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Abstract

Titanosauria is a globally distributed clade of usually extremely large Mesozoic herbivorous sauropod dinosaurs. On the basis of current evidence these giant dinosaurs seem to have reproduced in highly particular and localized nesting sites. ~~Yet,~~ no investigations have been performed to understand the possible ecological and geological biases that acted for the selection of these nesting sites worldwide. In this study, observations were performed on the best-known Cretaceous nesting sites around the world. Our observations strongly suggest their eggs were incubated with environmental sources of heat, in burial conditions. Taking into account the clutch composition and geometry, the nature and properties of the sediments, the eggshells structures and conductance, it would appear that titanosaurs adopted nesting behaviors comparable to the modern Australasian megapodes, using burrow-nesting in diverse media and mound-building strategies.

INTRODUCTION

Titanosaur sauropods ~~are~~ Mesozoic dinosaurs (Bonaparte & Coria, 1993; Wilson & Upchurch, 2003; Curry Rogers, 2005) that reached gigantic sizes (Upchurch, Barrett & Dodson, 2004; Sander et al., 2011; Benson et al., 2014) but also ~~were miniaturized~~ in insular ecosystems (Benton et al., 2010; Stein et al., 2010; Csiki et al., 2010). These quadrupedal herbivores are easily recognizable by their long necks and tails (Fig. 1A), small heads (Fig. 1A-B) and a characteristic wide-gauge stance (Fig. 1C; Wilson & Carrano, 1999; Carrano, 2005; Wilson, 2005a).

~~The~~ titanosaurs populated every continent including Antarctica (Curry Rogers, 2005; Mannion et al., 2011; Cerda et al., 2012) and according to Mannion & Upchurch~~,~~ (2010, 2011) they preferred inland rather than coastal habitats. They experienced a great expansion during the Late Cretaceous, chiefly in South America, where ~~they diversified in~~ more than 20 genera (Upchurch & Barret, 2005; Zaher et al., 2011; Mannion et al., 2011; García et al., 201~~4~~; Vieira et al., 2014).

Eggs and egg clutches classified in Megaloolithidae, a parataxonomic ~~classification~~ of eggs without any modern biological principles, have been assigned to titanosaurs (as well as other taxa) (Vianey-Liaud et al., 1994; Mikhailov, 1997). Although in recent years numerous studies explored several aspects of ~~the~~ titanosaur~~s~~ reproductive biology (Cousin & Breton, 2000; Jackson et al., 2008; Sander et al., 2008; Vila et al., 2009, 2010), most of them were limited ~~by~~ the description and comparison of eggs and eggshells in a non-phylogenetic context (i.e. fossil parataxonomy). Titanosaur eggs and eggshells have only been positively identified in few instances with the discovery of embryos *in ovo* (Chiappe et al., 1998; Chiappe, Salgado & Coria, 2001; Wilson et al., 2010; Grellet-Tinner et al., 2011, 2012) and/or with cautious morphological characterizations of eggs and eggshells (Grellet-Tinner, Chiappe & Coria, 2004; Grellet-Tinner et al., 2006, 2011, 2012; Grellet-Tinner, Fiorelli & Salvador, 2012) that allow identification of phylogenetic characters.

Species survival is contingent on several factors: food availability, predation, competition and reproduction. Just as amniote oviparity freed vertebrates from water-bound reproduction, viviparity entirely disconnected environmental factors from hatching to maximize reproductive success. Modern archosaurs lay amniotic eggs in nests and their reproduction is thus more constrained by environmental drivers than viviparous amniotes. Therefore, judicious nesting-site selection becomes a critical factor, as parents cannot compensate post-hatching for a poor choice of nesting environment (Shine & Harlow, 1996; Kolbe & Janzen, 2002; Kamel & Mrosovsky, 2005; Grellet-Tinner & Fiorelli, 2010; Grellet-Tinner, Fiorelli & Salvador, 2012). Modern archosaurs are known to build two main nest types: “ground dweller” and “arboreal” nests. Although ~~the latter is~~ quite interesting and ~~has fostered~~ several studies (Collias, 1964, 1997; Hansell, 2000; Gill, 2007; Walsh et al., 2010), including phylogenetic analyses (Winkler & Sheldon, 1993; Zyskowski & Prum, 1999; Hansell, 2007), ~~it does~~ not offer a valid model for titanosaur reproduction. Hence, this study focuses on the nests of ground dwelling species. Ground nests interface in various degrees with the sediments~~, where~~ they are constructed. Among th~~o~~se, two types of structures are recognized based on the incubating temperature and humidity requirements (Booth & Thompson, 1991): ~~N~~ests~~,~~ ~~where~~ eggs are deposited in the air-sediment interface~~;~~ open-nests sensu Collias (1964)~~;~~ and nests ~~where~~ eggs are buried in the substrate (Collias 1964; Seymour & Ackerman, 1980; Larson, 1998; Jones & Göth, 2008; Brazaitis & Watanabe, 2011).

The odds of preserving any of these nesting structures in the fossil record are extremely poor (Hasiotis et al., 2007) and/or their preservation could easily be misinterpreted. Therefore, according to the taphonomy of behavior (Plotnick, 2012), we focus this investigation not only on ichnology but also behavioral biology, offering the following revised nest definitions in the context of this study to help identify and discriminate nests from egg clutches in the fossil record~~.~~

Archosaur nest: Any recognizable structure or modification of environment that is voluntarily made by the parents to ovideposit their eggs.

Archosaur nest function: Mediates and optimizes environments in order to insure successful egg incubation and hatching.

Archosaur nest diagnosis: An identifiable structure recognized to result from parental nesting behavior that contains at least either autochthonous egg remains or eggshell fragments.

~~W~~e review ~~here world-wide distributed~~ nesting sites (Fig. 2)~~,~~ that have been assigned to titanosaurs, their eggs, eggshell microstructures, and sedimentary data, ~~to~~ attempt to understand the reasons sauropods were able to reproduce globally, but use particular localized nesting sites characterized by an overwhelming abundance of egg clutches and eggs. Understanding their nesting and incubation strategies through the megapode model ~~may~~ shed light on the enigmatic reproductive behavior of these extinct behemoths.

MATERIALS AND METHODS

The fossil record of "titanosaur" eggs and shells extends to Europe, Asia, South America and Africa. However, less than 10 years have passed since their first inclusion in a phylogenetic study (Grellet-Tinner et al., 2006). In contrast, most of the earlier (e.g. Mikhailov, 1997; Mohabey, 1998, 2001; Garcia & Vianey-Liaud, 2001a; Vianey-Liaud & Zelenitsky, 2003) and several current studies (Fernández & Khosla, 2015; Sellés & Vila, 2015) provide descriptions lacking enough detail and/or skewed by the use of parataxonomic criteria (Grellet-Tinner et al., 2012). In addition to the egg and eggshell morphology, the study of titanosaur nesting strategies requires the combination of an array of sources of data, such as clutch geometry and spacing, description of the nesting sediments and their stratigraphic context, possible geothermal activity, availability of vegetal materials and paleoclimatic conditions.

It is unavoidable that data on some nesting sites are more comprehensive than others because some localities ~~were~~ more intensively researched than others, and with different purposes (e.g. stratigraphy, parataxonomy). The need for a full and accurate record prevented ~~include~~ in this study, for example, the findings of isolated eggshells in Morocco and Tanzania, in Africa (Garcia et al., 2003; Gottfried et al., 2004). In addition, it should be noted that the localities in Spain are much more restricted geographically than ~~others~~ in South America and Asia. Considering that in some cases they are ~~closer than~~ 100 m ~~from~~ each other (Sellés & Vila, 2015), several of them could belong to the same nesting areas. As such, the more than 220 localities with eggs and eggshells in Southern Pyrenees, (Sellés & Vila, 2015) are not directly comparable in terms of scale with other localities around the world. Although not as close together as in Spain, many of the localities reported in Southern France have also been studied ~~with~~ parataxonomic and biostratigraphic purposes (Garcia & Vianey-Liaud, 2001a,b; Vianey-liaud, Khosla & Garcia, 2003; Cojan, Renard & Emmanuel, 2003), hence not providing enough information on morphology and/or egg spatial distribution. In addition, most fossil eggs and eggshells discovered during the nineteenth and twentieth century were not recovered ~~under~~ appropriate stratigraphic control and/or using archaeological field techniques (Cousin & Breton, 2000). The same problem arises with the many localities reported in China and Mongolia, which yield an extensive record of megaloolithid and faveoloolithid eggs and eggshells (Carpenter & Alf, 1994; Liang et al., 2009).

Considering the above-mentioned constraints, we selected ~~8~~ ~~world-wide distributed~~ nesting sites that provide enough data (Table S1) for comparison with modern analogues: Sanagasta (Argentina), Gyeongsang Basin (South Korea), Haţeg (Romania), Dholi Dungri (India), Rennes-le-Château and Albas (France), Coll de Nargó (Spain), and Auca Mahuevo (Argentina). It should be noted that all the selected nesting sites preserve autochthonous and/or parautochthonous fossil material in contrast to eggs and eggshells found in lithologies that belong to different environmental settings (Table 1), hence creating preservation biases.

We selected Megapodiidae for modern nesting analogues. This avian family consists of 22 species that are limited to Australia, New Guinea, Micronesia, Melanesia and Polynesia (Dekker, 2007; Harris, Birks & Leaché, 2014). They are unique among living dinosaurs by exclusively using environmental heat sources rather than body heat to achieve incubation (Jones & Birks, 1992; del Hoyo, Elliott & Sargatal, 1994).

RESULTS

Sanagasta, Argentina

Although this site has been cautiously classified as a neosauropod nesting ground (Grellet-Tinner & Fiorelli, 2010; Fiorelli et al., 2012; Grellet-Tinner, Fiorelli & Salvador, 2012), some paleontologists have regarded eggs with similar morphology as titanosaurs (de Valais, Apesteguía & Udrizar Sauthier, 2003; Simón, 2006). Hence on this basis, we include this Cretaceous nesting site (Grellet-Tinner & Fiorelli, 2010; Fiorelli et al., 2012) in our study (Table 1). The Sanagasta nesting site located in La Rioja, Argentina (Tauber, 2007; Grellet-Tinner & Fiorelli, 2010; Fiorelli et al., 2012), represents the first account of synchronous geothermal activity and “titanosaur” nesting strategy in the fossil record (Grellet-Tinner & Fiorelli, 2010). Several clutches were recovered from a single outcrop of the Los Llanos Formation in the Sanagasta Valley (Tauber, 2007; Grellet-Tinner & Fiorelli, 2010; Fiorelli et al., 2012). The nesting sediments consist of medium to coarse-grained grey and whitish arkosic sands deposited in a hydrothermal setting (Fiorelli et al., 2012). The eggs exhibit a thick eggshell (thickness 7.9 mm-1.2 mm; mean = 3.84 mm; Grellet-Tinner, Fiorelli & Salvador, 2012) regarded as an adaptation to resist acid erosion during geothermal incubation (Grellet-Tinner & Fiorelli, 2010). The thick single structural layer of the Sanagasta eggshells displays nodular rounded structures on the outer surfaces and long eggshell units with slender concentric and convex growth lines, including secondary dichotomic branching outwards (Figs. 3A-D). The spongy appearance of the eggshell is produced by a high concentration of wide pores that meander and branch between the eggshell units (Grellet-Tinner, Fiorelli & Salvador, 2012). Moreover, the large (~4800 cm^3) subspherical eggs (Fig. 3E; Table 1) are perforated by ~482000 pores leading to a water vapor conductance of ~2850 mgH2O/day*Torr (Grellet-Tinner, Fiorelli & Salvador, 2012).

Several clutches (e.g., Fig. 3F) were discovered regularly placed nearby preserved geothermal relics, encrusted with silcrete-calcrete structures, some with up to 30 eggs (Grellet-Tinner & Fiorelli, 2010; Fiorelli et al., 2012; Grellet-Tinner, Fiorelli & Salvador, 2012). Although the eggs spatial distribution in two superposed rows, whereas the upper row has a greater amount of eggs (Tauber, 2007; Grellet-Tinner & Fiorelli, 2010; Fiorelli et al., 2012), suggesting that they were deposited in ~~dug out-nests~~, close to geothermal vents, springs, or pools, no nesting structure has been preserved (Fiorelli et al., 2013). Therefore, these fossil assemblages are referred only as egg clutches, although the oological data (Table 1) strongly support parental placement of dug out-nests with eggs in close proximity of hydrothermal structures.

Gyeongsang Basin, South Korea

The nesting paleoenvironment of Sanagasta was compared with South-Korean nesting sites in the Gyeongsang Basin (Fiorelli et al., 2012), where continental sedimentation, volcanism and hydrothermalism occurred concomitantly during the Late Cretaceous (Choi, 1986; Chough et al., 2000; Choi et al., 2005, 2006). The development of this basin was associated with subduction in an Andean-type continental margin during this period (Choi, 1986). The Korean egg clutches consist of faveoloolithid eggs (Paik, Huh & Kim, 2004) similar to those found in Sanagasta. The eggs are recovered in several Upper Cretaceous localities, preserved in sandy tuffaceous sandstones interpreted as floodplain deposits and related to meandering rivers. According to previous descriptions, the faveoloolithid eggs found in Boseong (one of the most studied localities of the Gyeongsang Basin) vary in diameter from 15 to 20 cm and have extremely porous eggshells of 1.33 to 2.20 mm thick (Huh & Zelenitsky, 2002; Kim et al., 2009). The taphonomic and paleoenvironmental analyses conducted by Paik, Huh & Kim (2004) and Paik, Kim & Huh (2012) revealed that several single-layered clutches of up to 16 eggs occur in different calcic paleosol levels, suggesting nesting site fidelity. Although many egg clutches were recovered, no nesting structures could be found in the encrusting sediments (Kim et al., 2009). However, Paik, Huh & Kim (2004) and Paik, Kim & Huh (2012) suggested that eggs were incubated buried in the substrate, thus laid in excavated nests. Interestingly, the geological origin and development of the Gyeonsang basin was related to subduction in an Andean-type continental margin (Choi, 1986), with epithermal deposits (Choi et al., 2005). As the latter are related to subaerial volcanism or shallow intrusions (Choi et al., 2005, 2006) and the nesting sediments are locally tuffaceous (Paik, Kim & Huh, 2012), Fiorelli et al. (2012) suggested that nesting in geothermal settings were not limited to a particular endemic neosauropod population but were used by allopatric populations of the same genus and comparable to the nesting strategies of the modern Malau megapode (*Megapodius pritchardii* Gray, 1864) in the Tongas Islands or the Maleo (*Macrocephalon maleo*, Muller, 1846) in Sulawesi, Indonesia.

Haţeg, Romania

Grellet-Tinner et al. (2012) examined a group of 11 titanosaur egg clutches discovered in the exposures of the Maastrichtian Sânpetru Formation, at Toteşti, Romania (Grigorescu et al., 1990;

Grigorescu, 1993; Codrea et al., 2002; Panaiotu & Panaiotu, 2010). Grellet-Tinner et al. (2012) mention the presence of geothermal-derived minerals in the eggshell pores and the presence of volcanic activities in the same basin concomitantly to the ovideposition of the eggs. Moreover, a tremendous ~~amount~~ of embryonic bones representing several taxa (titanosaurs, aves, and lepidosaurians~~) (~~Grellet-Tinner et al., 2012) were recovered in the same formation, supporting possible geothermal and hydrothermal activities related to the coeval Carpathians and Apuseni volcanism (Russo-Sändulescu & Berza, 1979; Kräutner, Vajdea & Romanescu, 1986; Ştefan et al., 1988). The egg clutches were encased in fine grained siltstone-mudstone sediments, typical of a low energy nesting environment (Bojar et al., 2005; Grellet-Tinner et al., 2012). The spherical eggs were deformed by lithostatic compression, to become subspherical (Codrea et al., 2002; Grellet-Tinner et al., 2012). Their phylogenetic characters match those of the eggs from the Auca Mahuevo layer 4 (AM L#4) (Grellet-Tinner et al., 2012) that were identified as nemegtosaurid titanosaurs (García et al., 2010), based on their embryos *in ovo*. As such, both the AM L#4 and Toteşti eggs display similar egg shape and size, eggshell thickness, identical structural single layer of the shell, consisting of acicular calcitic crystals radiating from nucleation centers located above the membrana testacea, the same Y-shaped vertical pore canals with funnel shaped pore apertures located between the nodular surficial ornamentation, similar unit and node shapes, as well as an horizontal pore canal network parallel to the membrana testacea (Figs. 4A–C; Grellet-Tinner, Chiappe & Coria, 2004; Grellet-Tinner et al., 2012). The Toteşti egg clutches (Fig. 4D) consist of groups of ~~4~~ eggs ~~in~~ average that are superposed similarly to those in Sanagasta, thus suggesting they were also buried in dug-out nests (Grellet-Tinner et al., 2012). However, like the previously described nesting sites (Kim et al., 2009; Grellet-Tinner & Fiorelli, 2010), no true nesting structure was recognized. As such, the inference of nests rests only on the spatial arrangement of eggs in each of the 11 clutches (see Table 1). Grellet-Tinner et al. (2012) also mention the presence at the same site of other isolated egg species which are larger and exhibit different eggshell macro and micro morphologies, thus belonging at least to an additional dinosaur species. The presence of several egg types at the same site and stratigraphic horizon may indicate a preferential nesting environment for the dinosaurs confined in the Haţeg insular system. Regardless of considering the exclusive presence of sauropod (mostly titanosaurs taxa) egg clutches or mixed egg fossils including ornithopod species, although not confirmed contra Grigorescu (2010) and Grigorescu et al. (2010), the interesting question remains why only Toteşti and Nălaţ-Vad, or Tustea were preferential laying grounds on the Haţeg Cretaceous volcanic island.

