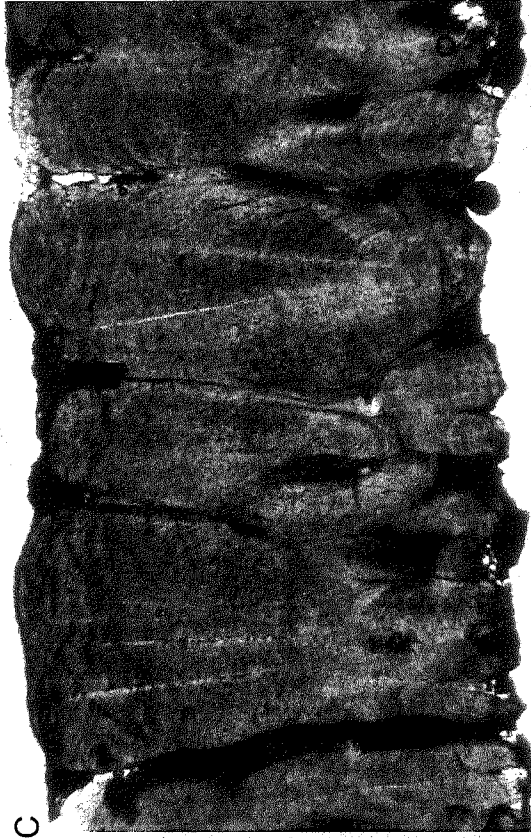
3. Egg parataxonomy

3.1 Egg parataxonomy at Auca Mahuevo

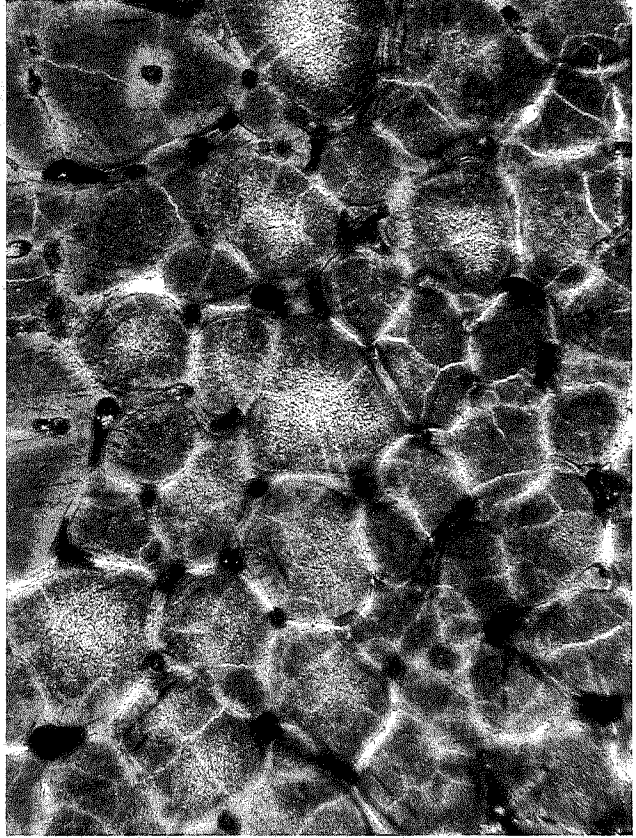
The eggs from Auca Mahuevo, Argentina, exhibit identical calcite microstructure to the oospecies *Megaloolithus patagonicus*, previously reported from the same formation (CALVO et al. 1997, GRELLET-TINNER 2004). This oospecies was claimed to be very similar to *M. jabalpurensis* from India by VIANEY-LIAUD et al. (2003) who tentatively synonymized *M. patagonicus* with *M. jabalpurensis* but did not provide information on shell porosity. *M. patagonicus* differs from *M. mammilare* from southern France and northern Spain in the smaller diameter of the Argentinian eggs (13–15 cm) compared to those from southern Europe (16–23 cm). Most importantly, the microstructure of the Argentinian eggs differs in the much lower number of pores compared to the southern European and Indian eggs (Text-fig. 6), suggesting that *M. patagonicus* is a valid oospecies because all other megaloolithid eggs for which this is known have a highly porous shell (DEEMING 2006).

3.2 Egg parataxonomy at the Catalan sites

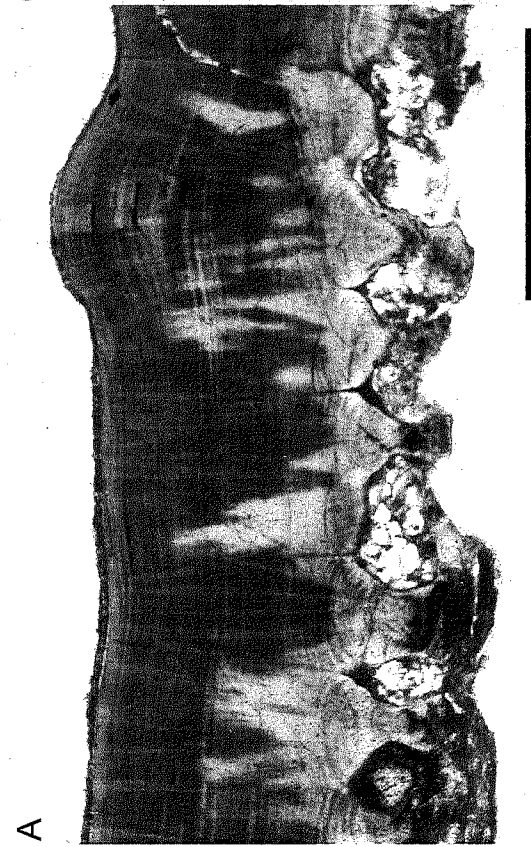
All eggs from the Catalan localities examined are assignable to a single oospecies, *Megaloolithus mammilare* (PEITZ 1999, 2000a, b). This conclusion differs from findings of French and Spanish workers who assign the eggshells from this region to numerous oospecies (e.g. VIANEY-LIAUD & LÓPEZ-MARTINÉZ 1997, BRAVO et al. 2000, LÓPEZ-MARTINÉZ 2000, LÓPEZ-MARTINÉZ et al. 2000, PANADÉS I BLAS 2002, 2005). Most material from these localities studied by these authors represents eggshell fragments rather than whole eggs, and the oospecies recognized differ primarily in eggshell thickness (MIKHAILOV 1997, CARPENTER 1999, PEITZ 1999, 2000a, b) (Text-fig. 7). We feel that establishing new oospecies on this basis requires caution and a thorough understanding of factors that influence eggshell thickness in a biological species. Eggshell thickness, and microstructural characters that co-vary with thickness, should not be used in megaloolithid eggshell parataxonomy. Thus, until microstructural characters are found that unambiguously distinguish *Megaloolithus* oospecies (independently of shell thickness), we feel that only a single oospecies should be recognized in the Catalan localities, *Megaloolithus mammilare* (PEITZ 1999, 2000a, b). This was the first species to be described, having page priority over some other



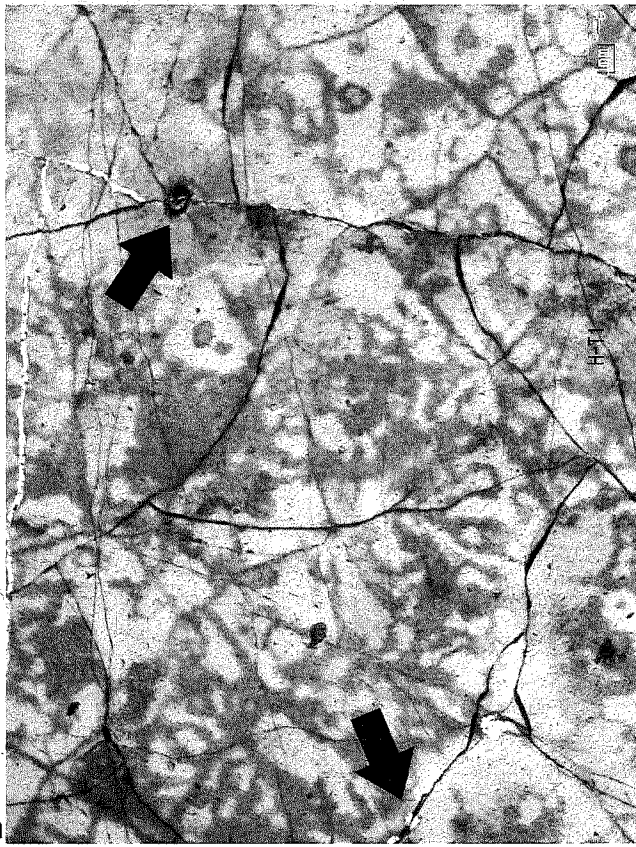
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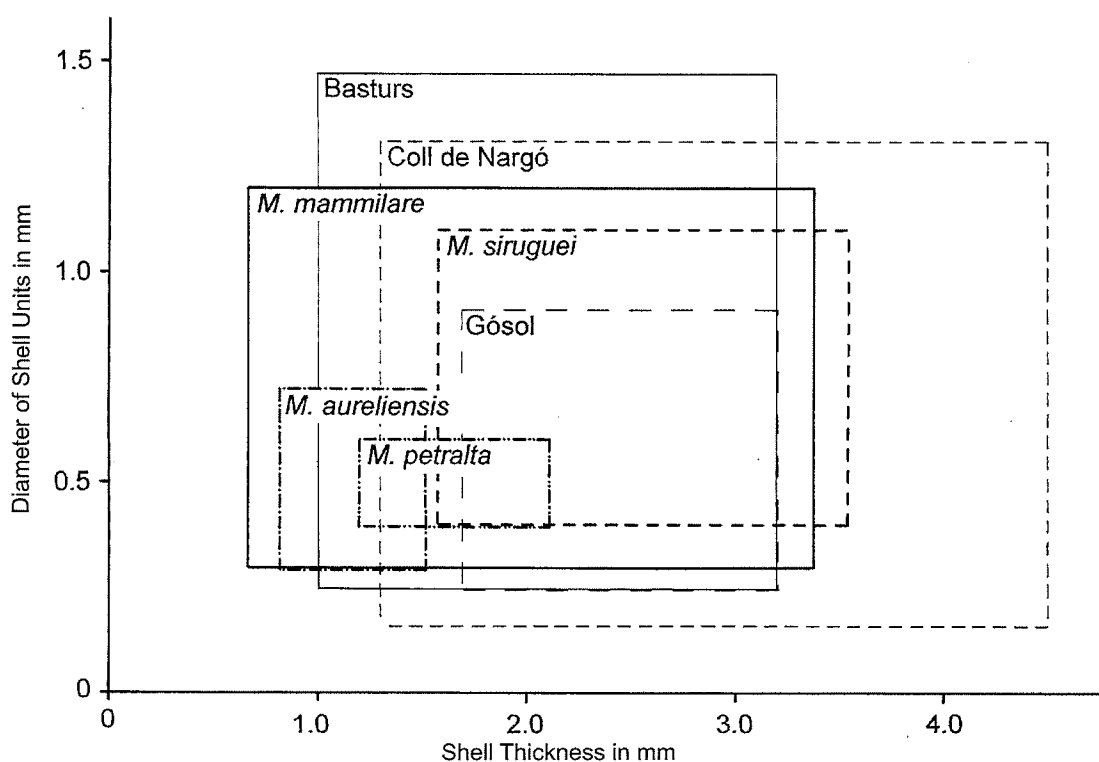
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A



