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RESEARCH ARTICLE

# The conservative structure of the ornithopod eggshell: electron backscatter diffraction characterization of *Guegoolithus turolensis* from the Early Cretaceous of Spain

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## Abstract

*Introduction* The Spheroolithidae oospecies *Guegoolithus turolensis*, putatively attributed to non-hadrosauroid styracosterns was first described in the Barremian of the Iberian Basin, and later reported in the Valanginian–Hauterivian of the Cameros Basin, with both occurrences separated by a few hundred kilometres but by over 10 million years.

*Methods* Here we apply electron backscatter diffraction to search for crystallographic and ultrastructural differences between both occurrences of this ootaxon.

*Results* Not only did not we found significant differences between eggshells from the two basins, probably laid by different non-hadrosauroid styracostern species but also, we found significant similitudes with the Late Cretaceous *Maiasaura* eggshells from North America. All Spheroolithidae eggshells are characterized by a profusion of low angle misorientation boundaries within larger orientation domains, that fan out from the eisospherite. A very quick reorientation of the c-axis of the crystals is observed, and explained partially via competitive growth.

*Conclusions* This conservative eggshell architecture suggests that the physical properties of the eggshell of styracosterns remain unchanged for at least 80 million years, implying similar nesting and breeding behaviours.

**Keywords** EBSD · Spheroolithidae · Barremian · Valanginian–Hauterivian · Maestrazgo basin · Cameros basin · Dinosaur

## Resumen

*Introducción* La ooespecie *Guegoolitus turolensis* de la oofamilia Spheroolithidae, atribuida putativamente a dinosaurios estiracosternos no hadrosauridos, fue descrita en el Barremiense de la Cuenca Ibérica, y posteriormente identificada en el Valanginiese-Hauteriviense de la Cuenca de Cameros, dos hallazgos separados por unos cientos de kilómetros, pero por más de diez millones de años.

*Métodos* En este trabajo utilizamos difracción de electrones dispersados para identificar posibles diferencias cristalográficas y ultraestructurales entre especímenes de estas dos localidades.

*Resultados* No solo no hemos encontrado diferencias significativas entre las cáscaras de ambas cáscaras, probablemente pertenecientes a huevos puestos por diferentes especies de estiracosternos no hadrosauridos; además hemos identificado similitudes importantes con cáscaras de huevo de *Maiasaura*, del Cretácico Tardío de Norteamérica. Todas las cáscaras de Spheroolithidae están caracterizadas por una abundancia de fronteras de desorientación de bajo ángulo, incluidas en dominios de orientación más grandes, que radian desde los eisosferitos. Hemos observado en todas las cáscaras una reorientación muy rápida de los ejes c, explicada parcialmente mediante crecimiento competitivo.

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*Conclusiones* Esta arquitectura de la cáscara tan conservativa sugiere que las propiedades físicas de las cáscaras de estiracosternos permanecieron invariables durante al menos ochenta millones de años, implicando comportamientos de nidificación y crianza similares.

**Palabras clave** EBSD · Spheroolithidae · Barremiense · Valanginiense–Hauteriviense · Cuenca del Maestrazgo · Cuenca de Cameros · Dinosaurio

# 1 Introduction

The identification of Spheroolithidae eggshells belonging to the oogenus *Guegoolithus* in several localities in the Early Cretaceous of Spain has expanded the record of an oofamily otherwise almost restricted to the Late Cretaceous (Moreno-Azanza et al. 2014, 2016). Spheroolithidae eggshells have been attributed to hadrosaurid dinosaurs, based on the associations of perinatal and juvenile individuals to nests containing Spheroolithidae eggshell fragments (Dewaele et al. 2015; Horner 1999), although the lack of members of Hadrosauria in the Early Cretaceous of Spain strongly suggest that the less derived styracosterns also laid Spheroolithidae eggshells. In fact, both styracostern bones and *Guegoolithus* eggshells are among the most abundant fossil remains in the dinosaur-bearing formations of the Lower Cretaceous of Spain (Canudo et al. 2010; Gasca et al. 2017).