Dholi Dungri, India

The Upper Cretaceous (Maastrichtian) Lameta Formation in India, overlain by the volcanic flows of the Deccan Traps, is well known for its rich record of dinosaur nesting sites (Mohabey, Udhoji & Verma, 1993; Mohabey, 1998). It consists of calcareous sandstones deposited by episodic transport in an alluvial-limnic paleoenvironment related to semiarid climate and secondarily affected by extensive pedogenesis (Mohabey, Udhoji & Verma, 1993; Mohabey, 1998, 2005; Wilson et al., 2010). Although many oospecies were recognized in the fossil parataxonomy (Mohabey, 1998), only the 3 eggs referred as *Megaloolithus dhoridungriensis* have been directly associated with titanosaurs, based on close association with a partial hatchling found at the exposures near Dholi Dungri locality, Gujarat, India (Mohabey, 1998; Wilson et al., 2010).

According to Wilson et al. (2010) the spherical eggs range from 14 to18 cm in diameter with an eggshell thickness of 2.26-2.36 mm and display discrete eggshell units similar to other~~s~~ megaloolithids. Although they are slightly larger and have thicker shells (Table 1), the Dholi Dungri eggs share only a few similarities with Auca Mahuevo (AM) fossils in their shape and single structural layer with acicular calcitic crystals radiating from nucleation centers located above the missing membrana testacea, a similar nodular surficial ornamentation, and a horizontal pore canal network parallel at the base of the shell with straight vertical pore canals and funnel shaped apertures outward. However, the vertical pores do not appear to have the atypical Y-shaped ramifications and are significantly more numerous than titanosaur eggs from AM (Wilson et al., 2010). Their overall morphological characters are closer to the unidentified Toteşti and Nălaţ-Vad egg species with thicker eggshell (Grellet-Tinner et al., 2012), than the AM eggs. The Dholi Dungri titanosaur eggs have a volume of ~2150 cm^3, an egg mass of ~2300 g, and appear isolated or grouped in clutches of up to 12 eggs, with an average clutch mass (6 to 12 eggs per clutch) of ~21000 g (Wilson et al., 2010).

Like other Indian sites, no nesting structures have been observed at this locality (Wilson et al., 2010), but the high porosity of the eggshells suggests burial incubation (Sander et al., 2008; Wilson et al., 2010). Tandon et al. (1995) noted that some of the different nesting sites in the Lameta beds appear to be topographically related and widely distributed in similar lithologies, suggesting a "practiced sense of site selectivity".

Rennes-le-Château and Albas, France

Since the late 1800s, several titanosaur egg clutches have been discovered in Cretaceous exposures in Southern France (Freytet, 1965; Kerourio, 1981; Cousin et al., 1989, 1994).

However, according to Cousin and Breton (2000), the vast majority of the fossils were recovered with inadequate field techniques and/or inappropriate stratigraphic control. Therefore, we focus on the detailed excavations of the nesting sites at the Upper Maastrichtian, Rennes-le-Château (Cousin et al., 1994) and Albas (Cousin & Breton, 2000), as these two sites were quarried with archaeological techniques, thus providing a good overview of the taphonomy and nesting environment (Cousin & Breton, 2000).

The eggs typically exhibit eggshell thicknesses of up to 2.5 mm, although some samples show thinning by dissolution (Cousin & Breton, 2000). As in other titanosaur eggs, the French eggs display nodular rounded structures on their outer surfaces and spherulitic eggshell units with slender concentric and convex growth lines formed by acicular calcitic crystals radiating from nucleation centers located above the missing membrana testacea. Moreover, they display a horizontal pore canal network, parallel to the base of the shell, with straight vertical pore canals for gas conductance (some of them with complex branching network of secondary transverse canals and dichotomic Y-shaped ramifications), and pore apertures around the base of the external nodes. These eggshells are quite similar to those of titanosaur “megaloolithid” eggshells from Spain which, according to Jackson et al. (2008), have a high pore density and elevated gas conductance, nearly 4000 mgH_2O/day*Torr (an overestimate due to a calculation error for gas conductance of the eggshells by these authors). The 17 to 20 cm eggs have a volume of ~2100 cm^3, an egg mass of ~2300 g and a clutch mass varying from ~18500 g (Rennes-le-Château) to ~35000 g (Albas). In Rennes-le-Château the eggs were found isolated or in small arcuate rows, but also in clusters of 3 to 8 eggs (Cousin et al., 1989). The careful excavation revealed that the egg clutches were preserved *in situ* (Cousin & Breton, 2000; Cojan, Renard & Emmanuel, 2003) and deposited in different stratigraphic levels, thus, suggesting nesting site fidelity (Cousin et al., 1989; Cousin & Breton, 2000). The sedimentary evidence does not support the presence of true nests (as above-defined), although Cousin and Breton (2000) suggested that the eggs of the Albas clutch could have been deposited in shallow pits. Therefore, the lack of any supporting sedimentary structure does not allow the inference of sauropod nests at these two sites. Although the egg clutches from Southern France do not indicate any organic matter in the surrounding sediments, the possibility of incubation in nests with vegetal mounds has been suggested by Kerourio (1981) and Cousin and Breton (2000), based primarily on high conductance of the eggshells. Yet, Grellet-Tinner, Fiorelli & Salvador (2012) suggested that high conductance values alone do not imply incubation in mounds, but just environments with elevated moisture contents.

Coll de Nargó, Spain

Several sauropod egg clutches were reported in Northeastern Spain (Vila et al., 2009, 2010, 2011; Vila, Jackson & Galobart, 2010), a region that was also tectonically active at the time the eggs were oviposited (Puigdefàbregas, Muñoz & Vergés, 1992). These fossils were classified in the Megaloolitidae oofamily and later loosely associated ~~to~~ titanosaurs (Sander et al., 2008; Vila et al., 2009, 2010) after the discovery of titanosaur embryos in the eggs of *Megaloolithus patagonicus* (Chiappe et al., 2003), and *M. dhoridungriensis* (Wilson et al., 2010). According to Sellés et al. (2013), more than 30 egg-bearing stratigraphic levels distributed in two lithofacies, representing a fluvial paleoenvironment, are recognized in the Upper Cretaceous Tremp Formation (Sander et al., 2008; Vila, Jackson & Galobart, 2010; Vila et al., 2010). Both lithofacies and eggs show evidences of stress deformation, consistent with the tectonic stress orientation of the region (Vila et al., 2010).

The eggs and eggshells have been described by several authors (Jackson et al., 2008; Vila et al., 2009; Vila, Jackson & Galobart, 2010; Sellés et al., 2013). They are spherical and reach 20 cm in diameter (Vila, Jackson & Galobart, 2010). Their 2.5 mm thick eggshells show typical discrete units with slender concentric and convex growth lines of acicular calcite crystals radiating from the nucleation centers, as well as a pore network system with branching –dichotomic Y-shaped ramifications– and secondary transversal ones.

According to Sellés et al. (2013) the 75 clutches found *in situ* at Pinyes (a subsite at Coll de Nargó locality) support a nest site fidelity behavior. However, Vila et al. (2010) indicated that these clutches represent a single event, albeit no sedimentary evidence independently confirms their interpretation (Sander et al., 2008). Three types of egg clutches were recognized by Vila et al. (2010). The "type 1", consists of clutches with 20-28 eggs separated by 3 to 6 m and buried in bowl kidney-shaped depressions (Vila, Jackson & Galobart, 2010; Vila et al., 2010). However, in previous interpretations these were considered as superimposed clutches with fewer eggs (Peitz, 1998; Sander et al., 1998, 2008). According to Vila et al. (2010) and Vila, Jackson & Galobart (2010) but contra Sander et al. (2008), the egg spatial arrangement in these putative complete clutches coupled with the high water vapor conductance (G_{H2O}) of the eggshells (Deeming, 2006), would suggest the eggs were buried during incubation.

Auca Mahuevo, Argentina

This Campanian locality (Dingus et al., 2000) in the Anacleto Formation (Argentina) was the first report ~~of~~ titanosaur embryonic bones and soft tissues *in ovo* (Chiappe et al., 1998; Chiappe, Salgado & Coria, 2001; Salgado, Coria & Chiappe, 2005). They were recently re-identified as nemegtosaurids (García et al., 2010). The eggs are in four egg-bearing strata (Chiappe et al., 2003, 2004) consisting of reddish-brown siltstones and mottled mudstones (Chiappe et al., 2000, 2004; Garrido, 2010a), deposited in an alluvial plain (Sander et al., 2008; Garrido, 2010a) under the regime of a warm and seasonal climate (Garrido, 2010a). The eggs and eggshells were described in detail by Grellet-Tinner, Chiappe & Coria (2004) and Grellet-Tinner (2005). According to these authors the well-preserved eggshell specimens, averaging 1.30 mm thick, display a pronounced ornamentation of single nodes and a pore network that consists of vertical channel openings in funnel-like structures located between the surficial nodes (Figs. 5A–B). Some vertical pores branch in a “Y” pattern, a derived feature originally described for these eggs but shared with other titanosaurs (Figs. 5C–D; Grellet-Tinner, Chiappe & Coria, 2004; Grellet-Tinner, Fiorelli & Salvador, 2012). Additionally, they show horizontal canals located between the bases of the eggshell units –nucleation centers– and above the membrana testacea (Figs. 5C–D). The unhatched eggs range from 13 to 15 cm in diameter (Fig. 5E; Chiappe et al., 1998; Grellet-Tinner, Chiappe & Coria, 2004) and are preserved in clutches of 15 to 40 eggs (Fig. 5F; Chiappe et al., 2000; Grellet-Tinner, Chiappe & Coria, 2004). Although supposedly in their original position, egg clutches became undistinguishable from one another due to soft sediment deformations (field observations; Chiappe et al., 2003; Jackson, Schmitt & Oser, 2013). Like the above-mentioned European, Asian, and South American nesting sites, the dense accumulation of clutches (11 eggs/m^2; Sander et al., 2008) in egg layers 3 and 4, led to interpretations of gregarious and nesting site fidelity behaviors (Chiappe et al., 2000, 2003). Paradoxically despite the extent of this nesting site, no nesting structures were reported in these overbanking sedimentary layers which were, according to Garrido (2010a), the preferred laying grounds close the stream channel for these nemegtosaurids. However, six trace fossils interpreted as nests with accumulations of eggs were reported in alluvial deposits (Chiappe et al., 2004) of an abandoned channel in the AM L#4 (Chiappe et al., 2003; Sander et al., 2008), which clearly contradict "the preferred areas close to stream channels" of Garrido (2010a). The six rimmed, sub-circular to kidney-shaped structures contain 4 to 35 randomly disposed eggs in 1 or 2 superposed rows. They were interpreted as rimmed-nests, ranging from 85 to 125 cm, and 10 to 18 cm deep (Chiappe et al., 2004; Sander et al., 2008). The six fossil assemblages were regarded as nests and an "open nest" strategy was suggested for the entire, assumed monospecific nesting site (Chiappe et al., 2004; Sander et al., 2008). However, a recent re-evaluation of the putative nests concluded that the rimmed structures were titanosaur footprints in an abandoned channel (Grellet-Tinner, Fiorelli & Salvador, 2012) that randomly trapped eggs during the several episodic floods. This interpretation is consistent with all the geological data and supported by the inconsistency of an "open nest" hypothesis (Chiappe et al., 2004; Jackson et al., 2008; Sander et al., 2008), considering the high G_{H2O} of the eggshells (Grellet-Tinner, Fiorelli & Salvador, 2012). Like other titanosaurs, the AM eggs' morphology indicates they were likely incubated in relatively high nesting humidities (Grellet-Tinner, Chiappe & Coria, 2004; Grellet-Tinner et al., 2006).

DISCUSSION

Titanosaur nesting strategies

The taphonomy of behavior emphasizes the need ~~of~~ defining trace fossils in terms of both classical ichnology and modern behavioral biology (Plotnick, 2012). Furthermore, the concept of behavioral fidelity, expressed as the "extent to which trace fossils preserve original behavioral signals" (Plotnick, 2012), allows behavioral interpretations contrastable to currently existing data. Considering solely the sedimentological evidence, none of the above-mentioned nesting sites display a diagnostic fossil nest structure. In the absence of direct evidence of preserved fossil nests, eggs and their spatial grouping, eggshell morphologies, coupled with observations of surrounding sediments, provide the only data with respect to nesting moisture content and heat, as those are the main extrinsic parameters that are paramount for hatching success. Pore canals allow the diffusion of gases and water vapor through the eggshell (Paganelli, 1980). Their size, geometry, and number reflect a specialization to the habitat where nesting occurs (Williams, Seymour & Kerourio, 1984; Cousin, 1997; Grellet-Tinner, Fiorelli & Salvador, 2012). Eggshell ornamentation (or lack thereof) is another morphological characteristic from which a nesting paleoenvironment can be hypothesized. Cousin (1997) and Cousin and Breton (2000) used the characteristics of the nodular appearance of eggshells from the Late Cretaceous of France as an indicator of the substrate, or nesting material, surrounding the eggs. This character (Grellet-Tinner, Chiappe & Coria, 2004; Grellet-Tinner & Zaher, 2007; Grellet-Tinner et al., 2011) was regarded as a specialization increasing gas conductance through the pores that are located around and at the base of each node, by preventing nesting debris from plugging their apertures (Sabath, 1991). The densely packed nodular structures typically observed on the outer surfaces of pristine titanosaur eggshells provide a substantial increase of surface in contact with the surrounding environment, suggesting they could also have acted to buffer acidic erosion during long periods of incubation, an interpretation consistent with GGT and colleagues (unpublished data) observations on modern megapode eggshells and associated nesting environments in Australia. Gas diffusion occurs through the pores and can be quantified by the eggshell's G_{H2O} (Seymour, 1979). It is commonly obtained for modern birds and reptiles by measuring water loss in a known vapor gradient across the shell (Ar et al., 1974). G_{H2O} for fossil eggs can be estimated from eggshell thickness and pore-system geometry and so forms a valuable proxy for assessing the moisture content in dinosaur nests, their environments (Seymour, 1979; Seymour &

Ackerman, 1980), and nesting strategies (Ar et al., 1974; Seymour, 1979; Birchard & Kilgore, 1980; Seymour et al., 1987; Grellet-Tinner, Chiappe & Coria, 2004; Deeming, 2006; Grellet-Tinner, Fiorelli & Salvador, 2012).

Titanosaurs could not have used the classic contact incubation strategy typical of most modern dinosaurs (Seymour, 1979; Werner & Griebeler, 2011; Ruxton, Birchard & Deeming, 2014), thus must have relied on external environmental heat for incubating their eggs. Interestingly, the extant Australasian megapodes are one of the most intriguing avian dinosaur families because they exhibit a practice unique among modern birds, regarded as a reversal character, of incubating their eggs by utilizing only environmental heat sources rather than body heat (Booth & Thompson, 1991; Jones & Birks, 1992; del Hoyo, Elliott & Sargatal, 1994). Moreover, they display the most diversified incubation behaviors among ground nesting archosaurs (Jones & Birks, 1992; del Hoyo, Elliott & Sargatal, 1994; Harris, Birks & Leaché, 2014), which are associated with species specific nesting strategies and nesting sites (Boles & Ivison, 1999; Harris, Birks & Leaché, 2014). These are: (1) mound-building; (2) burrow-nesting using geothermal heat; (3) burrow-nesting using solar-heated beaches; (4) burrow-nesting using decaying tree roots; (5) mound parasitism. As such, Megapodiidae potentially offers a valid proxy for titanosaur reproductive behaviors.