B

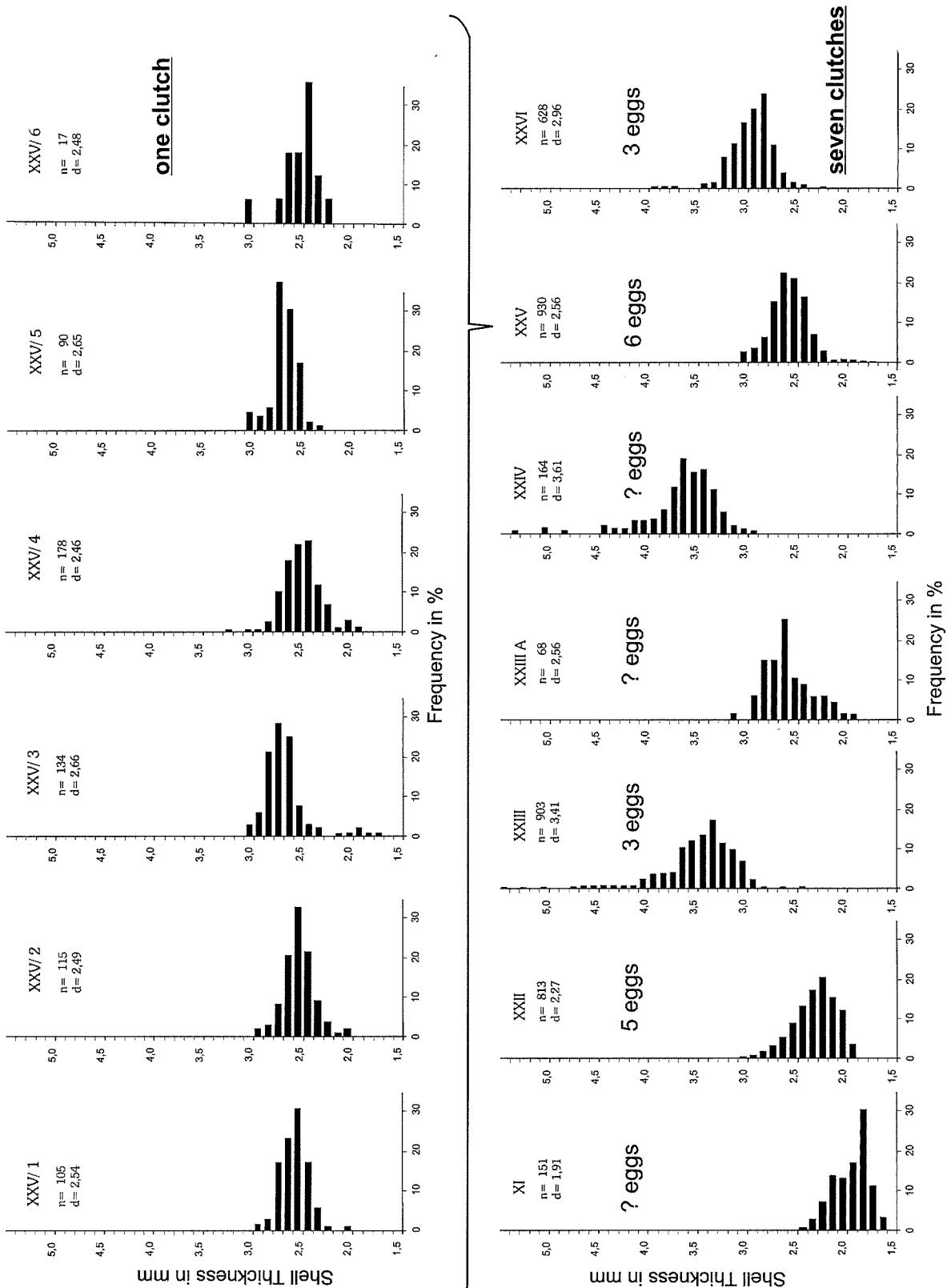


Text-fig. 7. Relationship of shell thickness and shell unit diameter in species of *Megaloolithus* from northern Spain and southern France. Note that the values of all named species overlap to such an extent that they can not be diagnosed from the shell thickness/shell unit diameter ratio alone. The samples from the Catalan sites of Coll de Nargó and Basturs cover nearly the entire range of variation of the named species. Plots for Coll de Nargó and Basturs are based on measurements made in numerous thin sections of shell samples kept in the collections of the Institute of Paleontology of the University of Bonn, Germany. Plots for the named species are from the literature.

species (VIANEY-LIAUD et al. 1994). This suggestion applies to the recent study by PANADÉS I BLAS (2005) as well which again concludes that there are several species of eggshell represented in the Catalan sites, but again is based on isolated eggshell and does not provide the control on sampling deemed necessary by us and discussed in the following section.

Detailed investigations of the Catalan material (SANDER et al. 1998, PEITZ 1999, 2000a, b), particularly at Coll de Nargó, have provided a better understanding of patterns of eggshell thickness variation (Text-fig. 8). At Coll de Nargó, SANDER & PEITZ assessed thickness in a single egg, among eggs of a single clutch, and among clutches in the same and different stratigraphic levels. It should be noted that none of the shell material studied showed any diagenetic thinning as indicated by the outer surface and the mammillary layer being intact. Within a single egg, thickness variation was negligible (Text-fig. 8). Similarly, examination of numerous *Megaloolithus* clutches from Coll de Nargó also showed little variation of shell thickness for eggs within the same clutch (Text-fig. 8) (PEITZ 1999, 2000a, b). Comparing different clutches revealed the greatest variation (Text-fig. 6) (PEITZ 1999, 2000a, b). Thus, the clutch with the thinnest shells had an average shell thickness of 1.91 mm (Text-fig. 6, clutch XI), while the clutch with the thickest shells has an average of 3.41 mm (Text-fig. 6, clutch XXIII), without overlap in range.

Text-fig. 6. Comparison of shell microstructure and porosity. *Megaloolithus patagonicus* from Auca Mahuevo, Argentina: A) cross section, specimen PVPH 113, an egg containing an embryo, and B) tangential sections of an uncatalogued egg. Note that there are only two pores visible in this section (arrows), with a third one possibly located between the arrows. *Megaloolithus mamillare* from Coll de Nargó, Spain: C) cross section and D) tangential sections of egg XXII/4. Note the numerous pores, located at the junction of the shell units. The shell samples figured in A) and B) are in the collections of the Museum of the Rockies, Bozeman, Montana, USA, and those figured in C and D are in the collections of the Institute of Paleontology of the University of Bonn, Germany. Scale bar is 1 mm and applies to all images.



Text-fig. 8. Shell thickness variation of *Megaloolithus mammillare* based on measurements of individual eggshell fragments at the Spanish site of Coll de Nargó among six eggs of one clutch (top row) compared to variation between seven different clutches with all eggs combined (bottom row). Note that shell thickness varies little among different eggs of the same clutch but varies greatly between different clutches from this locality. Shell samples on which the measurements are based are kept in the collections of the Institute of Paleontology of the University of Bonn, Germany.

Even directly adjacent clutches often exhibited significant thickness variation, e.g. clutch XXII (average shell thickness 2.27 mm) and clutch XXVIII (average shell thickness 3.41 mm) which were found only 4.5 m apart in the same horizon (Text-figs. 5, 8). With such a large and continuous variation in eggshell thickness between clutches having the same eggshell microstructure, egg morphology, and clutch morphology, this parameter alone should not be used as a character in differentiating ootaxa.

Contrary to expectation (e.g. SEYMOUR 1979, FIGUEROA & POWELL 2000), this variation in eggshell thickness did not result in a concordant variation in gas conductance of the shell. Our calculations, based on the corrected version (SABATH 1991, MIKHAILOV et al. 1994) of the formula of SEYMOUR (1979), show that there is no tight correlation between shell thickness and gas conductance (Text-fig. 9). Increased shell thickness was largely offset by increased pore diameter and increased pore density (Text-fig. 9), as already observed by SCHMIDT-NIELSEN (1984, p. 54) for modern birds.

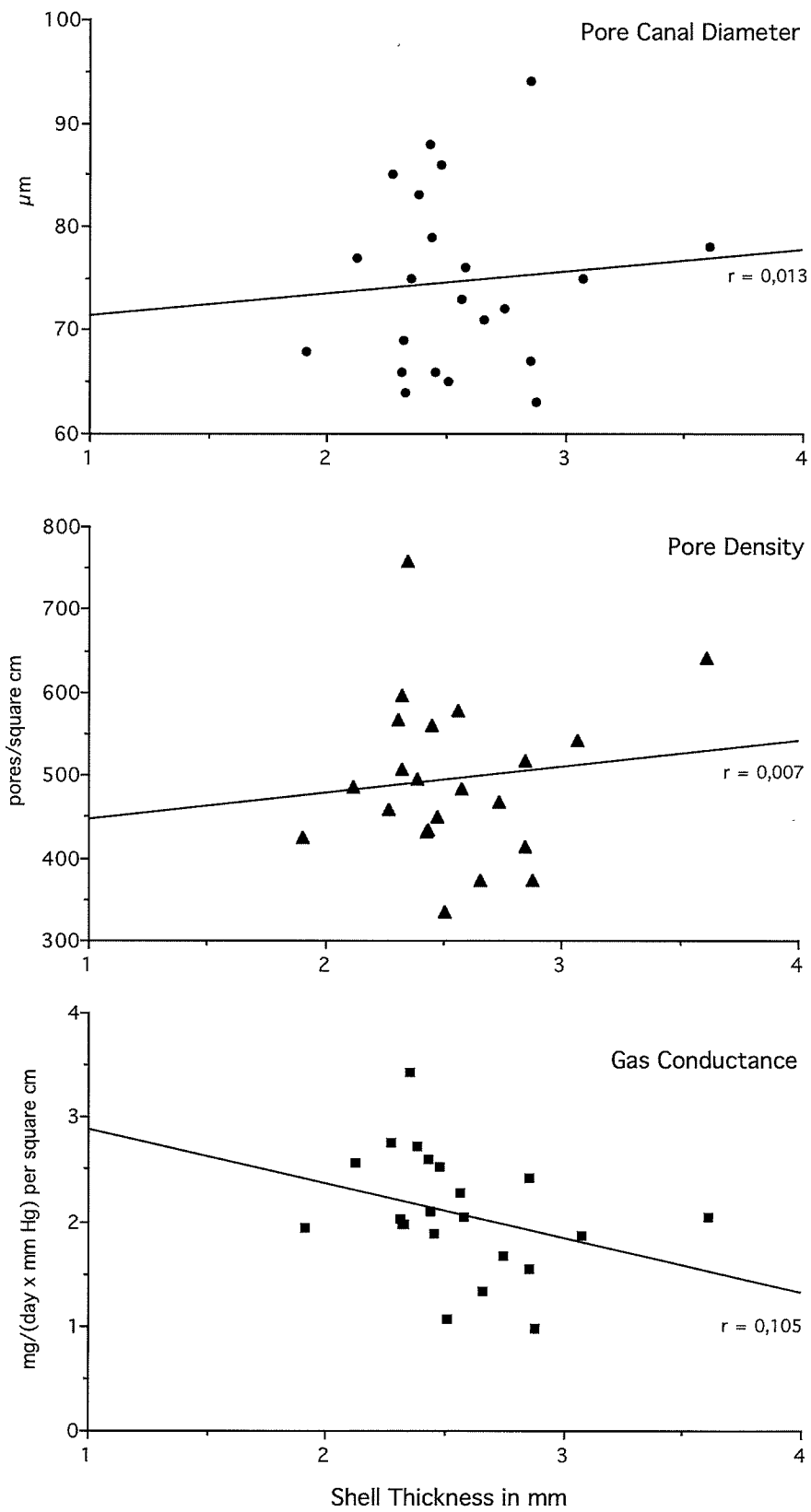
3.3 Egg parataxonomy in southern France

Due to their abundance and early discovery, the microstructure of eggs from southern France has been extensively studied. Pioneering work by ERBEN and others established the concept of eggshell structural types (ERBEN 1970, ERBEN et al. 1979), now superseded by egg parataxonomy (MIKHAILOV 1997). The advantage that parataxonomy provides over older classifications based only on shell microstructure and thickness is the inclusion of data on egg and clutch size, shape and morphology. Nevertheless, the parataxonomy of the southern French eggs is still heavily biased towards shell microstructure and thickness. VIANEY-LIAUD et al. (1994) were first to classify eggs from southern France within the framework of egg parataxonomy, establishing the oogenera *Megaloolithus*, *Carainoolithus*, and *Dughiolithus* and describing several oospecies for these oogenera (see also VIANEY-LIAUD et al. 2003). However, our work at the Spanish sites (Text-fig. 7) suggest the French egg parataxonomy is “oversplit”, and that there are only very few species of megaloolithid eggs, pertaining to a single oogenus, *Megaloolithus*, just as in Catalunya (PEITZ 2000a, b). This view is shared by CARPENTER (1999).

COUSIN (2002) also synonymized several species of *Megaloolithus*, as well as *Dughiolithus* with *Carainoolithus*. Furthermore, he tentatively suggested that *Cairanoolithus* eggs may not belong to the Megaloolithidae and that these eggs may have been laid by ornithopods. The major feature distinguishing *Cairanoolithus* from *Megaloolithus* is the less nodular to smooth shell surface of the former, a feature which has been suggested to result from erosion (CARPENTER 1999) and dissolution (COUSIN 2002). In addition, the growth lines of the columnar shell units of *Cairanoolithus* are considered less arched than in *Megaloolithus*. Until there is clear evidence to the contrary, we follow CARPENTER (1999) in regarding *Cairanoolithus* close to (if not a junior synonym of) *Megaloolithus*. We therefore include sites producing *Carainoolithus*, such as Founbit near Rennes-le-Chateau (COUSIN 2002) in our review of *Megaloolithus* eggs.

