VI Symposium on DINOSAUR 2017 PORTUGAL

ABSTRACT BOOK Miguel Moreno Azanza & Octávio Mateus (Eds.)

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Welcome!

Welcome to the VI Symposium on Dinosaur Eggs and Babies, the return of this periodic gathering to the Iberian Peninsula, when it hatched eighteen years ago. From the slopes of the Pyrenees, we have followed the first steps of dinosaurs through France, Argentina, the United States and China. Today, we come back and see the coast where the first theropod embryos were discovered twenty years ago.

Since the end of the last century, Paleoology, much like other branches of palaeontology, has evolved thanks to the advance of new methodologies and analytical tools, becoming a progressively more interdisciplinary area of knowledge. Dinosaur babies and embryos, rare findings back when these meetings started, seem to be everywhere now that we learn to look for them under the light of the microscope. New astonishing specimens allow us to understand how Mesozoic dinosaurs mate and reproduce. Oology, our parent discipline in the modern world, has made great advances in understanding the form and function of the egg, and its applications on poultry industry are countless.

More than thirty contributions evidence that our field remains small but alive and healthy. We hope that you find in this Symposium an opportunity to share knowledge and open new lines of collaboration. And do not forget to enjoy your stay in Portugal.

The host committee

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HOW TO GET TO THE FCT

Here are some suggestions, although there are other possibilities, combining public transportation. An interactive map can be found in the FCT web page: https://www.fct. unl.pt/en/about-fct/how-get-fct

From Lisbon (Portela Airport)

Using public transportation

There is a special shuttle bus (Carris nr 91), that takes passengers to Lisbon downtown in 20 minutes. This bus also stops at "Cais do Sodré" Train Station, next to the Ferry Station, where you can take a ferryboat to "Cacilhas". Once in "Cacilhas" you can take a tram to "Universidade", hopping off on its terminus (located near one of the campus entrances).

In Cacilhas you can also take one of the following TST buses: "Marisol", "Fonte da Telha" or "Costa de Caparica – via Almada". They all stop next to the FCT main entrance.

(In the airport there are other town bus lines: 5, 22, 44, 45 and 83 to Lisbon).

By Taxi

There are always plenty of taxis at the Arrivals and Departures Halls. All the taxis have meters, a ride to FCT NOVA costs approximately €30, depending on the traffic. During weekends, nights, and holidays there is a 20% surcharge.

From Lisbon (Praça de Espanha)

Using public transportation

You can use the TST bus to "Costa da Caparica" and get out at the bus stop located right in front of FCT main entrance.

From Lisbon (Cais do Sodré)

In the "Cais do Sodré" Ferry Station, you can take a ferryboat to "Cacilhas". Once in Cacilhas you take a tram to "Universidade", hopping off on its terminus (located near one of the campus entrances).

In Cacilhas you can also take one of the following TST buses: "Marisol", "Fonte da Telha" or "Costa de Caparica – via Almada". They all stop next to the FCT main entrance.

From Lisbon (Santa Apolónia Train Station)

Using public transportation

Metro to "Amadora Este" (blue line), get out in "Jardim Zoológico" station. Take the Fertagus train to "Coina" or "Setúbal" and get out in "Pragal". Once there, take the tram to "Universidade", hopping off on its terminus (located near one of the *campus* entrances).

By Taxi

There are always plenty of taxis outside the station. All the taxis have meters, a ride to FCT NOVA costs approximately \in 25, depending on the traffic. During weekends, nights, and holidays there is a 20% surcharge.

From Lisbon (Belém)

Take the ferry to "Trafaria". Once there, take the TST bus to "Cacilhas", getting out on the bus stop next to FCT.

From Costa de Caparica

Take a TST bus to "Cacilhas – via Almada" and get out in the bus stop right in front of FCT main entrance.



Dinosaur Eggs and Babies

Symposium venues

- FCT Symposium Venue Wed. 4th and Thu 5th
- Museu Geológico Ice breaker
 - Tuesday 3rd, 18:00 h

Meeting points

- Rato Meeting point for Ice breaker - Tuesday 3rd, 17:30
- Marquês de Pombal Friday 6th field trip - Meeting point 2 8:30
- Pragal Metro Station Friday
 6th field trip Meeting point 1
 8:00h
- National Museum of Natural History and Science - Saturday 7th Field trip meeting point -9:00h

Transport

- Almada Metro Station
- Pragal Metro Station
 - Cacilhas
- Bete Rios Train Link to symposium Venue
- Boat link to venue Cais do Sodré



VI Symposium on Dinosaur Eggs and Babies. Caparica, October 2017

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We want to thank the Faculdade de Ciências e Tecnologia / Universidade Nova de Lisboa for allowing us to host the VI Symposium on Dinosaur Eggs and Babies in their Campus in Caparica and their support in all aspects of the organization of this gathering. Thanks to the Departamento de Ciências da Terra for theur support, and special thanks to Prof. José Carlos Kullberg, head of the department, for his hard work and priceless advice. We thank the Divisão de Eventos e Projectos Especiais, particularly Anabela Seita, for their help with all the small and big details that allowed this meeting. Thanls to the staff of the Library of the FCT, for helping us with the technical details of the meeting, and to Nova.ID, for taking care of the financial aspects.

Thanks to the Museu da Lourinhã, for supporting us and taking care of the field trip. Thanks to the Museu Geologico/LNEG for hosting the Ice breaker party. Thanks to the Dino Park Lourinhã for opening their installations to us so close to inauguration and to the Camara Municipal de Lourinhã for providing transportation for the field trip.

Finally, thanks to all of our sponsors, including Duplix, Transmitting Science and the European Association of Palaeontology. If you enjoyed your stay in Caparica, please come back next year for the XVI EAVP Annual Meeting will from June 26th to July 1st, 2018.

PROGRAM

Tuesday-October 3rd		
18:00	Ice braker	Welcome party at Museu Geologico

Wednesdey-October 4th		
8:00	Registration	Library of the FCT
9:00	Ferguson	Nest site taphonomy of colonial ground nesting birds at Bowdoin National Wildlife Refuge, Montana.
9:20	Moreno-Azanza	Distribution of eggshell fragments as a proxy for lake dynamics.
9:40	Varricchio	Modern comparative taphonomy: the relationship between nesting site skeletal assemblages and reproductive attributes.
10:00	SellésGlobal and quantitative analyses indicate titanosauria nesting on inland environments.	
10:20	Coffee and Poster Session	
11:00	Welcome Ceremony	
11:30	KEYNOTE: Octávio Mateus	Fossil clutches, eggs and embryos from Portugal.
12:30	Lunch	
14:00	Oser	Dinosaur egghshell of the Western Interior Basin, USA: A new Assemblage from the Upper Cretaceous (Campa- nian) Kaiparowits Formation of Grand Staircase-Escalante National Monument, Utah.
14:20	Barta	Eggshell associated with a new troodontid taxon from the Upper Cretaceous Ukhaa Tolgod Locality, Mongolia.
14:40	Vremir	Megaloolithid eggs and nests from the late Maastrichtian of Sebes area (Transylvanian Basin, Romania).
15:00	Zheng	Bone histology and osteology of the juvenile <i>Liaoningo-saurus paradoxus</i> (Ornithischia: Ankylosauria).
15:20	Zhang Reuse of mixed-dinosaur-species breeding site on fluid deposits of Yunxian Basin, Hubei, China.	
15:40		Coffee Break
16:00	KEYNOTE: Mark Norell	Eggs, nest and babies of Ukhaa Tolgod- a Late Creta- ceous Locality in Mongolia´s Gobi Desert.

Thursday-October 5th		
9:00	Sellés	A singular sauropod eggshell-type from the lower Maastrich- tian (Upper Cretaceous) of the Coll de Nargó nesting area (Southern Pyrenees, Spain) with comments to the iberian sauropod diversity.
9:20	Leuzinger	Preliminary clumped isotope data from Late Cretaceous titanosaur (Sauropoda) eggshells: preservation of the origi- nal isotopic signal and implications for palaeoecological and palaeobiological interpretations.
9:40	Wiemann	The biomolecular paleontology of dinosaur eggshells: a synte- tic, chemoecological perspective.
10:00	Zelenkov	Neogene to Pleistocene fossil ostrich eggshell: evolution of Struthionidae in the Old World correlated with evolutionary history of bird faunas.

10:20	Coffee and Poster Session	
11:00	Deeming	Pelvis morphology suggests that early Mesozoic birds and dinosaurs were to heavy to contact incubate their eggs.
11:20	Mikhailov	Squamatic ultrastructure as a key character of ornithoid-type eggshell.
11:40	KEYNOTE: Yves Nys	Mechanisms of bird eggshell formation: structure, molecular control of mineralization and biological regulation in hens.
12:30	Lunch	
14:00	Araújo	The first ornithomimid embryo in a shell with a single structural layer: a challenge to orthodoxy.
14:20	Chapelle	Studying some of the world's oldest known dinosaurian embr- yos using synchrotron microtomography.
14:40	Yang	A new embryo-bearing egg-clutch revelas asynchronous hat- ching of oviraptorid dinosaurs.
15:00	Fabbri	A troodontid clutch demonstrates a dinosaurian origin of the avian single oviduct.
15:20	Pereira	Hatching a new geopark.
15:40	Coffee break	
16:00	KEYNOTE: Martin Kundrát	Paleoembryology - an interdisciplinary science.
17:00	Presentation of candidates for the VII Dinosaur Eggs & Babies.	