Among the titanosaurs nesting sites reviewed in this investigation, only two have been positively related with geothermalism: The well-documented Sanagasta and the South Korean eggs (Table 1). The compact arrangement of the Sanagasta eggs, in clutches of one or two layers, led Grellet-Tinner & Fiorelli (2010) and Fiorelli et al. (2012) to suggest incubation in excavated nests; a strategy already inferred by Paik, Huh & Kim (2004) and Paik, Kim & Huh (2012) for the eggs from Seonso Formation (Gyeongsang Basin, South Korea) (Table 1). The eggs from these sites have a similar morphology (but a thinner eggshell thickness in Gyeongsang) and they also share sedimentary and geological features of geothermal activities concomitant with the oviposition. This supports the hypothesis that geothermal heat sources could have been used by certain species of Cretaceous titanosaurs. Several megapode species –*Macrocephalon maleo*, *Eulipoa wallacei* Gray, 1861 and many *Megapodius* sp. – use burrow nesting with vegetal decomposition, solar radiation and/or geothermalism (inclusive here of volcanism) as incubating strategies (Frith, 1956; Dekker & Brom, 1960; Jones & Birks, 1992; del Hoyo, Elliott & Sargatal, 1994; Göth & Vogel, 1997; Dekker, 2007; Bowen, 2010; Harris, Birks & Leaché, 2014). The remarkable instance of opportunistic nesting in geothermal settings represents an adaptive case in which species avoid thermally heterogeneous nesting environments by exploiting geothermal conditions that maintain higher and more constant temperatures and moisture levels in egg clutches (Werner, 1983; Göth & Vogel, 1997; Chen, Kam & Lin, 2001; Wu & Kam, 2005; Guo et al., 2008; Huang et al., 2009; Sas, Antal & Covaciu-Marcov, 2010; Grellet-Tinner & Fiorelli, 2010; Grellet-Tinner, Fiorelli & Salvador, 2012). For example, the malau (*M. pritchardii*) digs pits more than 2 m deep to utilize underground geothermal heat (Frith, 1956; del Hoyo, Elliott & Sargatal, 1994; Göth & Vogel, 1997). In addition, because burrow nests in geothermal ecosystems are less susceptible than mounds to predation, burrow-nesting megapodes can abandon their nests after burying their clutch (Dekker, 1989; del Hoyo, Elliott & Sargatal, 1994), a strategy consistent with the titanosaur behavior inferred from the fossil record (Sander et al., 2008, 2011; Werner & Griebeler, 2011; Ruxton, Birchard & Deeming, 2014), where nesting sites were often located and synchronous with geothermal activities. Paradoxically, megapodes' nest-burrows are dug preferably in soft soils, in volcanic sands, environments that inhibit preservation of such structures in the fossil record because they easily collapse (Frith, 1956; Dekker & Brom, 1960; Roper, 1983; Bowen, 2010).

Although~~,~~ the first reports of AM nesting site implied a monotaxic titanosaur assemblage, further refined to nemegtosaurid titanosaur (García et al., 2010), one of the co-authors (Eagle et al., *in press*) has determined that the egg-laying titanosaurs in AM L#4 may represent a different nemegtosaurid species, certainly closely related to those nesting in Auca Mahuevo layers 1-3 (AM L#1-3) but displaying sufficient autapomorphies to justify a species variation (Table 1). This species variation is also supported by an environmental change. Celestite geodes and barite are ubiquitous in AM L#1-3 (Garrido, 2010a, 2010b). These two minerals are readily produced in geothermal and evaporitic settings, both equally possible at AM due to its particular geology (Jackson, Schmitt & Oser, 2013). Moreover geochemical analyses reveal a higher concentration of magnesium and lithium in AM L#1-3 than AM L#4 (R. Eagle et al., *in press*). These two minerals are prevalent in continental brines, which could be also formed under high evaporitic conditions or geothermalism. However the evidence available suggests AM have been selected first by a certain nemegtosaurid species (AM L#1-3) for its presence of limited rivers in a semiarid environment and then, after a climatic change toward wetter conditions, replaced by another closely related species with more conspicuous nodular eggshell ornamentation, adapted to a more humid nesting environment (Table 1). Climatic and environmental changes are also documented in the clay fabric in the 4 AM layers (Jackson, Schmitt & Oser, 2013). Interestingly, among the modern Megapodiidae a similar niche partition is observed in Australasia. The mound-builder *Alectura lathami* Gray, 1831 (brush-turkey) nests in wetter environments in coastal Australian regions with respect with its congener *Leipoa ocellata* Gould, 1840 (malleefowl) that nests in semi-arid settings. Although both species are contemporaneous their geographical niche partitioning is related to vegetation and climatic differences. Such species specific nesting partitioning in modern Australia may explain the nemegtosaurid successive species replacement in AM from a dryer environment nesting adaptation, such as occurs in AM L#1-3, to a wetter setting, recorded upwards by the transition to the Allen Formation's estuarine-coastal sediments (Garrido, 2010a, 2010b). Combined with the lack of convincing geothermal evidence, although not entirely discounted due to the episodic explosive volcanism (Jackson, Schmitt & Oser, 2013), the horizons with egg clutches and the eggshell structures would suggest mound-building nesting strategies with a dryer climate for AM L#1-3 which display shallower nodular eggshell ornamentation and wetter for AM L#4 with pronounced nodular ornamentation (Table 1). The oological material from AM L#4 and Haţeg are very similar, sharing several synapomorphies including egg size, shape and eggshell microstructure (Grellet-Tinner, Chiappe & Coria, 2004; Grellet-Tinner et al., 2012). The complexity of their pore systems is consistent with a morphological adaptation to high moisture nesting environments, typical of burial conditions. Furthermore, in AM a semiarid dry/wet climate coupled with episodic volcanism contributed to vertisol horizons development at the floodplain areas (Garrido, 2010a; Jackson, Schmitt & Oser, 2013). Rhizoliths and root traces as well as small fossil logs found there (Garrido, 2010a, 2010b; Jackson, Schmitt & Oser, 2013) suggest a floristic abundance that would promote ideal conditions for mound-nesting behaviors.

Although crocodilians' mound-nests also average 1 m high and 3m in diameter (Joanen, 1969; Webb, Messel & Magnusson, 1977; Seymour & Ackerman, 1980; Waitkuwait, 1989), it is important to distinguish this type of vegetal mounds from those of the Australian brush-turkey megapodes, built from humus, soil and smaller amounts of true vegetal matter. Modern megapodes construct surprisingly large nest~~s~~-mounds, ~~if compared~~ to their egg and clutch sizes.

Although a few mounds could reach 4 m in height, 18 m in length and 5 m in width, a typical brush-turkey mound commonly measure 1 by 4 m (height and diameter respectively) and requires up to 5 tons of soil mixed with vegetal matter (Seymour & Ackerman, 1980; Jones & Birks, 1992; del Hoyo, Elliott & Sargatal, 1994; Harris, Birks & Leaché, 2014). Conversely, nesting structures smaller than 0.75 m high and 2 m long are not functional (Jones & Birks, 1992; del Hoyo, Elliott & Sargatal, 1994; Jones & Göth, 2008). In contrast, malleefowl mounds consist mostly of sandy material with terrigeneous clasts. Malleefowl build their mound, and then dig out the center into which semi-arid to arid vegetation, like spinifex, is introduced before the rainy season (Frith, 1959; Jones & Birks, 1992; Jones & Göth, 2008; D. Booth, pers. comm.). Eggs are laid around this center core that induces sufficient heat from vegetal decomposition to support embryonic development. This results in all eggs being placed relatively centrally within a mound (D. Booth, pers. comm.). Temperatures in the mound range from 27 to 38 ºC, although eggs mostly lie in the range of 32 to 36 ºC (Booth, 1987). In contrast brush-turkey females burrow into the mound obliquely. The litter material does not collapse around the tunnel as sand would in a malleefowl mound (D. Booth, pers. comm.). Hence, eggs can be dispersed throughout the place in large mounds and not just in the central core as in the malleefowl ones. One strategy would result in eggs grouped together in a compact clutch, while the other results in eggs isolated or lined up in small groups when the mound is eroded away. In comparison, the latter matches the pattern already observed in the titanosaur nesting sites of Southern France, where Cousin et al. (1989) and Cousin and Breton (2000) interpreted that small groups of eggs (2 to 4) are not randomly distributed but belong to circular "supergroups" of up to 15 eggs and 3.5 m in diameter (see Fig. 10 in Cousin & Breton, 2000) substantially separated from others (Cousin et al., 1989; Cousin & Breton, 2000). Additionally, the few-egg clutches found in close association in Coll de Nargó that were interpreted by Vila et al. (2010) as partially preserved ~25-egg clutches, show similar patterns. As such, the egg spatial distribution, in small clusters linearly to compactly grouped, but contained in round shaped areas of up to 2.3 m (see Table 1; Vila et al., 2010), would either support burrow- or mound-nesting (Cousin & Breton, 2000).

The Upper Cretaceous eggs and eggshells found at the reviewed nesting sites of Southern France and Northern Spain share many characteristics. Regarding their similarities (Table 1), and considering the high conductance values of the Pinyes' eggs, a highly humid incubation environment can be inferred for both locations. Although the evidences at hand suggest burial incubation, no record of organic matter or hydrothermal relics has been identified in their fine surrounding sediments. Regarding the morphological aspects, the minimal differences in size between eggshell pores and the fine sediments reported in both cases obscure the inference of vegetation as nesting material.

Although there are no published analyses on gas conductance for the Dholi Dungri eggs, the high values obtained from other Indian localities, ranging between 2650 mgH2O/(day*torr) and 3490 mgH_2O/(day*torr) (Sahni et al., 1994), suggests a high moisture nesting microenvironment. Considering the nodular appearance of the eggshells as a good indicator of the surrounding nesting material (Cousin & Breton, 2000) the provision of substantial amounts of plant debris as constructing material cannot be discarded. Although the sediment itself is coarse enough to prevent pore obstruction, the well-developed ornamentation of the eggshells could be a mechanism to prevent the external eggshell erosion, by the acid formed by decomposing microbes and fungi during an extended incubation period, like in modern megapodes. The morphological and sedimentological evidences at hand, coupled with the interpretation of a semiarid, tropical dry-wet climate for the Lameta Formation during Maastrichtian (Tandon et al., 1995; Tandon & Andrews, 2001; Wilson et al., 2010; Prasad & Sahni, 2014), allows to infer an *A. lathami*-like nesting strategy, similar to that suggested for AM L#4 (Table 1). However, regarding the magnitude of the volcanism responsible of the Deccan Traps deposition, during Late Cretaceous, the geothermalism could also be regarded as an equally plausible alternative heat source for egg incubation. Interestingly, although Tandon et al. (1995) suggest the nesting activity in the Lameta Formation was contemporaneous with the first Deccan lavas, questions regarding its possible relationship still require further research.

Many species of modern megapodes are known to use mound-nesting strategies to incubate their eggs (Harris, Birks & Leaché, 2014). However, they are also known to revert to less conspicuous nesting strategies such as burrow-nesting (Dekker, 1989) because of their behavioral lability (Harris, Birks & Leaché, 2014). As such, although dusky megapode (*Megapodius freycinet* Gaimard, 1823) populations are categorized as mound-builders, they are also burrow-nesters and exploit geothermal resources for heat and moisture in New Britain and the Solomon Islands (Roper, 1983). This species demonstrates an interesting behavioral plasticity (Frith, 1956), yet still relying on environmental heat only. Additionally, the Moluccan megapodes (*Eulipoa wallacei*) lay their eggs in black volcanic sands and silt utilizing solar heat (del Hoyo, Elliott & Sargatal, 1994; Dekker, 2007) but also are known to switch to geothermal and microbial decomposition. Because of the scarcity of suitable nesting areas, burrow-nester megapodes (e.g., *M. freycinet*, *M. maleo*, and *M. pritchardii*) commonly adopt colonial nesting behaviors and site fidelity (del Hoyo et al., 1994; Dekker et al., 2000). Similarly, strong nesting environment selectivity and colonial nesting were related to the massive occurrence of eggs and egg clutches in similar lithofacies, in some of the best known titanosaur nesting sites (Sahni et al., 1994; Mohabey, 2001). Although some titanosaur species may have adopted nesting strategies relying on various styles of mound-nests, it is entirely plausible that a few of them ~~may~~ have reverted to such opportunistic behaviors when available, ~~this~~ particularly in settings like Haţeg (Grellet-Tinner et al., 2012), India (Tandon et al., 1995) and AM (Jackson, Schmitt & Oser, 2013) where volcanism and related processes were coeval with nesting titanosaurs (Table 1).

Seymour and Ackerman (1980) emphasized that vegetal decomposition through microorganisms could be critical in terms of gas tension for mound-builder archosaurs. When clutches are large, as occurs with the ~20 egg clutches of the Australian brush-turkey, the gas tensions as well as the temperature in the mound vary with the reworking of the mound by parents (Seymour & Ackerman, 1980; del Hoyo, Elliott & Sargatal, 1994; Priddel & Wheeler, 2003). Assuming similar incubation strategies, it seems that the sizes of the sauropods could have ~~prohibited~~ active reworking of the mound to compensate gas and temperature variations. Yet, such post-oviposition activities ~~may have not~~ been required, e.g. in modern alligators, that exhibit similar “~~i~~n masse” laying behaviors.

CONCLUSION

Titanosaurs reproduced in globally distributed but highly particular and localized nesting sites (Sahni et al., 1994; Mohabey, 2001). The geological-sedimentological record of the reviewed titanosaur sites suggests that different titanosaurs species may have evolved an array of reproductive strategies comparable to those of modern megapodes. The observed eggshell features indicate high nesting moisture content, yet with variable nesting humidities as expressed by the geometry of the pore canals used for gas diffusion through the eggshells. The egg spatial positions in clutches suggest excavated holes (e.g., Fig. 6A) as well as mound incubation (Fig.

6B). Mound-nesting incubation in its various forms as observed in modern megapodes, although not entirely supported because of the absence or paucity of organic matter or plant debris in close association with all the eggs or egg clutches in the fossil record, may be quite plausible. The sites –Haţeg, Dholi Dungri, Rennes-le-Château, Albas, Coll de Nargó and AM– seem to support mound incubating, but tectonism associated with volcanism was recorded in these sites, thus leaving an open door for opportunistic geothermal incubation strategies. In that regard geothermal and hydrothermal settings (Fig. 6) have undoubtedly been exploited by in Sanagasta and the South Korean southern peninsula for their external heat and moisture.

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REFERENCES

Ar A, Paganelli C V, Reeves RB, Greene DG, Rahn H. 1974. The avian egg: water vapor conductance, shell thickness, and functional pore area. *Condor* 76:153–158.

Birchard GF, ~~Kilgore DLJ.~~ 1980. Conductance of water vapor in eggs of burrowing and nonburrowing birds: implications for embryonic gas exchange. *Physiological Zoology* 53:284–292.

Benson RBJ, Campione NE, Carrano MT, Mannion PD, Sullivan C, Upchurch P, Evans DC. 2014. Rates of dinosaur body mass evolution indicate 170 million years of sustained ecological innovation on the avian stem lineage. *PLoS Biology* 12:e1001853.

Benton MJ, Csiki Z, Grigorescu D, Redelstorff R, Sander PM, Stein K, Weishampel DB. 2010. Dinosaurs and the island rule: the dwarfed dinosaurs from Haţeg Island. *Palaeogeography, Palaeoclimatology, Palaeoecology* 293:438–454.

Bojar A-V, Grigorescu D, Ottner F, Csiki Z. 2005. Palaeoenvironmental interpretation of dinosaur- and mammal-bearing continental Maastrichtian deposits, Haţeg basin, Romania. *Geological Quarterly* 49:205–222.

Bojar A-V, Csiki Z, Grigorescu D. 2010. Stable isotope distribution in Maastrichtian vertebrates and paleosols from the Haţeg Basin, South Carpathians. *Palaeogeography, Palaeoclimatology, Palaeoecology* 293:329–342.

Boles WE, Ivison TJ. 1999. A new genus of dwarf megapode (Galliformes: Megapodiidae) from the Late Oligocene of central Australia. *Smithsonian Contributions to Paleobiology* 89:199–206.

Bonaparte JF, Coria RA. 1993. Un nuevo y gigantesco saurópodo titanosaurio de la Formación Río Limay (Albiano-Cenomaniano) de la Provincia del Neuquén, Argentina. Ameghiniana 30:271–282.

Booth DT. 1987. Effect of temperature on development of mallee fowl *Leipoa ocellata* eggs. *Physiological Zoology* 60:437–445.

Booth DT, Thompson MB. 1991. A comparison of reptilian eggs with those of megapode birds. In: Deeming DC, Ferguson MWJ eds. *Egg incubation: its effects on embryonic development in birds and reptiles*. Cambridge University Press, 325–344.

Bowen J. 2010. Notes on the Vanuatu Megapode Megapodius layardi on Ambrym, Vanuatu. *Bird Conservation International* 6:401–408.

Brazaitis P, Watanabe ME. 2011. Crocodilian behaviour: a window to dinosaur behaviour? *Historical Biology* 23:73–90.

Calvo JO, Porfiri JD, González-Riga BJ, Kellner AW a. 2007. A new Cretaceous terrestrial ecosystem from Gondwana with the description of a new sauropod dinosaur. *Anais da Academia Brasileira de Ciências* 79:529–41.

Carpenter K, Alf K. 1994. Global distribution on dinosaur eggs, nests and babies. In: Carpenter K, Hirsch KF, Horner JR eds. *Dinosaur Eggs and Babies*. United States of America: Cambridge University Press, 15–30.

Carrano MT. 2005. The evolution of sauropod locomotion: morphological diversity of a secondarily quadrupedal radiation. In: Curry Rogers KA, Wilson JA eds. *The Sauropods: Evolution and Paleobiology*. University of California Press, 229–251.

Cerda IA, Paulina Carabajal A, Salgado L, Coria RA, Reguero MA, Tambussi CP, Moly JJ. 2012. The first record of a sauropod dinosaur from Antarctica. *Naturwissenschaften* 99:83–7.

Chen TC, Kam YC, Lin YS. 2001. Thermal physiology and reproductive phenology of *Buergeria japonica* (Rhacophoridae) breeding in a stream and a geothermal hotspring in Taiwán. *Zoological Science* 18:591–596.

Chiappe LM, Coria R, Dingus L, Jackson F, Chinsamy A, Fox M. 1998. Sauropod dinosaur embryos from the Late Cretaceous of Patagonia. *Nature* 396:258–261.