Electron backscatter diffraction (EBSD) is a high-resolution analytical technique that allows crystallographic characterization of materials at micrometre scale (Prior et al. 1999). Although being a widespread technique in Material and Earth Sciences, it has only recently being used in palaeontology (Coronado et al. 2013, 2015; Lee et al. 2007), although its applications in the study of fossil materials are numerous (Cusack 2016). Paleoecology is one of the paleontological fields where the use of EBSD is more extended, probably because the inherent dual nature of the eggshell as biominerals, and the consequent tradition of using advanced microscopy techniques (Erben 1970). The first characterization of the eggshell structure of recent birds was carried by Dalbeck and Cusack (2006), and since then the methodology has been replicated to better describe the crystallography of both recent and fossil eggshell material. Works have been mainly focused in the description of the original eggshell crystallographic architecture (Grellet-Tinner et al. 2011), studies concerning eggshell formation (Moreno-Azanza et al. 2013), or in the characterization of taphonomic processes that altered the original crystallographic structure of the eggshell (Eagle et al. 2015; Jain et al. 2016; Moreno-Azanza et al. 2016).

In the present work, we provide a detailed description of the crystallographic architecture of two eggshell fragments previously attributed to the oospecies *Guegoolithus turolensis*, from the Valanginian–Hauterivian and the Barremian of Northern Spain.

# 2 Materials and methods

*Guegoolithus turolensis* thin sections housed in both the Museo de Enciso (MENC, n = 3) and the Museo de Ciencias Naturales de la Universidad de Zaragoza (MPZ; n = 25, including the holotype of the oogenus) where exanimated under the polarizing microscope, to identify possible alterations as recyclization or epitaxial overgrowths of the eggshell, to select pristine eggshells. One thin section of each collection was selected: MENC-TREN-1, from El Horcajo locality (Trevijano, La Rioja province; Moreno-Azanza et al. 2016) and MPZ 2013/848, from the paratype of *Guegoolithus turolensis*, collected in the type locality of this oospecies, Cuesta Corrales 2 (Galve, Teruel province; Moreno-Azanza et al. 2014).

The thin sections where produced embedding eggshell fragments in epoxy resin and following standard procedures of thin section preparation. Preparation of samples for EBSD is a delicate process, that requires a perfect polishing, as irregular surfaces may compromise the quality of the acquired data, commonly resulting in the lack of indexation in large areas (Prior et al. 1999). The thin sections where polished with decreasing in size abrasives, first with powered alumina down to slightly over 30 μm, them with diamond powder for a final thickness of 30 μm. Finally, the specimens were chemo-mechanically polished using colloidal silica during 20 min.

EBSD analyses were performed in the CamScan X500 CrystalProbe field-emission gun (FEG) SEM (MENC-TREN-1) and a Philips XL30 standard SEM (MPZ 2013/848), both housed in the Electron Microscopy Laboratory – EBSD-SEM of the Department of Earth, Ocean and Ecological Sciences of the University of Liverpool. Electron backscatter diffraction patterns (EBSPs) were obtained using 20 kV acceleration voltage, 35 nA beam current, and 25 mm working distance. These were automatically indexed and then analysed using the software package CHANNEL 5, licenced to the University of Zaragoza. The grid spacing used was 2 μm for MENC-TREN-1 and 2 μm for MPZ 2013/848. Multiple maps across the eggshell thickness were stitched together using the CHANNEL 5 software.