Friday-October 6th	
8:00	Meeting in Caparica.
9:30	Visit to Paimogo nesting site.
11:30	Visit to Parque dos Dinosauros da Lourinhã.
13:00	Lunch
14:30	Visit to Peralta nesting site.
16:00	Visit to the Museu da Lourinhã.
18:30	Symposium dinner.
21:30	Return to Lisbon and Caparica

Saturday-October 7th	
9:00	Meeting point in Lisbon.
13:00	Lunch (not included).
16:00	Visit to Lisbon Aquarium (optional, not included).

Poster Session		
1	Batista	Dinosaur nesting sites and eggs from the Late Cretaceous of Urugay: the development of the paleo-oology in the last 10 years.
2	Dhiman	Dinosaur eggshell fragments from the Upper Cretaceous deposits of Cauvery Basin.
3	Fernández	A mixed vertebrate eggshell assemblage from the transylvanian Late Cretaceous.
4	Fernández	The first avian egg from Río Negro Province, Argentina (Allen Formation, Upper Cretaceous).
5	Gascó	Dinosaur egg clutches from the Upper Cretaceous of Guadalajara (Cen- tral Spain).
6	Moreno-Azanza	Sliced eggs: the use of non-standard thin sections in the study of eggs- hells.
7	Núñez-Lahuerta	First record of avian eggshells in the Pleistocene site of Gran Dolina (Atapuerca, Spain).
8	Díaz-Berenguer	Evidences of a turtle rookery in the Sobrarbe Fm. (Eocene, Northern Spain).
9	Panadès i Blas	Testing the utility of gaussian mixture models in parataxonomic analyses.

ABSTRACTS

THE FIRST ORNITHOMIMID EMBRYO IN A SHELL WITH A SINGLE STRUCTURAL LAYER: A CHALLENGE TO ORTHODOXY

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The hypothesis that additional structural layers evolved in theropod eggshell microstructure through time is broadly accepted. Basal theropods, such as megalosauroids, have one structural layer, whereas non-avialan coelurosaurians have two structural layers and avialan dinosaurs three. However, no previous ornithomimid eggs and embryos were found, but were expected to have two structural layers due to their phylogenetic position deeply nested within Coelurosauria.

Here, we report the discovery of a nearly complete *in ovo* ornithomimid embryo from the Campanian of Alabama that challenges the orthodox hypothesis.

The external morphology and microstructure of this egg (AUMP 1235 from the Mooreville Chalk near the Cahaba River) was originally published nearly 40 years ago; however, subsequent mechanical preparation revealed the presence of an embryo. We therefore employed propagation phase contrast synchrotron micro-computed tomography at the ID17, European Synchrotron Radiation Facility in Grenoble, France to study the bones in situ. Several morphological characters support referral to Ornithomimidae including the presence of an accessory condyle on the quadrate, the position and extension of the quadrate foramen, and the sutural arrangement of the frontal with the prefrontal and nasal. Additionally, the dentary is edentulous as in derived ornithomimosaurs. New eggshell thin sections analyzed by polarizing light microscopy and scanning electron microscopy confirm a single structural layer. The presence of an ornithomimid dinosaur in an egg with a single structural layer is incongruent with the currently accepted evolutionary model of theropod eggshells and underscores the need for broader sampling and analyses. Etching of the mammillary layer due to the late development of the embryo can be ruled out as the mammillae are perfectly visible. This is also the first morphological description of an ornithomimid embryo and provides insights into the ontogeny of this important dinosaur clade.

EGGSHELL ASSOCIATED WITH A NEW TROODONTID TAXON FROM THE UPPER CRETACEOUS UKHAA TOLGOD LOCALITY, MONGOLIA

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A new troodontid dinosaur specimen (IGM 100/1323) from the Upper Cretaceous Djadokhta Formation at Ukhaa Tolgod, Mongolia, represents a rare association of skeletal remains and eggshell. The new troodontid is described on the basis of a nearly complete, articulated skull with partial articulated postcranial skeleton, probably from a subadult individual. Six small fragments of eggshell are closely associated with, and in some cases in contact with, the skeleton. The specimen is small-bodied and short-snouted, like early-diverging paravians, but otherwise presents several derived characters that unite it with other Late Cretaceous troodontids.

Though the eggshell has been diagenetically altered, some diagnostic features are still visible. Examination of the smooth-surfaced eggshell with both light microscopy and scanning electron microscopy reveals that it is approximately 0.4 mm thick, and consists of a mammillary layer and overlying prismatic layer. These microstructural features allow assignment to Prismatoolithidae indet., and we note further similarities with the similarly thin-shelled eggshell associated with troodontid perinates from Ukhaa Tolgod, as well as the ootaxon *Protoceratopsidovum minimum*.

Given that some prismatoolithid eggs from Mongolia and North America are assigned to troodontids on the basis of embryos in ovo and clutch-contacting adults, it is plausible that the eggshell associated with IGM 100/1323 was laid by the new taxon. However, we cannot rule out other interpretations, such as predation or accidental association with eggshell from a different taxon. Despite similarly high levels of diversity among troodontid skeletal remains and prismatoolithid eggs in Djadokhta-equivalent formations, correlating taxonomic and ootaxonomic diversity remains difficult, owing to the scarcity of close associations between eggs and skeletal material.

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DINOSAUR NESTING SITES AND EGGS FROM THE LATE CRETACEOUS OF URUGUAY: THE DEVELOPMENT OF THE PALAEO-OOLOGY IN THE LAST 10 YEARS.

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Dinosaur nesting sites, eggs and eggshells are well known in Cretaceous formations worldwide, and Uruguay is not an exception. Since the 80's dinosaur eggshells, eggs and egg clutches have been largely reported in the country from several sites of Mercedes and Queguay formations. In the last 10 years, however, palaeo-oology has growth in relevance as a paleontological discipline in Uruguay, especially due to new findings. Here we report a series of brand new dinosaur nesting sites, eggs and eggshells from the Late Cretaceous (Campanian-Maastrichtian for Mercedes Formation –based on palinomorphs–, and the age is still discussed for Queguay Formation) of Uruguay, displaying a wide diversity of dinosaurs not verified by bone remains. Classic and new outcrops were explored at central and western regions of the country, allowing the discovered of several nesting sites in both units. These formations are characterized by conglomeratic sandstones with levels of ferricretes, silcretes, and calcretes. The morphologic and systematic analysis of these materials provide important evidences of its taxonomic assignment. We can describe with certain evidences that the most important fossil site, located in a private establishment close to Algorta city, with many clutches containing dozens of in situ eggs and abundant eggshells belongs to neosauropods. Isolated eggs and eggshells represent a high biodiversity (Sauropoda: Titanosauria; Theropoda: Avetheropoda, Averostra and Avialae), and are very common in other localities. In this abstract, we present an amended diagnosis of Sphaerovum erbeni and Tacuarembovum oblongum, however the parataxonomic assignment of these specimens not represent a valid methodology to fossil eggs classification as a biologic entity with evolutionary information. Dinosaur egg remains from the Late Cretaceous units of Uruguay have particular diagenetic history (high silicification), product of epigenetic processes that suffered both units. Palaeobiology and taphonomy, along with the geological characteristics, will shed light on nesting behaviour and palaeoenvironmental aspects of egg-bearing units, which will reveal important aspect on dinosaur reproduction and the biological evolution of amniotic egg. We suggest that the current western Uruguay had large and extensive nesting sites and reproductive colonies of titanosaurs. The study of these Uruguayan dinosaur nesting sites and their eggs, as well as of its geo-paleoenvironment, will contribute to the knowledge of amniote communities in South America during the Late Cretaceous.

STUDYING SOME OF THE WORLD'S OLDEST KNOWN DINOSAURIAN EMBRYOS USING SYNCHROTRON MICROTOMOGRAPHY

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Massospondylus carinatus Owen 1854 is an emblematic South African basal sauropodomorph dinosaur from the Early Jurassic. Golden Gate Highlands National Park in the Free State Province of South Africa preserves a well-known nesting locality for this taxon. Two partially prepared embryonic skeletons preserved in a single clutch of eggs (BP/1/5347A) from this locality represent some of the world's oldest known dinosaurian embryos to date. This study uses scans (at 3-6µm resolution) obtained by synchrotron microtomography to digitally reconstruct these embryos, revealing features not visible on the surface. Our results show several surprising discoveries, including: 1) the presence of a previously undescribed third embryo in one of the unprepared eggs; 2) embryonic teeth in at least two of the embryos with first-generation morphological features such as lack of denticles; and 3) differences in the ossification stages of braincase bones, such as the presence/absence of basipterygoid processes. Our high-resolution scans allow us to stage these embryos and to tentatively conclude that different embryos developed at heterogeneous rates within a single clutch of eggs. Our data provides crucial early data for understanding the pre-hatching ontogeny of Massospondylus carinatus.