Chiappe LM, Dingus L, Jackson F, Grellet-Tinner G, Aspinall R, Clarke JA, Coria RA, Garrido AC, Loope DB. 2000. Sauropod eggs and embryos from the Late Cretaceous of Patagonia. *First international symposium on dinosaur eggs and babies, extended abstracts*. 23–29.

Chiappe LM, Coria RA, Jackson F, Dingus L. 2003. The Late Cretaceous nesting site of Auca Mahuevo (Patagonia, Argentina): eggs, nests, and embryos of titanosaurian sauropods. *Palaeovertebrata* 32:97–108.

Chiappe LM, Schmitt JG, Jackson FD, Garrido AC, Dingus L, Grellet-Tinner G. 2004. Nest structure for sauropods: sedimentary criteria for recognition of dinosaur nesting traces. *Palaios* 19:89–95.

Chiappe LM, Salgado L, Coria R a. 2001. Embryonic skulls of titanosaur sauropod dinosaurs. *Science* 293:2444–6.

Choi HI. 1986. Sedimentation and evolution of the Cretaceous Gyeongsang Basin, southeastern Korea. *Journal of the Geological Society* 143:29–40.

Choi S-G, Ryu I-C, Pak SJ, Wee S-M, Kim CS, Park M-E. 2005. Cretaceous epithermal gold–silver mineralization and geodynamic environment, Korea. *Ore Geology Reviews* 26:115–135.

Choi S-G, Pak SJ, Kim CS, Ryu I-C, Wee S-M. 2006. The origin and evolution of mineralizing fluids in the Cretaceous Gyeongsang Basin, Southeastern Korea. *Journal of Geochemical Exploration* 89:61–64.

Chough SK, Kwon S-T, Ree J-H, Choi DK. 2000. Tectonic and sedimentary evolution of the Korean peninsula: a review and new view. *Earth-Science Reviews* 52:175–235.

Codrea V, Smith T, Dica P, Folie A, Garcia G, Godefroit P, Van Itterbeeck J. 2002. Dinosaur egg nests, mammals and other vertebrates from a new Maastrichtian site of the Haţeg Basin (Romania). *Comptes Rendus Palevol* 1:173–180.

Cojan I, Renard M, Emmanuel L. 2003. Palaeoenvironmental reconstruction of dinosaur nesting sites based on a geochemical approach to eggshells and associated palaeosols (Maastrichtian, Provence Basin, France). *Palaeogeography, Palaeoclimatology, Palaeoecology* 191:111–138.

Collias NE. 1964. The evolution of nests and nest-building in birds. *American Zoologist* 4:175–190.

Collias NE. 1997. On the origin and evolution of nest building by passerine birds. *The Condor* 99:253–270.

Cousin R, Breton G, Fournier R, Watte J-P. 1989. Dinosaur egg-laying and nesting: the case of an Upper Maastrichtian site at Rennes-Le-Chateau (Aude, France). *Historical Biology* 2:157–167.

Cousin R, Breton G, Fournier R, Watte J-P. 1994. Dinosaur egglaying and nesting in France. In: Carpenter K, Hirsch KF, Horner JR eds. *Dinosaur Eggs and Babies*. Cambridge: Cambridge University Press, 56–74.

Cousin R. 1997. Les gisements d'ceufs de dinosauriens des Hautes Corbières et des Corbières Orientales (Aude): Ponte, nidification, microstructure des coquilles. *Bulletin de la Société d'Études Scientifiques de l'Aude* 97:29–46.

Cousin R, Breton G. 2000. A precise and complete excavation is necessary to demonstrate a dinosaur clutch structure. In: *First international symposium on dinosaur eggs and babies, extended abstracts*. 31–42.

Csiki Z, Codrea V, Jipa-Murzea C, Godefroit P. 2010. A partial titanosaur (Sauropoda, Dinosauria) skeleton from the Maastrichtian of Nălaţ-Vad, Haţeg Basin, Romania. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen* 258:297–324.

Curry Rogers KA. 2005. Titanosauria: a phylogenetic overview. In: Curry Rogers KA, Wilson JA eds. *The Sauropods: Evolution and Paleobiology*. University of California Press, 50–103.

Deeming DC. 2006. Ultrastructural and functional morphology of eggshells supports the idea that dinosaur eggs were incubated buried in a substrate. *Palaeontology* 49:171–185.

Dekker RWRJ. 1989. Predation and the western limits of megapode distribution (Megapodiidae; Aves). *Journal of Biogeography* 16:317–321.

Dekker RWRJ. 2007. Distribution and speciation of megapodes (Megapodiidae) and subsequent development of their breeding behaviour. In: Renema W ed. *Biogeography, time, and place: distributions, barriers, and islands*. Dordrecht, The Netherlands: Springer, 93–102.

Dekker RWRJ, Brom TG. 1960. Megapode phylogeny and the interpretation of incubation strategies. *Zoologische Verhandelingen* 278:19–31.

Dingus L, Clarke J, Scott GR, Swisher III CC, Chiappe LM, Coria RA. 2000. Stratigraphy and magnetostratigraphic/faunal constraints for the age of sauropod embryo-bearing rocks in the Neuquén Group (Late Cretaceous, Neuquén Province, Argentina). *American Museum Novitates* 3290:1–11.

Eagle RA, Enriquez M, Grellet-Tinner G, Perez-Huerta A, Hu D, Tütken T, Montanari S, Loyd S, Ramirez P, Tripati A, Kohn M, Cerling T, Chiappe LM, Eiler J. *in press*. Isotopic (13C-18O) ordering in eggshells reflects body temperatures and suggests differing thermophysiology in two Cretaceous dinosaurs. *Nature Communications*.

Fernández MS, Khosla A. 2015. Parataxonomic review of the Upper Cretaceous dinosaur eggshells belonging to the oofamily Megaloolithidae from India and Argentina. *Historical Biology* 27:158–180.

Fiorelli LE, Grellet-Tinner G, Alasino PH, Argañaraz E. 2012. The geology and palaeoecology of the newly discovered Cretaceous neosauropod hydrothermal nesting site in Sanagasta (Los Llanos Formation), La Rioja, northwest Argentina. *Cretaceous Research* 35:94–117.

Fiorelli LE, Grellet-Tinner G, Argarañaz E, Salgado L. 2013. Tafonomía del sitio de nidificación de neosaurópodos de Sanagasta (La Rioja, Argentina): ejemplo de preservación excepcional en un paleoambiente hidrotermal del Cretácico. *Ameghiniana* 50:389–406.

Freytet P. 1965. Découverte d'oeufs de Dinosaures à Saint-André-de-Roquelongue (Aude). *Bulletin de la Société d'Etudes de la Science de l'Aude* 65:121–124.

Frith HJ. 1956. Breeding habits in the family Megapodiidae. *Ibis* 98:620–640.

Frith HJ. 1959. Breeding of the mallee fowl, *Leipoa ocellata* Gould (Megapodiidae). *Wildlife Research* 4:31–60.

Garcia G, Vianey-Liaud M. 2001a. Nouvelles données sur les coquilles d'œufs de dinosaures Megaloolithidae du Sud de la France: systématique et variabilité intraspécifique. *Comptes Rendus de l'Académie des Sciences - Series IIA - Earth and Planetary Science* 332:185–191.

Garcia G, Vianey-Liaud M. 2001b. Dinosaur eggshells as biochronological markers in Upper Cretaceous continental deposits. *Palaeogeography, Palaeoclimatology, Palaeoecology* 169(1-2):153–164.

Garcia G, Tabuce R, Cappetta H, Marandat B, Bentaleb I, Benabdallah A, Vianey-Liaud M. 2003. First record of dinosaur eggshells and teeth from the North-West African Maastrichtian (Morocco). *Palaeovertebrata* 32:59–69.

García RA, Salgado L, Coria RA, Chiappe LM. 2010. Osteología embrionaria de saurópodos titanosaurios de Neuquén (Argentina): aspectos ontogenéticos y evolutivos. *Ameghiniana* 47:409–430.

García R, Salgado L, Fernández M, Cerda I, Paulina Carabajal A, Otero A, Coria R, Fiorelli L. 201~~4~~. Paleobiology of titanosaurs: reproduction, development, histology, pneumaticity, locomotion and neuroanatomy from the South American fossil record. *Ameghiniana* 52:29–68

Garrido AC. 2010a. Paleoenvironment of the Auca Mahuevo and Los Barreales sauropod nesting-sites (Late Cretaceous, Neuquén Province, Argentina). *Ameghiniana* 47:99–106.

Garrido AC. 2010b. Estratigrafía del Grupo Neuquén, Cretácico Superior de la Cuenca Neuquina (Argentina): nueva propuesta de ordenamiento litoestratigráfico. *Revista del Museo Argentino de Ciencias Naturales* 12:121–177.

Gill FB. 2007. Nests and Incubation. In: Gill FB ed. *Ornithology*. New York: W. H. Freeman and Company, 431–466.

Gottfried MD, O'Connor PM, Jackson FD, Roberts EM, Chami R. 2004. Dinosaur eggshell from the Red Sandstone Group of Tanzania. *Journal of Vertebrate Paleontology* 24:494–497.

Göth A, Vogel U. 1997. Egg laying and incubation of Polynesian megapode. *Annual Review of the World Pheasant Association* 1996-97:43–54.

Grellet-Tinner G. 2005. Membrana testacea of titanosaurid dinosaur eggs from Auca Mahuevo (Argentina): Implications for exceptional preservation of soft tissue in Lagerstätten. *Journal of Vertebrate Paleontology* 25:99–106.

Grellet-Tinner G, Chiappe L, Norell M, Bottjer D. 2006. Dinosaur eggs and nesting behaviors: A paleobiological investigation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 232:294–321.

Grellet-Tinner G, Sim CM, Kim DH, Trimby P, Higa A, An SL, Oh HS, Kim T, Kardjilov N. 2011. Description of the first lithostrotian titanosaur embryo in ovo with Neutron characterization and implications for lithostrotian Aptian migration and dispersion. *Gondwana Research* 20:621–629.

Grellet-Tinner G, Codrea V, Folie A, Higa A, Smith T. 2012. First evidence of reproductive adaptation to “island effect” of a dwarf Cretaceous Romanian titanosaur, with embryonic integument in ovo. *PloS One* 7:e32051.

Grellet-Tinner G, Chiappe LM, Coria RA. 2004. Eggs of titanosaurid sauropods from the Upper Cretaceous of Auca Mahuevo (Argentina). *Canadian Journal of Earth Sciences* 41:949–960.

Grellet-Tinner G, Fiorelli LE. 2010. A new Argentinean nesting site showing neosauropod dinosaur reproduction in a Cretaceous hydrothermal environment. *Nature Communications* 1:32.

Grellet-Tinner G, Fiorelli LE, Salvador RB. 2012. Water vapor conductance of the Lower Cretaceous dinosaurian eggs from Sanagasta, La Rioja, Argentina: Paleobiological and paleoecological implications for South American faveoloolithid and megaloolithid eggs. *Palaios* 27:35–47.

Grellet-Tinner G, Zaher H. 2007. Taxonomic identification of the Megaloolithid egg and eggshells from the Cretaceous Bauru Basin (Minas Gerais, Brazil): Comparison with the Auca Mahuevo (Argentina) Titanosaurid eggs. *Papéis Avulsos de Zoologia* 47:105–112.

Grigorescu D, Seclamen M, Norman DB, Weishampel DB. 1990. Dinosaur eggs from Romania. *Nature* 346:417.

Grigorescu D. 1993. The latest Cretaceous dinosaur eggs and embryos from the Haţeg Basin - Romania. *Revue De Paléobiologie* 7:95–99.

Grigorescu D. 2010. The "Tustea Puzzle": hadrosaurid (Dinosauria, Ornithopoda) hatchlings associated with Megaloolithidae eggs in the Maastrichtian of the Hateg Basin (Romania). *Ameghiniana* 47:89–97.

Grigorescu D, Garcia G, Csiki Z, Codrea V, Bojar A-V. 2010. Uppermost Cretaceous megaloolithid eggs from the Haţeg Basin, Romania, associated with hadrosaur hatchlings: Search for explanation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 293:360–374.

Guo P, Liu SY, Feng JC, He M. 2008. The description of a new species of *Thermophis* (Serpentes: Colubridae). *Sichuan Journal of Zoology* 27:321.

Hansell MH. 2000. *Bird nests and construction behaviour*. Cambridge: Cambridge University Press.

Hansell MH. 2007. *Built by animals: the natural history of animal architecture*. Oxford: Oxford University Press.

Harris RB, Birks SM, Leaché AD. 2014. Incubator birds: biogeographical origins and evolution of underground nesting in megapodes (Galliformes: Megapodiidae). *Journal of Biogeography* 41:2045–2056.

Hasiotis ST, Platt BF, Hembree DI, Everhart MJ. 2007. The trace-fossil record of vertebrates. In: Miller W ed. *Trace fossils: concepts, problems, prospects*. Amsterdam, The Netherlands: Elsevier, 196–218.

del Hoyo J, Elliott A, Sargatal J. 1994. *Handbook of the birds of the world. Vol 2. New World vultures to guinea fowl*. Barcelona: Lynx Edicions.

Huang S, Liu S, Guo P, Zhang Y, Zhao E. 2009. What are the closest relatives of the hot-spring snakes (Colubridae, *Thermophis*), the relict species endemic to the Tibetan Plateau? *Molecular phylogenetics and evolution* 51:438–46.

Huh M, Zelenitsky DC. 2002. Rich dinosaur nesting site from the Cretaceous of Bosung county, Chullanam-Do province, South Korea. *Journal of Vertebrate Paleontology* 22:716–718.

Jackson FD, Varricchio DJ, Jackson RA, Vila B, Chiappe LM. 2008. Comparison of water vapor conductance in a titanosaur egg from the Upper Cretaceous of Argentina and a *Megaloolithus siruguei* egg from Spain. *Paleobiology* 34:229–246.

Jackson FD, Schmitt JG, Oser SE. 2013. Influence of vertisol development on sauropod egg taphonomy and distribution at the Auca Mahuevo locality, Patagonia, Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology* 386:300–307.

Joanen T. 1969. Nesting ecology of alligators in Louisiana. *Proceedings of the Annual Conference of Southeastern Association of Game and Fish Commissioners* 23:141–151.

Jones D, Birks S. 1992. Megapodes: Recent Ideas on Origins, Adaptations and Reproduction. *Trends in Ecology and Evolution* 7:88–91.

Jones DN, Göth A. 2008. *Mound-builders: malleefowl, brush turkeys and scrubfowl*. Collingwood, Victoria, Australia: CSIRO Publishing.

Kamel SJ, Mrosovsky N. 2005. Repeatability of nesting preferences in the hawksbill sea turtle, *Eretmochelys imbricata*, and their fitness consequences. *Animal Behaviour* 70:819–828.

Kerourio P. 1981. Nouvelles observations sur le mode de nidification et de ponte chez les dinosauriens du Crétacé terminal du Midi de la France. *Compte rendu sommatre des sélances de la Sociéité Géologique de France* 1:25–28.

Kim C-B, Al-Aasm IS, Ghazban F, Chang H-W. 2009. Stable isotopic composition of dinosaur eggshells and pedogenic carbonates in the upper cretaceous seonso formation, South Korea: Paleoenvironmental and diagenetic implications. *Cretaceous Research* 30:93–99.

Kolbe JJ, Janzen FJ. 2002. Impact of nest-site selection on nest success and nest temperature in natural and disturbed habitats. *Ecology* 83:269–281.

Kräutner HG, Vajdea E, Romanescu O. 1986. K–Ar dating of the banatitic magmatites from the southern Poiana Ruscă Mountains (Rusca Montană sedimentary basin). *DS Inst Geol Geofiz* 70-71:373-388.

Larson PL. 1998. The theropod reproductive system. *Gaia* 15:389–397.

Liang X, Wen S, Yang D, Zhou S, Wu S. 2009. Dinosaur eggs and dinosaur egg-bearing deposits (Upper Cretaceous) of Henan Province, China: Occurrences, palaeoenvironments, taphonomy and preservation. *Progress in Natural Science* 19:1587–1601.

Mannion PD, Upchurch P, Carrano MT, Barrett PM. 2011. Testing the effect of the rock record on diversity: a multidisciplinary approach to elucidating the generic richness of sauropodomorph dinosaurs through time. *Biological Reviews* 86:157–81.

Mannion PD, Upchurch P. 2010. A quantitative analysis of environmental associations in sauropod dinosaurs. *Paleobiology* 36:253–282.

Mannion PD, Upchurch P. 2011. A re-evaluation of the “mid-Cretaceous sauropod hiatus” and the impact of uneven sampling of the fossil record on patterns of regional dinosaur extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology* 299:529–540.

Mikhailov KE. 1997. Fossil and recent eggshell in amniotic vertebrates: fine structure, comparative morphology and classification. *Special Papers in Palaeontology*:83.

Mohabey DM. 1998. Systematics of indian Upper Cretaceous dinosaur and chelonian eggshells. *Journal of Vertebrate Paleontology* 18:348–362.

Mohabey DM. 2001. Indian dinosaur eggs: a review. *Journal of the Geological Society of India* 58:479–508.