Differentiation of fossil material by shell thickness also played a role in Cretaceous-Tertiary extinction hypotheses. In an influential paper, ERBEN et al. (1979) observed that eggshell thickness in the Rousset section (Basin of Aix-en-Provence) decreased as one approached the K/T boundary, without a corresponding change in structural type. Based on previous work on domestic fowl (ERBEN 1969, 1972), the authors attributed this shell thinning to increasing stress levels in successive populations of a single dinosaur species. The stress allegedly resulted from deteriorating environmental conditions towards the end of the Cretaceous and documented the extinction process locally. KÉROURIO (1981a), however, considered at least one of the eggshell localities examined by ERBEN to represent material reworked from the underlying strata. Furthermore, a section spanning the K/T boundary at Coll de Nargó did not show this eggshell thinning (ASHRAF & ERBEN 1986), and the concept did not gain general acceptance (for further discussion, see JACKSON et al. 2004).

VIANEY-LIAUD et al. (1987, 1994, 2003), on the other hand, attributed the thinning trend to a succession of different egg types, despite the limited thickness variation in the shells they examined (Text-fig. 7). Based on our studies of the Catalan sites (PEITZ 1999, 2000a, 2000b), we feel that all previous studies lack sufficient control on shell thickness variation for two reasons: First, ERBEN et al. (1979) did not provide any data on the number of samples, measurements recorded, or statistical methods used to document the purported increased thinning over a stratigraphic interval at Rousset (JACKSON et al. 2004). The conclusions, therefore, remain questionable without further verification. Second, the eggshells used in most studies represent dispersed fragments rather than in situ eggs or clutches, thereby reflecting a time-averaged accumulation of unknown duration (JACKSON et al. 2004).



Text-fig. 9. Relationship between shell thickness and pore canal diameter (A), pore density (B), and gas conductance (C). Gas conductance was calculated based on the formula of SEYMOUR (1979) as corrected by SABATH (1991). Note poor correlation between shell thickness and pore canal diameter, respectively pore density. Gas conductance shows only a slight decrease with increasing shell thickness. Shell samples on which the measurements are based are kept in the collections of the Institute of Paleontology of the University of Bonn, Germany.

Studies by VIANEY-LIAUD et al. (1987, 1994, 2003) most likely include eggshell from different clutches produced by the same biological species, reflecting inter-clutch variation in shell thickness and concordant differences in eggshell microstructure (Text-figs. 7, 8). Verification of these results requires a systematic study to determine to what extent eggshell thickness and structure varies within the same clutch. For example, do multiple “oospecies” occur within the same clutches? Variation among clutches of the same and different horizons must also be documented in order to determine if shell morphology is unique to specific clutches or horizons. If several oospecies are present, one would expect variation to be discontinuous, i.e. show several maxima for a particular value or character. As documented by our study of the Catalan sites, very little variation exists within a single egg and in eggs of the same clutches, but considerable variation exists between clutches. Therefore, a well-founded understanding of thickness variation is essential for recognition and interpretation of trends in eggshell structure. The potential presence of several *Megaloolithus* oospecies contributes little to an improved understanding of sauropod diversity in this region. Titanosaur diversity based on osteological remains is poorly understood in southern France and northern Spain (LE LOEUFF 1995, 2003) and cannot be tested against the fossil record of megaloolithid eggs. The same situation applies to the Indian occurrences as well (see below).

3.4 Egg parataxonomy in the Lameta Formation

The *Megaloolithus* eggs from the Lameta Formation of India are assigned to numerous oospecies based on shell microstructure (KHOSLA & SAHNI 1995, MOHABEY 1998, VIANEY-LIAUD et al. 1987, MOHABEY 2001). The most recent comparative study on Indian dinosaur eggs (VIANEY-LIAUD et al. 2003) reduced Indian *Megaloolithus* oospecies from fourteen to nine. In view of our work on *Megaloolithus* eggs and clutches from northern Spain (see above), we agree with CARPENTER (1999) that the actual diversity is much lower, with possibly only one oospecies present. Furthermore, VIANEY-LIAUD et al. (2003) recognized similarities among some Indian and southern French oospecies, as well as with *M. patagonicus* from South American (see above). The Indian eggs vary in diameter between 12 cm and 20 cm (VIANEY-LIAUD et al. 2003). SAHNI et al. (1994, p. 221, fig. 13.15) argued that greater diameters (up to 28 cm) were due to a diagenetic increase in size caused by calcrete precipitation processes but did not discuss or illustrate this hypothesis in detail.

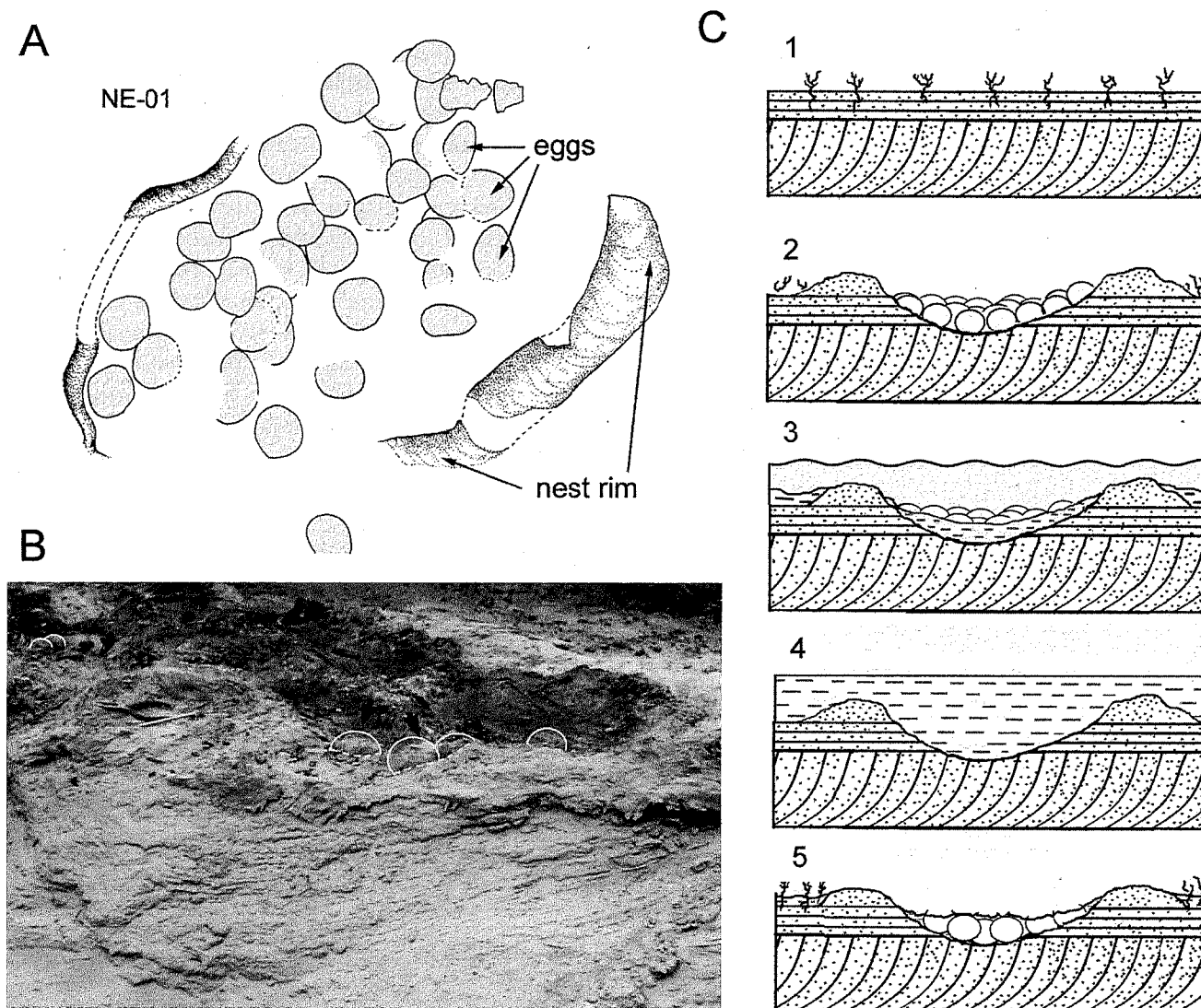
4. Patterns of egg occurrence

4.1 Egg occurrences at Auca Mahuevo, Argentina

Four well-separated egg-bearing horizons are present within exposures of the Anacleto Formation at the Auca Mahuevo locality (Text-fig. 2). However, egg beds 3 and 2 can be subdivided into two layers (CHIAPPE et al. 2005), thus indicating the existence of 6 egg-bearing layers. Egg beds 3 and 4 are laterally continuous for at least 8 kilometers and exhibit paleosol features such as blue-gray mottled root traces and small caliche nodules. Work at the two adjacent localities Barreales Norte and Barreales Escondido suggests that these egg beds could extend laterally for a much greater distance but detailed stratigraphic correlation is needed. Mudstones surrounding the eggs at Auca Mahuevo exhibit abundant slickensides of highly variable orientation characteristic of paleoverisols (LOOPE et al. 2000). Similar high clay content vertisols form today in semi-arid to sub-humid regions with seasonally wet and dry climatic regimes (CHIAPPE et al. 2000).

4.1.1 Nesting trace fossils at Auca Mahuevo, Argentina

Dinosaur “nests” are often mentioned in the literature, but most are inferred by the geometry of the eggs rather than the sedimentary structure of the host strata (for an exception, see VARRICCHIO et al. 1997, 1999). At Auca Mahuevo eggbeds 3 and 4 contain thousands of in situ unhatched eggs clutches (DINGUS et al. 2000, CHIAPPE et al. 2000). The uniformity of the mudstone facies provides no lithologic evidence of nest structure. However, thin, fine-to-medium grained channel and crevasse splay sandstones (some containing egg clutches) interfinger with the overbank deposits. In egg bed 4, five egg-filled depressions occur in the upper surface of a channel deposit and a sixth clutch is present in a crevasse splay sand lobe from the same horizon. These six



Text-fig. 10. Nesting traces and clutch morphology at the Auca Mahuevo site, Neuquén, Argentina. A) An egg clutch within a nesting trace (NE-01). Note the loose and irregular packing of the eggs. B) Field photograph of a nesting trace in vertical section. The nesting trace consists of a mudstone-filled pit excavated into cross-bedded sandstone. Note pliers for scale. C) Sequence of events that led to preservation of nesting trace with clutch. 1 = Soil forms after fluvial deposition of cross-bedded and horizontally bedded sand. 2 = Female dinosaur excavates pit with sediment piled up on the margins, deposits eggs, and leaves them exposed. 3 = Flood drowns clutch. 4 = Waning flood waters cover nest, clutch and preexisting land surface with mud. 5 = Recent erosion exhumes nesting trace and clutch. A) and C) from CHIAPPE et al. 2004.

clutches represent the first trace fossil nest excavated by a sauropod dinosaur (CHIAPPE et al. 2004). Some of these nests are separated by a few meters only, although it is not possible to determine if they were laid during the same nesting season.

The five clutches in the channel sandstone occur less than a meter below a layer containing thousands of carbonate-filled sauropod footprints (LOOPE et al. 2000). The lateral continuity of this footprint layer provides an index horizon for establishing that the egg-filled depressions occur within the same channel sandstone (CHIAPPE et al. 2004). Nest shape varies from sub-circular, to sub-elliptical, to kidney-shaped and from 85 to 125 cm across their maximum plan-view axes, with a maximum depth from 10 to 18 cm (Text-fig. 10). The egg-filled depressions truncate primary sedimentary structure such as trough cross bedding, horizontal stratification, or ripple laminations, and are encircled by a rim of structureless sandstone that resulted from piled debris (CHIAPPE et

al. 2004). Green mudstone fills the depression and interstitial spaces between these eggs. These muddy sediments resulted from suspension settling of fine-grained material during flooding of the abandoned channel. The lithologic difference between the sandstone host strata and the green mudstone that fills the depressions indicates that all six nests were open at the time of flooding (Text-fig. 10) (CHIAPPE et al. 2004). This is in accordance with the low porosity of the Auca Mahuevo eggshell (Text-fig. 6) and strongly suggests that the eggs were not incubated in the substrate nor in a vegetation mound.