PELVIS MORPHOLOGY SUGGESTS THAT EARLY MESOZOIC BIRDS AND DINOSAURS WERE TOO HEAVY TO CONTACT INCUBATE THEIR EGGS

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Numerous fossils of birds have driven an interest in their pattern of reproduction. Avian eggs are rare in the fossil record and none have been found in contact with adult skeletons, which would make assigning them to a species unambiguous. Such paucity of evidence hampers our understanding of the evolution of reproductive biology in early birds, particularly contact incubation, which is a defining feature of extant birds. Current views include the idea that contact incubation evolved first in theropod dinosaurs and persisted in early birds but such evidence has not been universally accepted. Our study used an indirect approach to predict egg size in extinct avian species based on pelvic morphology. The presence of a pubic symphysis in non-ornithurine birds defines a pelvic canal and hence a maximal egg breadth. Using elongation ratios of Mesozoic bird eggs, we predicted egg mass for a total sample of 20 fossil avian species. Data from modern birds allowed us to calculate the load mass an egg could endure before cracking. Body masses of fossil birds were predicted from data for humerus and femur lengths. For non-ornithothoracine birds body mass was 135% of the load mass of the eggs. For Enantiornithes body mass and egg load mass were comparable to that predicted for extant birds, but some early Cretaceous ornithuromorphs were 132% heavier than their eggs could support. By contrast, eggs of extant birds of comparable sizes can support three times the mass of the adult. Available evidence for predicted body mass and egg mass of theropod dinosaurs also suggests that contact incubation was not possible because of the risk of crushing the eggs. This problem would be exacerbated by higher estimates for body mass. Our results suggest that contact incubation evolved comparatively late in birds and was not inherited from a theropod ancestor.

DINOSAUR EGGSHELL FRAGMENTS FROM THE UPPER CRETACEOUS DEPOSITS OF CAUVERY BASIN

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Fossilized dinosaur eggs, nests and eggshell fragments have been reported from the Upper Cretaceous Lameta Formation from a number of sites in central and western parts of India within the Deccan Volcanic Province (DVP). Ultrastructural studies of fossil eggshells from these sites have shown a high diversity of sauropod dinosaur oospecies. Currently nine oospecies are known from these sites viz. *Megaloolithus cylindricus, M. jabalpurensis, M. megadermus, M. dhoridungriensis, M. khempurensis, Fusioolithus baghensis, F. padiyalensis, F. mohabeyi, and F. dholiyaensis.* As compared to this high diversity in dinosaur oospecies from the DVP, only one report of a dinosaur egg is known from the Cauvery Basin. In fact, the first fossil egg identified as a chelonian egg was reported from the Aptian - Albian Karai Formation of Cauvery basin in 1957. Following this a solitary egg of a titanosaurid dinosaur was described from the Upper Cretaceous (Early Maastrichtian) Kallankuruchhi Formation, Cauvery basin in 1996. More recently, we have recovered isolated eggshell fragments from the marine Upper Cretaceous (Late Maastrichtian) Ottakoil Formation which succeeds the Kallankuruchhi Formation vertically.

Based on SEM and polarizing microscope studies, the eggshell fragments from Ottakoil are assigned to the oospecies *Fusioolithus baghensis* because of compactituberculate external ornamentation, fan-shaped radiating spheroliths, arching growth lines which merge with the growth lines of coalescing spheroliths and swollen basal cap units. Prior to this find, *F. baghensis* has been recorded from the Lameta Formation of Bagh area, Jabalpur and Pisdura in central India, and Balasinor and Anjar in western India. The new find from Cauvery basin is important from a paleobiogeographic point of view as the oofamily Fusioolithidae is found in the Upper Cretaceous strata of India, France, and Argentina, supporting the previous works in which possible terrestrial connections between India and Eurasia have been suggested.

EVIDENCES OF A TURTLE ROOKERY IN THE SOBRARBE FM. (EOCENE, NORTHERN SPAIN)

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Here we describe an unusually high concentration (several tenths of thousands) of turtle eggshell fragments from the Castejón de Sobrarbe-41 (CS-41) fossil site (Lutetian, middle Eocene). CS-41 is a sirenian dominated bonebed located in the Sobrarbe Formation, Ainsa Basin, Huesca, Northern Spain. CS-41 is associated with overbank settings, related to the dynamic of the tributary channels of the deltaic plain. Macrofossils are dominated by sirenian bones, but Pleurodire turtle remains collected include a complete carapace 60 cm in length and postcraneal bones.

The eggshells recovered are single layered and formed by subcylindrical shell units with radial ultrastructure. Outer surfaces are slightly sculptured, with compactituberculated ornamentation. In thin sections, the eggshells are highly recrystallized, with its original composition completely lost. This contrasts with the apparent fine preservation of the ultrastructure under secondary electrons. We postulate that during the fossildiagenesis, fine details of the ultrastructure were preserved due to a very slow replacement of the original aragonitic eggshell with low magnesian calcite, growing as mineral phantoms. All preserved features are consistent with fossil and modern turtle eggshells. We assign them to the oofamily Testudoolithidae, and discuss their affinities to the Eocene oogenus *Haininchelys*.

Over 200 eggshell fragments were recovered per kilogram of sediment by screen washing, doubling the number of eggshells recovered in other similarly sampled localities, but formed by attrition or active transport and accumulation of fragments. The high numbers of eggshell fragments suggest that the assemblage formed in the proximities of a nesting area. Complete and/or hatched eggs were exhumed, broken and washed during a storm, which accumulated the eggshell fragments in an abandoned channel. Recent pleurodire turtles are known to nest in lentic and lotic environments within modern deltaic systems. Further prospection of the more proximal deltaic facies may yield more complete specimens and nests.

A TROODONTID CLUTCH DEMONSTRATES A DINOSAURIAN ORIGIN OF THE AVIAN SINGLE OVIDUCT

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The avian reproductive system is among the most sophisticated in the animal kingdom. One of the most important innovations is supposedly the presence of a single functional oviduct involved in egg formation. On the other hand, clutches attributed to non-avian theropod dinosaurs, such as oviraptors, show a paired arrangement of the eggs, indicating that two reproductive tracts were present in these taxa. Based on the fossil evidence, a single functional oviduct is regarded as present only in birds.

We report here a theropod clutch from Ukhaa Tolgod, Djadoktha Formation, Mongolia. The nest is attributed to Troodontidae based on the vertical disposition of the eggs, reduced eggshell ornamentation and asymmetrical shape. Fifteen eggs are counted in the clutch, and two almost complete skeletons belonging to hatchlings are preserved on top of the clutch. Cranial and postcranial remains are preserved for both the individuals. The presence of a lateral maxillary groove in the skulls allows to attribute the two perinates to the taxon Byronosaurus. The two skeletons are interpreted as belonging to hatching rather than embryonic individuals based on the high degree of skeletal ossification and the abundance of associated scattered eggshell fragments. Randomization of egg position in space and cluster analysis were performed to test the probability for a paired arrangement of the eggs, as documented for oviraptors. We find no support for a paired partition of the eggs, supporting the presence of a single oviduct in Troodontidae. This result suggests that a bird-like ovarian tract evolved already in non-avian theropods. The presence of only two perinates on the nest supports a heterochronous hatching in Troodontidae. In the end, a shed tooth belonging to an adult individual and referable to Troodontidae is found next to the two skeletons of the hatching Byronosaurus, on top of a hatched egg. We suggest that adult Byronosurus were visiting the nest to check over the offspring.

NEST SITE TAPHONOMY OF COLONIAL GROUND NESTING BIRDS AT BOWDOIN NATIONAL WILDLIFE REFUGE, MONTANA

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Nesting localities of extant birds and reptiles provide taphonomic models for interpreting nesting sites in ancient archosaurs. Here we describe assemblages of nesting gulls (Larus delawarensis and L. californicus), American white pelicans (Pelecanus erythrorhynchos), and double-crested cormorants (Phalacrocorax auritus). Twentyfive gull, 20 pelican, and 25 cormorant nests yielded 172 invertebrate fragments, 2580 bones, and 2308 eggshells. Gulls constructed vegetation nests from 19-72 cm in diameter and 3-5 cm in height. Associated elements consist of birds (65.7%), fish (22.7%), and mammals (10.5%). Half of skeletally mature avian elements comprised gulls. Gull eggshell was uncommon (19%). Pelicans made scratch nests 40-77 cm in diameter and 3-4 cm in height. Fish dominate (49.3%) the assemblage, followed by mammals (26.0%) and birds (18.5%). Juvenile pelicans dominate nester elements (87%). Cormorant nests were 20-30 cm in height, 34-50 cm in diameter and made from sticks, bones, and man-made debris. Fish elements predominate (61.4%), followed by birds (26.8%), and crayfish (9.8%). Juvenile cormorants predominate nester elements (92%). Elements associated with pelican and cormorant nests generally occurred outside the nests (47-82%), whereas most gull debris was inside (40.9%). Eggshell concave up and concave down ratios (CU:CD) on the surface of gull nests compared closely to predated assemblages (57:43). Pelican and cormorant surface ratios were approximately 50:50, suggesting trampling by altricial young. Weathered bones in the subsurface of cormorant and pelican nests, and layers of predated eggshell in gull nests, suggest multi-year accumulations. The amount of material associated with the nests and the age of the nester bones provides a means of distinguishing altricial and semi-precocial nesting sites. Nesting grounds for gulls with semi-precocial young yielded a higher proportion of mature gull bones and less associated skeletal material, whereas those for altricial pelican and cormorant nests were dominated by young birds and a higher percentage of additional skeletal elements.