Mohabey DM. 2005. Late Cretaceous (Maastrichtian) nests, eggs, and dung mass (coprolites) of sauropods (titanosaurs) from India. In: Tidwell V, Carpenter K eds. *Thundelizards: the Sauropodomorph Dinosaurs*. Bloomington and Indianapolis: Indiana University Press, 466–489.

Mohabey DM, Udhoji SG, Verma KK. 1993. Palaeontological and sedimentological observations on nonmarine Lameta Formation (Upper Cretaceous) of Maharashtra, India: their palaeoecological and palaeoenvironmental significance. *Palaeogeography, Palaeoclimatology, Palaeoecology* 105:83–94.

Paganelli C V. 1980. The physics of gas exchange across the avian eggshell. *American Zoologist* 20:329–338.

Paik IS, Huh M, Kim HJ. 2004. Dinosaur egg-bearing deposits (Upper Cretaceous) of Boseong, Korea: occurrence, palaeoenvironments, taphonomy, and preservation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 205:155–168.

Paik IS, Kim HJ, Huh M. 2012. Dinosaur egg deposits in the Cretaceous Gyeongsang Supergroup, Korea: Diversity and paleobiological implications. *Journal of Asian Earth Sciences* 56:135–146.

Panaiotu CG, Panaiotu CE. 2010. Palaeomagnetism of the Upper Cretaceous Sânpetru Formation (Haţeg Basin, South Carpathians). *Palaeogeography, Palaeoclimatology, Palaeoecology* 293:343–352.

Peitz C. 1998. Megaloolithid dinosaur eggs from the Maastrichtian of Catalunya (NE-Spain) - parataxonomic implications and stratigraphic utility. In: *First International symposium on dinosaur eggs and babies, extended abstracts*. 155–159.

Pigati JS, Rech JA, Quade J, Bright J. 2014. Desert wetlands in the geologic record. *Earth-Science Reviews* 132:67–81.

Plotnick RE. 2012. Behavioral biology of trace fossils. *Paleobiology* 38:459–473.

Prasad GVR, Sahni A. 2014. Vertebrate fauna from the Deccan volcanic province: Response to volcanic activity. *Geological Society of America Special Paper 505*.

Priddel D, Wheeler R. 2003. Nesting activity and demography of an isolated population of malleefowl (*Leipoa ocellata*). *Wildlife Research* 30:451–464.

Puigdefàbregas C, Muñoz JA, Vergés J. 1992. Thrusting and foreland basin evolution in the Southern Pyrenees. In: McClay KR ed. *Thrust tectonics*. The Netherlands: Springer, 247–254.

Riera V, Anadón P, Oms O, Estrada R, Maestro E. 2013. Dinosaur eggshell isotope geochemistry as tools of palaeoenvironmental reconstruction for the upper Cretaceous from the Tremp Formation (Southern Pyrenees). *Sedimentary Geology* 294:356–370.

Roper DS. 1983. Egg incubation and laying behaviour of the incubator bird *Megapodius freycinet* on Savo. *Ibis* 125:384–389.

Russo-Sändulescu D, Berza T. 1979. Banatites from the western part of the South Carpathians. *Rev. Roum. Geol. Geophys. Geogr.* 23:149–158.

Ruxton GD, Birchard GF, Deeming DC. 2014. Incubation time as an important influence on egg production and distribution into clutches for sauropod dinosaurs. *Paleobiology* 40:323–330.

Sabath K. 1991. Upper Cretaceous amniotic eggs from the Gobi Desert. *Acta Palaeontologica Polonica* 36:151–189.

Sahni A, Tandon SK, Jolly A, Bajpai S, Sood A, Srinivasan S. 1994. Upper Cretaceous dinosaur eggs and nesting sites from the Deccan volcano-sedimentary province of peninsular India. In: Carpenter K, Hirsch KF, Horner JR eds. *Dinosaur eggs and babies*. Cambridge: Cambridge University Press, 204–226.

Salgado L, Coria RA, Chiappe LM. 2005. Osteology of the sauropod embryos from the Upper Cretaceous of Patagonia. *Acta Palaeontologica Polonica* 50:79–92.

Sander PM, Peitz C, Gallemi J, Cousin R. 1998. Dinosaurs on a red beach? *C. R. Acad. Sci. Paris* 327:67–74.

Sander PM, Peitz C, Jackson FD, Chiappe LM. 2008. Upper Cretaceous titanosaur nesting sites and their implications for sauropod dinosaur reproductive biology. *Palaeontographica Abt. A* 284:69-107.

Sander PM, Christian A, Clauss M, Fechner R, Gee CT, Griebeler E-M, Gunga H-C, Hummel J, Mallison H, Perry SF, Preuschoft H, Rauhut OWM, Remes K, Tütken T, Wings O, Witzel U. 2011. Biology of the sauropod dinosaurs: the evolution of gigantism. *Biological Reviews* 86:117–55

Sas L, Antal C, Covaciu-Marcov SD. 2010. Tropics patch in the Holarctic: a new case of wintertime breeding of a *Pelophylax ridibundus* population in North-Western Romania. *North-Western Journal of Zoology* 6:128–133.

Sellés AG, Bravo AM, Delclòs X, Colombo F, Martí X, Ortega-Blanco J, Parellada C, Galobart À. 2013. Dinosaur eggs in the Upper Cretaceous of the Coll de Nargó area, Lleida Province, south-central Pyrenees, Spain: Oodiversity, biostratigraphy and their implications. *Cretaceous Research* 40:10–20.

Sellés AG, Vila B. 2015. Re-evaluation of the age of some dinosaur localities from the southern Pyrenees by means of megaloolithid oospecies. *Journal of Iberian Geology* 41:125–139.

Seymour RS. 1979. Dinosaur eggs: Gas conductance through the shell, water loss during incubation and clutch size. *Paleobiology* 5:1–11.

Seymour RS, Vleck D, Vleck CM, Booth DT. 1987. Water relations of buried eggs of mound building birds. *Journal of Comparative Physiology B* 157:413–422.

Seymour RS, Ackerman RA. 1980. Adaptations to underground nesting in birds and reptiles. *American Zoologist* 20:437–447.

Shine R, Harlow PS. 1996. Maternal manipulation of offspring phenotypes via nest-site selection in an oviparous lizard. *Ecology* 77:1808–1817.

Simón ME. 2006. Cáscaras de huevos de dinosaurios de la Formación Allen (Campaniano-Maastrichtiano), en Salitral Moreno, provincia de Río Negro, Argentina. *Ameghiniana* 43:513–528.

Stein K, Csiki Z, Rogers KC, Weishampel DB, Redelstorff R, Carballido JL, Sander PM. 2010. Small body size and extreme cortical bone remodeling indicate phyletic dwarfism in

Magyarosaurus dacus (Sauropoda: Titanosauria). *Proceedings of the National Academy of Sciences* 107:9258–63.

Ştefan A, Lăzăr C, Berbelac I, Udubaşa G. 1988. Evolution of banatitic magmatism in the Apuseni Mountains and associated metallogenesis. *D.S. Inst Geol Geofiz* 72-73:195–213.

Tandon SK, Sood A, Andrews JE, Dennis PF. 1995. Palaeoenvironments of the dinosaur-bearing Lameta beds (Maastrichtian), Narmada Valley, Central India. *Palaeogeography, Palaeoclimatology, Palaeoecology* 117:153–184.

Tandon SK, Andrews JE. 2001. Lithofacies associations and stable isotopes of palustrine and calcrete carbonates: examples from an Indian Maastrichtian regolith. *Sedimentology* 48:339–355.

Tauber AA. 2007. Primer yacimiento de huevos de dinosaurios (Cretácico Superior) de la provincia de La Rioja, Argentina. *Ameghiniana* 44:11–28.

Upchurch P, Barrett PM, Dodson P. 2004. Sauropoda. In: Weishampel DB, Dodson P, Osmolska H eds. *The Dinosauria*. Berkeley, California: University of California Press, 259–322.

Upchurch P, Barrett PM. 2005. Phylogenetic and taxic perspectives on sauropod diversity. In: Curry Rogers KA, Wilson JA eds. *The Sauropods: Evolution and Paleobiology*. University of California Press, 104–124.

de Valais S, Apesteguía S, Udrizar Sauthier D. 2003. Nuevas evidencias de dinosaurios de la Formación Puerto Yeruá (Cretácico), Provincia de Entre Ríos, Argentina. *Ameghiniana* 40:631–635.

Vianey-Liaud M, Mallan P, Buscail O, Montgelard C. 1994. Review of French dinosaur eggshells: morphology, structure, mineral and organic composition. In: Carpenter K, Hirsch KF, Horner JR eds. *Dinosaur Eggs and Babies*. Cambridge University Press, 151–183.

Vianey-Liaud M, Zelenitsky DK. 2003. Historical and new perspectives on the parataxonomy of fossil eggs. *Palaeovertebrata* 32:189–195.

Vianey-liaud M, Khosla A, Garcia G. 2003. Relationships between European and Indian Dinosaur eggs and eggshells of the oofamily Megaloolithidae. *Journal of Vertebrate Paleontology* 23:575–585.

Vieira WLS, Vieira KS, Nóbrega RP, Montenegro PFGP, Pereira Filho GA, Santana GG, Alves RRN, Almeida WO, Vasconcellos A. 2014. Species Richness and Evidence of Random Patterns in Assemblages of South American Titanosauria during the Late Cretaceous (Campanian–Maastrichtian). *PLoS ONE* 9:e108307.

Vila B, Galobart À, Oms O, Poza B, Bravo AM. 2009. Assessing the nesting strategies of Late Cretaceous titanosaurs: 3-D clutch geometry from a new megaloolithid eggsite. *Lethaia* 43:197–208.

Vila B, Jackson FD, Fortuny J, Sellés AG, Galobart A. 2010. 3-D modelling of megaloolithid clutches: insights about nest construction and dinosaur behaviour. *PloS one* 5:e10362.

Vila B, Riera V, Bravo AM, Oms O, Vicens E, Estrada R, Galobart À. 2011. The chronology of dinosaur oospecies in south-western Europe: Refinements from the Maastrichtian succession of the eastern Pyrenees. *Cretaceous Research* 32:378–386.

Vila B, Jackson FD, Galobart À. 2010. First data on dinosaur eggs and clutches from Pinyes locality (Upper Cretaceous, Southern Pyrenees). *Ameghiniana* 47:79–87.

Waitkuwait WE. 1989. Present knowledge on the West African slender-snouted crocodile, *Crocodylus cataphractus* Cuvier 1824 and the West African dwarf crocodile, *Osteolaemus tetraspis* Cope 1861. In: IUCN ed. *Crocodiles. Their Ecology, Management and*

Conservation. IUCN/SSC Crocodile Specialist Group. IUCN Publications. Gland, Switzerland, 259–275.

Walsh PT, Hansell M, Borello WD, Healy SD. 2010. Repeatability of nest morphology in African weaver birds. *Biology letters* 6:149–51.

Webb GJW, Messel H, Magnusson W. 1977. The nesting of *Crocodylus porosus* in Arnhem Land, northern Australia. *Copeia* 1977:238–249.

Werner DI. 1983. Reproduction in the Iguana *Conolophus subcristatus* on Fernandina Island, Galapagos: Clutch Size and Migration Costs. *The American Naturalist* 121:757–775.

Werner J, Griebeler EM. 2011. Reproductive biology and its impact on body size: comparative analysis of mammalian, avian and dinosaurian reproduction. *PloS one* 6:e28442.

Williams DLG, Seymour RS, Kerourio P. 1984. Structure of fossil dinosaur eggshell from the Aix Basin, France. *Palaeogeography, Palaeoclimatology, Palaeoecology* 45:23–37.

Wilson JA, Upchurch P. 2003. A revision of *Titanosaurus* Lydekker (Dinosauria–Sauropoda), the first dinosaur genus with a ‘Gondwanan’ distribution. *Journal of Systematic Palaeontology* 1:125–160.

Wilson JA. 2005a. Overview of sauropod phylogeny and evolution. In: Curry Rogers KA, Wilson JA eds. *The Sauropods: Evolution and Paleobiology*. University of California Press, 15–49.

Wilson JA. 2005b. Redescription of the Mongolian sauropod *Nemegtosaurus mongoliensis* Nowinski (Dinosauria: Saurischia) and comments on Late Cretaceous sauropod diversity. *Journal of Systematic Palaeontology* 3:283–318.

Wilson JA, Mohabey DM, Peters SE, Head JJ. 2010. Predation upon hatchling dinosaurs by a new snake from the Late Cretaceous of India. *PLoS biology* 8:e1000322.

Wilson JA, Carrano MT. 1999. Titanosaurs and the origin of wide-gauge trackways a biomechanical and systematic perspective on sauropod locomotion. *Paleobiology* 25:252–267.

Winkler DW, Sheldon FH. 1993. Evolution of nest construction in swallows (Hirundinidae): a molecular phylogenetic perspective. *Proceedings of the National Academy of Sciences* 90:5705–5707.

Wu C-S, Kam Y-C. 2005. Thermal tolerance and thermoregulation by Taiwanese rhacophorid tadpoles (*Buergeria japonica*) living in geothermal hot springs and streams. *Herpetologica* 61:35–46.

Zaher H, Pol D, Carvalho AB, Nascimento PM, Riccomini C, Larson P, Juarez-Valieri R, Pires-Domingues R, da Silva NJ, Campos DDA. 2011. A complete skull of an Early Cretaceous sauropod and the evolution of advanced titanosaurians. *PloS one* 6:e16663.

Zyskowski K, Prum RO. 1999. Phylogenetic analysis of the nest architecture of neotropical ovenbirds (Furnariidae). *The Auk* 116:891–911.

FIGURES

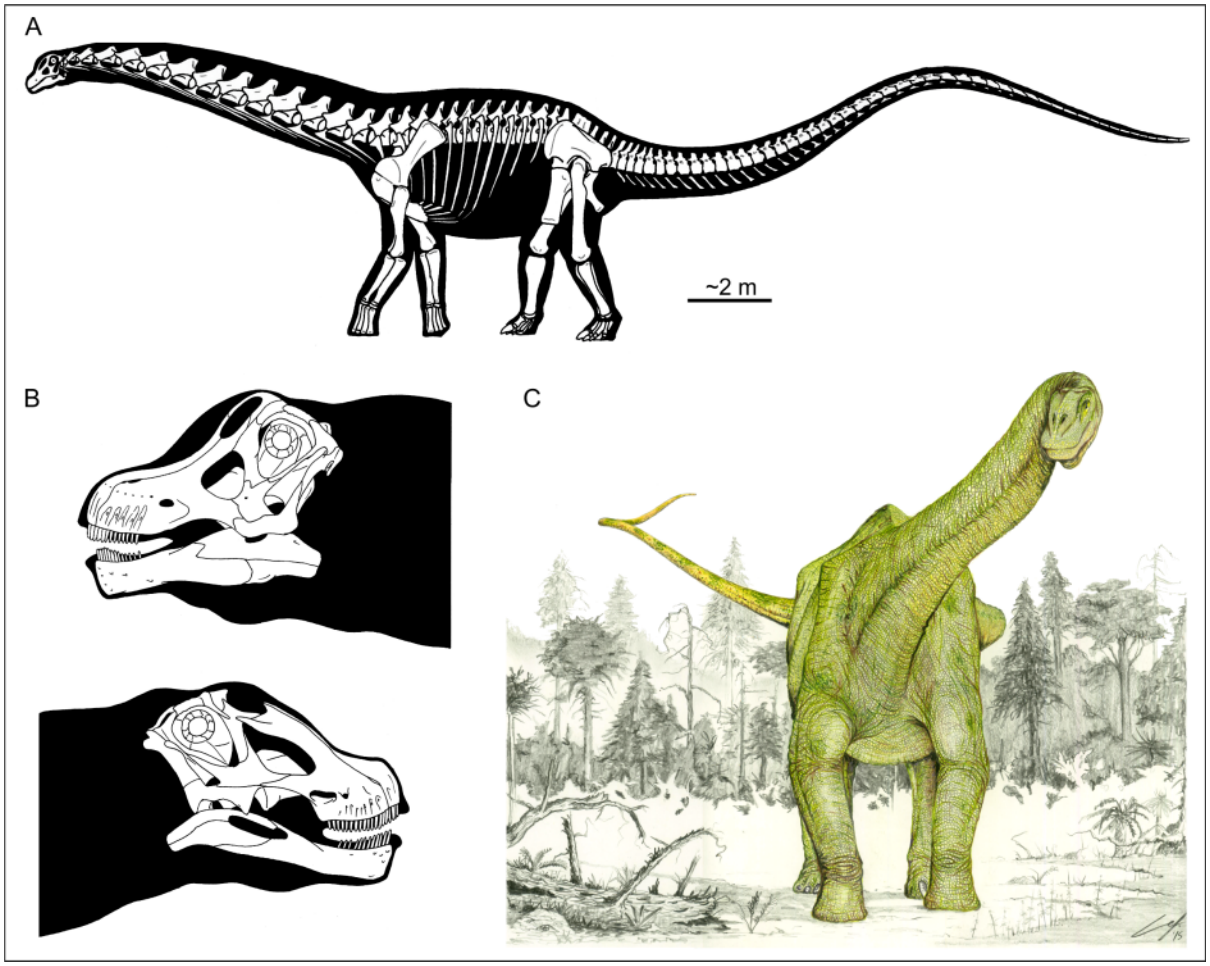

Figure 1 Skeletal and live reconstructions of titanosaur sauropods. (A, C) Based on *Futalognkosaurus dukei* (Calvo et al., 2007). (B) Skull reconstructions of (up) *Nemegtosaurus mongoliensis*, Nowinski 1971 and (down) *Tapuiasaurus macedoi* Zaher et al., 2011 (based on Wilson, 2005b and Zaher et al., 2011, respectively).