# 3 Geological and geographical setting

The north-eastern area of the Iberian Peninsula (Fig. 1) presents an almost continuous record of Lower Cretaceous continental and transitional formations, from the Lower
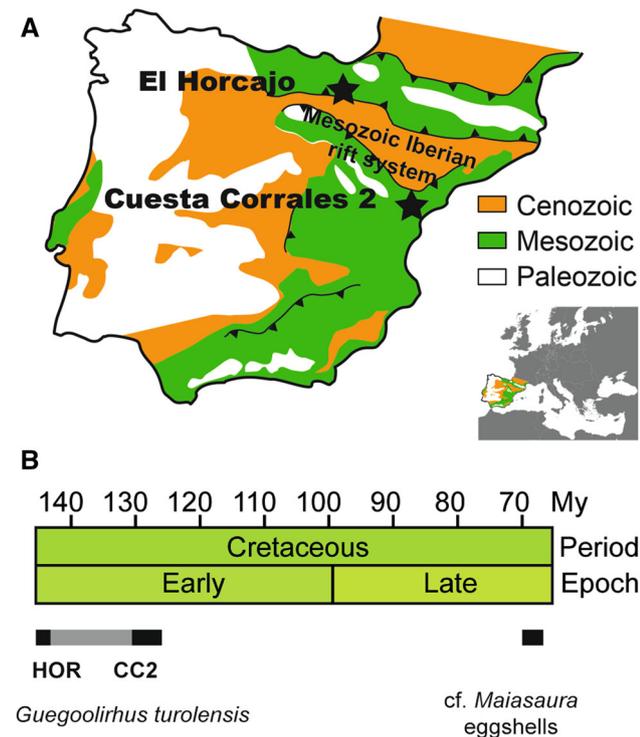
**Fig. 1 a** Simplified geological sketch of the Iberian Peninsula, showing the location of El Horcajo and Cuesta Corrales two sites. **b** Age of the ootaxa discussed in this work. *Black bars* correspond to actual occurrences. *Grey bar* represents inferred occurrence



**Fig. 2** *Guegoolithus turolensis* cross-polarized light microphotographs of 30 micron thin sections before chemo-mechanical polishing. MPZ2014/848 (**a**). MENC-TREN-1 (**b**). *Scale bars* equal 200 μm

Berriasian to the Albian (Salas et al. 2001). The complex tectonic history of the area, together with the present semiarid climate, has provided good and extensive outcrops that have historically yielded abundant fossil vertebrate remains, building a vast skeletal, ichnological and eggshell fossil collections (Canudo et al. 2010; Castanera et al. 2016; Ruiz-Omeñaca et al. 2004). Two of the most productive areas in this region are the Cameros Basin, known worldwide for its extensive record of dinosaur footprints (Castanera et al. 2013; Díaz-Martínez et al. 2015; Ezquerra et al. 2007; Pérez-Lorente 2002), and the Maestrazgo Basin, where more than a hundred of fossil vertebrate localities have been described for the last thirty years (Canudo et al. 2012; Cuenca-Bescós et al. 2014; Gasca et al. 2015; Ruiz-Omeñaca et al. 2004).

Both the Cameros and the Maestrazgo basins are part of the Mesozoic Iberian rift system. The Iberian basins were formed by normal faults active during the Late Jurassic to the Early Cretaceous, and subsequently inverted during the alpine orogeny in the Cenozoic (Mas Mayoral et al. 1993; Salas et al. 2001). This rifting resulted in a series of independent basins and sub-basins where different palustrine, lacustrine and transitional environments developed. The El Horcajo microvertebrate site (HOC) is in the vicinity of the village of Trevijano, in La Rioja province. It
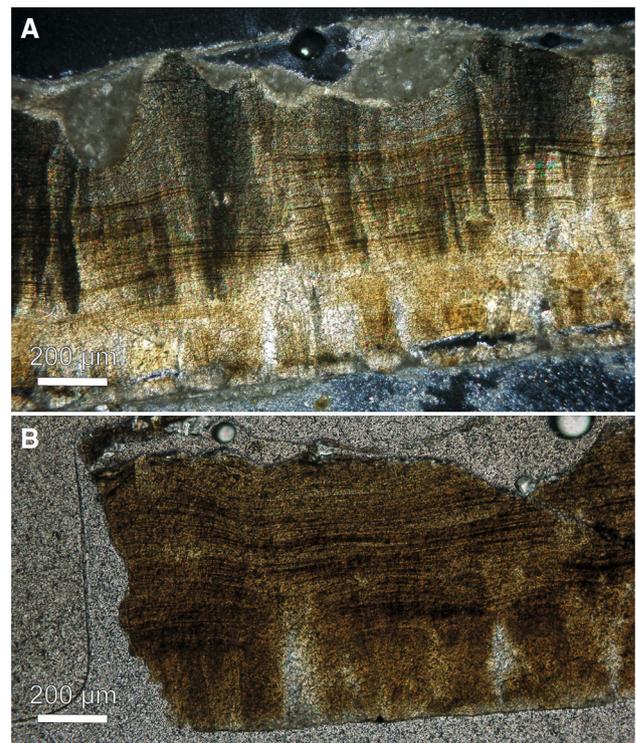
has been interpreted as a small pond in lacustrine-palustrine environment, and has yielded several microvertebrate remains, including eggshells of theropod and ornithopod dinosaurs, crocodiles, turtles and probably geckos (Moreno-Azanza et al. 2016). Cuesta Corrales 2 (CC2) its located near the village of Galve, in Teruel province. It is a large accumulation of eggshell fragments, most of them assignable to *Guegoolithus turolensis*, in a grey marl level deposited in a lacustrine environment (Moreno-Azanza et al. 2014).