A MIXED VERTEBRATE EGGSHELL ASSEMBLAGE FROM THE TRANSYLVANIAN LATE CRETACEOUS

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To date, the vertebrate oological fossil record is mainly dominated by monospecific egg and nest associations, with few rare exceptions. Among the extant fauna, however, there are numerous examples of disparate taxa sharing nesting areas or even the same nests. Based on these occurrences, it is parsimonious to predict similar behaviours in the past.

A Late Cretaceous-aged multi-taxon nesting accumulation from the Oarda site close to the city of Sebes, Romania, where eggs are preserved in three dimensions, reveals a new example of nest site sharing between diverse vertebrate lineages in the fossil record. Eggshell and osteological evidence, mixed in a single accumulation, shows that at least four vertebrate taxa including enantiornithine and neornithine birds, crocodylomorphs, and gekkotan squamates were nesting at the same site. Communal nesting in enantiornithines was previously described from this site; we present the first fossil evidence that other vertebrates also nested in the same area, perhaps exploiting the presence of a large bird colony. We describe the four different eggshell morphotypes present at this site and draw palaeoecological inferences based on this inter-class nesting association.

The Oarda accumulation is thus unique in the vertebrate fossil record: it is a multispecies nesting assemblage that reveals the earliest record of disparate animals sharing the same nesting area.

We speculate that perhaps a plain area, created by seasonal flooding, offered the birds safety from predators and that the nest environments themselves offered shelter to smaller reptiles that benefitted from the security provided by those birds guarding their own nests, as is often the case in extant mixed-nesting assemblages.

Acknowledgments: We would like to thank PICT 2013-1901 for funding this investigation. Paula Troyon from CNEA, who took the pictures at SEM.

THE FIRST AVIAN EGG FROM RÍO NEGRO PROVINCE, ARGENTINA (ALLEN FORMATION, UPPER CRETACEOUS)

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We report the first record of an ornithoid egg from Río Negro Province, in Upper Cretaceous (Campanian-Maastrichtian) rocks of the Allen Formation (Salitral Ojo de Agua locality, Arriagada II site), with organic remains from their testaceous membrane.

The egg was found near of a faveoloolithid nest previously studied, it appeared isolated in the ground without any sedimentological feature who suggest a nest structure. It preserves a single pole with a smooth surface. Its measurements are 5.38 cm in length (long axis) and 3.06 cm in width (short axis). Three samples of eggshells have been observed under scanning electron microscope. The ultrastructure of the eggshells reveals a two layered egg, with an ornithoid basic type and a ratite morphotype. The well-developed mammilary layer is 154 μ m thick with petal-shaped mammilla; the squamatic layer is 251 μ m thick. The complete thickness of the eggshell is about 400 μ m. The ratio CL:ML is 1:1.6. The shell microstructure of this egg is consistent with Laevisoolithidae, an ootaxon traditionally associated with enantiornithid birds.

The egg has an excellent preservation, including fibers of the testaceous membrane have preserved their shape in 3 dimensions, at the moment no organic remains have been found. The fibers display a flattened shape, with a thickness of 1.1µm and a width of 4.8µm each. The fibers have an arrangement similar to those seen in extant reptiles and display a random arrangement. The preservation and replacement of the testaceous membrane suggests an excellent site conditions. EDAX analysis reveals that the fibers have been enriched and replaced with trace of Mg, Al, Si, P, F, and K, elements that are also present in one or more examples of both extant and fossil shell membrane.

Acknowledgments: We would like to thanks PICT 2013-1901 for funding this investigation. Paula Troyon from CNEA, who took the pictures at SEM and performed EDAX analysis.

DINOSAUR EGG CLUTCHES FROM THE UPPER CRETACEOUS OF GUADALAJARA (CENTRAL SPAIN)

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Castilla-La Mancha is one of the richest regions in the Cretaceous of Spain for fossil remains of dinosaurs and other reptiles. Its importance has been growing since the discovery of the Lo Hueco site (Fuentes, Cuenca) in the Villalba de la Sierra Formation, more than ten thousand specimens of Campanian-Maastrichtian reptiles were discovered. However, no eggshells were recognized there.

Until now, the only record of eggshells in Castilla-La Mancha comes from Portilla (Cuenca), also in the Villalba de la Sierra Formation. They were preliminarily identified as *Megaloolithus siruguei*, an oospecies attributed to titanosaur sauropods.

In 2016 a new discovery occurred in the area of Buendía (Sacedón, Guadalajara), where an isolated titanosaur vertebra had been previously described. This area is also located in the Villalba de la Sierra Formation. This recent survey provided the finding of two main fossiliferous levels, one with fossil bones, including some of a middle-sized theropod, and the other with both eggshells and complete eggs that seem to be grouped in clutches. The presence of both complete eggs and clutches is new for the Central Area of Spain. The excavation and study of the morphology of some of these eggs and potential clutches will be carried out in the coming months.

The preliminary study of some isolated eggshell fragments from Buendía allows us identifying them as belonging to a dinosauroid spherulitic type, where the eggshell units are almost fused, so the boundaries between them hardly can be recognized. They show ondulating and uniformly arranged growth lines and very few pore channels. The outer surface shows a dispersituberculate ornamentation. The mammillary zones show different states of resorption. The overall microstructure differs from the oospecies *Megaloolithus siruguei*, so far, the only one identified in this Formation. Its microstructure could be described as prolatospherulithic-like.

VII SYMPOSIUM ON DINOSAUR EGGS AND BABIES IN QINGLONGSHAN GEOPARK IN HUBEI, CHINA

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The Late Cretaceous basins in China are renowned for their enormous amount of dinosaur eggs. Since 1993, over than 50000 dinosaur eggs were discovered in the Xixia Basin, south-western Henan, China. Due to immature protection policies, the fossils in the Xixia Basin were at high risk for devastation by human activities and illegal excavations. Conversely, in the past decade, more dinosaur-egg-bearing strata were reported in north-eastern Hubei, but better protected. Geological evidence indicates that red basins in south-western Hubei (Yunyang Basin) and north-eastern Henan (Xixia Basin, Liguangiao Basin, and Yichuan Basin) belonged to the same tectonic regime during the Late Cretaceous period. Among the basins in north-eastern Hubei and south-western Henan, Qinglongshan area in the western Yunyang Basin yields the best and largest in-situ preserved dinosaur egg clusters. Over than 500 egg clutches in Gaogou Formation were exposed and protected by complete enclosing constructions. Most eggs are spherical and assignable to dendroolithid eggs. Unlike the Sigou Formation in south-western Henan that bears mostly elongatoolithid eggs, Qinglongshan area probably represents an earlier prosperous dinosaur flock during the early Late Cretaceous period. Recently, more dinosaur eggs are also exposed in several regions near Qinglongshan area, demonstrating the scientific potential to facilitate more research on the paleoecology and reproductive biology of dinosaurs.

The Qinglongshan Dinosaur Egg-Cluster National Geopark is located at around 30 km to Shiyan City in Hubei. The meeting will be hosted in the museum building with in-situ preserved outcrops. We would like to sincerely invite all palaeontologists and students to visit the museum and in-situ preserved outcrops. In our potential preand post-symposium trips, we would explore some outcrops of Gaoguo Formation in Qinglongshan and neighbouring area, probably as well as the classical quarries in Xixia Basin, Yichuan Basin, and Liguanqiao Basin.

PALEOEMBRYOLOGY – AN INTERDISCIPLINARY SCIENCE

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Fossils preserved inside eggs (*in ovo*) are useful in particular for establishing biological relationships between different egg morphologies, or/and nesting strategies, and known dinosaur taxa. Fossilized embryos are also irreplaceable sources of information for understanding the development of extinct animals and prenatal developments. The level of information available from fossil eggs can be enhanced using different technological tools. Two main kinds of approaches, invasive and non-invasive, have been used to access embryonic remains within fossilized eggs.

Mechanical and chemical techniques have been applied in early paleoembryology to access the preserved *in ovo* remanis of dinosaurs. In addition, non-invasive x-ray-imaging techniques have recently also been utilized to extract biological information from egg fossils and translate these data into precise 3D virtual replicas of fossilized tissues. These novel approaches have prooved

revolutionary in studying precious fossils without cutting/etching them, but nevertheless most have also been insufficient in providing meaningful information due the lack of third dimension (radiography), and a low absorption contrast corresponding to high density of these objects (medical computed tomography and laboratory compued microtomography), both limiting further exploitation of x-ray data.