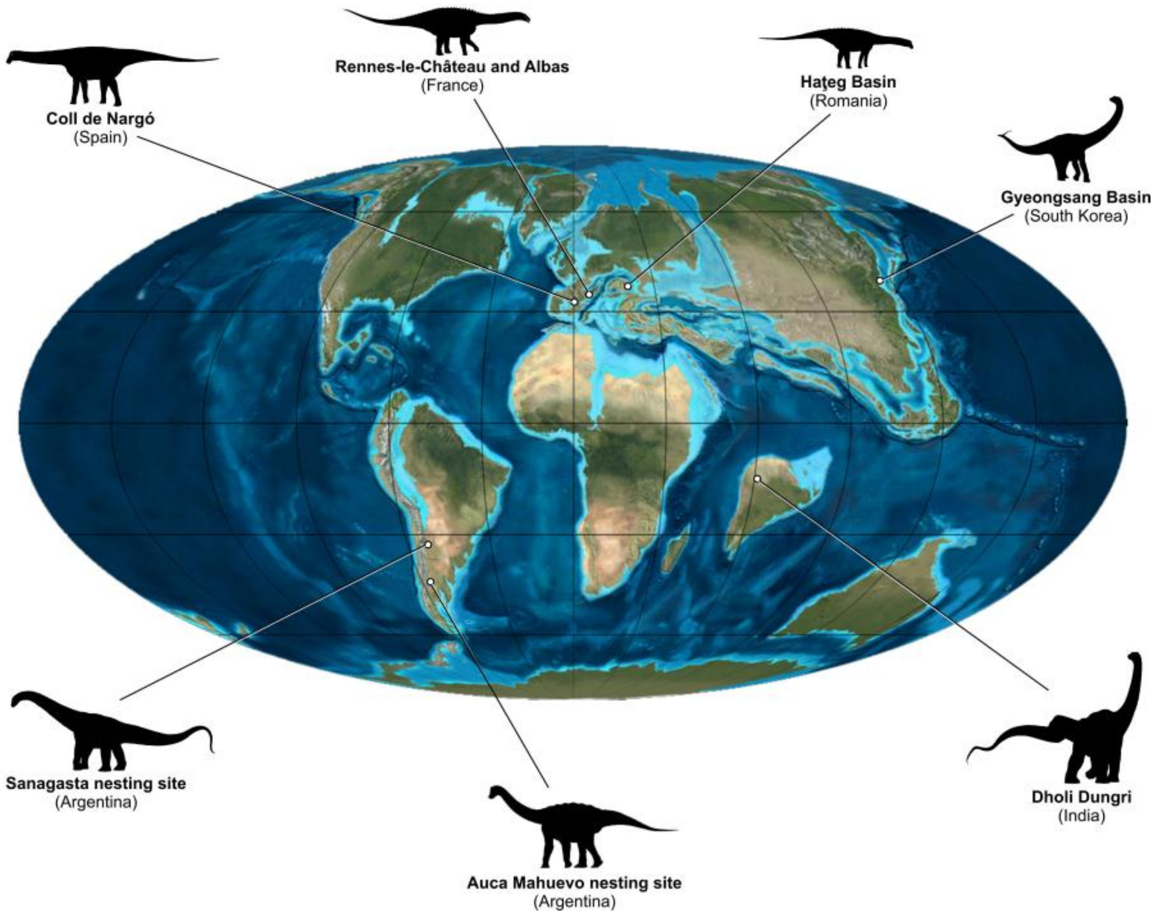

Figure 2 Upper Cretaceous paleogeography and distribution of the reviewed titanosaur nesting sites. Map modified from Ron Blakey, Colorado Plateau Geosystems, Inc.

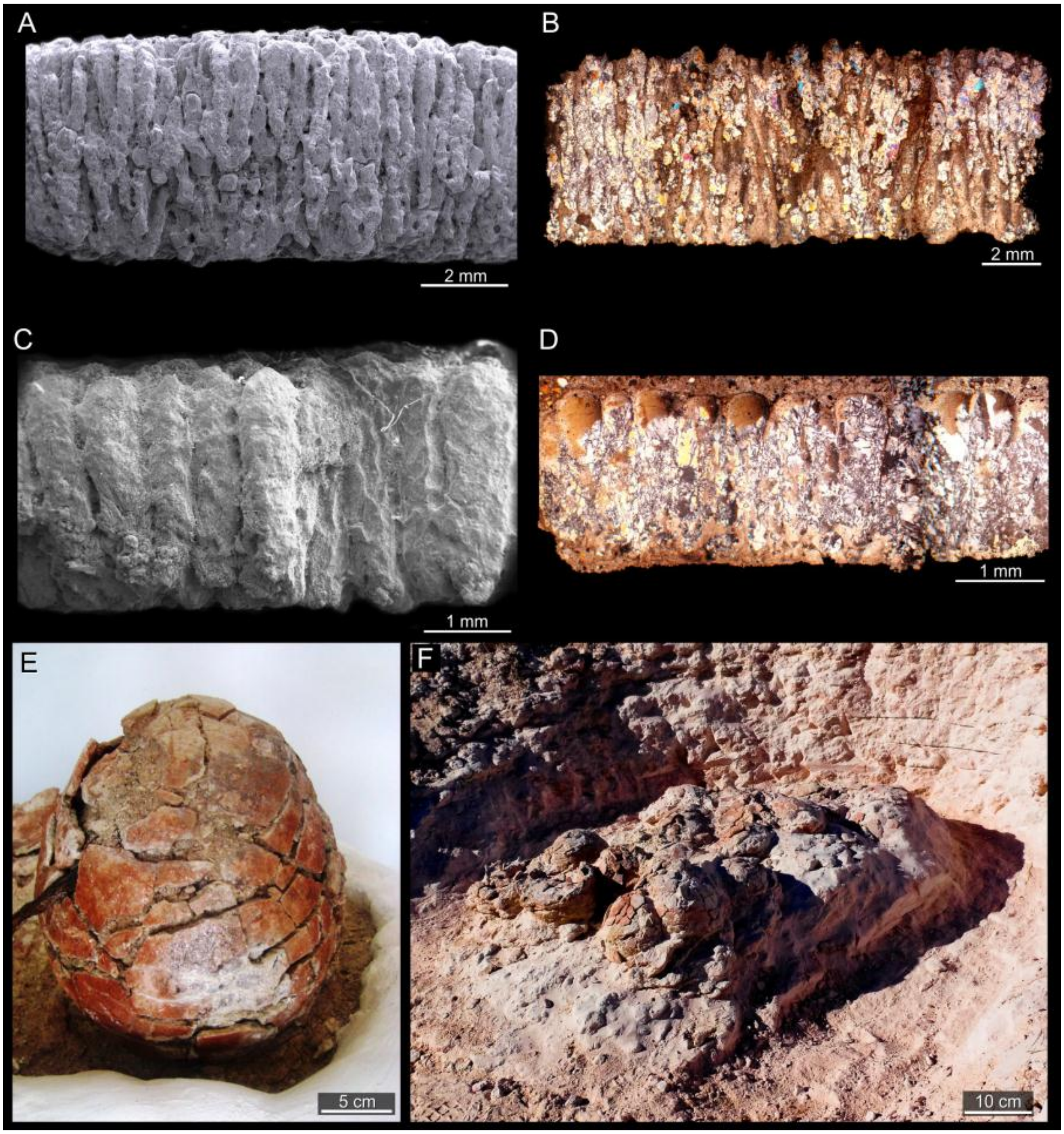

Figure 3 Sanagasta nesting site. (A, C) Radial thin sections of eggshell fragments seen under Scanning Electron Microscope (SEM) and (B, D) under stereomicroscope. (E) Complete egg (CRILAR Pv-400 SA-C6-e1). (F) Egg clutch (exposed *in situ* at the Sanagasta Geologic Park).

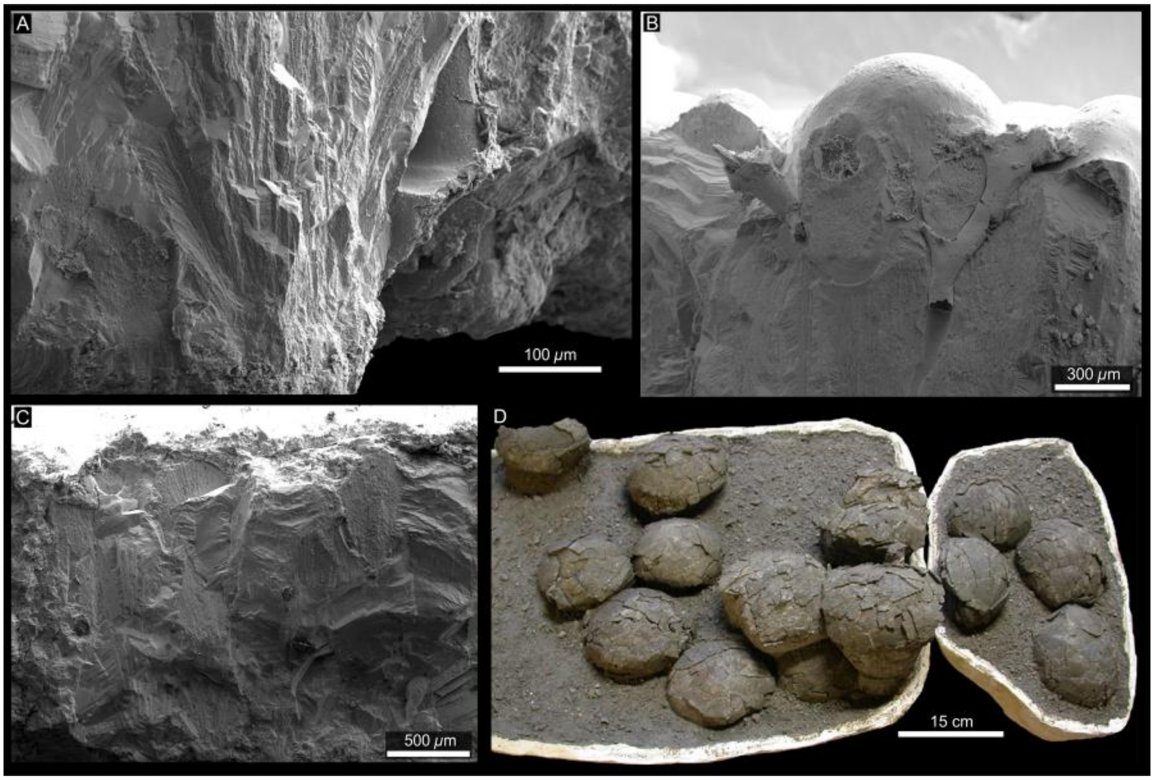

Figure 4 Haţeg Basin. (A–C) Nemegtosaurid eggshell fragments seen under SEM. (D) Three egg clutches (TO O–01; IRSNB Cast-Vert 32) exhibit at the University of Cluj and the Royal Belgian Institute of Natural Sciences**.** From Grellet-Tinner et al., 2012.

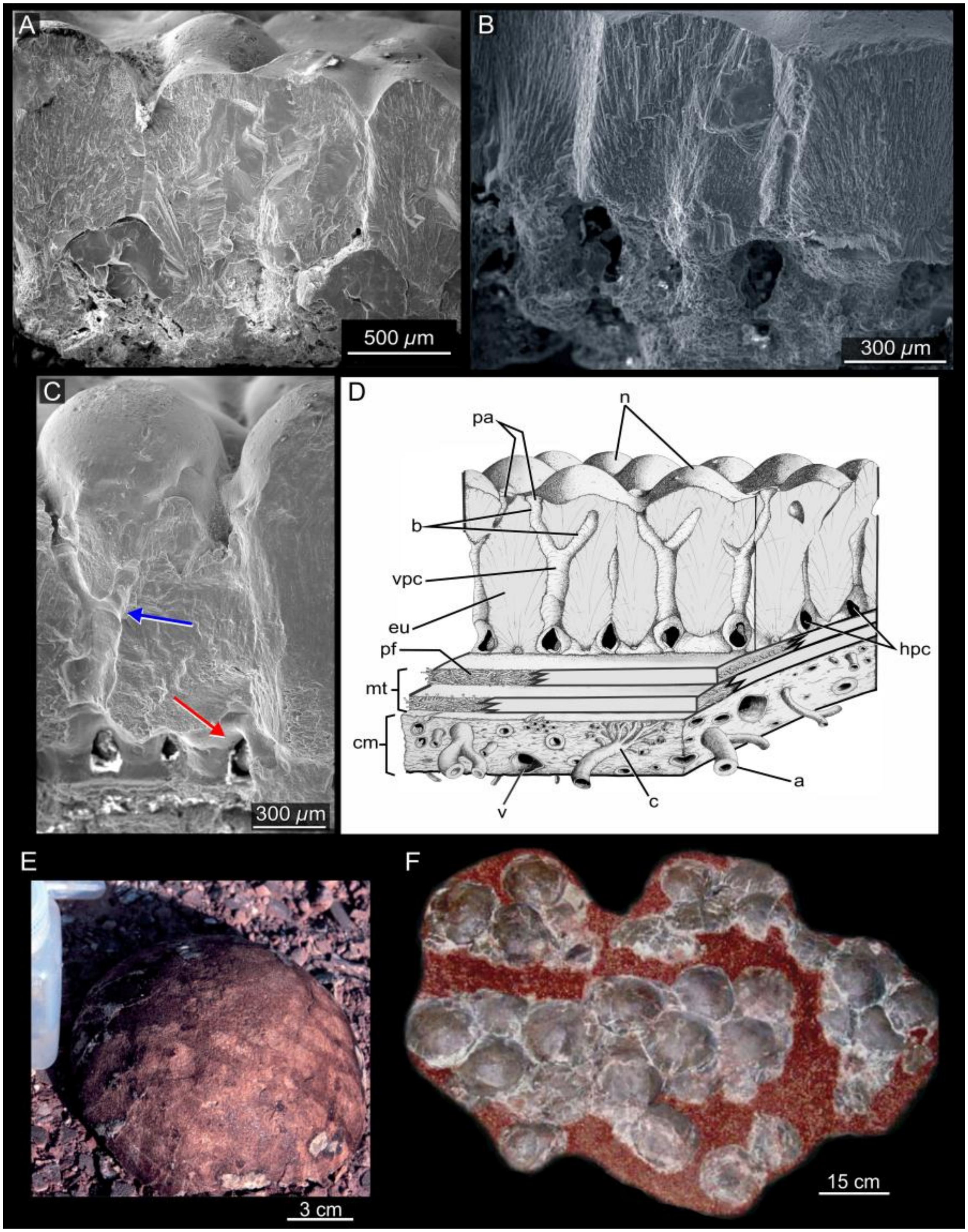

Figure 5 Auca Mahuevo nesting site. (A-C) Radial section of titanosaur eggshell fragments (From Grellet-Tinner, Chiappe & Coria, 2004; Grellet-Tinner & Zaher, 2007). Note in (C) the transverse Y-shaped vertical pore canals (blue arrow) and the horizontal network system (red

arrow). (D) Schematic interpretation of an eggshell from AM L#3, according to Grellet-Tinner, Chiappe & Coria (2004) SEM observations (modified from Grellet-Tinner, Fiorelli & Salvador, 2012). a = arteries; b = branches of pore canal; c = capillaries; cm = corioallantoid membrane; eu = eggshell unit; hpc = horizontal pore canals; mt = membrana testacea; n = node on outer eggshell surface; pa = pore aperture; pf = protein fibers of the membrana testacea; v = veins; vpc = vertical pore canals. (E) Complete egg AM L#3. F) Egg clutch recovered from AM L#3 (LACM 149648; from Grellet-Tinner, Chiappe & Coria, 2004). LACM = Natural History Museum of Los Angeles County.