This observation is contrary to recent suggestions that incubation likely occurred in a moist nesting environment that resulted from the clutches having been covered with vegetation by a parent animal (GRELLET-TINNER et al. 2004). Their conclusion was based on three lines of evidence: (1) alleged similarity with the pore system present in French eggshell, (2) surface ornamentation, and (3) organic remains in a trace fossil nest previously reported by CHIAPPE et al. (2004). In addition, UPCHURCH et al. (2004) report similar information from the Auca Mahuevo locality. We feel that these conclusions are misleading for the following reasons.

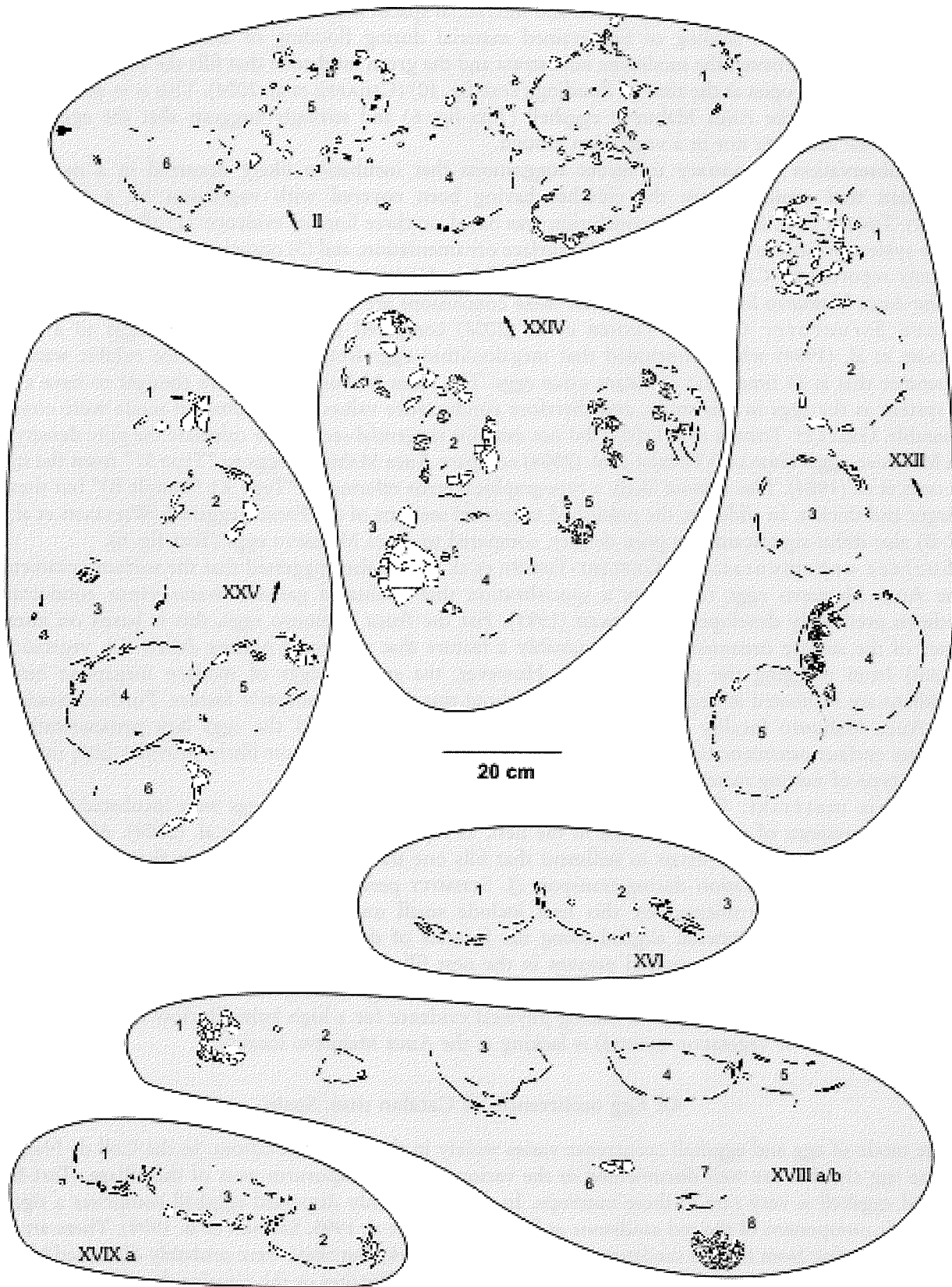
Pore Structure: GRELLET-TINNER et al. (2004) compared the Auca Mahuevo eggs to a study by WILLIAMS et al. (1984) which concluded that megaloolithid eggs from southern France exhibit water vapor conductance that is 24 times that of extant avian eggs. The Auca Mahuevo eggs were thought to have a similar pore system as the eggs in this study, and therefore conductance values and incubation mode were considered comparable. GRELLET-TINNER et al. (2004) did not examine tangential sections or calculate the pore density of the Auca Mahuevo eggs. GRELLET-TINNER et al. (2004) compare Auca Mahuevo eggs to "Type 31" from the study of WILLIAMS et al. (1984). This is most likely a typographical error referring to "Type 3.1 (Sample B)" but these eggs are larger and thicker. In addition, the published tangential sections of the French eggshell (WILLIAMS et al. 1984, fig. 2-B) also differ significantly in pore density, compared to Auca Mahuevo eggs (Text-fig. 6).

Surface ornamentation: GRELLET-TINNER et al. (2004) also suggested that the surface ornamentation in the Auca Mahuevo eggs represents a specialization that facilitated gas and water vapor conductance, a hypothesis previously developed by SABATH (1991). For the Auca Mahuevo eggs, this is based on internodal distance of the surface ornamentation, presumably a feature that prevented nesting debris (i.e. vegetation and sediment) from plugging the pore apertures. However, the smooth eggs of modern megapode birds and crocodylians are incubated in vegetation mounds without this purported adaptive feature. Further, extant turtles at the Auca Mahuevo locality bury eggs in fine-grained sediment, and the eggs lack ornamentation. The tuberculate surface ornamentation of the Auca Mahuevo titanosaur eggs most likely provides little information about the type of nesting material and nest construction.

Organic material: GRELLET-TINNER et al. (2004) suggested that the eggs were incubated in vegetation based on the presence of organic material in the nest, as reported by CHIAPPE et al. (2004). Although sparse, minute carbonaceous remains occur in sediment that fills one trace fossil nest, the fact that the particle size is commensurate with maceration during transport (J. SCHMITT pers. comm.) make this evidence unwarranted. Furthermore, the strata truncated by this nest include small mudstone rip-up clasts and an even greater concentration of organic material aligned along the foresets of the weakly cross bedded, fine-grained sandy sediments. The sparse organic material present in the nest fill, like that of the underlying strata, most likely represents transported material that was washed into the nest during flooding. Although some light covering may have concealed the titanosaur eggs, convincing physical evidence for a high humidity/low oxygen environment (e.g. substrate burial or vegetation mound) is lacking at the Auca Mahuevo locality.

4.2 Egg occurrences at Catalan sites, Spain

The mode of egg and eggshell occurrence varies widely in the Catalan localities. In the Coll de Nargó area, complete egg clutches are well documented in the various badland exposures west of the village (Text-fig. 11). Dispersed eggshell is very rare in these outcrops. In contrast, evenly dispersed eggshell comprises a significant petrographic component of the red sandstone at Basturs (SANZ et al. 1995, SANDER et al. 1998). There are several clutches weathering from the red sandstone at Basturs (Text-fig. 4), but these were probably disrupted by nesting activities in subsequent seasons (see below, SANDER et al. 1998). Clutches or the remains thereof also occur at the other localities such as Suterranya and Sallent, and their appearance in the field is consistent with the clutch morphology seen at Coll de Nargó.



Text-fig. 11. Representative tracings of clutches in outcrop at Coll de Nargó. The upper four clutches are seen in map view, while the lower three clutches are seen in vertical section. Stippled shell fragments are seen from the outside and white ones from the inside. Note the irregular and loose arrangement, and the limited vertical spacing of the eggs. The vertical sections clearly show the shell piles at the bottom of many hatched eggs. Clutch XVIII a/b is actually two superimposed clutches. Shaded areas are visualization aids and do not represent nesting traces.

4.3 Egg occurrence in southern France

Eggs occur at numerous localities and include a wide variety of lithologies. The locality Founbit near Rennes-les-Chateau (Department Aude) has received the most detailed study, facilitated by the soft sediment encasing the eggs (COUSIN et al. 1989, 1994, COUSIN 2002). Common problems with other localities include the limited extent of the excavation or outcrop exposure, thus resulting in poor control of clutch morphology and spacing (see below and COUSIN 2002).

4.4 Egg occurrence in the Lameta Formation, India

Egg localities are restricted to the so-called Lameta Limestone, a reddish to brown sandstone overprinted by pedogenic processes that contributed the carbonate component as calcrete to the sediment (SAHNI & KHOSLA, 1994). The egg-bearing bed in the Lameta Limestone is a few to several meters thick, and the eggs occur throughout the bed, unrestricted to a specific horizon. At least two egg occurrences may be superimposed (SAHNI et al. 1994, SAHNI & KHOSLA 1994, MOHABEY 2001).

5. Clutch morphology

5.1 Clutch morphology at Auca Mahuevo, Argentina

The arrangement and distribution of eggs within titanosaurid clutches is well documented at the Auca Mahuevo locality (Text-figs. 2, 10). Since 1999, nearly 500 in situ eggs have been mapped in a quarry excavated in egg bed 3 (CHIAPPE et al. 2000, 2005). The clutches contain 15 to nearly 40 spherical to subspherical eggs (CHIAPPE et al. 2004, 2005), approximately 15 cm in diameter. The eggs are in direct contact with one another or loosely packed with random distribution in single or multiple layers (Text-figs. 2, 10), with a maximum of three layers observed thus far (JACKSON et al. 2004).

5.2 Clutch morphology at Catalan sites, Spain

The exposures of the Coll de Nargó area provide an excellent opportunity to study *Megaloolithus* clutch morphology (Text-fig. 11). Here, groups of hatched or unhatched but intact eggs are widely separated by egg- and shell-free sediment. Over 30 such clutches were studied in detail in the field (Text-figs. 5, 11) (PEITZ 2000a, b). Due to the high rates of erosion in the badlands, some clutches deteriorated during the course of our (PEITZ & SANDER) fieldwork, while new groups were exposed. When the outcrop surface was parallel to the bedding plane, eggs within a clutch were traced directly from the rock, using a sheet of clear plastic and a black marker (Text-fig. 11). Similarly, vertical sections through clutches were recorded if the erosional surface cut the bedding plane at a high angle (Text-fig. 11). Sometimes, the remains of additional eggs of a clutch occur as accumulations of egg-shell fragments covering the surface of the outcrop.

Clutch size at Coll de Nargó varies from three to six eggs (Text-fig. 11), compared to a maximum of 7 at Basturs. The high rate of weathering in the badlands suggests that clutches of less than 3 eggs represent erosional remnants of larger clutches. A higher number of eggs (> six) occurred in only two, obviously superimposed clutches (Text-fig. 11). One could argue that the largest clutches of six eggs represent erosional remnants of once larger clutches as well. However, this is unlikely because of their recent exposure to erosion and lack of eggshell float that would suggest other eggs were originally present.

The locality of Basturs is less suited than the outcrops at Coll de Nargó for studying clutch morphology in the Catalan *Megaloolithus* eggs. On the one hand, this is because the weathering rate is low and no eggshell is found as float, making it impossible to detect eggs lost from weathering. On the other hand, the extreme density of dispersed eggshell in the sediment suggests that those clutches that are preserved may have been compromised by later processes such as bioturbation (trampling, nesting activity) and pedogenesis that also produced the immense amount of dispersed eggshell.