The most advanced technological tools capable of accurate visualizing 3D preserved embryonic bones embedded in matrix of comparable density are large high-energy synchrotrons. Third generation synchrotrons, in particular, are well-optimized for tuning the energy of hard x-rays to provide best possible imaging results in absorption contrast mode. These results can be dramatically enhanced when the edge detection technique is superimposed on absorption contrast, phase contrast microtomography. The best effect of the phase contrast for the precise imaging of dinosaurs eggs interiors can be achieved using monochromatic, highly coherent, and parallel beams produced by bending magnets and the insertion devices of third generation synchrotrons and a long propagation distance.

In this lecture, I provide several examples of experimental outcomes when imaging different *in ovo* preserved dinosaur embryos from Mongolia, China, USA, and Argentina. I also present two examples of *in toto* immunolabelling and *in ovo* ablation and transplantation experiments carried out on modern crocodilians and birds. These experiments are to demonstrate our ability to learn and reconstruct early stages of morphogenesis which is unlikely to preserved as fossils.

PRELIMINARY CLUMPED ISOTOPE DATA FROM LATE CRETACEOUS TITANOSAUR (SAUROPODA) EGGSHELLS: PRESERVATION OF THE ORIGINAL ISOTOPIC SIGNAL AND IMPLICATIONS FOR PALAEOECOLOGICAL AND PALAEOBIOLOGICAL INTERPRETATIONS

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For several decades, scientists have relied on stable isotope analyses on fossils and associated sediments for palaeoecological and palaeoenvironmental reconstructions. The fractionation of oxygen and carbon isotopes between a mineral and the original fluid it precipitated from depends on temperature. Information related to climate, environment and/or physiology can thus be inferred from the isotopic composition of both, the mineral and original fluid, by means of established fractionation equations. The most limiting factor of this method is that the isotopic composition of the original fluid (e.g. meteoric water, body water, marine water) is unknown for geological and fossil samples and must consequently be estimated.

A recently developed stable isotope method called 'carbonate clumped isotope thermometry' now allows to calculate the precipitation temperature of a mineral independently of the isotopic composition of its original fluid, basing only on the abundance of ¹³C-¹⁸O bonds within a carbonate molecule, which is temperature-dependant. When applied on fossils (eggshells, carbonate fraction in tooth apatite...), clumped isotope analyses give direct information on the body temperature of the animal, provided that the primary isotopic composition is preserved.

We ran classical oxygen and carbon, as well as clumped isotope analyses on Late Cretaceous dinosaur eggshells, associated pedogenic carbonate nodules and hydrothermal crystals from three different titanosaur nesting sites of La Rioja province, NW Argentina. The results show that the eggshells of two sites are isotopically poorly preserved, meaning that the calculated precipitation temperature (>40°C) most probably corresponds to that of secondary calcite. However, the eggshells of the third one show values different from associated, diagenetic carbonate and can thus be used to answer palaeophysiological questions. We will provide preliminary information on body temperature of titanosaurs and on the environmental conditions that prevailed in these three study sites, likely ideal for nesting.

SQUAMATIC ULTRASTRUCTURE AS A KEY CHARACTER OF ORNITHOID-TYPE EGGSHELL

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The squamatic ultrastructure (SqU) is the key character of the outer (continuous) layer in avian eggshell, documented in all recent bird taxa at family level. This fine architecture defines particular interconnection between organic and inorganic phases which makes this layer to be strongest eggshell stratum (resistant to shocks or static load) versus its relative thickness. SqU also defines specific spongy quality of the layer, e.g. allowing it to absorb liquid plastic. Finally, the other layer with SqU is formed faster than the inner (mammillary) layer. All this suggests that SqU represents a particular functional level in the organization of the hard eggshell of the vertebrates.

However, the recognition of SqU in the Mesozoic eggshells is not always easy, which leads to some mistakes and finally to very different results in cladistic analysis of theropod eggs. Among the Cretaceous sauropsids, SqU is detected in enantiornithine birds (oofamilies Subtiliolithidae and Gobioolithidae) and in certain maniraptoran theropods (oofamilies Elongatoolithidae and Oblongoolithidae), in particular in oviraptorids and dromaeosaurids; also in some other non-avian or avian theropods: oogenera *Nipponoolithus*, *Belonoolithus* and *Dimorphoolithus*. At the same time SqU is absent in Jurassic basal theropods such as *Torvosaurus* (megalosaurids) and in basal maniraptorans such as therizinosaurids. The ultrastructure of the outer eggshell layer remains uncertain in avian-like eggs such as *Parvoolithus*, *Montanoolithus*, *Parvoblongoolithus* and *Pachycorioolithus*, yet is highly probable in *Troodon*. The outer layer in the elongated eggs of Prismatoolithidae lacks SqU.

SLICED EGGS: THE USE OF NON-STANDARD THIN SECTIONS IN THE STUDY OF EGGSHELLS

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Thin sections have been used to examine fossil and recent eggshells since the 19th century. They provide information on the eggshell histology, pore system and extinction pattern, all of them key characters in the description of eggshells. Most paleoological studies use standard 30 µm thin sections. This type of preparation has important advantages: the methods of mineralogical identification are calibrated for standard thin sections, and most commercial laboratories are optimized for this thickness. Nevertheless, standard thin sections may not be the most adequate preparations for the study of eggshells.

Important histostructural features of the eggshells, such as the presence and shape of growth lines, may be too faint in standard thin sections. Experience from both eggshell and bone histological preparations suggests that 50 to 100 μ m thin sections are the best to study these histological features. Also, crystallographic features, such us crystal shape, orientation and extinction pattern usually reflect structures that are much smaller than 30 μ m. Therefore, these features can be misinterpreted in standard thin sections. In recent eggshells, the high organic content of the eggshell may hinder the crystallography of the mineral phase, where as in fossil eggshells, some abnormal crystallographic features, such as dog tooth spar texture may be hidden in standard thin sections.

Once the mineralogy of an eggshell has been determined, producing both thicker and thinner thin sections may increase the understanding of its histostructrure and crystallography. As an alternative, taking photographs at different thickness during section preparation allows to acquire all data from a single fragment. This second approach has limits: 1) fine polishing at each thickness is required for the pictures to be informative, adding steps to the preparation process; and 2) it is destructive, so resulting pictures should be curated with care to avoid data loss.

DISTRIBUTION OF EGGSHELL FRAGMENTS AS A PROXY FOR LAKE DYNAMICS.

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The site Cuesta Corrales 2 (CC2) comprises an eggshell assemblage found in shallow lacustrine facies of the El Castellar Formation (Galve, Spain, early Barremian). The site is the type locality of the ootaxon *Guegoolihus turolensis*. Several thousands of eggshell fragments, 95% of them belonging to *Guegoolithus* where collected in an area of 7 m², in a 1,40-meter-thick stratum of grey marks corresponding to basinal lacustrine deposits..

Guegoolithus fragments are large (2 cm²) and significantly more abundant at the middle of the level, here defined as the maximum accumulation horizon (MAH). In this horizon, clusters of up to 60 fragments have been interpreted as crushed partial eggs. Eggshell fragments are present through the whole stratum, decreasing in abundance from the MAH. There is a dominance of concave up eggshell fragments in the MAH. Further away from this horizon the orientation of the fragments is randomized between concave up, concave down and vertical eggshells.

Analysis of the eggshell fragments not belonging to *Guegoolithus* (5% of the assemblage) shows that they increase in abundance towards the top of the stratum. These fragments are smaller (<0,25 mm²) and show different degrees of preservation. They represent the typical ootaxa assemblage of the Barremian of the Iberian Basin (i.e. *Trigonoolithus, Mycomorphoolithus, Krokoolithes*, etc).

CC2 was deposited during a shallowing cycle of the lake. The MAH can be explained by a quick retraction of the water table on a low-gradient lakeshore during a phase of lake level drop which was profited by dinosaurs to nest in the resulting mudflat. An alternative hypothesis is that the eggs where discarded into the lake after hatch, because of a nest cleaning behaviour. The accumulation was later modified by the sedimentological and biological dynamics of the lacustrine environment.

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FIRST RECORD OF AVIAN EGGSHELLS IN THE PLEISTOCENE SITE OF GRAN DOLINA (ATAPUERCA, SPAIN)

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The archaeological-palaeontological site of Gran Dolina (TD) is one of the numerous cavities of the Sierra de Atapuerca karst complex (Burgos, Spain). It is known by their exceptional Quaternary stratigraphic and paleontological record. It has a 19-m-thick Lower and Middle Pleistocene infilling, which is divided in eleven levels. This work is focused on the level TD6 (0.78-0.86Ma). It consists of a succession of debris flow and fluvial facies with a high diversity of small microvertebrates and large mammals, including *Homo antecessor*, the first species of *Homo* in the Iberian Peninsula.