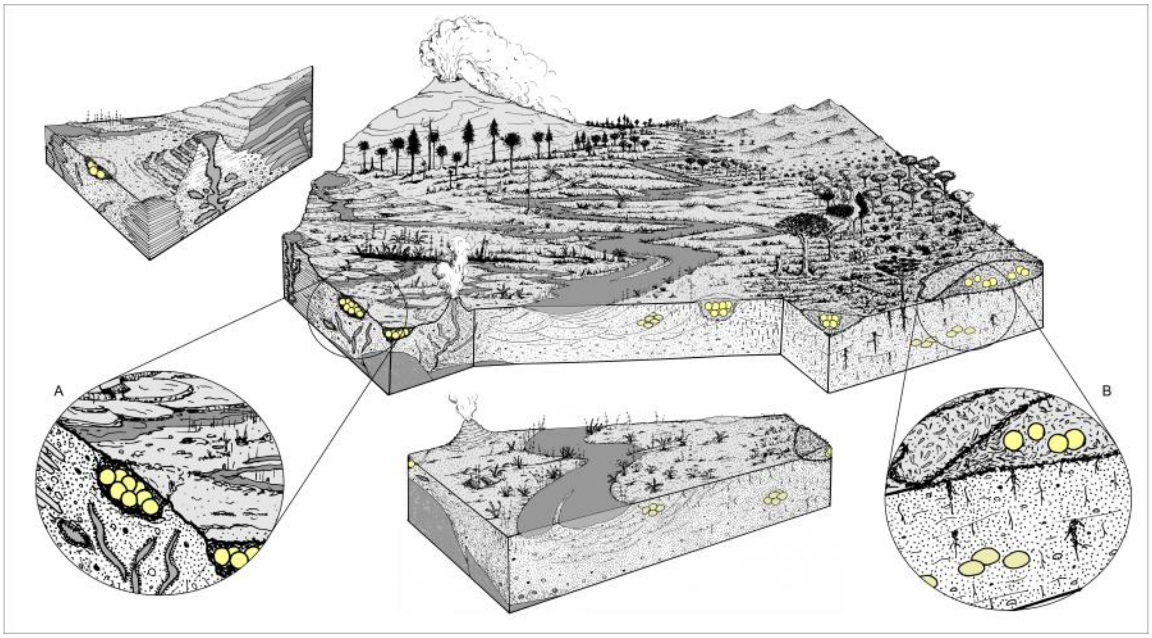

Figure 6 Schematic reconstruction of different nesting environments and the nesting strategies suggested for the Cretaceous titanosaur dinosaurs. (A) Detail of borrow-nesting in geothermal environments. (B) Detail of mound-nesting and eggs buried in a soil profile.

Table 1 Egg and eggshell morphologies, temporal and spatial distribution and nesting paleoenvironments. [a]Choi, 1986; Chough et al., 2000; Choi et al., 2005, 2006. [b]Bojar, Csiki & Grigorescu, 2010. [c]Tandon et al., 1995; Tandon & Andrews, 2001; Prasad & Sahni, 2014. [d]Cojan, Renard & Emmanuel, 2003. [e]Riera et al., 2013. [f]Garrido, 2010a,b. [g]Jackson, Schmitt & Oser, 2013. MAP= mean annual precipitation. MAT= mean anual temperature. MT= membrana testacea.

Table S1. List the of known Cretaceous "titanosaur" egg-bearing localities/areas that preserve at least complete eggs. Nesting sites selected for the current study correspond to the localities/areas that are highlighted in grey. AL= allochthonous; AU= autochthonous; PA= parautochthonous; X = known data; ? = imprecise information; - = unknown data.

TABLE

Table 1

Sites		Sanagasta	Gieongsang Basin	Haţeg	Dholi Dungri
Authors		Fiorelli et al., 2012; Grellet-Tinner et al., 2012b	Huh & Zelenitsky, 2002; Kim et al., 2009.	Grellet-Tinner et al., 2012a	Wilson et al., 2010
Formation		Los Llanos	Boseong	Sânpetru	Lameta
Age - stage		Hauterivian?-Cenomanian?	Upper Cretaceous	Maastrichtian	Maastrichtian
Eggs	egg shape	sub-spherical	spherical	sub-spherical	spherical
	egg size (cm)	21	15-20	11-13	14-18
	eggshell thickness (mm)	1.2-7.95 (mean=3.84)	1.33-2.2	1.7-1.8	2.26 - 2.36
	pore canal morphology	Y-shaped	?	Y-shaped	straight
	pore aperture morphology	round and funnel shape	?	round and funnel shape	round and funnel shape
	ornamentation morphology	nodular-single nodes and coalesecent nodes	nodular	nodular-single nodes and coalesecent nodes	nodular
	ornamentation size (mm)	Ø=0.58-0.62	?	Ø= 0.6-0.7	?
	MT size (mm)	0.025-0.09	?	0.19	?
Egg spatial distribution	grouping	clutches; up to 30 eggs	clutches; up to 16 eggs	clutches; average 4 eggs	isolated or in clutches; up to 12 eggs
	geometry	bowl, linear, random	?	bowl-round	bowl-round
	layers	2	1	2	?
Paleoenvironment	sediment	medium to coarse-grained grey and whitish arkosic sands	sandy tuffaceous sandstones	fine grained siltstone-mudstone sediments	calcareous sandstones
	setting	geothermal	floodplain deposits / geothermal / paleosols	floodplain / paleosols/geothermal	alluvial-limnic / paleosols
	volcanism	present	present[a]	present	present[c]
	paleoclimate	semiarid	semiarid	warm (MAT= 14º)	semi-arid[c]
	vegetation	?	C3 veg.	C3 veg.[b]	dominantly herbaceous; C3 veg.[c]

Rennes-le-Château and Albas	Coll de Nargó	Auca Mahuevo layers 1-3	Auca Mahuevo layer 4
Cousin and Breton, 2000; Cousin et al. 1989	Vila et al., 2010a, 2010b	Grellet-Tinner et al., 2004; Grellet-Tinner, 2005	
Marnes rouges inférieures	Tremp	Anacleto	
Upper Maastrichtian	Maastrichtian	Campanian	
sub-spherical	spherical	spherical	spherical to sub-spherical
16-20	20	13-15	12.5 -14
up to 2.5	1.3-4.5	1 - 1.78	1.7- 1.8
?	Y-shaped	straight	Y-shaped
round?	round-elliptical	round-elliptical and funnel shape	round and funnel shape
nodular	nodular	nodular-single nodes and coalesecent nodes	nodular-single nodes and coalesecent nodes
?	Ø=0.64-0.87	Ø=0.35-0.65	Ø=0.68
?	?	?	0.2-0.25
isolated or in clutches; 3 to 8 eggs	clutches; up to 20-28 eggs	clutches; 15-50 eggs	
bowl-round / supergroups (Ø=3,5 m)	linear-round (inferred kidney shape)	bowl-kidney	
1	2-3?	1-2	
very soft variegated marls	mudstones intercalated with medium-coarse sandstone bodies	reddish-brown siltstones and mottled mudstones[f]	
floodplain? / paleosols	lagoon / marsh / fluvial / paleosols	floodplain deposits[f] / paleosols[f,g]	
?	?	present[g]	
tropical-subtropical / semi-arid episodes[d]	warm (MAT= 21º) / MAP=1200 mm/yr[e]	warm and seasonal[f] dryer	warm and seasonal[f] wetter
C3 veg. riparian forest / open vegetation (Aix-en-Provence Basin)[d]	C3 veg.[e]	palustrine plant remains[f]	

1

Skeletal and live reconstructions of titanosaur sauropods.

(A, C) Based on *Futalognkosaurus dukei* (Calvo et al., 2007). (B) Skull reconstructions of (up) *Nemegtosaurus mongoliensis*, Nowinski 1971 and (down) *Tapuiasaurus macedoi* Zaher et al., 2011 (based on Wilson, 2005b and Zaher et al., 2011, respectively).

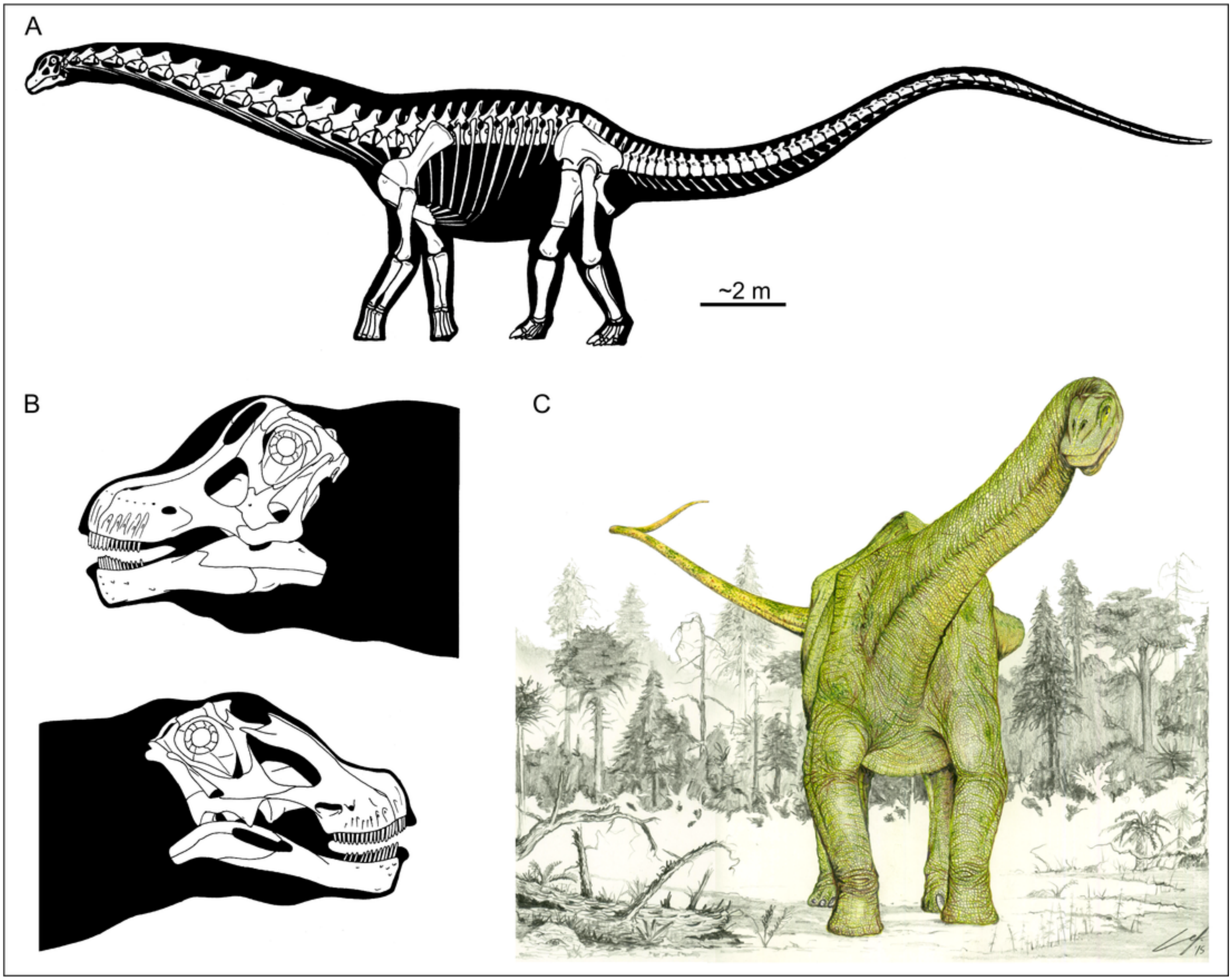

Figure 2(on next page)

Upper Cretaceous paleogeography and distribution of the reviewed titanosaur nesting sites.

Map modified from Ron Blakey, Colorado Plateau Geosystems, Inc.

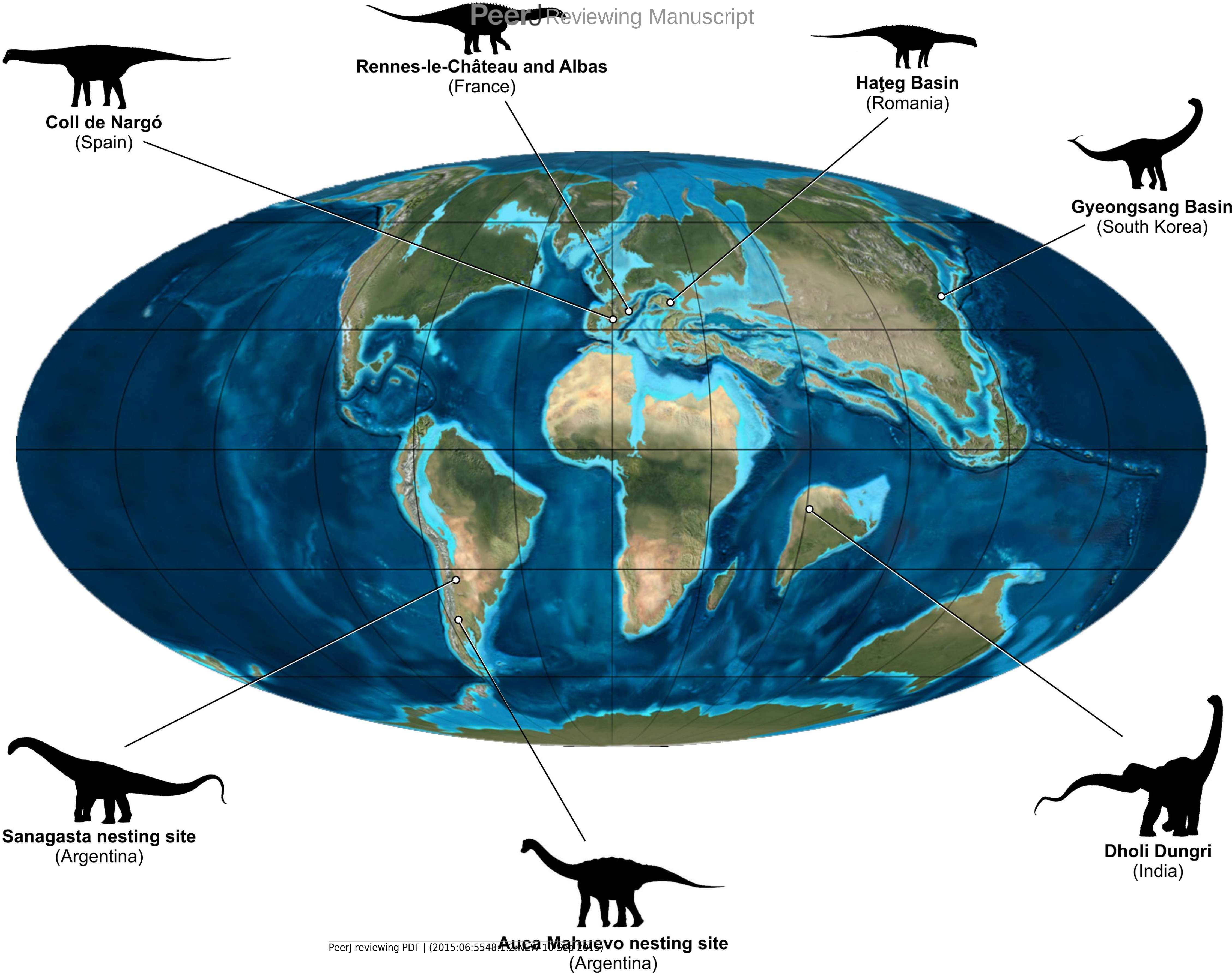
Coll de Nargó
(Spain)
Rennes-le-Château and Albas
(France)
Haţeg Basin
(Romania)
Gyeongsang Basin
(South Korea)
Sanagasta nesting site
(Argentina)
Auca Mahuevo nesting site
(Argentina)
Dholi Dungri
(India)

Figure 3(on next page)

Sanagasta nesting site.

(A, C) Radial thin sections of eggshell fragments seen under Scanning Electron Microscope (SEM) and (B, D) under stereomicroscope. (E) Complete egg (CRILAR Pv-400 SA-C6-e1). (F) Egg clutch exposed *in situ* at the Sanagasta Geologic Park.