## 4 Results

As noted by Moreno-Azanza et al. (2016), the resemblance of the Barremian and Valanginian–Hauterivian specimens is notable (Fig. 2). Both specimens present similar eggshell thickness, a well-developed sagenotuberculated ornamentation, undulating extinction under cross-polarized light, eisospherites with acicular ultrastructure that progressively develop into tabular ultrastructure. In the two upper thirds of the eggshell thickness, brown growth lines cross between shell units, varying between slightly wavy at the middle part of the eggshell to undulating and sub-parallel to the ornamentation in the upper part of the eggshell.

Kikuchi pattern indexation was relatively high in both samples (MPZ 2013/848 = 55%, 67% after processing; MENC-TREN-1 = 42%, 69% after processing) but significantly higher in the Barremian specimen, as evidenced by the voids with no data shown in Fig. 2b. This contrast with the general better preservation of the specimens from El Horcajo, but most probably is due to a worse polish of the sample. Nevertheless, the resulting indexing is good enough to provide details of the crystallographic architecture of the eggshell.

All-Euler maps (Fig. 3) show a progressive increase from the internal to the external surfaces in the size of calcite crystalline domains (i.e. eggshell areas with the same crystallographic orientation). Domains with their c-axis oriented oblique to the eggshell growth direction are sub-circular or slightly elongated. On the other hand, domains with c-axis subparallel to the eggshell growth direction are fan shaped, expanding towards the eggshell surface, revealing that the 3D shape of these domains is conical, progressively opening from the domain nucleation (the eisosphere) along the c-axis of the domain. The ornamentation development shapes the morphology of the domains. Crystalline domains forming the shell units ending in valleys of the ornamentation are less fanned, whereas domains that contribute to the crests open wider. There are no significant differences in the shape, relative orientation and size of the domains between both specimens.

Eggshell grain boundary maps (Fig. 4a, b) reveal that the crystalline domains are characterized by high angle boundaries (>20°). Within domains, low angle boundaries (2–5°) are abundant, causing the observed undulating extinction under cross-polarized light. These low angle boundaries surround elongated areas of equal orientation, which represent each of the acicular crystals that radiate from the eisosphere. MPZ 2013/848 presents a higher number of low angle boundaries than MENC-TREN-1, although this is most probably due to the differences in the step size during acquisition. Nevertheless, in both eggshell de distribution of grain boundaries is skewed to the low angle boundaries (Fig. 4c, d).

Finally, inverse pole figure maps (Fig. 5a, b) show the typical arrange of the orientation of the c-axis of the crystals described for other dinosaur eggshells. The bases of the shell units, where the eisospherites are located, show concentric arranges growing in all directions from the organic core outward. The crystals grow until reaching neighbouring crystals, and quickly—approximately at the bottom quarter of the eggshell thickness—only the "vertical" crystals survive, forming a parallel fabric for the rest of the eggshell. This competitive growth can also be observer at the scale of the shell units, where the shell units that are part of the eggshell ornamentation "kill" neighbouring shell units (Figs. 4, 5). Thus, pole figures of the lower fifth of the eggshells show non-preferred orientation but c-axis quickly oriented from the second fifth onwards