Here we describe eggshell fragments recovered by screen washing of sediments collected during the archaeological excavations. They are rare, and despite of the several tons of sediment processed in this level, only 22 eggshell fragments have been recovered.

Fragments are of small size (<5 mm2) and poorly preserved, with clear signals of abrasion. All eggshells present smooth outer surfaces, densely packed mammillae in the inner surfaces, and are multilayered. Thus, they can be identified as avian eggshells. The degree of abrasion of the radial sections hinders the identification of ultrastructural characters, but cathodoluminescence analyses allow discarding recrystallization. In the best-preserved fragments, differences in eggshell thickness and relative proportions between the mammillary layer and the continuous layer, and between the squamatic zone and external zone suggest the presence of three ootaxa. This result may be affected by the small size of the sample, as these disparities may be explained by intraoospecific variability.

Birds are a common component of the faunal association of TD6, with over 30 taxa identified. The scarcity and poor preservation of eggshell remains suggest that the fragments where transported inside the karstic system, and do not represent evidence of cave nesting birds. This is congruent with the taphonomic and sedimentological models proposed for the infilling of TD6.

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MECHANISMS OF BIRD EGGSHELL FORMATION: STRUCTURE, MOLECULAR CONTROL OF MINERALIZATION AND BIOLOGICAL REGULATION IN HENS.

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The chicken egg is a giant reproductive cell protected by an eggshell. The eggshell is a porous bioceramic that regulates the exchange of metabolic gases and water, and serves as a calcium reservoir for the developing embryo. It forms daily in the distal segment of oviduct, in an acellular uterine fluid that contains inorganic and organic precursors of the shell. Its distinctive features, as compared to bone or teeth, are the nature of the mineral and the absence of cell-directed assembly during its fabrication on eggshell membranes. Eggshell is made of 95% calcium carbonate (calcite) and 3.5% organic matrix (proteins and proteoglycans). The organic matrix plays a key role in the nucleation and stabilization of calcium carbonate on specific sites on the eggshell membranes, determining polymorphic phase selection, regulating crystal morphology and growth rate. These interactions between both mineral and organic matrix constituents result in a highly ordered structure of the eggshell, with unique mechanical properties. The sequential events of mineralization correspond to the following phases: 1) the widespread deposition of amorphous calcium carbonate (ACC), 2) ACC transformation into crystalline calcite aggregates, 3) formation of larger calcite crystal units followed by 4) the development of a columnar structure with preferential calcite crystal orientation and 5) the termination of calcification prior the oviposition. Transcriptomic and proteomic studies have identified a wealth of protein matrix candidates that may regulate shell mineralization. Their involvement has been demonstrated by numerous *in vitro* and *in vivo* evidences. The mechanisms regulating the precipitation of calcium carbonate and the structural organization of the eggshell and its constituting crystals will be reviewed. Eggshell formation requires large amounts of CaCO, as the hen exports 10% of her total body calcium (2 g) each day. Neither ion (Ca²⁺ and HCO₃) is stored in the uterus, but they are continuously supplied during eggshell formation by the blood via uterine trans-epithelial transport. Such intense Ca²⁺ metabolism challenges calcium homeostasis in hens which develop numerous physiological adaptations. This review will, in addition, describe ionic transporters supplying shell mineral precursors and introduce some regulating factors contributing to the control of eggshell strength in hens.

DINOSAUR EGGSHELL OF THE WESTERN INTERIOR BASIN, USA: A NEW ASSEMBLAGE FROM THE UPPER CRETACEOUS (CAMPANIAN) KAIPAROWITS FORMATION OF GRAND STAIRCASE-ESCALANTE NATIONAL MONUMENT, UTAH.

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Western North America preserves a spectacular record of late Cretaceous environments and biotas deposited along the Laramidian shore of the Cretaceous Interior Seaway. Subsidence coupled with abundant sediment supply resulted in thick, continuous, highly fossiliferous deposits aligned along the Cordilleran foreland basin. Multiple contemporaneous formations comprised of these sediments collectively form the Western Interior Basin (WIB) system, including: the Dinosaur Park Formation of southeastern Alberta, Canada; the Two Medicine Formation of western Montana; the Kaiparowits Formation, exposed at Grand Staircase-Escalante National Monument (GSENM) in southern Utah; and the Fruitland Formation of northwestern New Mexico. These formations provide a unique, 2 Ma-long window into well-preserved Campanian environments and ecosystems along a latitudinal gradient. Studies of vertebrate terrestrial assemblages from the WIB report latitudinal shifts in fauna; however, eggshell studies suggest similar assemblages throughout. The objectives of this study are to identify the eggshell preserved in the Kaiparowits Formation of GSENM and to compare this assemblage to other coeval assemblages along the WIB. Twenty-two specimens (each represented by multiple fragments) were selected and photographed prior to destructive analyses. Thirty-seven thin sections were then prepared and imaged with a petrographic microscope and analyzed with ImageJ software.

The dinosaur eggshell assemblage preserved in the Kaiparowits Formation of GSENM displays a high oodiversity consisting of at least five dinosaur ootaxa, including: *Portituberoolithus, Continuoolithus, Prismatoolithus, Spheroolithus* (including an abnormal, double-layered specimen), and Elongatoolithidae. *Continuoolithus* and *Prismatoolithus* occur in all four formations discussed here, while *Spheroolithus* and *Portituberoolithus* occur in three formations. The northern formations display a higher oodiversity than the southern formations, which may reflect changes in preservation potential (e.g. paleoenvironment, reproductive behavior) and/or collecting biases. Further, this study adds to the growing wealth of paleobiological data preserved within GSENM and is a reminder that conserving public lands is deeply beneficial to the scientific community.

TESTING THE UTILITY OF GAUSSIAN MIXTURE MODELS IN PARATAXONOMIC CLASSIFICATION OF FOSSIL EGGS

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Fossil eggs and eggshells are very seldom associated with skeletal or dermal remains and can rarely be assigned taxonomically. This has resulted in oologists creating an alternative classification system for fossil eggs and eggshells: the parataxonomy of fossil eggs. Under parataxonomy, fossil eggs are classified in oospecies, oogenera and oofamilies according to qualitative characters (e.g. shape of the shell units and ornamentation) and highly heritable quantitative characters (e.g. height of unit, HU, and width of unit, WU).

Megaloolithus oospecies, which have previously been partially attributed to both *Titanosaurus* and hadrosaurid dinosaurs, are defined by the shape of their units, quantification of the morphometric variation and variability of their microstructures (HU and WU of eggshell units). Two competing interpretations of the observed morphological variation of the eggshell units have been proposed: 1) different megaloolithic morphologies are indicative of different dinosaur species; and 2) the same dinosaur species was responsible for all the variation seen in megaloolithic eggshell units.

In this study, a Gaussian mixture model was applied to test both interpretations. This probabilistic model assumes all the data points are generated from a mixture of a finite number of Gaussian distributions with unknown parameters. We compared the morphometric distributions of HU and WU in eggshells, eggs and clutches belonging to 8 *Megaloolithus* oospecies from Catalonia to the defined morphometric variation seen in the eggshell microstructures of two extant turtle species and two crocodile species.

The resulting Gaussian model was best defined for four distributions of HU and WU representing the extant turtle and crocodile oospecies, and three distributions consisting of one or more *Megaloolithus* oospecies. Thus, the variation of megaloolithic eggshell units in Catalonia were produced by the same dinosaur species.

Acknowledgments: this study is dedicated to the memory of Professor Nieves López Martínez: without understanding the past, we cannot deal with the future, we shall thus live in the moment.

HATCHING A NEW GEOPARK: DINOSAUR EGGS AND BABIES IN THE BIRTH OF A SUSTAINABLE GEOTOURISM IN PORTUGAL

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The Lourinhã formation is known for its dinosaur and fossilized clutches and eggs, some with embryos. The theropod nesting site of Paimogo, discovered in 1993, and in display in the Museum of Lourinhã since 1997 is one of the highlights of the exhibition. The display includes holotype of the oospecies Krokolithes dinophilus. The theropod and crocodylomorph eggs and embryos from Paimogo, Porto das Barcas, Peralta and Casal da Rola have been subject of various scientific publications and recognition. Besides eggs and tracks, the Museu da Lourinhã also displays the holotypes of Lourinhanosaurus antunesi, Zby atlanticus, Miragaia longicollum, Torvosaurus gurneyi, Allosaurus europaeus, Draconyx loureiroi and Dinheirosaurus lourinhanensis that were all found within a 10 km radius of the town of Lourinhã. This abundance of paleontological findings boosted the numbers of visitors of the Museu da Lourinhã. Nearly 25.000 people visit the Museu da Lourinhã every year. A new touristic thematic park, the Parque dos Dinossauros da Lourinhã, is scheduled to open in 2018 promoting even more the paleontological tourism in the region, is expected to receive more than 200.000 visitors per year.