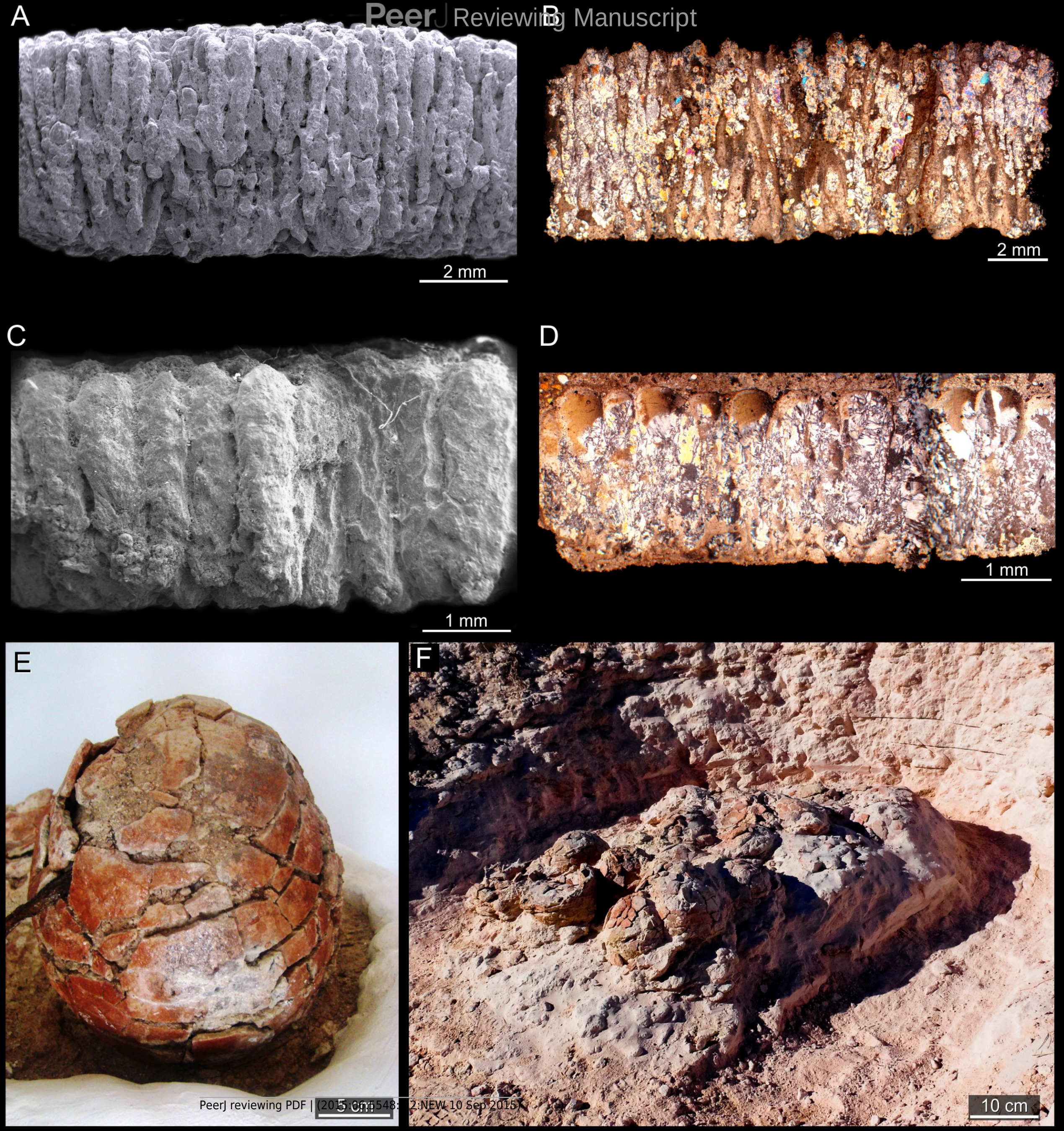
A
2 mm
B
2 mm
C
1 mm
D
1 mm
E
5 cm
F
10 cm

Figure 4(on next page)

Haţeg Basin

(A–C) Nemegtosaurid eggshell fragments seen under SEM. (D) Egg clutches (TO O–01; IRSNB Cast-Vert 32) exhibit at the University of Cluj and the Royal Belgian Institute of Natural Sciences**.** From Grellet-Tinner et al., 2012.

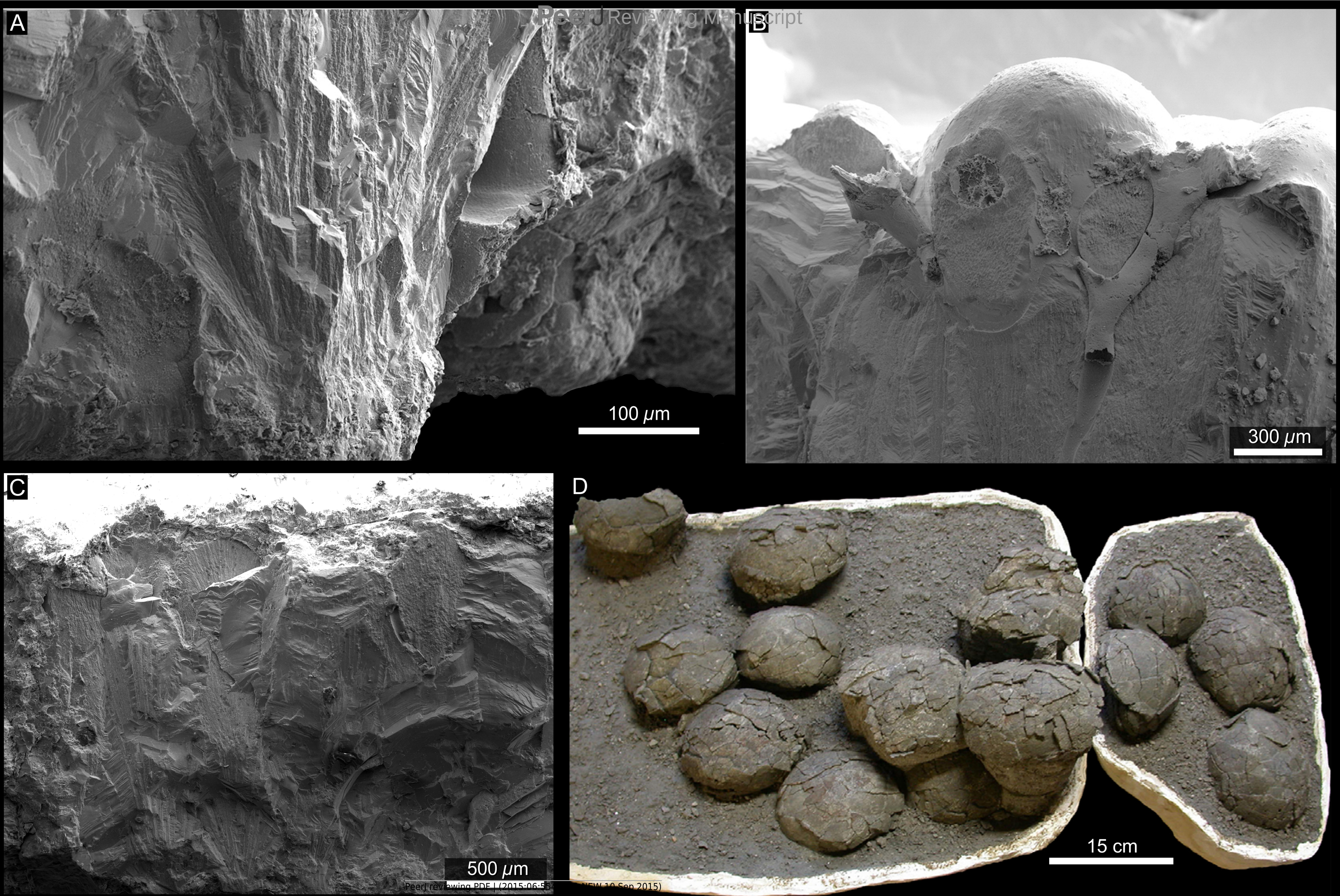
A
B
100 μm
300 μm
C
D
500 μm
15 cm

Figure 5(on next page)

Auca Mahuevo nesting site

(A-C) Radial section of titanosaur eggshell fragments (From Grellet-Tinner, Chiappe & Coria, 2004; Grellet-Tinner & Zaher, 2007). Note in (C) the transverse Y-shaped vertical pore canals (blue arrow) and the horizontal network system (red arrow). (D) Schematic interpretation of an eggshell from AM L#3, according to Grellet-Tinner, Chiappe & Coria (2004) SEM observations (modified from Grellet-Tinner, Fiorelli & Salvador, 2012). a = arteries; b = branches of pore canal; c = capillaries; cm = corioallantoid membrane; eu = eggshell unit; hpc = horizontal pore canals; mt = membrana testacea; n = node on outer eggshell surface; pa = pore aperture; pf = protein fibers of the membrana testacea; v = veins; vpc = vertical pore canals. (E) Complete egg AM L#3. F) Egg clutch recovered from AM L#3 (LACM 149648; from Grellet-Tinner, Chiappe & Coria, 2004). LACM = Natural History Museum of Los Angeles County.

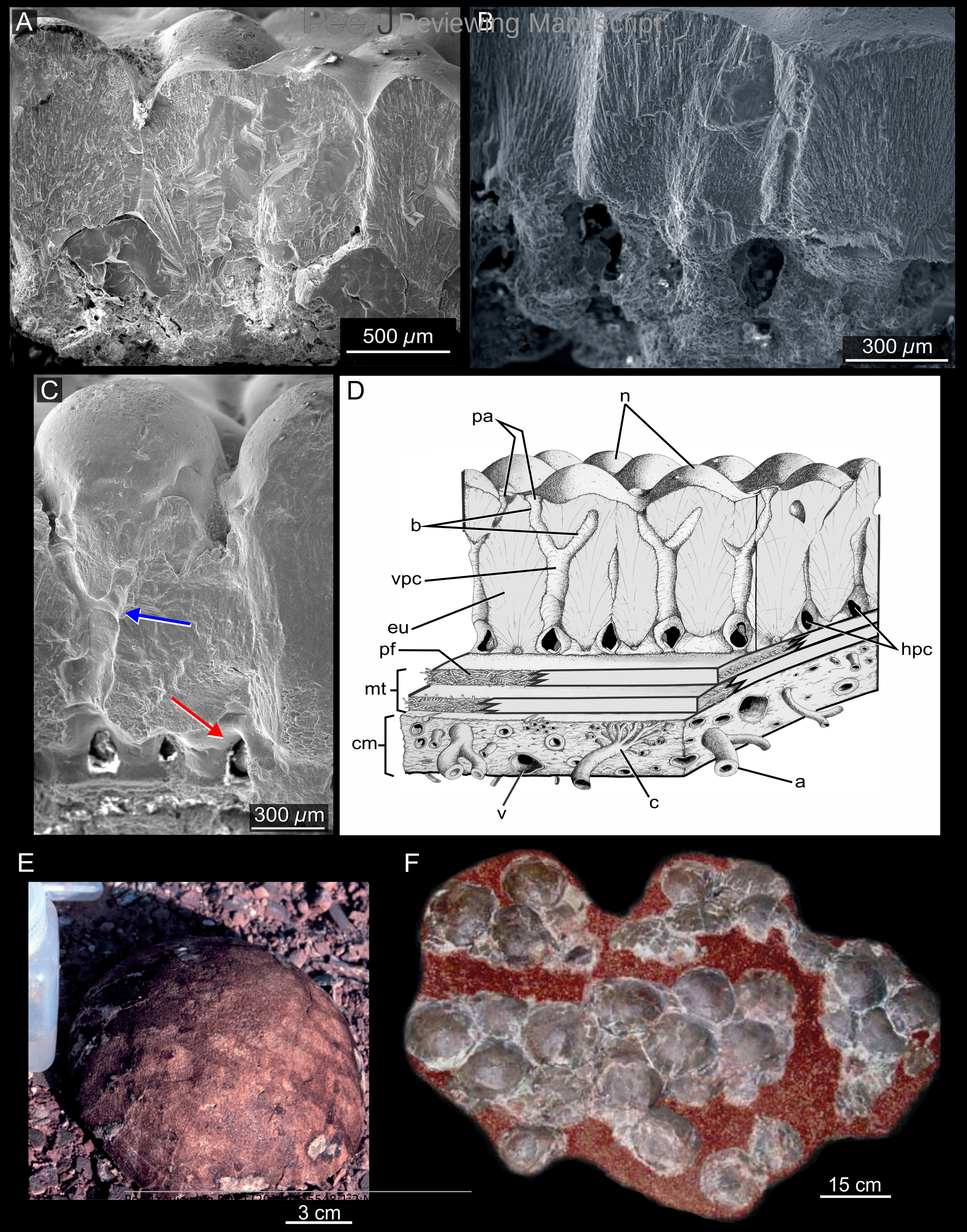
A
500 μm
B
300 μm
C
300 μm
D
n
pa
b
vpc
eu
pf
mt
cm
hpc
a
c
v
E
3 cm
F
15 cm

Figure 6(on next page)

Schematic reconstruction of different nesting environments and the nesting strategies suggested for the Cretaceous titanosaur dinosaurs.

(A) Detail of borrow-nesting in geothermal environments. (B) Detail of mound-nesting and eggs buried in a soil profile.

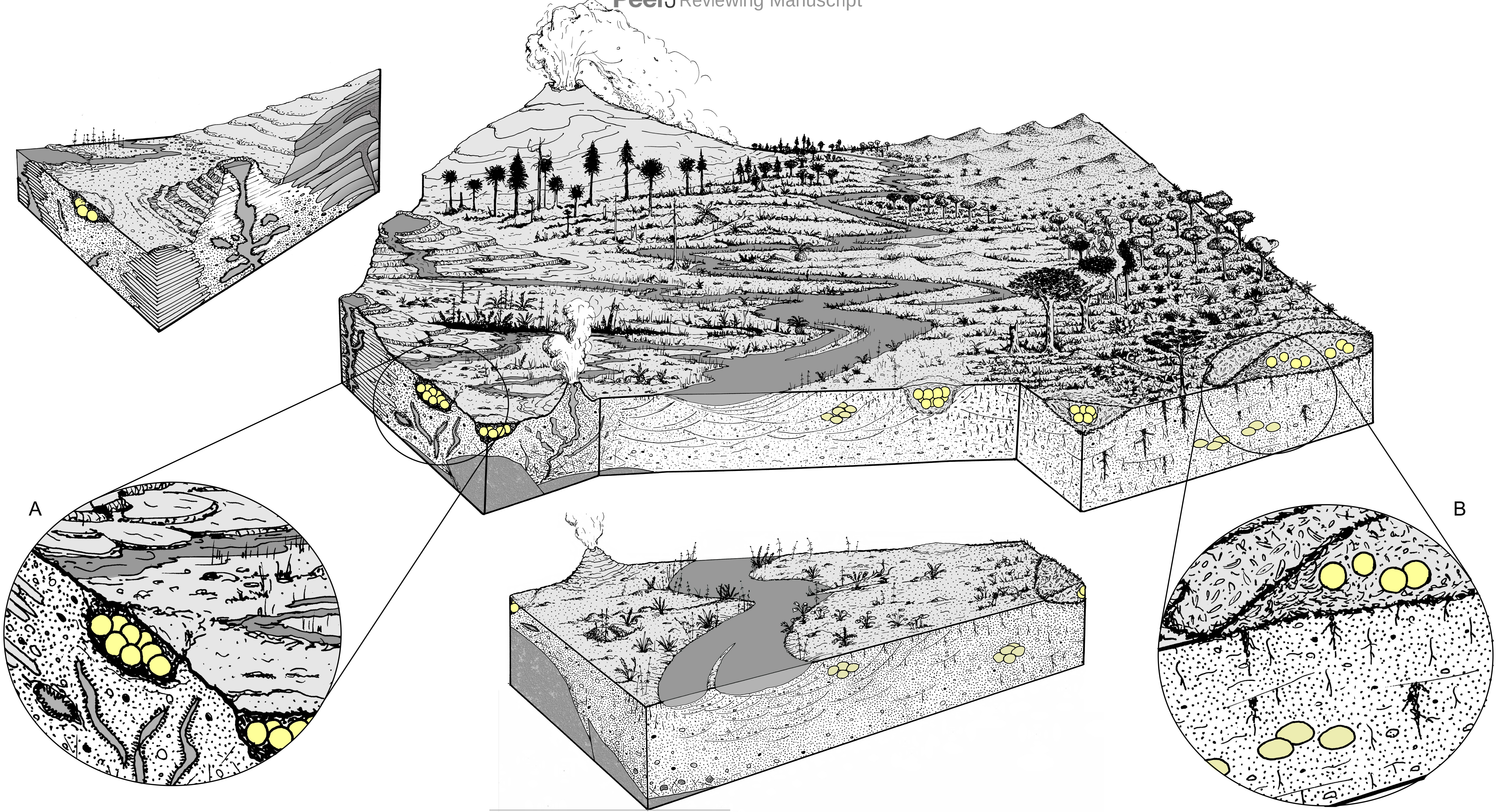
A
B

Table 1(on next page)

Table 1: Egg and eggshell morphologies, temporal and spatial distribution and nesting paleoenvironments.

[a]Choi, 1986; Chough et al., 2000; Choi et al., 2005, 2006. [b]Bojar, Csiki & Grigorescu, 2010. [c]Tandon et al., 1995; Tandon & Andrews, 2001; Prasad & Sahni, 2014. [d]Cojan, Renard & Emmanuel, 2003. [e]Riera et al., 2013. [f]Garrido, 2010a,b. [g]Jackson, Schmitt & Oser, 2013. MAP= mean annual precipitation. MAT= mean anual temperature. MT= membrana testacea.

Sites		Sanagasta	Gieongsang Basin	Haţeg	Dholi Dungri
Authors		Fiorelli et al., 2012; Grellet-Tinner et al., 2012b	Huh & Zelenitsky, 2002; Kim et al., 2009.	Grellet-Tinner et al., 2012a	Wilson et al., 2010
Formation		Los Llanos	Boseong	Sânpetru	Lameta
Age - stage		Hauterivian?-Cenomanian?	Upper Cretaceous	Maastrichtian	Maastrichtian
Eggs	egg shape	sub-spherical	spherical	sub-spherical	spherical
	egg size (cm)	21	15-20	11-13	14-18
	eggshell thickness (mm)	1.2-7.95 (mean=3.84)	1.33-2.2	1.7-1.8	2.26 - 2.36
	pore canal morphology	Y-shaped	?	Y-shaped	straight
	pore aperture morphology	round and funnel shape	?	round and funnel shape	round and funnel shape
	ornamentation morphology	nodular-single nodes and coalesecent nodes	nodular	nodular-single nodes and coalesecent nodes	nodular
	ornamentation size (mm)	Ø=0.58-0.62	?	Ø= 0.6-0.7	?
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	volcanism	present	present[a]	present	present[c]
	paleoclimate	semiarid	semiarid	warm (MAT= 14°)	semi-arid[c]
	vegetation	?	C3 veg.	C3 veg.[b]	dominantly herbaceous; C3 veg.[c]

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C3 veg. riparian forest / open vegetation (Aix-en-Provence Basin)[d]	C3 veg.[e]	palustrine plant remains[f]	