In map view, the eggs from all five study sites show an irregular distribution, described by CARPENTER (1999, caption to fig. 10.8) as “random, loosely packed”. While some clutches are roundish or oval groups, others appear

linear in arrangement. However, the eggs never occur in a clear row. Eggs are closely spaced with some, but not all, in direct contact with at least one other egg. The eggs in a clutch lie at slightly different levels, varying by approximately three-quarters of an egg diameter above or below the average egg level (Text-figs. 11, 12). There is no uniform pattern to the vertical distribution of eggs within the clutch. For example, the lowest egg does not necessarily occur in the middle of the clutch (Text-figs. 11, 12). This geometry is consistent with eggs deposited in a small, confined pit excavated by the female sauropod (Text-fig. 12). Furthermore, this arrangement argues against a previous interpretation by DUGHI & SIRUGUE (1958a, b, 1966, 1976) that megaloolithid eggs were deposited on a level, preexisting surface. Deposition on a preexisting surface was also suggested by LÓPEZ-MARTINÉZ et al. (2000) for a clutch of seven eggs from Biscarri at the eastern rim of the Tremp Basin. The clutch was found in the lower member of the Tremp Formation, which the authors interpreted as lagoonal and tidal flat deposits, based on paleosols characterized by watersaturated conditions. They argue that this lithology provides evidence of above-ground nesting mounds that included at least some vegetation. However, clutch morphology at the Biscarri site does not appear to differ from the other Catalan occurrences of *Megaloolithus* studied by SANDER & PEITZ.

Clutch morphology also indicates a more complex process of egg laying than the female simply depositing eggs in a shallow excavation (Text-fig. 12). The separation and loose packing suggest that one or more eggs may have been covered with soil or plant matter before additional eggs were deposited in the excavation. The addition of sediment or vegetation to the excavation, therefore, may account for the observation that in some cases the eggs at the edge of the clutch are lower than those at the clutch center (Text-fig. 11). If the eggs would have been laid into a shallow excavation without intervening matter, one would expect them to touch each other and the eggs in the center of the clutch to be the lowest. Although vegetation or sediment may have covered the eggs, the enclosing matrix provides no evidence of preserved plant matter. Unlike the six clutches preserved in sandstone at Auca Mahuevo (CHIAPPE et al. 2004), there is no apparent truncation of sedimentary structure by nest excavation or difference in lithology between the host strata and sediment surrounding the eggs.



Text-fig. 12. Reconstruction of a *Megaloolithus* clutch from Coll de Nargó before burial by the female. The depth of the pit is not based on sedimentological evidence but on the high porosity of the shell indicating substantial cover by sediment or plant material. For details, see text.

5.3 Clutch morphology in southern France

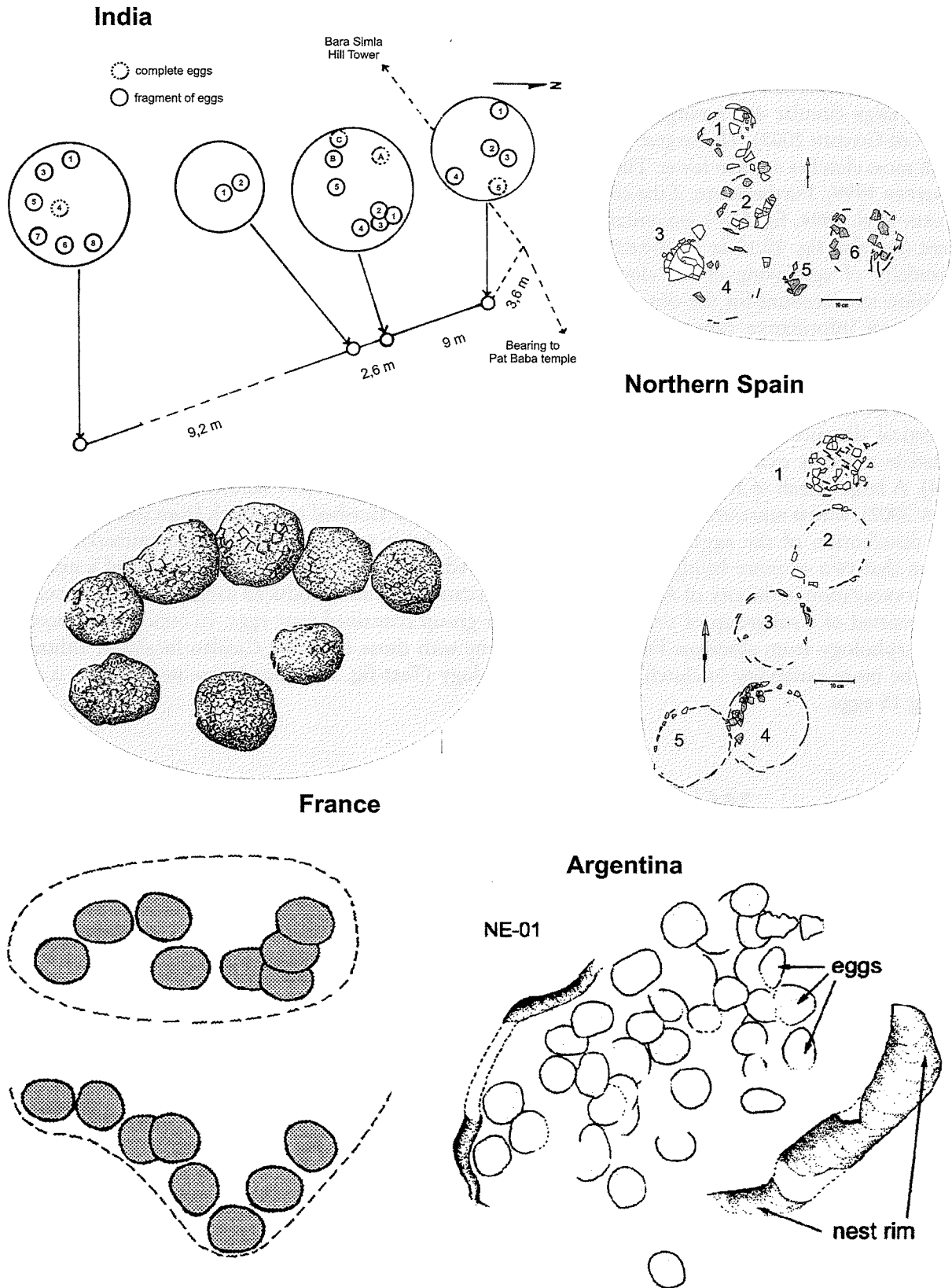
COUSIN et al. (1989, 1994) and COUSIN (2002) described two different clutch morphologies from Founbit, near Rennes-les-Chateau: irregular small, random, and loosely packed clutches of the type present in northern Spain and large circular egg arrangements comprised of multiple elongate groups of up to four eggs ("superclutches" of COUSIN 2002). The largest random, loosely packed clutches at Rennes-le-Chateau consist of 10 eggs, although most clutches contain fewer. The interpretation of the "superclutches" has subsequently been questioned (CARPENTER 1999). Furthermore, if the circle lines are removed from the excavation map (COUSIN et al. 1989, fig. 2, COUSIN et al. 1994, fig. 5.17), no circular pattern emerges and only individual eggs and small egg clusters are apparent (see also fig. 10.10 in CARPENTER 1999 with alternative circle lines). Since no evidence exists for the synchronicity of egg-laying of the elongate groups comprising the egg circles, repeated use and differential preservation may account for the observed pattern at this site.

The most informative papers describing isolated clutches and small groups of clutches from the other southern French localities are those of ERBEN et al. (1979), KÉROURIO (1981b), COUSIN et al. (1994), and COUSIN (2002). The clutches described by ERBEN et al. (1979) and KÉROURIO (1981b) also show an irregular pattern of egg distribution. One clutch illustrated by KÉROURIO contains eight eggs, but the specimens are distributed over a large vertical distance (Text-fig. 13). KÉROURIO (1981b) interpreted this distribution as resulting from eggs deposited in a deeply excavated pit. Two separate egg-laying events, however, cannot be ruled out (COUSIN et al. 1994). A large clutch of 15 loosely spaced eggs was recovered from a hard sandstone near Albas, Dept. Aude (COUSIN 2002), which represents the highest number of eggs ever ascribed to a clutch from southern France. The vertical distribution of the eggs in this clutch was rather great as well (several egg diameters). There is no indication that two or more laying episodes were involved. However, there is no indication of a nest structure either. An excavation in the city of Aix-en-Provence (COUSIN 2002) also produced irregular clutches; one elongate group consisted of a subgroup of six eggs and another group contained four eggs. In conclusion, most data on clutch morphology from southern France are consistent with those from the Catalan localities, although there seems to be more variability in clutch size and morphology (Text-fig. 13). Clutch size nevertheless is small, not exceeding 15 eggs.

5.4 Clutch morphology in the Lameta Formation, India

Little detailed information has been published on clutch morphology. Schematic illustrations of clutches by JAIN (1989) and SAHNI et al. (1994) show an irregular and loose egg arrangement and vertical distribution of eggs that is similar to the Catalan sites (Text-fig. 13). This is also documented in an illustration of an additional locality (Bara Simla Hill - SAHNI & KHOSLA 1994). MOHABEY (1990, 1996, 2001) described and illustrated such clutches, noting their irregular pattern and limited vertical egg range. Some eggs in these photographs and drawings appear to be touching, while others are more loosely spaced. MOHABEY (1990, 1996) notes that there is little lithologic evidence for a nest structure, other than better sorting and coarser sediments that surround the eggs, compared to the host strata. SAHNI et al. (1994) mention no difference between clutch matrix and host rock.

Although isolated eggs do occur, the minimum number of eggs in these clutches appears to be three, with the caveat that this may reflect egg loss due to erosion or incomplete exposure of clutches in the hard sandstone. Although SAHNI et al. (1994) refer to a maximum of seven eggs, several clutches show eight eggs (fig. 13.14 in SAHNI et al. 1994, fig. 1 in SAHNI & KHOSLA 1994). These illustrations are in general accordance with the descriptions and photographs provided by MOHABEY (1990, 1996, 2000, 2001). The largest clutches at the Rahioli site contain seven and eight eggs (MOHABEY 2000, figs. 4 and 5), but MOHABEY (1990, 1996) also describes clusters as large as 18. It is unclear from his brief descriptions and illustrations, however, whether these large clusters actually represent two or more clutches. Some clusters consist of superimposed egg layers, thereby suggesting this possibility. Although significantly larger clutches may be present, the maximum number of eggs per clutch (seven or eight eggs, Text-fig. 13) appears only slightly higher than in northern Spain.



Text-fig. 13. Comparison of *Megaloolithus* clutch morphology from around the world, in clockwise arrangement: India (from JAIN 1989), northern Spain (this paper), Argentina (from CHIAPPE et al. 2004), and southern France (from COUSIN 2002). Note the general similarity of all clutches, best described as random, loosely packed (CARPENTER 1999). All clutches have >nine eggs, except those from Argentina which consist of up to 40 eggs. The clutch from France in the lower left is seen in map view (top) and vertical section (bottom).

6. Patterns of preservation of individual eggs

6.1 Egg preservation at Auca Mahuevo, Argentina

The great majority of eggs at Auca Mahuevo are clearly unhatched. Eggs that are missing the upper shell surface typically result from recent erosion, and the fragmented eggshell is locally concentrated, with little or no dispersal between clutches. The absence of definitive evidence for hatched eggs is in strong contrast to the European and Indian localities. Egg preservation at Auca Mahuevo varies according to the lithology of the host rock. Eggs preserved in mudstone show moderate to extensive compression from lithologic compaction and/or pedogenic processes. Egg bed 4 often produces highly deformed agglomerations of alternating concave-up/concave-down eggshell layers, representing compaction of multiple eggs from a single clutch. This phenomenon most likely results from shrinking and swelling of clays in the nesting horizon. In contrast, eggs enclosed by sandstone often show minimal compression and three-dimensional morphology (Text-fig. 10).

6.2 Egg preservation at Catalan sites, Spain

The different Catalan sites all show similar egg preservation, although crushing from diagenetic compaction varies from minimal in sandstones (e.g. Basturs, Suterranya), to significant in calcareous mudstone (e.g. Coll de Nargó). Although some eggs are intact and unhatched, the upper surface of most eggs typically lacks eggshell (Text-fig. 11). Inside the egg, the remains of the cap are found at the bottom, typically in several layers (Text-fig. 11; see also PEITZ 2000b, figs. 58, 64, LÓPEZ-MARTINÉZ 2000). Close inspection of these fragments reveals that they generally are preserved with the outer surface facing down, i.e. facing externally. In addition, there are isolated fragments dispersed in the matrix that fills the egg (MUELLER-TÖWE et al. 2002). All this suggests that the majority of eggs thus far discovered hatched prior to burial.