**Fig. 3** *Guegoolithus turolensis* all-Euler maps showing relative orientation of crystal domains. Note the progressive increase of size of the domains. *White arrows* point to the widening of the shell unit fan that can also be observed in Fig. 5. MPZ2014/848 (**a**); MENC-TREN-1 (**b**). *Scale bar* equal 200 μm
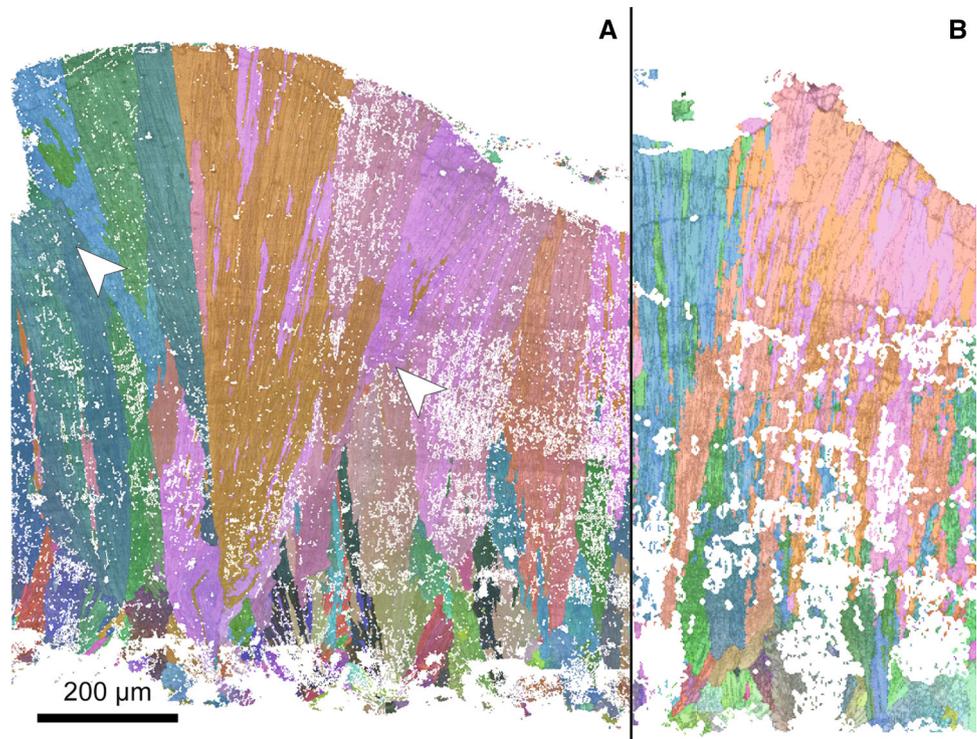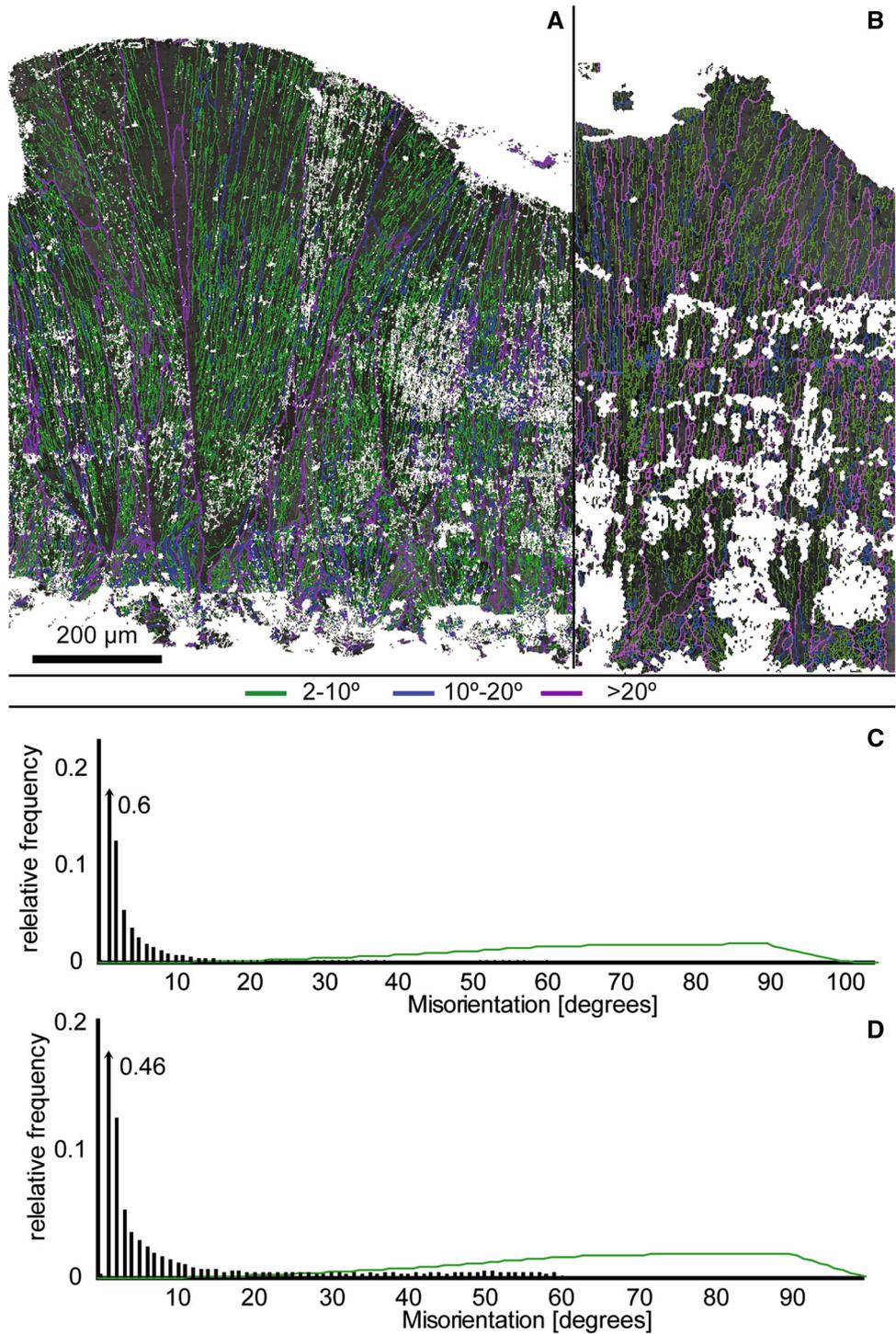
**Fig. 4** *Guegoolithus turolensis* grain boundary maps and relative distribution of misorientation angles. **a, b** Misorientation boundaries between grains: *green line* 5°–10° boundaries; *blue line* 10°–20° boundaries; *purple line* >20° boundaries. Note the profusion of low angle boundaries in both specimens. Relative fewer boundaries are seen in MENC-TREN-1 due to the double step size used during data acquisition. **c, d** Histogram showing the relative frequency of the misorientation angles. Both distributions are unimodal, and skewed to the low angle boundaries. *Green line* represents probability of random distribution. *White arrows* in both maps and pole figures point to the widening of the shell unit fan that can also be observed in Fig. 2. MPZ2014/848 (**a, c**); MENC-TREN-1 (**b, d**). *Scale bar* equal 200 μm