Lourinhã is in a center of an area known as 'Oeste', which has as pillars of its sustainable tourism based on: the sand beaches, the scenic atlantic coast, the surf, the paleontology, and nature hiking; all of which are result of the geological context, which lead the municipalities of Bombarral, Lourinhã, Óbidos, Peniche and Torres Vedras to gather in 2017 and prepare an application to a new GeoPark that aspires to receive UNESCO approval, after an idea hatched in the Museu da Lourinhã and its neonate first steps are still being taken.

Portugal already has 4 UNESCO GeoParks, with remarkable success in attraction of tourists and revenues for the regions within a magnitude of hundred of millions of euros per year in same cases.

A SINGULAR SAUROPOD EGGSHELL-TYPE FROM THE LOWER MAASTRICHTIAN (UPPER CRETACEOUS) OF THE COLL DE NARGÓ NESTING AREA (SOUTHERN PYRENEES, SPAIN) WITH COMMENTS TO THE IBERIAN SAUROPOD DIVERSITY

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The uppermost Cretaceous continental strata from southern Europe are known for yielding an abundant diversity of oological remains attributed to various groups of dinosaurs. Southern Pyrenean basins (northern Iberian Peninsula) are especially rich in eggshell fragments, eggs, and clutches attributed to titanosaurian sauropods (oofamily Megaloolithidae). Among the hundreds of egg-sites reported from the Iberian Pyrenees, the Coll de Nargó area emerges as the most important locality for producing an enormous quantity of this fossil record.

After intensive paleontological surveys carried out for more than 10 years in the Coll de Nargó nesting area, five oospecies, distributed along 45 stratigraphic levels, have been recognized. Here we report the occurrence of a new and singular dinosaur eggshell-type. The new material was collected from three different strata of the "lower red unit" of the Tremp Fm. (early Maastrichtian in age). Eggshells are composed of single-layered, partially fused, elongated fan-shape units crossed by a reticulate pore system, leading us to ascribe them to the oogenus *Megaloolithus*. They exhibit a distinctive ornamental pattern consisting of irregular, triangle-shaped nodes with rounded pore openings on their top, not shared with any described oospecies of this oogenus.

In recent times, the oological record has been postulated as a proxy to infer taxonomic diversity for certain regions. In this way, the current megaloolithid diversity and its chronological distribution in SW Europe roughly match with the known sauropod diversity at the region. Between four and six titanosaurian taxa and three megaloolithid oospecies are known from the early Maastrichtian of northern Iberian Peninsula, while four indeterminate titanosaurians and only two oospecies are distinctive from the late Maastrichtian. Despite some disagreements, both records support the hypothesis of a sauropod faunal change during the Maastrichtian in the Iberian region.

MODERN COMPARATIVE TAPHONOMY: THE RELATIONSHIP BETWEEN NESTING SITE SKELETAL ASSEMBLAGES AND REPRODUCTIVE ATTRIBUTES

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To better understand fossil nesting assemblages, we taphonomically surveyed nesting sites for a variety of extant amniotes. Ultimately, we aim to quantitatively assess the relationships between reproductive attributes and skeletal assemblages generated at nesting localities. Surveyed taxa included two turtles, two crocodylians, and 13 birds, capturing a range of reproductive behaviours. Nesting localities occur on beaches and small islands, adjacent to inland waterways, near wetlands, in grasslands, and in arboreal colonies. Hatchlings range from precocial (turtles, crocodylians, ducks, crane) to semi-precocial (gulls, tern), semi-altricial (great blue heron), and altricial (pelican, cormorant). Parental care of young varies from none (turtles) to assistance at hatching (crocodylians), to more extensive care (most birds) and is proportional to post-hatching residence time. Data collection involved mapping, counts, taxonomic indentification, and taphonomic assessment of biotic materials (bone, eggs, eggshell, pellets). Shallow excavations were conducted at some localities. Nesters with precocial young generated assemblages consisting of eggshell and largely intact hatched or unproductive eggs, except crocodylians where assistance of adults during hatching produces a large spread of fragmented shell. Eggshell is far less abundant with semi-precocial to altricial hatchlings. Instead, skeletal remains of young and adult nesters represent a significant component and, as young become more altricial, the proportion of prey items appears to increase. Eggshell orientation, although variable from nest to nest and across taxa, largely falls between 60:40 to 50:50 concave up versus concave down. But ratios favoring concave down occur in areas with potentially greater trampling, e.g. crocodile adults assisting hatching, altricial young, and subsurface assemblages. The associated ground assemblage for the arboreal nester (heron) compared closely to those of other birds with similar young. Subsurface assemblages mimicked those at the surface but with lower eggshell content. Embryos within a clutch may die asynchronously, challenging the assessment of asynchronous hatching in fossil assemblages.

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GLOBAL AND QUANTITATIVE ANALYSES INDICATE TITANOSAURIANS NESTING ON INLAND ENVIRONMENTS

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Eggs and clutches of the Megaloolithidae oofamily, profusely reported in Europe, India and South America, have been ascribed to titanosaurian sauropods. A key-point in the study of reproduction in titanosaurians is the selection of the nesting site which was most probably constrained by finding an environment with optimal incubation conditions that ensures the offspring success and avoid the pressure of predators.

In order to test what, if any, habitat preferences existed among the titanosaurians during nesting season or if environmental versatility is statistically significant, we constructed a global database, based on literature and containing 132 sites with *in situ* megaloolithid eggs and clutches. The primary (inland and coastal) and the secondary (fluvial/palustrine-lacustrine/aeolic; barrier beach/lagoon/tidal flat) environments were specified for each site and the relationship between megaloolithid eggs and certain environments was tested by using statistical chi-square analyses.

The results of the first chi-test found a global, statistically significant association of megaloolithid eggs with inland environments (86% of the sites). Split by regions, this association is positive in Europe and India (86% and 100% of the sites) whereas there is a random distribution in both inland and coastal habitats in South America (54% and 46% of the sites, respectively). The tests made with the secondary environments call into question that the titanosaurians were versatile in the selection of nesting environments; regional analyses indicate that, as a rule, these sauropods show a clear and strong preference for nesting on a variety of fluvial (Europe) and palustrine-lacustrine (India) settings, usually in mature paleosols developed in overbank deposits. This setting seems to fulfil the optimal conditions for incubation, irrespective of the varied lithologies of the nesting substrate. The small South-American sample (n=13) still provides ambiguous results on this regard, with data indicating that megaloolithid eggs were laid both in tidal flats and fluvial settings.

MEGALOOLITHID EGGS AND NESTS FROM THE LATE MAASTRICHTIAN OF SEBEȘ AREA (TRANSYLVANIAN BASIN, ROMANIA)

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Late Cretaceous (Maastrichtian) megaloolithid dinosaur eggs are well known from several localities in the Hateg Basin, southwest Romania. Here, all the megaloolithid eggs were assigned to *Megaloolithus siruguei* oospecies, spherical to sub-spherical in shape, 14-16 cm in diameter, exhibiting nodular ornamentation, and eggshell thicknesses of 2.2-2.8 mm. Numerous clutches and nests were documented, particularly at the Tuştea nesting site, where hatchling hadrosauroid bones were found closely associated with the eggs/nests. Controversy regarding the parent animals in of the Hateg nesting sites persists, and a clear answer cannot be obtained without diagnostic *in-ovo* embryonic remains. However, few options are known: besides the aforementioned basal hadrosauroids (*Telmatosaurus*), titanosaurids (*Magyarosaurus*, *Paludititan*) are rather common, alongside numerous rhabdodontids (*Zalmoxes*).

A recently discovered latest Maastrichtian megaloolithid egg nesting site in southwest Transylvaniain Sebes area, outside the Hateg basin, provides new data regarding megaloolithid ootaxonomic diversity, nesting behaviour, and the possible identity of the parent animals. Preliminary evaluation indicates the presence of isolated or grouped megaloolithid eggs, distributed in at least three egg horizons within red siltyclaystone floodplain deposits. Several clutches were unearthed, the largest of which contain minimum 24 eggs, and shows grouped-linear arrangement, sometimes in two or even three levels. The majority of eggs and clutches were laid on the ground surface in shallow pits, being surrounded by numerous rhyzoliths. The eggs are subspherical, with diameters of 15-16 cm (volume up to 1480 cm³), compactituberculate ornamentation, and eggshell thicknesses of 0.7-0.9 mm, showing fused shell units. An asymmetric pit-like nest structure on sandy substrate, containing a closely packed group of nine eggs is also documented. In this nest, the eggs are subspherical in shape with diameters of 13-14 cm and egg-shell thickness of 1,4-1,7 mm, tubospherulitic with a tubocanaliculate pore system. Preliminary data indicate two nest structure types and two eggshell thickness classes, which may represent *Megaloolithus baghensis* and a different *Megaloolithus* oospecies, and thus possibly two different parent animals sharing the same nesting site.