6.3 Egg preservation in southern France

Egg preservation varies according to lithology in southern France. Eggs preserved in sandstones show little deformation, while eggs from mudstones are often compacted to a fraction of their former diameter. For most sites there is no census data regarding hatched versus unhatched eggs. However, specimens preserved in the collections of the Institute of Paleontology, University of Bonn (IPB R 268 and IPB R 270 from the Aix Basin), suggest that most eggs are hatched. Statistics for Founbit near Rennes-le-Chateau indicate that 98% of the clutches are hatched (COUSIN et al. 1989). Many of the hatched eggs from southern France show remains of the cap at the bottom of the egg (see also MUELLER-TÖWE et al. 2002). In the case of Founbit near Rennes-le-Chateau, the only locality for which this information has been published (COUSIN et al. 1989, 1994), the outer surface of the cap or its fragments face externally (COUSIN et al. 1994, figs. 5.15, 5.16).

6.4 Egg preservation in the Lameta Formation, India

Eggs in the Lameta Formation are usually hatched, with the remains of the cap found in several layers at the bottom of the egg (“concentric circles” of SAHNI & KHOSLA 1994). The outer surfaces of most shell fragments face externally, although some face internally. The condition of all fragments facing internally was not observed. This pattern was interpreted as resulting from collapse of unhatched eggs (SAHNI & KHOSLA 1994, SAHNI et al. 1994, but see section 6.5). Dispersed eggshell is commonly associated with the Indian clutches. With the exception of some intertrappean beds, dispersed eggshell (without nearby eggs) has not been observed in the Lameta Formation sites (MOHABEY 2001). Apparently, no intact and unhatched eggs were positively identified (SAHNI et al. 1994, MOHABEY, 1990).

7. Clutch spacing and density

7.1 Clutch density at Auca Mahuevo, Argentina

Spatial analysis of egg location (x, y and z coordinates) at Auca Mahuevo revealed high egg density (11 eggs/m²) and discrete egg clustering in the egg bed 3 quarry (Text-fig. 2; CHIAPPE et al. 2000, 2005). However, two distinct and laterally continuous egg levels occur in some portions of the excavation, separated by several centimeters of sediment. Both contain predominantly whole eggs, with little or no fragmented eggshell in between the clutches, thus suggesting the existence of two separate egg-laying events (CHIAPPE et al. 2005).

Mapping of in situ clutches exposed on an erosion surface at a second, stratigraphically equivalent locality produced 74 and 31 randomly distributed egg clutches within 1.701 m² and 486 m², respectively (Text-fig. 2; CHIAPPE et al. 2000, 2005). The maximum stratigraphic thickness at this second site is less than 70 cm, and the clutches are typically 3 to 6 m apart. A third and similar erosional surface within a mudstone facies in egg bed 4 produced comparable clutch density, distribution, and spacing as the two sites mapped in egg bed 3 (CHIAPPE et al. 2004). Due to the criteria used in the mapping projects, the total number of clutches (Text-fig. 2) possibly represents only a small portion of those originally present in these localities. Furthermore, pedogenic processes also contribute to the difficulty of assessing egg and clutch density in the mudstone facies. However, clutches preserved in crevasse splay and channel sandstones that intercalate with the mudstones in egg bed 4 (see section 2.5) show a similar distribution. For example, the three clutches preserved in the upper surface of a single sandstone body are 3.6 to 3.9 m apart, compared to 3 to 6 m for clutches in egg bed 3.

7.2 Clutch density at Catalan sites, Spain

Clutch spacing in the Catalan sites can be studied best in the extensive badlands along the Riu Sallent and its tributaries west of the village of Coll de Nargó. Rapid sedimentation rates (see above) in this part of the stratigraphic section combined with laterally continuous mudstone beds provide excellent control on clutch synchronicity. SANDER & PEITZ interpret as synchronous those clutches that either were exposed in precisely the same mudstone horizon or on the same bedding plane. The rapid sedimentation rate resulted in wide, vertical spacing of egg horizons (see Text-fig. 5), and the locally traceable marker beds of well indurated mudstone allow correlation of clutches at the outcrop level. The outcrop dimensions are from 20 to 100 m laterally and up to 35 m vertically. The minimum horizontal distance between clutches in any one horizon is approximately 1 m, although wider spacing (e.g. 2.3, 4.5, 7, 10, and 12 m) is the rule (SANDER et al. 1998, PEITZ 2000a, b). Even wider spacing is indicated by the commonly made observation that only a single clutch per horizon is found in an outcrop (Text-fig. 10).

7.3 Clutch density in southern France

Despite the long history of research, very little is known about clutch density and spacing in the southern French sites because of limited outcrop exposure and difficulty of time resolution. The occurrence of isolated clutches at some localities (COUSIN et al. 1994, COUSIN 2002 – pers. observation PMS) suggests an irregular and wide clutch spacing, similar to that documented at Coll de Nargó. No southern French locality offers convincing evidence for colonial nesting such as regularly spaced clutches with demonstrated synchronicity of nesting.

7.4 Clutch density in the Lameta Formation, India

Documentation of clutch spacing in the Indian nesting sites is limited, and the synchronicity of the clutches is poorly constrained because of the homogeneous and unstratified nature of the egg-bearing sediment. It remains unclear if one or several nesting events are preserved. However, the descriptions by SAHNI et al. (1994), SAHNI & KHOSLA (1994) and MOHABEY (1990, 2000) indicate that considerable distance sometimes separates the clutches, while a few meters or less separate other clutches. The most detailed information is presented in maps of the nesting sites (SAHNI et al. 1994), in which clutches are spaced less than 1 m and up to 92 m apart (Text-fig. 13). Intermediate clutch spacing of several meters is common as well.

8. Duration of occupation of nesting sites

8.1 Duration of occupation at Auca Mahuevo, Argentina

Some portions of the egg-bearing horizons at Auca Mahuevo may represent a single nesting season, e.g. the ones preserved with nesting trace fossils (see above). However, the clutches often occur at slightly different levels within the thin (70 cm) egg bed 3, possibly reflecting paleotopographic surfaces or multiple nesting seasons. Nevertheless, the clutch density and lateral continuity of egg beds 3 and 4 suggests gregarious nesting behavior in the Auca Mahuevo titanosaurs (CHIAPPE et al. 2000, 2005). In addition, the high number of unhatched eggs in the egg beds would also be consistent with a single catastrophic event (flood?) killing off numerous densely spaced clutches (K. CARPENTER, pers. comm.). The presence of at least four egg-bearing horizons within the 85 m thick Auca Mahuevo section also suggests repeated use of this area over an unknown time interval.

8.2 Duration of occupation at Catalan sites, Spain

The Basturs locality offers strong evidence for prolonged use of this area for nesting. Using the data for clutch size and clutch density per nesting season collected at Coll de Nargó, SANDER et al. (1998) estimated that the dispersed eggshells in the red sandstone units at Basturs represent 300,000 eggs. This suggests an estimated occupation time of approximately 10^5 years if nesting females occupied the site annually (for details of the calculations, see SANDER et al. 1998). This time frame is in agreement with that required for the development of a mature soil. Justification for comparing the Basturs site and those west of Coll de Nargó is provided by all sites preserving exactly the same egg types and clutch morphology (SANDER et al. 1998, PEITZ 2000a).

8.3 Duration of occupation in southern France

Very little can be deduced about duration of occupation in the southern French sites because of limited outcrop exposure and difficulty of time resolution. However, the high density of eggs and dispersed eggshell in the sediment at Founbit near Rennes-les-Chateau (COUSIN et al. 1994, COUSIN 2002) suggests repeated use.

8.4 Duration of occupation in the Lameta Formation, India

Due to the poorly constrained synchronicity of clutches in any of the Lameta nesting sites, estimates of the duration of occupation must rely on other evidence. For example, repeated use of the site may be indicated by the possible presence of superimposed clutches (e.g. MOHABEY 1990, 2001). Similarly, sites with high concentrations of dispersed eggshell between clutches suggest repeated use over a longer time period.

9. Synthesis: review of the evidence and first-order inferences

The comparative approach taken in this synthesis paper allows identification of similarities and differences between well-studied Upper Cretaceous *Megaloolithus* nesting sites on three continents. This resulted in the recognition of two fundamentally different reproductive strategies in titanosaurs for the European and Indian sites on one hand, and the Argentinian site of Auca Mahuevo on the other.

9.1 Environmental setting and substrate

All localities share a lowland setting on distal alluvial or coastal plains (possibly even tidal flats; LÓPEZ-MARTINÉZ et al. 2000). Remarkable variation in lithology characterizes the *Megaloolithus* nesting sites. Host sediments include sandstone, siltstone, and calcareous mudstones, suggesting no substrate preference by the female titanosaurs. However, pedogenesis is common to most nesting sites, with some exhibiting mature paleosols that formed prior to nesting activity (e.g. at Basturs, SANDER et al. 1998, LÓPEZ-MARTINÉZ 2000). The pattern that emerges indicates preference for egg-laying in well-developed soils rather than freshly deposited sediment.

9.2 Clutch morphology

Clutch morphology is rather uniform among the European and Indian sites and conforms to the “random, loosely packed” pattern of CARPENTER (1999). A clutch consists of a round to elongate group of three to eight eggs (exceptionally up to 18), loosely to closely spaced or touching each other (Text-fig. 13). No apparent egg arrangement exists (i.e. no parallel lines, circles, preferred long axis orientation etc.). Importantly, the eggs occur at different depths, with those closest to the center usually but not always lying deeper than those at the periphery. Vertical spacing of clutches is minimal, not exceeding 1.5 egg diameters. Although the Argentinian clutches are similar in their unordered egg arrangement and vertical spacing pattern, significant differences exist: clutches are larger (15 to <40 eggs), eggs occur in 1 to 3 layers, and eggs are more closely spaced within the clutches (Text-fig. 13).

9.3 Nest structure

In the absence of nesting traces in the European and Indian localities, three primary lines of evidence suggest that *Megaloolithus* eggs there were normally deposited in an excavation and covered with soil and/or vegetation.

1. The vertical distribution of the eggs in the clutch (some eggs lower than others, Text-figs. 11–13) indicates that the eggs were not laid on a level, preexisting surface, but deposited in a shallow pit excavated into the substrate (Text-fig. 12).
2. Clutches at Coll de Nargó are embedded in paleosols; the eggs, however, lack evidence of modification by intersecting root traces or *Ophiomorpha* burrows (Text-fig. 11). This suggests that the eggs were buried after soil formation occurred, rather than entombed by depositional processes related to a flood event, as in the case of Auca Mahuevo.
3. High eggshell porosity documented for eggs from the southern French (SEYMOUR 1979, DEEMING 2006) and Catalan sites (Text-figs. 6, 9) (PEITZ 2000b) represents the third line of evidence. Published micrographs of radial sections of the Indian specimens consistently show very porous shells (KHOSLA & SAHNI 1995, MOHABEY 1998, VIANEY-LIAUD et al. 1987, 2003) as well.

High eggshell porosity in recent amniote eggs reflects incubation in a vegetation mound or substrate burial of eggs (SEYMOUR 1979, DEEMING 2006; for megopodid birds see SEYMOUR & RAHN 1978). In the Indian and European sites, no sedimentological evidence exists for fossilized vegetation or an excavated pit. The lack of such evidence, however, may reflect preservation bias in these localities or pedogenic processes that altered sedimentary structures. Alternatively, some titanosaurs may have occasionally produced a raised nesting mound of sediment that also incorporated plant matter (LÓPEZ-MARTÍNÉZ et al. 2000). Such flexibility within one species is also observed in at least one extant species of crocodile, *C. acutus*, which usually digs a hole nest but constructs a mound in beach environments in Florida (COOMBS 1989).

The inferred nest structure (based on clutch morphology, Text-fig. 12) of European and Indian *Megaloolithus* eggs is confirmed by the nesting traces from Auca Mahuevo. These six nests provide sedimentological evidence for nests excavated in sand; mud filled the depressions and surrounded the egg clutches (Text-fig. 10) (CHIAPPE et al. 2004). However, the Auca Mahuevo clutches and nests differ from the European and Indian localities in several ways: (1) all six nests were open at the time of mud deposition, rather than buried in the substrate (Text-fig. 6); (2) some clutches contain up to three egg levels; and (3) the clutches contain a higher number of eggs (close to 40 in some clutches, Text-fig. 6). This far exceeds the maximum of 13 eggs per clutch predicted by SEYMOUR (1979) for *Megaloolithus* eggs incubated under cover. This prediction, based on the gas conductance through the cover and the oxygen consumption of the embryos, is consistent with clutch size in the European and Indian localities. The larger-than-predicted clutch size at Auca Mahuevo is explained by the low porosity of the eggshell (Text-fig. 10), which also suggests that these eggs were not incubated within the substrate or a vegetation mound. Because DEEMING (2006) did not study egg and eggshell from Auca Mahuevo, these interpretations are not in conflict with his conclusion that all dinosaur eggs were incubated buried in a substrate. However, DEEMING's (2006) conclusion does highlight the unusual nature of the Auca Mahuevo nesting site.