(Fig. 5c, d). In MPZ 2013/848, there is a small increase in the range of orientations, related to the slight widening of the shell units observed in all-Euler maps (arrows in Figs. 3 and 5). This is not observed in MENC-TREN-1, where the ornamentation of the selected eggshell fragment is sharper and the fan of crystals does not broad.

## 5 Discussion

The two analysed eggshell fragments present the radial extinction pattern and sagenotuberculated ornamentation characteristic of the oofamily Spheroolithidae, which together with the prominent ornamentation, strongly marked growth lines, and apparent two layers, confirms the
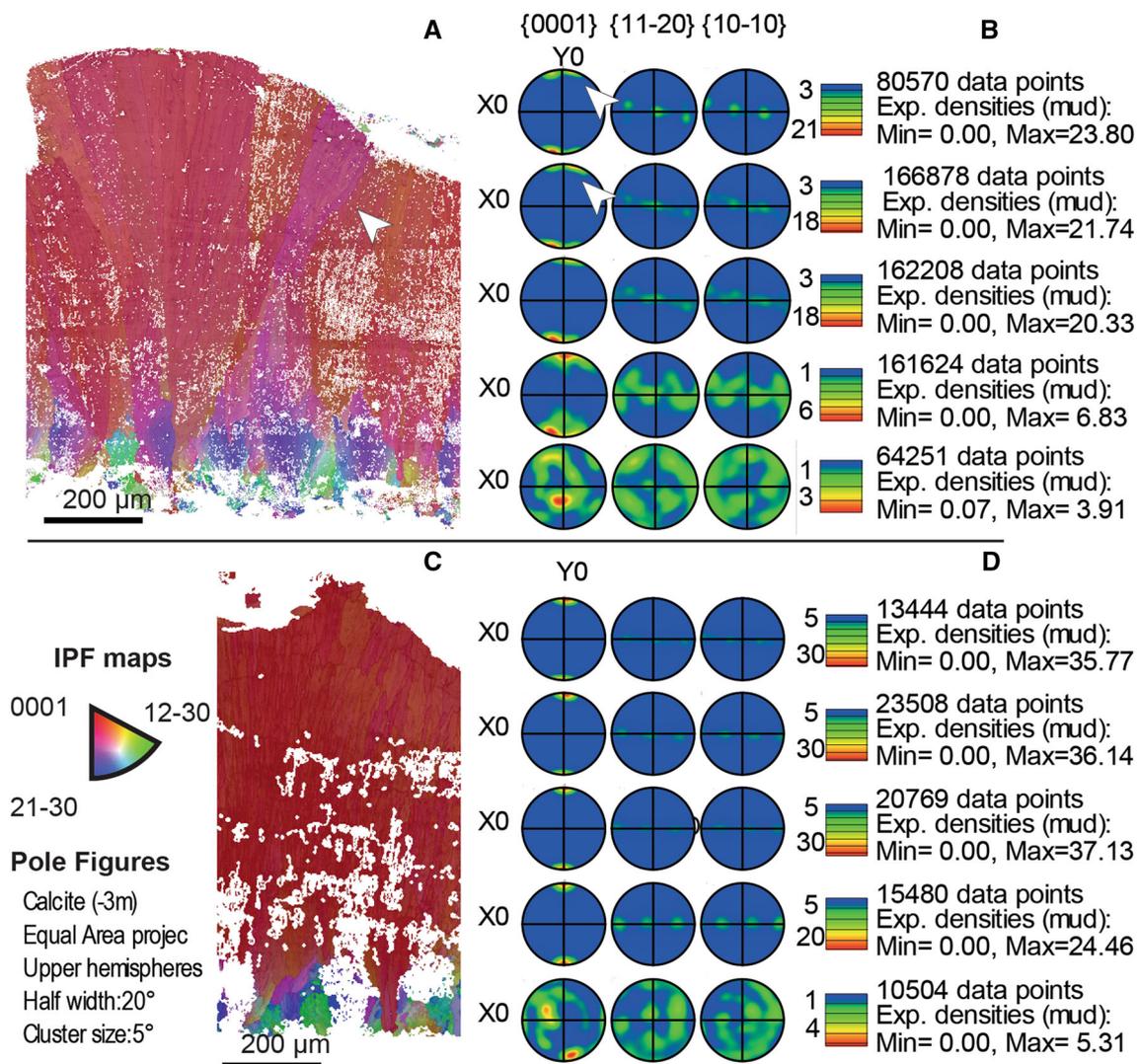
**Fig. 5** *Guegoolithus turolensis* relative orientation of the *c-axis* of crystal grains. **a**, **c** Inverse pole figure maps, with axis oriented perpendicularly to the acquisition surface. *White arrows* point to the widening of the shell unit fan that can also be observed in all-Euler maps in Fig. 3. **b**, **d** Pole figures of five equal-area sections of the eggshell through the eggshell thickness. All pole figures are equal-area projections of the upper hemispheres. Contours are calculated with a half width of 20° and a cluster size of 5°. *Scale bars* equal 200 μm. MPZ2014/848 (**a**, **c**); MENC-TREN-1 (**b**, **d**). *Scale bars* equal 200 μm

assignation of these eggshell *to Guegoolithus turolensis* (Moreno-Azanza et al. 2014, 2016). EBSD shows two differences between both eggshells: the less proportion of low angle boundaries in MENC-TREN-1, which as noted above is probably due to the lower resolution of the acquired aps; and the broader nature of the fans of crystals in the upper part of the eggshell. Nevertheless, no significant structural differences have been observed in the ornamentation of the Valanginian–Hauterivian and Barremian eggshells, other than a different degree of abrasion in the outer surfaces (Moreno-Azanza et al. 2014, 2016). Thus, our study farther supports the long temporal extension of *Guegoolithus turolensis* as an ooespecies, from the Valanginian-Hauterivian to the Barremian. This temporal

gap—no less than 5 and up to 10 million of years (Cohen et al. 2013)—it is unlikely to represent an unusual long lasting dinosaur species, furthermore when styracosterns are regarded as having relatively high speciation rates within dinosaurian (Sakamoto et al. 2016). Considering the above, it is plausible that *Guegoolithus turolensis* eggs where laid by different styracostern species throughout the Early Cretaceous.