THE BIOMOLECULAR PALEONTOLOGY OF DINOSAUR EGGSHELLS: A SYNTHETIC, CHEMOECOLOGICAL PERSPECTIVE

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The investigation of the biomolecular material associated with dinosaur eggshells is not only the key to understanding egg soft-tissue fossilization, but also a tool for reconstructing chemoecological interactions between the dinosaur egg and its parents, conspecifics, predators, and the environment. Here we present the first complete analysis of dinosaur eggshell organics and use chemoecological inferences to provide evolutionary insights into avian reproductive strategies in a phylogenetic context. We sampled 35 fossil eggshells comprising Protoceratops, Maiasaura, Titanosauria, Oviraptorosauria, Troodontidae, Enanthiornithes, and Paleognathae, and 20 modern eggshells including Alligator, Crocodylus, all paleognath families, Galloanseres, and Passeriformes. Preserved fossil and modern soft tissue remains were subjected to Confocal Raman Microspectroscopy, High-performance Liquid Chromatography coupled to ESI Mass Spectrometry, UV/Vis Spectrophotometry, and Fluorescence Microscopy. Soft tissue morphology and molecular preservation demonstrated that embryonic and shell membranes, and eggshell spongy layer, color pigments, and waxy cuticle survive in fossils. We compare the chemical composition and tissue architecture of preserved chorioallantoic tissues in fossil eggshells belonging to complete clutches as diagnostic criterion of the fertilization state of fossil eggs. We discuss the architecture of the spongy layer that gives rise to the crystallites of the prismatic zone, and deduce incubation strategies. We consider the binding mechanism of avian eggshell pigments and their taphonomy, and we present pigment data for all investigated dinosaur taxa in the context of multiple origins of colored eggs. The interface between an egg and its environment is the waxy outer cuticle: we compare thicknesses of cuticle in different taxa, and use the data to provide further information on incubation, paleotemperature and humidity during the breeding season, and predation. Thus we aim to maximize the chemoecological data available from dinosaur eggshell.

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A NEW EMBRYO-BEARING EGG-CLUTCH REVEALS ASYNCHRONOUS HATCHING IN OVIRAPTORID DINOSAURS

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Dinosaur eggs with embryos inside have been discovered in a number of localities around the world, and provide insights into dinosaur reproductive biology and breeding ecology. The majority of the known embryo-containing eggs can be referred to oviraptorid theropods. However, most of these eggs cannot be referred to a specific clutch, and, so far, only one partial, poorly preserved embryo-bearing oviraptorid egg-clutch has been reported, stemming from the Late Cretaceous Nemegt Formation of Mongolia. Here we report another partial, but better preserved oviraptorid clutch including three eggs containing embryos, a pair and a single one, from the Late Cretaceous Nanxiong Formation near Ganzhou in Jiangxi Province, southern China. These embryobearing eggs are distinct from those of the Mongolian clutch, and are assigned to Macroolithus based on the external ornamentation and internal microstructure of the eggshells. Osteological and histological analyses reveal that the embryo of the single egg was closer to hatching than those of the egg pair, indicating an asynchronous hatching mode in oviraptorid dinosaurs. This new clutch, together with the Mongolian clutch, suggests that asynchronous hatching might be a synapomorphy of oviraptorid dinosaurs. Asynchronous hatching occurs when the development of the embryos is not simultaneously triggered. In extant birds, asynchronous hatching has been suggested to constitute an adaptation to cope with food shortage, although several subsequent ecological experiments could not provide significant evidence for this hypothesis. Alternatively, asynchronous hatching in oviraptorids could be explained by polygamy behavior, where several females are contributing to a clutch, in combination with no incubation.

NEOGENE TO PLEISTOCENE FOSSIL OSTRICH EGGSHELL: EVOLUTION OF STRUTHIONIDAE IN THE OLD WORLD CORRELATED WITH EVOLUTIONARY HISTORY OF BIRD FAUNAS

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The fossil ostrich eggshell is fairly common in the Neogene and Pleistocene localities of Africa and Eurasia. This exceptional record allows tracing the evolutionary history of one particular bird lineage across a broad timespan (at least 21 MYA). Modern ostriches and most likely their fossil ancestors are tightly connected with open landscapes, and it is thus notable that the inferred evolutionary history of the ostriches is well correlated with the history of the avian faunas of Asian open landscapes across the entire Neogene and Pleistocene. Ostriches first appear in the early Miocene of Africa and one of their lineages, represented by the so called type-A pore pattern eggshell morphotype, later achieved a wide distribution in Eurasia in the latest middle to early late Miocene. This broad distribution of ostriches is correlated with the first Eurasian appearance of several other bird lineages of presumably African origin, including bustards (Otididiae) and sandgrouses (Syrrhaptes). In the latest Miocene, the type-A lineage was replaced by a lineage with type-A-S pore pattern, which at that time was distributed across the whole mid-latitudes of the Eurasia. This episode is correlated with a wide range of arid-adapted avian faunas, spreading from Western Europe to East China. These late Miocene to early Pliocene faunas evolved in Eurasia (also true for ostriches), but show affinities with the modern faunas of sub-Saharan Africa, i.e. in the presence of hornbills and lark buttonguails. In the second half of the Pliocene and in the early Pleistocene, the avian faunas of Eurasia achieve their fairly modern taxonomic composition, and this correlates with the appearance of the type-S eggshell morphotype of the ostriches, which enjoyed broad geographical distribution across Eurasia and Northern Africa in the latest Neogene. This lineage of ostriches apparently originated in Asia and likely gave rise to modern species of Struthio.

REUSE OF MIXED-DINOSAUR-SPECIES BREEDING SITE ON FLUVIAL DEPOSITS OF YUNXIAN BASIN, HUBEI, CHINA

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Colonial nesting behavior in dinosaurs has been described from clutch-clusters of sauropodomorph *Massospondylus* from South Africa, hadrosaurid *Maiasaura* from Montana, USA, and therizinosaurs from Mongolia; however, only constrained to monospecific colonial nesting. Here we report the first evidence of mixed-dinosaur-species breeding flocks (hereafter referred to as "flocking") in Yunxian Basin of Hubei Province, China. Yunxian Basin is a Late Cretaceous extensional basin filled with coarse sediments, such as conglomerates and sandstones. Late Cretaceous sediments in Yunxian Basin are divided into three formations. The lowermost, dinosaur-egg-bearing Gaogou Formation formed in the initial stage of Yunxian Basin's development according to angular grains in sediments, cut-and-fill beddings, and ichnotaxon *Ophiomorpha*.

Eggshell parataxonomy revealed three different oogenera, including *Dendroolithus*, probable *Faveoloolithus*, and an unknown ootype. Among these oogenera, dendroolithid eggs account for the majority of eggs discovered in Yunxian Basin. The clutch size of dendroolithid eggs varies from four to 77 eggs without specific arrangement. However, some egg clutches exhibit an arcuate nest architecture, indicating that dinosaurs laid eggs while moving. More than 30 dendroolithid egg clutches dispersed throughout the outcrop show that dinosaurs came here annually, or even every several years. Most eggs were incubated since the egg shape is well-preserved except for the hatching window.

Dendroolithid eggs from Mongolia are assigned to therizinosaurs that are considered as social herding animals. It is hence conceivable that therizinosaurs were probably the core species in the flocking of Late Cretaceous Yunxian Basin, as seen in extant mixed-bird-species flocks. Our study also indicates that Yunxian Basin was a nursery for various dinosaurs in the aftermath of each flooding event.

The whole quarry is now under the protection of a museum from erosion. More than three thousand eggs were recently exposed, indicating that this quarry was a frequently reused nursery for dinosaurs during the Late Cretaceous.

BONE HISTOLOGY AND OSTEOLOGY OF JUVENILE LIAONINGOSAURUS PARADOXUS (ORNITHISCHIA: ANKYLOSAURIA)

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Liaoningosaurus paradoxus is an ankylosaurian dinosaur from the famous Early Cretaceous Jehol Biota of Liaoning Province, China. It is known from dozens of skeletons, most with body length of less than 50 cm and are considered to be juvenile. However, a recent study suggests that these small specimens are probably adult, making Liaoningosaurus the smallest known ornithischian. Here we described the holotype and three new specimens of *Liaoningosaurus*, which have a femoral length of 28.5 mm, 29.7 mm, 31.5 mm, and 56.5 mm respectively. To better assess the ontogenetic stages of these specimens, we sampled three specimens for histological study for the first time, including the holotype, another small specimen with a femoral length (31.5 mm) similar to that of the holotype, and the large specimen (femoral length: 56.5 mm). The small specimen shows highly porous woven-fibered bone matrix and lacks any line of arrested growth, suggesting that the individual was in its early stage of growth. The large one, with a femoral length approximately twice that of holotype, shows fibro-lamellar tissue with only primary osteons in circular rows and lacks any lines of arrested growth. The histological features of these specimens suggest that they are all in the juvenile stage, consistent with their small size and skeletal fusion features. Furthermore, these new specimens provide new anatomical information for Liaoningosaurus, including a complete tail that confirms the absence of a tail club knob and complete forelimbs and hind limbs that help recover both manus and pes phalangeal formulas. The length ratios of selected limb bones to femur remain nearly constant in different-sized individuals, suggesting isometric growth in the early ontogenetic stage of Liaoningosaurus.



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