9.4 Clutch spacing and colonial/communal nesting

Among the European and Indian sites, clutch spacing can be estimated with confidence only at the Spanish locality of Coll de Nargó but not at Basturs (contra SANZ et al. 1995 and CARPENTER 1999, p. 9; see SANDER et al. 1998, LÓPEZ-MARTINÉZ 2000) nor in the Lameta Formation. At Coll de Nargó, clutch spacing is wide and irregular, which differs from the close spacing found in some communal nesting sites of extant sea turtles (e.g. BELLAIRS 1970, p. 424) and birds (e.g. HAYWARD et al. 1989). The point here is that, although we cannot exclude communal/colonial nesting at some of those European sites showing a high density of eggs, in none of these it can be proven that the eggs were deposited during the same nesting season. The only positive evidence we have for clutch spacing in *Megaloolithus* from Europe and India indicates isolated clutches.

The remarkably close spacing of clutches (~3 m) at the Auca Mahuevo locality strongly suggests some type of gregarious behavior (CHIAPPE et al. 2000). Although time-averaging of nesting events may have occurred in some areas, the dense, closely spaced clutches and egg-bed continuity supports gregarious behavior of the Auca Mahuevo titanosaurs and crowded nesting conditions.

9.5 Egg preservation

The absence of positively identified hatched eggs from Auca Mahuevo prevents discussion of issues that are applicable to European and Indian localities. Some European and Indian eggs are complete and represent unhatched specimens. Most, however, are damaged and are missing the top. The remains of the cap are typically preserved in several shell layers ("shell fragment pile" of MUELLER-TÖWE et al. 2002) at the bottom of the damaged eggs (Text-fig. 11). Depending on locality, all or the majority of the shell fragments exhibit the external surface facing outwards. If little or no sediment is enclosed between these fragments of the cap, diagenetic cementation can lead to misinterpretation of eggshell pathology because contact occurs between mammillae and the outer shell surfaces. This may account for the high frequency of pathological eggshell reported by ERBEN et al. (1979) from localities in southern France. CARPENTER (1999, p.106) appropriately addressed the problem of pseudo-pathologies and suggested the orientation of shell fragments can be used to detect abnormal conditions. For example, crushing of a single egg results in mammillae-mammillae contact, while crushing of two adjacent or superimposed eggs of a clutches produces outer surface-outer surface contact. However, the hatching process, combined with crushing, commonly results in mammillae-outer surface contact. Differentiation between multi-layered eggshell resulting from a pathological condition and diagenetically cemented shell fragments, therefore, is often only possible by petrographic thin sections or scanning electron microscopic imaging (JACKSON et al. 2004).

Several potential explanations exist for damage to the egg top and the subsequent arrangement of eggshell preserved inside the eggs (Text-fig. 11): hatching, predation, pedogenesis, and structural collapse due to sedimentary overburden. Although the latter three mechanisms cannot be discounted, we believe that damage to the eggs in Catalunya and elsewhere generally results from hatching (MUELLER-TÖWE et al. 2002). COUSIN et al. (1989, p. 160) were first to interpret eggshell fragments inside an egg from Founbit near Rennes-le-Chateau as the remains of the cap that entered through the hatching window. Contrary to SABATH (1991) and CARPENTER (1999), this eggshell arrangement may result from hatching if the eggs were covered by soil or vegetation and the hatchlings had to work their way out of this vegetation cover (MUELLER-TÖWE et al. 2002). If the eggs had hatched in the open, one would expect more variable and extensive damage. In addition, in modern animals, hatching in open nests does not result in concave-up shell fragments in the bottom of the egg (MUELLER-TÖWE et al. 2002).

9.6 Repeated use ("site fidelity")

In the ecology of extant animals, site fidelity is often defined as repeated use of a geographical area by a single female or a population for nesting. The term has also been applied to dinosaur nesting sites (e.g. HORNER 1982, SANZ et al. 1995). Given the difficulty of time resolution in the rock record, we prefer the term "repeated use" over "site fidelity" to describe the use of an area for nesting over a longer time period. We differentiate between repeated use in ecological time (i.e. $<10^2$ years, the time span covered by ecological studies) and geological time (i.e. $>10^4$ years). The isolated and widely spaced clutches commonly reported from Europe and India suggest that

only one or a few female titanosaurs deposited clutches in an area at any one time. Higher clutch density in some European and Indian sites, however, indicates some form of repeated use of certain areas by female titanosaurs over several years, i.e. in ecological time. Nesting beaches used by marine turtles may provide a modern analog for these sites (PETZ 2000b, LÓPEZ-MARTÍNÉZ 2000). Repeated use over geological time is indicated by multiple nesting horizons within a thick (>100 m) vertical sedimentary sequence. Reasons for this nest concentration in titanosaurs might include limited availability of appropriate nesting substrates and preferred vegetation.

The phenomenon of repeated use is apparent in all regions, but is best studied at the Basturs site. At this locality, an estimated annual use for at 10^5 years provides the strongest evidence to date for repeated use of a nesting area by titanosaurian dinosaurs (see above, SANDER et al. 1998).

10. Implications for reproductive biology and evolutionary ecology

This section has a twofold purpose: (1) to describe the processes of nesting and hatching in the European and Indian *Megaloolithus* nesting sites vs. the Argentinian sites based on the review in sections 2 to 6 and (2) to consider the implications of these and previous observations on reproductive biology for the evolutionary ecology of titanosaurs. We admit that some of the ideas put forward in this section are speculative but feel that they have the potential for verification by future research and thus are worth advancing.

10.1 Reproductive biology

The events from the beginning stages of nesting to the hatching of the young will now be described in a brief scenario, emphasizing the comparative approach among the different localities in general and the European/Indian sites vs. Auca Mahuevo in particular.

10.1.1 Nest site selection

Prior to egg-laying, the titanosaur female must have located a suitable environment to maximize hatching success and minimize egg or clutch loss due to environmental perturbations or predation. A variety of environments (flood plain, abandoned channel sands, coastal plain etc.) satisfied these requirements, but nearly all represented stable land surfaces with at least some plant cover, as indicated by preservation of most clutches in paleosols.

10.1.2 Preparation of nest and egg-laying

The female excavated a shallow pit and deposited the clutch, presumably from a crouching position. In the European and Indian sites, the clutch was then covered with soil and possibly plant material, although there is no direct evidence for use of plant material. In the case of Auca Mahuevo, the excavated sediment formed a rim around the pit, and the eggs were not buried in the substrate, as also indicated by the low shell porosity. This, however, leaves the question as to how the eggs in open nests were concealed from predators. While some vegetation may have covered the eggs for this purpose, adequate evidence is currently lacking.

It is unknown if the eggs in a clutch were all laid at once by the titanosaur female, as in modern reptiles, or sequentially, as in modern birds and oviraptorosaurian dinosaurs (SATO et al. 2005). Evidence based on extant phylogenetic bracketing and pathological eggshell is equivocal (JACKSON & VARRICCHIO 2003, JACKSON et al. 2004). However, the small clutch mass relative to adult female mass, random egg distribution within the clutches, and the uniform eggshell thickness within a single clutch suggests that the eggs of a clutch at the European and Indian localities were formed and laid at the same time and not sequentially.

10.1.3 Gregarious nesting

True colonial nesting with gregarious behavior, as reported in some birds, is difficult to document in the fossil record but may be represented by the dense and apparently synchronous clutches that occur in many areas of the Auca Mahuevo site in Argentina (CHIAPPE et al. 2000, 2005). Close clutch spacing at this site would likely have

resulted in inadvertent nest destruction by trampling. Although definitive evidence is lacking, a carbonate-filled footprint, similar to those in the extensive track horizon that overlies an egg-bearing horizon (see section 2.5), occurs beside an egg clutch in egg bed 3. Trampling of eggs in open clutches, however, would most likely result in dispersal of eggshell to the adjoining sediments, due to weathering and transport. The absence of shell fragments between clutches in the nesting horizon suggests that movement within the area was limited once the eggs were laid.

10.1.4 Nest guarding

No direct evidence exists for nest guarding or attendance at any nesting locality. At Auca Mahuevo, the lack of substrate burial of eggs, however, suggests the possibility of prolonged nest attendance or guarding. Based on the comparison with extant birds, a titanosaur egg of 1.5 kg (the size of an ostrich egg) would require about 60 days to hatch, using an avian model (RAHN & AR 1974). This duration would likely necessitate prolonged attendance of one or both parents in the vicinity to deter egg predation. The density of clutches suggests this parental care might have been limited to the periphery of the nesting ground (CHIAPPE & DINGUS 2001).

10.1.5 Hatching

Hatching in the European and Indian eggs is relatively well understood. The position of the cap within hatched eggs provides evidence that the hatchling cut open the egg with an egg tooth and then left the egg, working its way to the surface and, in the process, pushing the cap into the empty shell (MUELLER-TÖWE et al. 2002). The lack of hatched material at Auca Mahuevo prevents assessment of hatching mode, although an osseous equivalent of an egg tooth has been documented in the rostral portion of some embryos (GARCIA 2007) as predicted by MUELLER-TÖWE et al. (2002).

10.1.6 Post-hatching parental care

Within the extant phylogenetic bracket of sauropod dinosaurs, crocodylians guard their nest and provide post-hatching care (COOMBS 1989, ZUG et al. 2001), as do almost all birds. However, no evidence exists for post-hatching care of titanosaur young. For the Auca Mahuevo titanosaurs, minimal parental care may have occurred, based on apparent gregarious nesting and lack of substrate burial that would conceal the eggs from predators.

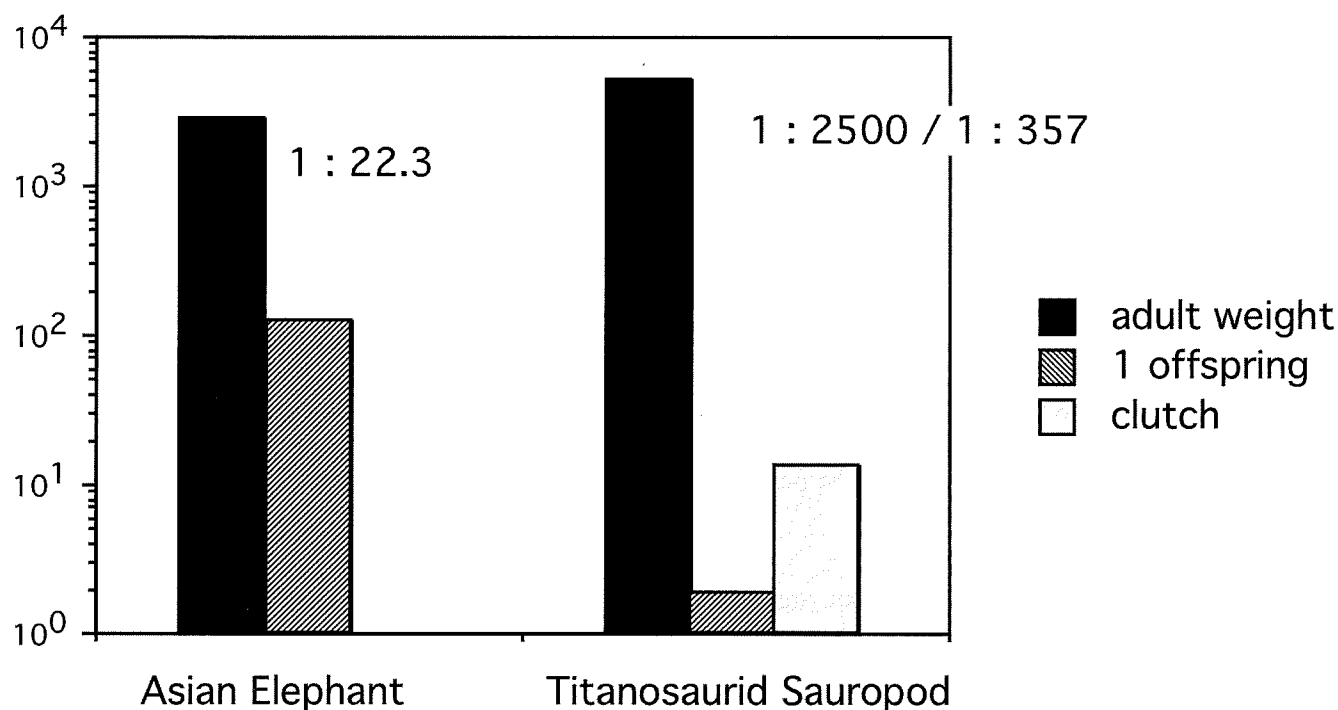
10.2 Evolutionary ecology

10.2.1 Apparent reproductive effort and implications for reproductive mode

Recently available data on titanosaur nesting sites allows the first quantitative estimates of sauropod reproductive effort, as expressed as a ratio of clutch mass to adult mass per nesting episode (i.e reproductive bout in the terminology of evolutionary ecology). It again is necessary to differentiate here between the European and Indian eggs on one hand and the Argentinian site of Auca Mahuevo on the other. Clutch mass is egg mass multiplied by clutch size. Estimates range from 12 kg for a six-egg clutch from Catalunya (based on our own data for egg mass, Text-fig. 14) or southern France (based on the average volume of 1900 cc per egg; SEYMOUR 1979) to 24 kg for a 30-egg clutch of eggs with a mass of 800 g from Argentina. DEEMING (2006), however, obtained a much greater egg mass of up to 5500 g for *Megaloolithus* eggs from southern France.