More interesting are the striking similarities between the crystallographic maps obtained for the Early Cretaceous specimens and the ones reported for the eggshells attributed to the Late Cretaceous hadrosaur cf. *Maiasaura* (Moreno-Azanza et al. 2013). The eggshells of cf. *Maiasaura* are characterized by the profusion of low angle

boundaries, as observed in *Guegoolithus* eggshells. Furthermore, the rapid realignment of the fabric from a radial to a sub-parallel organization of the c-axis of the crystals is also observed in both *Guegoolithus* and cf. *Maiasaura* eggshells. The ultrastructure of the eggshell controls the physical properties of the egg, including its hardness, and has been related to the nesting strategies of the laying species (Dalbeck and Cusack 2006). There is limited information on the nesting and breeding strategies on ornithischian dinosaurs. High water vapour conductance values reported suggest buried nests (Deeming 2006), a hypothesis also supported by evidence of hatchlings found within nests excavated in the substrate (Horner 1999). The study of incremental lines of von Ebner in embryonic teeth has allow to estimate unexpectedly long—171 days—incubation periods for the hadrosaurid *Hypacrosaurus* (Erickson et al. 2017). After hatch, offspring remained in the nest for long periods, as revealed by over a herd of year old juvenile *Maiasaura* found together in their nests (Horner and Makela 1979). Furthermore, the histological evidence points towards altricial development in hadrosauroids (Chure et al. 1994; Horner et al. 2001). Moreno-Azanza et al. (2013) postulated that the profusion of low angle misorientation boundaries might weaken the general eggshell structure, allowing altricial hatchlings to easily break the eggs at the moment of hatch. Although this hypothesis needs to be tested with both experimental data and modern analogues, the description of this trait in Early Cretaceous eggshells suggests that the physical properties of the eggshell of Spheroolithidae eggs have remain unchanged for at least 80 million of years. Thus, it can be concluded that both the incubation strategies and development of the egg layers of Spheroolithidae where stable during all the Cretaceous, allowing to infer both burial nesting and altricial development in non-hadrosauroid hadrosauriforms.

It is interesting that this quick realignment happens in eggshells that present well-spaced mammillae—i.e. high distance between centre of nucleation of the individual shell units—and that most of the rearrangement of crystals by annihilation non-vertical individuals happens before shell units contact. The recent discovery of an amorphous carbonate precursor of the eggshell calcite changed the paradigm of avian eggshell formation (Rodríguez-Navarro et al. 2015). In the model proposed by these authors, non-crystalline $CaCO_3$ is deposited around a scaffold of proteins, and mineralization occurs afterwards by the crystallization of the precursor into calcite. This model is compatible with competitive growth as postulated by (Garía-Ruiz and Rodriguez-Navarro 1994), but the requirement of a precursor plus protein template for the crystals to grow further restricts the space available for the crystals to grow. This additional constrain may explain both the formation of the isolated and well-spaced mammillary caps of *Guegoolithus* and the deviations from the power law model of crystal number decay observed in cf. *Maiasaura* eggshells (Moreno-Azanza et al. 2013).

# 6 Conclusions

Despite the up to 10 million year gap between both specimens, no significant differences are found between *Guegoolithus turolensis* eggshells recovered from the Valanginian-Hauterivian of the Cameros Basin and the Barremian of the Iberian Basin. Furthermore, the crystallographic architecture of the *Guegoolithus* eggshells is extremely similar of that reported for cf. *Maiasaura* eggshells from the Campanian of North America. We conclude that the conservative basic architecture of the eggshell during the evolution of ornithopod dinosaurs, unchanged for over 80 million of years, suggests also very conservative breeding and incubation strategies in this linage of ornithischian dinosaurs.

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