Estimating the mass of the female sauropod is difficult because of the paucity of body fossils associated with the nesting sites. *Ampelosaurus atacis* represents probably the best known titanosaur from southern France. This animal is a medium-sized sauropod, with a mature female weighing at least 10 t (based on data in LE LOEUFF 1995, 2005). Similarly, the most conservative mass estimates for mature females for any of the other localities is 5 t because there is not evidence for unusually small or even dwarfed sauropods in the respective deposits.

Estimates of reproductive effort (Text-fig. 14), therefore, vary between <0.12% (in the case of a 10t-*Ampelosaurus* producing the small Catalan clutches) and <1% (assuming the minimum 5 t-female at Auca Mahuevo). Using the higher egg masses computed by DEEMING (2006) for southern French *Megaloolithus* eggs, an intermediate value between the Catalan clutches and those from Argentina would obtain. These values for reproductive effort are all very low in comparison with recent vertebrates which typically have a substantial,



Text-fig. 14. Comparison of neonate size/hatchling size to mother size in a titanosaur (*Ampelosaurus ataxis*) and in a very large mammal, the Asian elephant. Data for Asian elephants are from KURT & U MAR (1996) and include seven captive mother-neonate pairs with a birth mass of 126 ± 28 kg and a mother body mass of 2814 ± 460 kg. Data for titanosaur sauropods are based on a very modest estimate of a mean body mass of 5 t for an adult *Ampelosaurus* female and a maximum clutch size of seven eggs with a volume of 2000 cc, as observed at Coll de Nargó, Spain. Offspring weight is assumed to have been slightly less than egg weight. Note relatively very low offspring mass in the sauropod.

although variable, reproductive effort (COCKBURN 1991, ZUG et al. 2001). This discrepancy between high adult female mass and low clutch mass in *Megaloolithus*-producing dinosaurs (Text-fig. 14) was previously noted by SEYMOUR (1979). While the value for reproductive effort may seem within the biologically reasonable limits for Auca Mahuevo, the European and Indian egg sites require further explanation.

10.2.2 Multiple clutches per season

Several hypotheses may be put forward to explain this apparently very low reproductive effort in the Indian and European titanosaurs. First, a scaling effect, because reproductive effort decreases with increasing body size, thus being relatively lower in very large animals. Second, these sauropods may have invested a "normal" reproductive effort by very extensive and energy-expensive parental care. No evidence, however, exist for either of these hypotheses. To the contrary, the evidence favors little or no parental care. A third hypothesis is that one female produced several relatively small clutches per reproductive season, laying them in different suitable locations of her home range. Alternative to a distinctive nesting season, clutches may have been produced in regular intervals throughout the year. More than one clutch per year is produced by some squamates (ZUG et al. 2001), most turtles (WILBUR & MORIN 1988, ZUG et al. 2001), at least one crocodylian (*Crocodylus palustris*; EWERT et al. 1984, LANCE 1989), as well as passerine birds.

Based on localities from southern France, a scenario in which titanosaurs in Europe and India produced several clutches per reproductive episode has been previously suggested (DUGHI & SIRUGUE 1966, SEYMOUR 1979). SEYMOUR based this scenario on his prediction (borne out by evidence from southern France and particularly from our recent work in Catalunya) that there is an upper limit to the size of a buried clutch set by respiratory physiology. Accordingly, deposition of several clutches would be necessary to produce a sufficiently large number of offspring per female per season. In addition, EWERT et al. (1984) proposed that

dinosaurs probably laid several clutches per season, based on abnormal multilayered eggshell. According to their hypothesis, retained eggs would receive additional eggshell layer(s) during a second or subsequent round of ovulation during the season. Further, they predicted that if complete clutches containing pathological eggs were eventually discovered, the abnormal eggs should lie near the bottom of the clutch, representing the first eggs expelled from the oviduct during the next laying episode (EWERT et al. 1984). However, the first in situ titanosaur clutches containing pathological eggs from Auca Mahuevo show that the abnormal eggs occur at the top rather than the bottom of the clutch (JACKSON et al. 2004). Therefore, evidence from the Auca Mahuevo locality remains equivocal in regard to multiple nesting seasons in the South American titanosaurs. Furthermore, as noted by EWERT et al. (1984), extant turtle eggs with as many as nine additional eggshell layers are known, yet no turtle species produces nine oviductal complements in a single season. Thus, the arguments used by EWERT et al. (1984) to support an annual multi-nesting scenario are questionable.

The difference in reproductive mode between Europe and India vs. Auca Mahuevo may explain why multiple clutches should be expected in the former but not necessarily in the latter. There are thus two independent lines of evidence suggesting multiple clutches in the European and Indian eggs. One is the small clutch size, the other is the hypothesized physiological limit of clutch size imposed by the incubation under cover. If correct, incubation under cover limited clutch size and led to the deposition of multiple clutches per season. The combination of much larger clutch size and evidence for open incubation (nesting traces and low shell porosity), necessitating prolonged nest attendance at Auca Mahuevo, suggest that the Argentinian titanosaurs may have produced only one clutch per season.

10.2.3 Obligatory r-strategy?

JANIS & CARRANO (1992) and PAUL (1994, 1997) previously hypothesized reproductive r-strategy in sauropod dinosaurs. Here, we argue that this life history strategy represented the only possibility for sauropods, due to constraints of the oviparous mode of reproduction. A striking contrast exists between the small size of *Megaloolithus* eggs and hatchlings, compared to adult female body size (Text-fig. 14). Among therian mammals today, reduction of the number of offspring accompanies an increase in the relative size of offspring. All megaherbivores (> 1 t body mass) produce no more than one or two offspring per reproductive bout (OWEN-SMITH 1988).

In birds, egg size shows a negative interspecific allometry (RAHN et al. 1975): the larger the bird, the relatively smaller the egg. Eggs are produced one at a time, from a single oviduct (CARPENTER 1999). Ostriches produce the largest extant bird egg, with a mass of 1.6 kg, compared to an adult mass of 150 kg. The largest known bird egg is that of *Aepyornis* from the Late Quaternary of Madagascar, with an egg volume 8.5 l (FEDUCCIA 1996), compared to an adult body weight of 275 kg (WORTHY & HOLDAWAY 2002). *Megaloolithus* eggs obviously do not scale with the avian curve or they would have weighed a few hundred kilograms. An extrapolation based on the formula of RAHN et al. (1975) and SCHMIDT-NIELSEN (1984; egg mass = $0.277 \times$ body mass to the 0.77th power) would result in an egg of 333 kg for a 10 t female! Such eggs would most certainly exceed the theoretical limit of egg size as discussed by AR et al. (1979). This limit is set by the shell thickness that is necessary to prevent breakage but still allow respiration of the embryo and successful hatching (ALEXANDER 1989 p. 157, SCHMIDT-NIELSEN 1984 p. 55). The theoretical size limit was probably approached by the *Aepyornis* egg (ALEXANDER 1989).

Crocodylians, the second group of extant archosaurs, produce larger clutches of much smaller eggs relative to female body weight (ZUG et al. 2001). Life history strategy in turtles is variable (WILBUR & MORIN 1988), from strongly K-selected taxa (e.g. *Cuora* spp.) to strongly r-selected species (e.g. marine turtles, Cheloniidae). Many birds and all large mammals are also K-strategists, while crocodylians are r-strategists. In titanosaurs, the combination of small offspring and probable large number of eggs (deposited in multiple clutches in the European and Indian titanosaurs) suggests they were r-strategists as well. R-strategy in sauropods comes as somewhat of a surprise because, based on the analogy with large endothermic tetrapods such as megaherbivores and large marine mammals, one would assume that sauropods were strongly K-selected. Endothermy in sauropods less derived than titanosaurs is suggested by their high growth rates documented by bone histology (CURRY 1999, ERICKSON et al. 2001, SANDER 2000, SANDER & TÜCKMANTEL 2003, SANDER et al. 2004). Although titanosaurian sauropods have not been studied histologically in detail, preliminary histologic evidence from *Ampelosaurus atacis* indicates that titanosaurs did not differ in this aspect from less derived sauropods.

One possible explanation for this discrepancy between sauropods and very large mammals could be constraints resulting from maximum egg size and absence of vivipary in all archosaurs. In modern sauropsids, the evolutionary step from ovipary to vivipary occurred relatively frequently and at low taxonomic levels. However, vivipary is not seen in sauropsids that produce rigid calcareous eggshells (turtles, some geckoes, all birds, and crocodylians). Vivipary generally evolves via prolonged egg retention and hatching of the embryo inside the mother. This evolutionary step is apparently incompatible with a rigid calcareous eggshell (PACKARD 1977). Thus, by being limited to an oviparous mode of reproduction, titanosaurian sauropods and, by extension, all sauropods were obligatory r-strategists because ovipary sets an absolute limit to offspring size. During an evolutionary size increase of a lineage, such as the one occurring in the origin of sauropod dinosaurs (SANDER et al. 2004), the limits to offspring size resulted in relatively very small offspring which had to be produced in large numbers to guarantee survival of at least a few individuals to reproduction.

11. Conclusions

Detailed fieldwork in nesting grounds provides an important source of information about dinosaur reproductive biology. This information, combined with analysis of eggshell microstructure, embryonic remains, and taphonomy allows much more refined interpretations of Late Cretaceous *Megaloolithus* nesting sites from Europe, India, and Argentina. Two reproductive modes for Late Cretaceous titanosaurs are inferred: In Europe and India, the female sauropod deposited a number of small clutches per year. Although the clutches were deposited primarily in soils comprised of fine grained or sandy sediment, no specific habitat or substrate preference is observed. Some sites were used for extended intervals of time. The clutch was laid in a pit covered by sediment or vegetation, and the eggs were incubated by solar heat or heat generated by decomposition of plant material, with no apparent post-hatching parental care of the young. This mode of incubation sets a limit to clutch size and thus necessitated multiple clutches per season to guarantee a sufficient reproductive effort.

At the Argentinian site of Auca Mahuevo, substrates used by females are primarily distal floodplain environments with soil development, but also include abandoned channel and crevasse splay sands. These sites, however, differ from the European and Indian localities in several aspects, including greater clutch density, significantly larger clutch size, and the arrangements of the eggs of a clutch in levels with a maximum of three stacked egg layers. The evidence indicates that Argentinian eggs were incubated in the open and may have been guarded by the parents in a nesting colony. Multiple clutches appear unlikely because of the prolonged incubation period. The single clutches at Auca Mahuevo thus should allow a precise estimate of the reproductive effort of these titanosaurs once the parent animals are sufficiently known.

The small egg size of *Megaloolithus* eggs, relative to adult titanosaur body size, suggests an obligatory r-strategy of reproduction for this group of dinosaurs. This may have been due to the biomechanical and physiological limitations on maximum egg size and the impossibility to evolve vivipary linked to the calcareous eggshell. In combination with the great body size, these factors blocked the evolutionary option of K-strategy for sauropods.

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